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Climatic and hydrologic effects on the regeneration of *Populus angustifolia* James along the Animas River, Colorado

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Abstract. I investigated the dates of origin of riparian forests dominated by *Populus angustifolia* James, and recent interannual fluctuation in *P. angustifolia* seedling abundance on a relatively undisturbed 6-mile reach of the Animas River in southwestern Colorado. The goal was to develop plausible hypotheses about the roles of floods and interannual climatic fluctuation in structuring these forests. I determined the year of origin of 242 recently-established seedlings and fifty-seven forest stands, and then developed empirical models relating seedling abundance and stand-origin events to climatic and hydrologic fluctuations. Seedlings were most abundant in years with cool winters, wet springs, and cool, wet falls (R^2_{adj}=0.98). Both good seedling years and stand-origin years were associated with winter blocking in the North Pacific and a persistent late-summer Arizona Monsoon. Extant stands originated in ten to thirteen discrete periods between 1848 and 1976, in years with both high spring and fall peak discharges. Expected seedling abundance and stand-origin dates since 1914 were reconstructed using climate data, and were extended to 1556 using tree-ring chronologies. Model results suggest good seedling years occurred more frequently (about every 3.4 years) than stand-origin years (about every 10–15 years). Good seedling years were 2–3 times, and stand-origin years were 5 times more common from 1848 to 1985 than from 1556 to 1848. Recent expansion of *P. angustifolia* may have been favoured by more frequent cool, wet years since 1848.

Key words. Riparian forests, *Populus angustifolia*, population dynamics, floods, disturbance, Colorado.

INTRODUCTION

Climate–vegetation relationships are apparent on several spatial and temporal scales, but often appear clearer on large areas and long time scales. On smaller land areas climate–vegetation relationships may be unclear because of the influence of other factors, such as parent materials or disturbance history (Daubenmire, 1956). Moreover, imperfect relationships between climate and vegetation may result if vegetation lags in its adjustment to climatic change (Davis, 1986), or is insensitive, as one model suggests, to short-term (e.g. interannual, decadal) climatic fluctuation (Davis & Botkin, 1985). In this paper I argue that, in spite of lags, vegetation may be sensitive to short-term climatic fluctuation, and may reflect climatic conditions atypical of decadal or longer-term mean conditions.

Empirical evidence suggests some rapid vegetational responses to decadal and interannual fluctuation in climate. Recent climatic warming on the decadal scale may have encouraged treelines to advance globally (Bray, 1971), trees to invade subalpine meadows (Franklin *et al.*, 1971), and woody plants to invade desert grasslands (Hastings & Turner, 1965). Lesser magnitude interannual climatic fluctuation may cause compositional shifts (Goldberg & Turner, 1986), fluctuations in primary production (Cable, 1975) and growth (Hughes *et al.*, 1982), and differential reproductive success (Neilson, 1986; Cawker, 1980). The effect of fluctuations in precipitation and temperature on riparian tree regeneration has not apparently been studied.

Climate may also influence vegetation through the disturbance regimes that affect vegetation structure and regeneration. In the riparian environment studied here, climate might affect vegetation indirectly through effects on the hydrologic regime. Low magnitude hydrologic fluctuations may affect tree growth along rivers (Wendland & Watson-Stegner, 1983). Higher magnitude flood flows may destroy existing riparian forests, providing opportunities for tree regeneration (Turner, 1930; Sigafoos, 1964; Yanosky, 1982). Regeneration may be favoured by low-flow intervals (Sigafoos, 1964) or sustained moderate-flow intervals (Noble, 1979). The relative importance of particular hydrologic conditions for riparian tree regeneration remains unclear.

In this paper, I (1) analyse interannual variation in the abundance of *Populus angustifolia* James seedlings; (2) relate this variation to fluctuations in annual and seasonal temperature, precipitation, and river discharge using multiple regression; (3) use this regression model and climatic records to reconstruct past annual seedling success; (4)

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develop a discriminant model to distinguish which hydrologic variables are important in originating riparian forest stands; (5) compare the years of reconstructed high seedling success with actual stand-origin dates; and (6) extend the seedling abundance model and stand-origin model to AD 1556 using published regional tree-ring chronologies.

METHODS

Field methods

I studied riparian forests along a 6-mile reach of the Animas River, a sinuous gravel-bed river in the San Juan Mountains of southwestern Colorado, in the summer of 1986. This river is unregulated and has a relatively undisturbed watershed, with the study reach (2390–2575 m in elevation) never grazed by domestic animals. Forests along the reach are dominated by *P. angustifolia, Picea pungens* Engelm., *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., and *Pseudotsuga menziesii* (Mirbel) Franco (Baker, 1987). The ecology of *P. angustifolia,* the subject of this study, is virtually unknown, in contrast to that of other cottonwoods.

I placed sampling plots (0.1 ha) within areas of similar-sized trees, or 'stands', with fifty-seven stands sampled consecutively along the reach, each stand being sampled by a single plot. Boundaries between stands were generally sharp and easily delimited in the field with the aid of 1:20,000 scale aerial photographs.

Ages of stems in the plots often suggested a common 'stand-origin date' (Heinselman, 1973). Preliminary determination of ages of stems in stands <12 years old revealed a truncated age class structure (many stems of the same age and none older), suggesting rapid simultaneous initial recruitment following stand-destructive disturbance. In most plots there were several stems of the oldest age, again suggesting a common date of origin. I identified the stand-origin date by determining the ages of the larger stems in each plot, by obtaining two or three increment cores at the base of each stem, or by a cross-section in the case of smaller stems. Cores and cross-sections were stained with phloroglucinol, and the rings were counted, by two people, in the field with a hand lens. Field counts were necessary because *P. angustifolia* rings often can only be counted when the core is fresh, lightly-stained, and held up to the sun before the stain dries. The 'larger stems' were chosen after a size class tally and measurement of diameter with a Biltmore stick. I determined the ages of approximately ten trees (range four to twenty-one) in each plot, beginning with the largest diameter tree. Often the gravel bars were small, so that this sample included most of the large, old trees in the plot. Origin dates for individual stands are probably accurate to within a few years for stands up to about 75 years old, but may be 5 years in error for older stands, although this estimated error is speculative.

Also within each plot I determined the age of approximately fifteen (range ten to twenty-five) healthy (terminal bud undamaged and stem free of disease) *P. angustifolia* seedlings encountered on a random walk through the plot. 'Seedlings' of *P. angustifolia* may include many root sprouts; the distinction is not important for the purposes of this study. Seedlings of other species were not studied because *P. angustifolia* is virtually always numerically dominant on new gravel bars. I determined the age of seedlings less than 6 or 7 years old by counting terminal bud scale scars (Hett & Loucks, 1976), after a preliminary test showed 100% agreement with ages determined by counting annual rings in cross-sections. Older seedlings were aged by counting annual rings in cross-sections. Data from all the plots were pooled for the subsequent seedling analyses.

Climatic and hydrologic effects on seedling abundance

The goal of this part of the study was to determine whether recent interannual variation in seedling abundance is related to fluctuation in climate and hydrology, and if so which climatic and hydrologic conditions favour regeneration. I used seedling abundance by year as the predicted variable and climatic and hydrologic time series as the predictor variables in a multiple regression model. The model is not limited to a particular theoretical form as there is no theory to draw upon. Model building in this case is 'exploratory' (Dillon & Goldstein, 1984), and is aimed only at developing plausible hypotheses and preliminary theory. For these reasons I allow the statistics to drive the model-building process as much as possible.

Analysis is restricted to seedlings less than or equal to 11 years old (originating between 1975 and 1985). The abundance of stands that originated in 1975, but not subsequently, suggests a stand-destructive flood occurred in 1975, but not since. Streamflow records (U.S. Geological Survey) show that discharge on the Animas River at Durango between 6 and 16 June 1975 was the highest spring flow since 1973. Seedling analysis is further restricted to gravel bars <45 years old, which are sparsely vegetated, suggesting that seedlings have been relatively free of competitive effects. Seedlings are uncommon in stands older than about 45–60 years of age (Baker, 1988).

Seedling mortality may have occurred after establishment, so that seedling abundance by age does not precisely reflect the abundance of seedlings established in a particular year. I found evidence in nine of fifty-seven stands, for example, that beavers harvest *P. angustifolia,* but they concentrate on stems larger than 3 cm d.b.h., which are generally older than 12 years. In a similar study of climatic effects, Cawker (1980) corrected for mortality by fitting negative exponential and power function models (after Hett & Loucks, 1976) to abundance by age data. Here, there is a slight (R^2=6.2%) but not significant negative trend in seedling abundance versus age, possibly from mortality. I considered both raw seedling numbers and residual seedling numbers (after removing the linear trend due to age) in all the subsequent analyses. The results did not differ appreciably, and only raw seedling numbers are used in the remainder of the paper.

Climatic data are from United States Weather Service records for Durango, Colorado, approximately 32 km downstream from the study site, at 1990 m elevation. Runoff data are for the Animas River at Durango. These data differ in absolute value from the actual data for the study reach, but the pattern of interannual variation is probably similar. A 'water-year' running from December to November was used, so that quarterly summaries (Table 1) would be more congruent with a division of the annual hydrograph. The instrumented record for Durango includes: (1) precipitation from 1896 to 1985, (2) temperature from 1896 to 1985, and (3) runoff from 1912 to 1985.

To be appropriate for multiple regression, time series should be free of serial autocorrelation. To produce the appropriate prewhitened series (Monserud, 1986) I fit standard time series autoregressive-integrated-moving average (ARIMA) models (Box & Jenkins, 1976; Salas *et al.*, 1980) separately to annual and quarterly precipitation, total runoff, peak discharge, and temperature series for the period of instrumented record. Prior to fitting the models, each series was checked for normality by inspecting histograms and comparing means and medians. The variables were transformed where necessary. I checked for non-stationary trends by analysis of variance of the full series divided into six to eight parts, and removed trends, if present, by nonseasonal differencing. Potential ARIMA models were identified by examining autocorrelation and partial autocorrelation functions in combination with an all-possible-models approach, where combinations of autoregressive and moving average parameters of orders 0–5 were examined. I then tried to improve these models by adding seasonal terms (Salas *et al.*, 1980), and included those models that passed the Portmanteau lack-of-fit test (Salas *et al.*, 1980), and whose parameters were all significant at the 5% level. Among those models remaining, I selected and estimated the most parsimonious model (Monserud, 1986) and used the residual series in all subsequent analyses. I used SPSSX (1986) for all calculations.

TABLE 1. Climatic and seedling variables included in the multivariate analyses. Winter=December, January, and February; Spring=March, April, and May; Summer=June, July, and August; Fall=September, October, and November.

Variable	Description
PC	Current year total precipitation
RC	Current year total runoff
TC	Current year mean temperature
PF	Following year total precipitation
RF	Following year total runoff
TF	Following year mean temperature
PC1–PC4	Current year winter (PC1), spring (PC2), summer (PC3), and fall (PC4) precipitation
RC1–RC4	Current year winter (RC1), spring (RC2), summer (RC3), and fall (RC4) runoff
TC1–TC4	Current year winter (TC1), spring (TC2), summer (TC3), and fall (TC4) mean temperature
PF1–PF4	Following year winter (PF1), spring (PF2), summer (PF3), and fall (PF4) precipitation
RF1–RF4	Following year winter (RF1), spring (RF2), summer (RF3), and fall (RF4) runoff
TF1–TF4	Following year winter (TF1), spring (TF2), summer (TF3), and fall (TF4) mean temperature
SN	Peak snowmelt discharge (April–June)
TH	Peak thundershower discharge (July–October)
SEEDRAW	Raw seedling numbers

Multicollinearity among the residual series was high. To avoid violating the multiple regression assumption that predictor variables are independent (Draper & Smith, 1981), I transformed the correlated predictor variables to orthogonal variables by principal components analysis (Dillon & Goldstein, 1984). Components were retained for further analysis if their eigenvalue exceeded 1.0 or if they were interpretable (only one or two variables with high loading).

Seedlings may have lagged responses to past climatic conditions or be affected by climate in the years following germination. Because the time series of seedling data is only 11 years long, insufficient degrees of freedom are available to include a full suite of lagged variables in the multiple regression model development phase. In a preliminary analysis, I used the principal components transformations of annual climatic series to explore the separate contributions of variously lagged data (from year^{+3} to year^{-3}) to current-year seedling numbers. Only current-year and following-year data made significant contributions (arbitrarily defined as $R^2>10\%$), and in the remainder of the analyses only these variables (Table 1) were used.

I developed multiple regression models separately using annual and quarterly principal components predictors of raw seedling numbers. The regression models were then of the form:

$$\begin{aligned}\mathrm{SEEDRAW}_i=b_0+b_1\,\mathrm{COM1}_i+b_2\mathrm{COM2}_i+\ldots\, b_n\mathrm{COM}n_i\\ +b_{n+1}\mathrm{COM1}_{i+1}+b_{n+2}\mathrm{COM2}_{i+1}\\ +\ldots\, b_{n+n}\mathrm{COM}n_{i+1}\end{aligned} \qquad (1)$$

where SEEDRAW$_i$ is the number of seedlings in year i, COMn_i is the value of the nth principal component of annual or quarterly climate data in year i, and b_0–b_n are the regression coefficients to be estimated. Final models were selected by an all-possible-regressions procedure (Draper & Smith, 1981), with the best equation having the maximum value of adjusted R^2. Residuals from fitted models were examined for trends, outliers, serial autocorrelation and normality.

Fitted models were then used to reconstruct seedling numbers for the period of instrumented record (1914–84). Unfortunately, model parameter stability could not be checked with another series, or by deletion of part of the calibration series, which is too short, so that the model relationships must be considered tentative.

I examined the atmospheric circulation patterns during good seedling years (arbitrarily defined as >0.5 SD above the mean) and bad seedling years (arbitrarily defined as >0.5 SD below the mean) using the synoptic climatic classifications and historical data of Barry, Kiladis & Bradley (1981) and Blasing & Lofgren (1980) to determine if particular synoptic patterns were associated with the climatic conditions favouring abundant seedlings.

Climatic and hydrologic effects on stand origins

Stand-destructive floods facilitate stand-origin in fully-occupied riparian environments, but is it a single large flood (seasonal peak discharge) or prolonged high flow (seasonal total runoff) that is a better predictor of stand-origins? Are the hydrologic conditions conducive to stand-origin different from those conducive to seedling success? To investigate these questions, I used discriminant function analysis (Dillon & Goldstein, 1984) to develop a classification of stand-origin and no-stand-origin years based on: (1) the residual series (after fitting a time-series model) from the instrumented record of peak seasonal discharge during the snowmelt period (April–June) and peak seasonal discharge during the period of convective thundershowers (July–October), and (2) the residual series from the instrumented record of quarterly total runoff, all measured at Durango. Annual discharges on the Animas River sometimes have two nearly equal peaks, the first related primarily to snowmelt and the second from intense short-duration convective thundershowers. Some of the largest historical discharges have been from the latter source (Follansbee & Sawyer, 1948).

I used a stepwise method to construct and compare the success of two discriminant functions. The first function is of the form:

$$Z=b_1\mathrm{SN}+b_2\mathrm{TH}+b_3\mathrm{SEEDRAW} \tag{2}$$

where Z is the Fisher linear discriminant function, SN is peak snowmelt discharge (April–June), TH is peak thundershower discharge (July–October), SEEDRAW is the reconstructed number of seedlings, and b_1–b_3 are the discriminant function coefficients to be estimated. The second function is of the form:

$$Z=b_1\mathrm{RC1}+b_2\mathrm{RC2}+b_3\mathrm{RC3}+b_4\mathrm{RC4}+b_5\mathrm{SEEDRAW} \tag{3}$$

where Z is the Fisher linear discriminant function, RC1 is winter total runoff, RC2 is spring total runoff, RC3 is summer total runoff, RC4 is fall total runoff, SEEDRAW is the reconstructed number of seedlings, and b_1–b_5 are the discriminant function coefficients to be estimated.

I used the period from 1930 to 1974 to develop the classification. For the stand-origin group of years I used only 1941 and 1957 (see Results), as these are the two clearest stand-origin years during this period. The no-stand-origin group consisted only of the years with no dated stand-origin (Fig. 3a).

Variables were checked for normality using histograms. Equality of variance–covariance matrices for the two groups could not be assessed due to the small size of the stand-origin group. Inequality of group dispersions may lead to distortion of the discriminant function and misclassification (Williams, 1983). As this potential source of error cannot be evaluated here, the results can be interpreted only as exploratory. I assigned prior probabilities based on the proportion of cases in each group for the calibration period, and used the minimization of Wilks lambda method to select variables for stepwise entry. I used an F-test to test the significance of the Mahalanobis' distance between groups (Dillon & Goldstein, 1984), and assessed variable contribution using standardized loadings.

The derived discriminant function was then used to classify the years between 1914 and 1984 as either a stand-origin year or a no-stand-origin year. The success of the predictions was evaluated by comparing predictions with stand-origin years determined in the field.

Extended reconstructions

If the interannual variation in seedling success and stand-origins on the Animas River is related to regional interannual climatic fluctuations, then it may be possible to reconstruct past seedling success and stand-origin years using regional tree-ring chronologies. Clark, Blasing & Fritts (1975) first used this approach to reconstruct interannual fluctuations in albacore tuna populations along the west coast of the United States from a set of western United States tree-ring chronologies.

I reconstructed past seedling success, prior to the beginning of the instrumented climate record, by: (1) fitting autoregressive-moving average (ARMA) time series models to six published tree-ring chronologies (Table 6) from sites near the Animas River (Drew, 1974, 1976; Stokes, Drew & Stockton, 1973), (2) deriving new uncorrelated (principal components) variables from the six residual tree-ring series, (3) using all-possible-regressions to derive a multiple regression model relating seedling success to the tree-ring principal components, lagged from +2 to −2 years. Appropriate time series models are ARMA models rather than ARIMA models because the tree-ring chronologies have already had growth trends removed, so that ring-indices have a constant mean (Monserud, 1986). Methods used in fitting the ARMA models are identical to those described earlier. I used only the period (1555–1961) common to all six chronologies as the reconstruction period, the reconstructed SEEDRAW estimates as the predicted data, and 1914–61 as the calibration period.

I reconstructed past stand-origin dates by using discriminant function analysis to develop a function to classify known stand-origin years and no-stand-origin years, based on the same principal components derived from six residual tree-ring chronologies. I used the period from 1905 to 1961 as the calibration period. As known stand-origin years I used only 1941 and 1957, as these are the two clearest stand-origin years during this period. The derived function was then used to classify the years between 1555 and 1961. Model adequacy was assessed as described previously.

RESULTS

Recent seedling dynamics and reconstruction

Seedling abundance varied interannually, from 1975 to 1985, from a low of one to a high of forty-two (Fig. 1). Residual climatic time series were derived from a variety of ARIMA models (Table 2). Multiple regression models relating SEEDRAW to principal components transformations (Table 3) of these residual climatic time series were much more successful using quarterly climatic variables than annual climatic variables (Table 4). The quarterly models have very high R^2 values, even after adjustment for the small number of observations. Such high R^2 values might suggest an underlying tautology, or an artefact of a statistically-driven model construction process. But, the

TABLE 2. Autoregressive-moving average models fit to climatic series.

Climate series*	ARIMA model†
1. Total annual precipitation	$(0, 1, 1)\times(1, 1, 0)_8$
2. Total annual runoff	$(0, 1, 3)$
3. Mean annual temperature	$(0, 1, 1)\times(1, 1, 0)_7$
4. Total quarterly precipitation	$(0, 1, 1)\times(0, 1, 1)_4$
5. Total quarterly runoff	$(0, 0, 4)\times(0, 1, 1)_4$
6. Mean quarterly temperature	$(0, 0, 4)\times(0, 1, 1)_4$
7. Peak snowmelt discharge	$(0, 1, 3)$
8. Peak thundershower discharge	$(0, 1, 4)$

*All series are from the instrumented record for Durango, Colorado.

†ARIMA $(p, d, q)\times(P, D, Q)_s$ models are: (1) a p order autoregressive, q order moving average model fitted to the dth nonseasonal difference of the series, and (2) coupled with a P order autoregressive, Q order moving average model fitted to the Dth seasonal difference, with period s, of the residual series of (1).

fact that the annual models, based on the same number of observations, do not have such high R^2 values suggests that the importance of quarterly climatic variables is undeniable. As the quarterly model is much better than the annual model (Table 4), I used this reconstruction in all subsequent analyses.

The best model using quarterly climatic data (Table 4) suggests that large numbers of seedlings are produced in a year with: (1) high winter and spring precipitation and high spring and summer runoff (Component 1), (2) high fall precipitation and runoff and low temperature (Component 2), and (3) low winter temperature and runoff (Component 4), particularly if followed by a year with high spring temperature, but not unusual runoff or precipitation (Component 3). Although all these components are significant, the change in R^2 upon removal of each component suggests a cool and wet year, especially with a cool and wet fall, is most critical for high seedling success (Table 4). This interpretation is based on principal components transformations of residual climatic series, but raw precipitation, runoff, and temperature patterns during five good seedling years and five bad seedling years support this interpretation (Fig. 2).

Cool and moist falls are the result of synoptic patterns like Blasing & Lofgren's (1980) Types 3 or 5, and Barry *et*

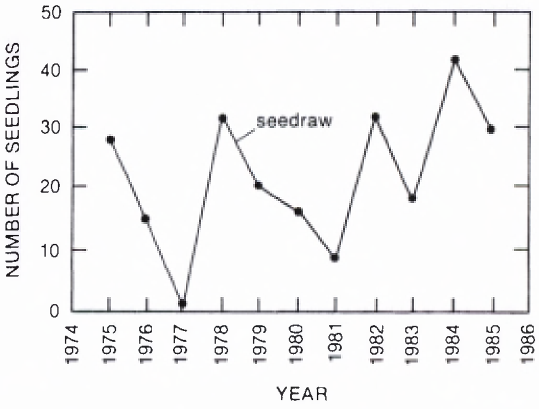

FIG. 1. Raw number of seedlings (SEEDRAW) in each year.

TABLE 3. Component loadings of annual and quarterly climatic variables.

Annual climatic variables

	Component		
	1	2	
Eigenvalue	1.501	0.941	
Variable			Communality
RC	0.839*	0.015	0.981
PC	0.661*	0.642	0.962
TC	−0.601	0.728*	0.990

Quarterly climatic variables

	Component					
	1	2	3	4	5	
Eigenvalue	2.942	1.973	1.451	1.228	1.052	
Variable						Communality
RC3	0.728*	0.179	−0.410	−0.025	0.235	0.875
RC2	0.679*	0.333	0.308	−0.165	0.089	0.935
PC1	0.696*	0.143	0.496	0.044	0.161	0.875
PC2	0.630*	0.319	−0.453	−0.042	0.058	0.853
PC4	−0.242	0.750*	−0.053	0.026	−0.029	0.934
RC4	−0.597	0.621*	−0.083	−0.003	0.148	0.874
TC4	0.139	−0.531*	0.228	0.523	0.290	0.997
TC2	−0.478	0.134	0.675*	−0.195	0.166	0.938
TC1	−0.291	0.238	−0.179	0.819*	−0.137	0.986
RC1	0.408	0.352	0.334	0.460*	−0.137	0.951
PC3	−0.362	0.304	−0.077	−0.035	0.670*	0.963
TC3	−0.159	−0.432	−0.264	−0.014	0.591*	0.984

*Variables which have their highest loading on a particular component.

TABLE 4. Best models from multiple regression of seedling numbers with annual and quarterly climatic components (see Table 3).

Predicted variable	Variable	Parameter value	Signif.	Removal R^2 change
Annual climatic variables				
SEEDRAW	Constant	22.034	0.005	
	COM1–current year*	7.182	0.022	0.421
	COM2–following year	−6.772	0.000	0.258
R^2=0.658, R^2_{adj}=0.561				
Quarterly climatic factors				
SEEDRAW	Constant	23.360	0.000	
	COM1–current year	4.532	0.000	0.253
	COM2–current year	9.291	0.000	0.464
	COM4–current year	−6.333	0.000	0.131
	COM3–following year	3.910	0.001	0.124
R^2=0.990, R^2_{adj}=0.982				

*The COM number refers to the respective principal component in Table 3.

al.'s (1981) Type 2, associated with a positive pressure anomaly over northern Canada or Siberia and northerly displacement of the Bermuda anticyclone, which encourages a persistent Arizona Monsoon (Bryson & Lowry, 1955; Carleton, 1985) in southern Colorado. Teleconnections with Pacific SST's are less clear (Kiladis, 1982). Also unclear is the importance of zonal or meridional flow patterns (Carleton, 1985).

Cold and normal or wet winters are associated with synoptic patterns like Blasing & Lofgren's (1980) Type 2 or 4, which are characterized by a weak Aleutian low or positive pressure anomaly in the north Pacific, and a meridional pattern with a trough of cold arctic air over the western United States. Several of Barry *et al.*'s (1981) synoptic types (including 2, 7 and 14) may also produce cold wet winters in the region. The general pattern may result from the strong blocking action of the north Pacific ridge, as occurred in the winter of 1983–84 (Quiroz, 1984), possibly associated with warmer sea surface temperatures (SSTs) in the central Pacific and cold SSTs along the west coast of the United States (Kiladis, 1982). There are other possible teleconnections with El Nino/Southern Oscillation events (Quiroz, 1984).

The reconstruction suggests that while seedlings are produced in most years, certain years were very good or bad seedling years. Good years would have occurred twenty-one times between 1914 and 1984 for a mean recurrence interval of about 3.4 years. Bad years would have occurred with about the same frequency.

Stand-origins

Stand-origin dates were determined for all fifty-seven stands, using a total of 469 aged trees. Origin dates (Fig. 3a) were clustered around 1848–54, 1878–83, 1896–1903, 1911, 1919–20, 1927–28, 1935, 1941–49, 1952, 1957, 1968 and 1975–76. There were no stands on the reach originating prior to 1848. Although dates of origin for stands must be interpreted with caution (Swetnam, Sutherland & Thompson, 1983), due to possible tree-dating errors, the likelihood of error is lower for younger stands. Moreover, coincidence of several individual stand-origin dates increases the likelihood that a particular year was, in fact, a stand-origin year. For example, 1941, 1957 and 1975 were certainly stand-origin years (Fig. 3a).

There are some apparent relationships between climatic–hydrologic time series (Figs. 3d–3g) and the stand-origin series (Fig. 3a), but no single series corresponds highly with the stand-origin series. In the precipitation (Fig. 3g) and runoff (Fig. 3d) time-series the peaks at 1941 and 1957 correspond with stand-origin years (Fig. 3a), but stands did not apparently originate during every year of high precipitation and runoff (e.g. not in 1965 or 1916). Moreover, stands did not originate in every year of high seedling success (e.g. not in 1965, 1961, 1914–16), and there is little relationship between the temperature series and the stand-origin series.

The discriminant analysis supports the primary importance of peak discharge in stand-origin. Model 1 (Table 5), which suggests that stand-origin years have both high peak snowmelt discharge and high thundershower discharge, had slightly better discriminating power ($P<0.15$) than Model 2 ($P<0.20$), which suggests that stand-origin years have both high spring and high fall total runoff. Moreover, Model 1 correctly classified five of fourteen of the actual stand-origin years between 1914 and 1985 that were not used as calibration years (Fig. 3a), while Model 2 did not correctly classify any of these years. Some of the stand-origin years missed by Model 1 are years scattered within a cluster, which could represent dating errors or a lagged regeneration response, rather than a distinct stand-origin event. Model 1 did identify all the clusters correctly, but predicted some that did not apparently occur (1914–16, 1970, 1980). Seedlings would have been abundant in most of the predicted stand-origin years (Fig. 3), but also during many years without stand-origins. With the possible exception of 1921 and 1943, stands originated only in years (during the 1914–85 period of instrumented record) with average or above average reconstructed seedling success (Fig. 3). These results suggest that stand-origin is favoured by stand-destructive high peak discharges during years also with the climatic and hydrologic conditions conducive to seedling abundance.

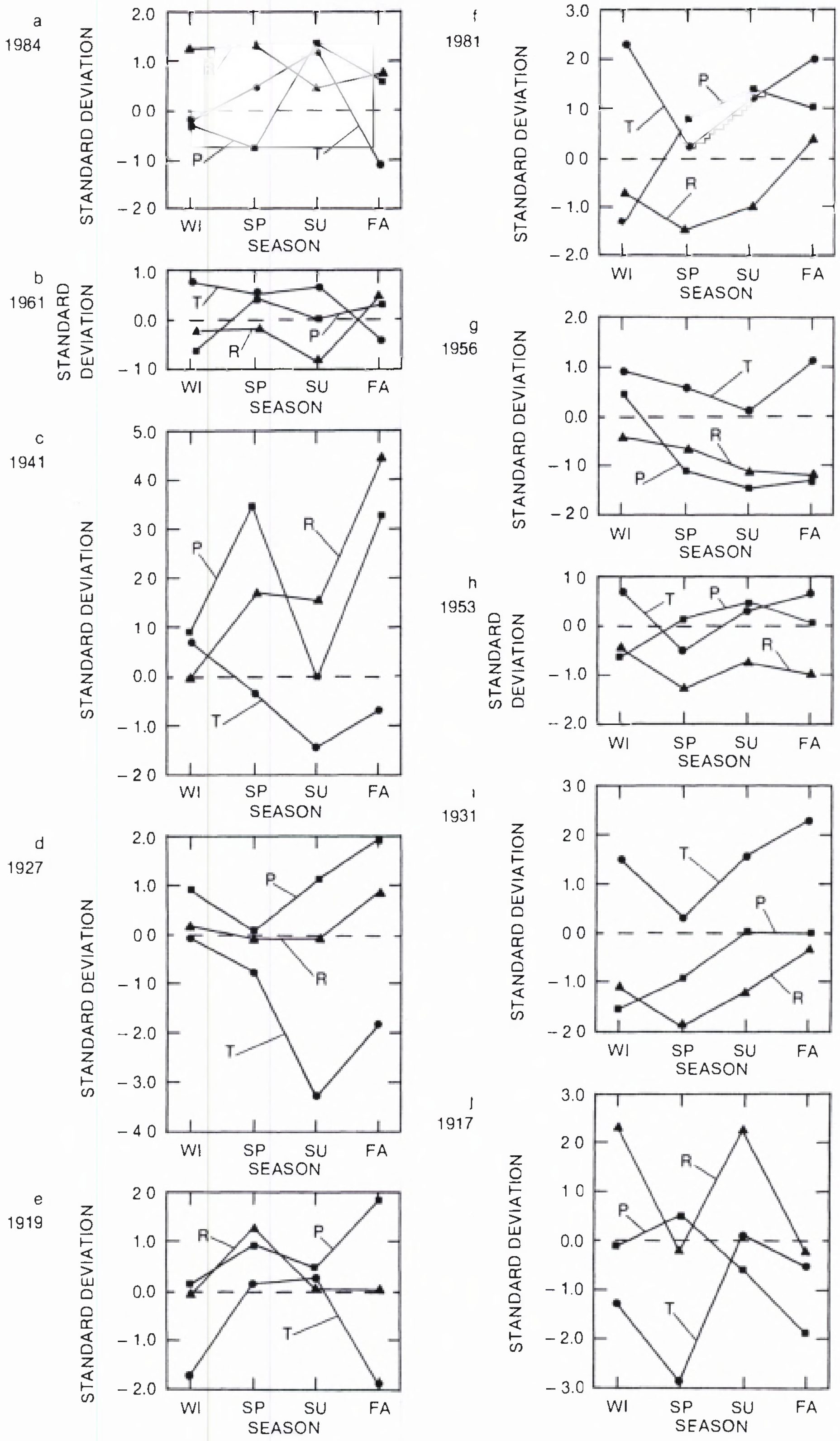

FIG. 2. Quarterly (seasonal) precipitation (P), runoff (R), and temperature (T) during some good (a–e) and bad (f–j) seedling years. Seasons are WI=winter, SP=spring, SU=summer and FA=fall.

TABLE 5. Discriminant loadings of peak discharge (Model 1) and quarterly runoff (Model 2) on discriminant functions separating stand-origin from no-stand-origin years. Variables listed are the only variables entered in the stepwise model.

Model 1: Peak discharge

Variable	Discriminant loading
SN	0.937
TH	0.496

Model significance $P<0.15$.
Number of years correctly classified=37 of 44.

Model 2: Total quarterly runoff

Variable	Discriminant loading
RC3	0.799
RC4	0.339

Model significance $P<0.20$.
Number of years correctly classified=34 of 44.

Synoptic climatic conditions that promote high spring peak discharges may be similar to those that are important in seedling success, although high peak spring discharges also occur following warm and wet winters not conducive to seedling abundance. High fall peak discharges are associated with intense thundershowers, which may represent brief, local departures from seasonal synoptic conditions.

The moderate success of the discriminant model suggests that peak discharge alone cannot explain all the stand-origin events. This may be partly because peak discharge data ignore variation in the character of the flood (e.g. the form of the flood hydrograph) and the antecedent conditions. Moreover, the capacity of a flood to destroy existing forests may be affected by the age of the forests, local stream gradient and other channel morphological variables, and the size and quantity of entrainable bed materials, all of which are ignored in simple peak discharge data.

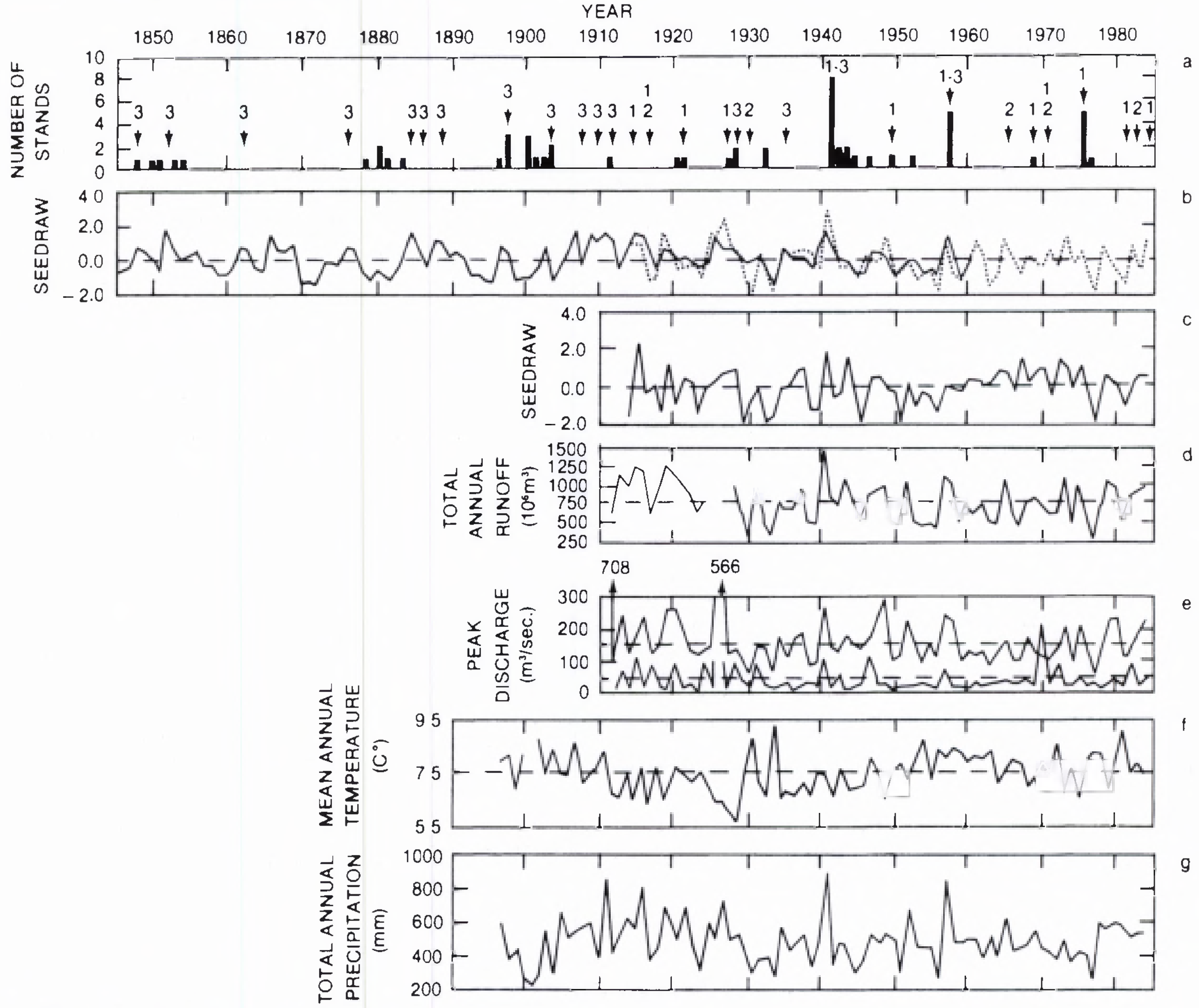

FIG. 3. Time series of stand origin dates, reconstructed seedling numbers, and climatic and hydrologic time series. (a) Number of stands originating in each year, based on field data (bars), and reconstructed stand-origin years (numbered arrows); numbers above arrows refer to: discriminant Model 1 (seasonal peak discharge), Model 2 (seasonal total runoff), or Model 3 (tree-ring chronologies), (b) reconstructed seedling numbers from quarterly climatic data (dashed line) and extended records from tree-ring time series (solid line), (c) reconstructed seedling numbers from annual climatic data, (d) total annual runoff for the Animas River at Durango for the period of instrumented record, (e) snowmelt (April–June) peak discharge (upper line) and thundershower (July–October) peak discharge (lower line) of the Animas River at Durango for the period of instrumented record, (f) mean annual temperature at Durango for the period of instrumented record, (g) total annual precipitation at Durango for the period of instrumented record.

How frequently do conditions suitable for stand-origin occur? Stands originated (Fig. 3a) primarily during years with peak snowmelt discharges of at least 200 m^3 s^{-1} (Fig. 3e). Twenty flows this size occurred from 1914 to 1985 (Fig. 3e), with a mean recurrence interval (MRI) of 3.6 years. But the discriminant model suggests that fall peak discharges are also important in stand-origin. Only six (MRI=11.8 years) of the twenty high snowmelt flows were accompanied by peak thundershower discharges above the mean (Fig. 3e). Thus, hydrologic conditions suitable for stand-origin occurred about every 12 years.

But, how often did stands actually originate? If stand-origin dates were all correct, then stands originated in thirty-two years (MRI=4.3 years) between 1848 and 1985 (Fig. 3a), but if some of these multiple years close together represent dating errors, then perhaps only thirteen to fifteen stand-origin years (MRI=9.2–10.6 years) occurred during this period. Thus, at least one stand may have originated about every 10 years.

Some years were exceptional stand-origin years. For example, 23% of the stands established between 1848 and 1985 (Fig. 3a) originated in two years (1941 and 1957). Only nine flows, of the size occurring during 1941 and 1957 (>225 m^3 s^{-1}), occurred between 1914 and 1984 (Fig. 3e), and only five of these (MRI=14.2 years) were accompanied by fall flows above the mean. Thus, flows large enough to initiate many new stands occur about every 14 or 15 years. This disturbance regime only characterizes the period since about 1850.

Good seedling years occurred about 3 times as often (MRI=3.4 years) as flood flows sufficient to originate a new stand (MRI=9.2–10.6 years), suggesting that periodicity of flood flows is the more significant regulator of riparian stand origins.

Extended reconstructions

ARMA (1,1) models were the predominant 'best' time series models for the six tree-ring chronologies (Table 6), supporting Monserud's (1986) hypothesis that the first order autoregressive-moving average process may be a common process in tree-ring chronologies.

The best multiple regression model relating SEEDRAW to principal components transformations (Table 7) of the tree-ring chronologies, accounts for about 40% of the variance in SEEDRAW (Table 8). Although this is only a moderately successful model, the pattern of overlap, between this tree-ring based model and the model based on the instrumented record, is reasonably good (Fig. 3b).

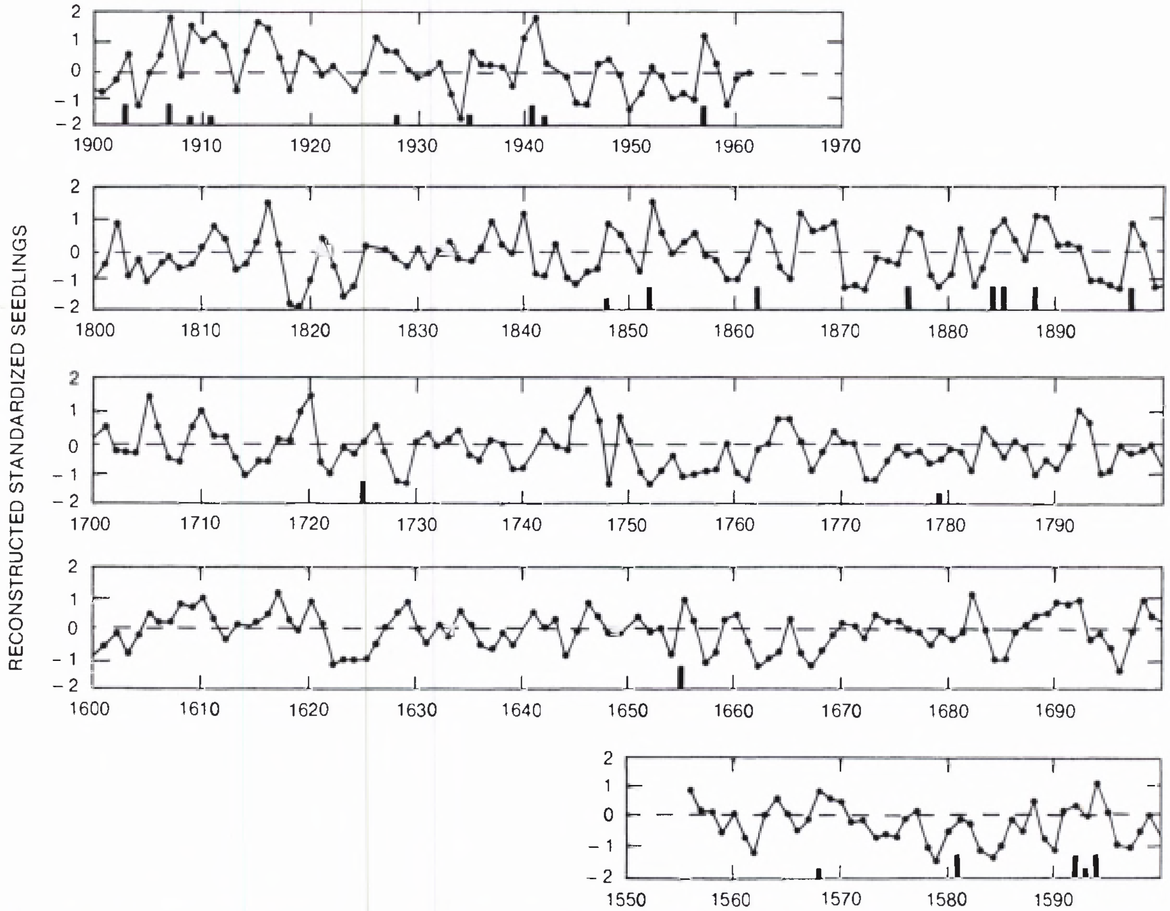

FIG. 4. Standardized seedling numbers (solid line), major stand-origin years (large solid bars) and minor stand-origin years (small solid bars) reconstructed from the tree-ring record. Major stand-origin years are defined arbitrarily as those years with a >0.85 probability of belonging to the stand-origin group of years. Minor stand-origin years have 0.50–0.85 probability of belonging to that group.

TABLE 6. Tree-ring chronologies used in reconstruction, and the autoregressive moving average (ARMA) models fit to each chronology. The trees are all *Pseudotsuga menziesii* (Mirbel) Franco, except at Almagre Mtn., where it is *Pinus aristata* Engelm.

Abbr.	Chronology	Source	ARMA Model*	Parameter estimates		
				ϕ_1	ϕ_2	θ_1
ALMA	Almagre Mtn.	Drew (1974)	(2, 0)	0.54	0.30	
ANTO	Antonito, site B	Drew (1974)	(1, 1)	0.66		0.40
BOBC	Bobcat Canyon	Drew (1976)	(1, 1)	0.85		0.66
SALI	Salida	Drew (1974)	(1, 1)	0.94		0.81
SAL	Salida, Site A	Drew (1974)	(1, 1)	0.83		0.75
SCHU	Schulman Old Trees	Stokes *et al.* (1973)	(1, 1)	0.91		0.75

*ARMA (p, q) models are p order autoregressive, q order moving average models. ARMA (1, 1) models are of the form: $Z_t=\phi_1 Z_{t-1}+a_t-\theta_1 a_{t-1}$. ARMA (2, 0) models are of the form: $Z_t=\phi_1 Z_{t-1}+\phi_2 Z_{t-2}+a_t$, where Z_t is the deviation at time t from the mean of an equally spaced stationary time series, a_t is an independently distributed normal deviate with zero mean and constant variance, and ϕ_1, ϕ_2 are the two autoregressive parameters, while θ_1 is the moving average parameter.

TABLE 7. Component loadings of tree-ring chronologies. Chronology abbreviations are as in Table 6.

	Component			
	1	2	3	
Eigenvalue	3.090	1.135	0.925	
Chronology				Communality
ALMA	0.253	0.416	0.873	1.000
ANTO	0.717	−0.079	−0.010	1.000
BOBC	0.819	−0.479	0.111	1.000
SALI	0.777	0.490	−0.233	1.000
SALA	0.768	0.481	−0.292	1.000
SCHU	0.805	−0.505	0.108	1.000

Using the tree-ring model, the pattern of reconstructed variation in seedling abundance since 1556 (Fig. 4) suggests that: (1) the period from about 1850 to the present was one with an unprecedented number of good seedling years, with thirty-five good years between 1850 and 1950, compared to only twelve to seventeen per century prior to 1850, (2) the number of bad seedling years has not changed appreciably since 1556, with about eighteen to twenty-five bad years per century.

The discriminant function (Model 3) separating stand-origin from no-stand-origin years, based on the tree-ring record (Table 9) significantly ($P<0.01$) separated these years, and correctly identified several of the unclassified stand-origin years between 1848 and 1961 (Fig. 3a). Some years were identified as stand-origin years (1862, 1876, 1884–85, 1888, 1907, 1909, 1935) which may not have been on the Animas River, but this may be only an apparent misclassification, due to: (1) errors in dating the stands, (2) lags in regeneration, or (3) subsequent destruction of stands originating in those years. The model does remarkably well considering the data limits.

Using this tree-ring model, the pattern of reconstructed variation in stand-origins since 1556 (Fig. 4) is similar to the pattern of reconstructed seedling success. The period from 1850 to the present also had an unprecedented number (seventeen) of stand-origin years, compared to the number (three) since 1595. The model suggests that the late 1500s (1568–95) may have been the only major period of stand-origin, at least for *P. angustifolia*, between 1556 and 1850.

DISCUSSION

Regeneration of *P. angustifolia*

Climatically-related interannual variability in seedling success such as that reported here has not apparently been observed in other riparian species. Some terrestrial trees (e.g. Pearson, 1923) and cacti (Brum, 1973) regenerate episodically in response to climatic fluctuations.

Climatic conditions favouring regeneration are characterized by particular seasonal synoptic patterns. Granger (1984) suggests that hemispheric warming results in a wetter climate in my study area, but global warming or cooling alone does not necessarily promote *P. angustifolia* seedling success. Moreover, good seedling years for *P. angustifolia* may occur during either zonal or meridional 'epochs' (Dzerdzeevskii, 1971), so that epoch conditions are not

TABLE 8. Best model from multiple regression of reconstructed seedling numbers (SEEDRAW) with tree-ring factors.

Predicted variable	Predictor variable*	Parameter value	Signif.
SEEDRAW	COM1–current year	0.347	0.004
	COM2–current year	−0.337	0.016
	COM3–current year	0.320	0.005
	COM1–following year	0.238	0.034
	COM2–previous year	−0.232	0.074

$R^2=0.466$, $R^2_{\mathrm{adj}}=0.403$.

*The COM number refers to the respective principal component in Table 7.

TABLE 9. Discriminant loadings of tree-ring factors (Model 3) on the discriminant function separating stand-origin from no-stand-origin years. Variables (factors) listed are the only factors entered in the stepwise model, out of five potential factors for current year, previous year, and following year.

Variable	Discriminant loading
COM1–current year	0.328
COM3–current year	0.448
COM1–following year	0.058
COM3–following year	0.259
COM1–previous year	0.240

good predictors of seedling success. Good seedling years are characterized by a within-year coincidence of particular seasonal synoptic patterns.

My data support Noble's (1979) observation that sustained moderate flow during the growing season is important in riparian species' regeneration, although temperature was also found to be important here, and more seedlings were produced in years with above average flows. Low-flow intervals, such as 1977, were not good years for regeneration, in contrast to Sigafoos' (1964) observation.

The Little Ice Age and recent vegetation change

Vegetation responded to the end of the Little Ice Age and subsequent global warming. This response is particularly apparent in changes in treelines (reviewed by Bray, 1971). Establishment patterns, reflected in forest age-class structures, often suggest: (1) limited establishment during the Little Ice Age, (2) a gradual post-1800 or post-1850 increase, and (3) a dramatic increase after 1920 (Payette & Filion, 1985; Kullman, 1987; Scott, Hansell & Fayle, 1987; Steijlen & Zackrisson, 1987). Other studies of forests (Hustich, 1958; Kullman, 1979; Franklin *et al.*, 1971) and shrublands (Cawker, 1980) reveal establishment peaks during the peak of the warming trend in the 1930s. These studies all cite 'warming' as the primary factor responsible for change.

Another pattern of increased post-1850 tree establishment has the peak post-1850 establishment periods before 1920 and after 1940 (Kullman, 1986a, b). My modelling data suggest *P. angustifolia* would have expanded between 1850 and 1920 and after 1940. There is photographic evidence of an expansion of *P. angustifolia*, beginning in the mid-1800s, that is not just restricted to the Animas River, but is regional in extent, and broadly synchronous (Baker, 1987).

Hypothesized causes of this second tree establishment pattern are based on assumptions about Little Ice Age climate that are not supported by recent tree-ring reconstructions or by my reconstruction of climatic factors influencing *P. angustifolia* regeneration. LaMarche (1973), for example, in a study of bristlecone pine at treeline in eastern California, suggested that cool, but relatively dry conditions during the Little Ice Age discouraged regeneration, which increased after the mid-1800s. However, tree-ring width indices near LaMarche's study area (Scuderi, 1987) were larger from 1500 to 1600 and from about 1725 to 1800 than after 1900, suggesting warm, rather than cool conditions during these parts of the 'Little Ice Age.' Neilson (1986) similarly suggested that cooling during the Little Ice Age, with meridional flow, favoured a mosaic of desert shrubland and desert grassland, but that this mosaic is not adapted to the present climate. Hastings & Turner (1965) found evidence that plant ranges in southwestern deserts moved upward after perhaps 1880, and similarly hypothesized that warmer and drier conditions beginning in about 1870 were responsible.

Tree-ring reconstructions for western North America do not support these authors' interpretations, but instead suggest a generally warmer and drier climate between 1602 and 1900 compared to 1901–70 (Fritts & Lough, 1985; Fritts in Brubaker & Cook, 1985). Very warm, dry western winters, like that of 1976–77, which resulted in almost no *P. angustifolia* seedlings in 1977, were up to 400% more common during certain periods, such as from 1615 to 1655 (Fritts, Lofgren & Gordon, 1979).

Tree-ring reconstructions also suggest the frequency of synoptic climate types changed. After 1700 there was a sharp increase in the frequency of Blasing & Lofgren's (1980) Winter Type 2 (a type favourable to *P. angustifolia*), a lesser decrease in Type 4 (a type favourable to *P. angustifolia* seedlings), and little change in the frequency of the Winter Types 1 and 3 (Blasing & Fritts, 1976; Fritts *et al.*, 1979), types that are generally unfavourable to *P. angustifolia*. A tree-ring reconstruction of climate since the mid-1500s for the Colorado Front Range suggests that fall and late spring/early summer cool and wet years were particularly common in the late 1500s and from about 1835 to 1900 (Hansen-Bristow, Ives & Wilson, 1988), the same time periods that my models predict *P. angustifolia* expansion. These authors' reconstruction also suggests predominantly warm and dry conditions during the 'Little Ice Age.'

In summary, the evidence that post-1850 warming has caused tree expansions is equivocal, particularly since climatic reconstructions suggest a complex pattern of temperature and precipitation fluctuations during and following the Little Ice Age in western North America. Circumstantial evidence might suggest that cooling following the mid-1800s is in some cases a more probable cause of tree expansion, and in the case of *P. angustifolia* there is more than circumstantial support for this interpretation.

The results suggest that it is essential to consider climatic conditions on a seasonal or at least annual basis in order to construct plausible hypotheses about past vegetation conditions. Decadal or longer-term estimates of regional zonal or meridional flow patterns may not be adequate or relevant. The tree-ring record may be one of the few sources that can provide appropriate annual and seasonal data needed to reconstruct plausible hypotheses about late-Holocene vegetation conditions.

Vegetation response to climatic change

Populations of organisms with short life-spans and high natality and mortality rates may track temporal fluctuations in environment fairly closely. Longer-lived organisms, such as trees, may lag in their population response to environmental fluctuations, and be less sensitive to fluctuations (Davis & Botkin, 1985).

But, while lags do affect sensitivity, sensitivity has more than one interpretation. In the riparian system studied here lags are apparent, as extant forests are dominated by trees established as early as 1848 (Fig. 5a, b, c). But insensitivity to climatic fluctuations is not apparent. Seedling abundance appears to closely track interannual and seasonal climatic fluctuation, but not every year has an effect, because where the riparian corridor is densely vegetated, as it is along the Animas River, stand-destructive floods must occur before seedling abundance fluctuations have substantial effect. On

FIG. 5(a). William H. Jackson, AD 1874, near Hot Sulphur Springs, Colorado, on the Colorado River. The shrubs on the floodplain are *Salix*. A few young *Populus angustifolia* are present (darker plants) on the sandier bars. (Colorado State Historical Society photo J-30349.)

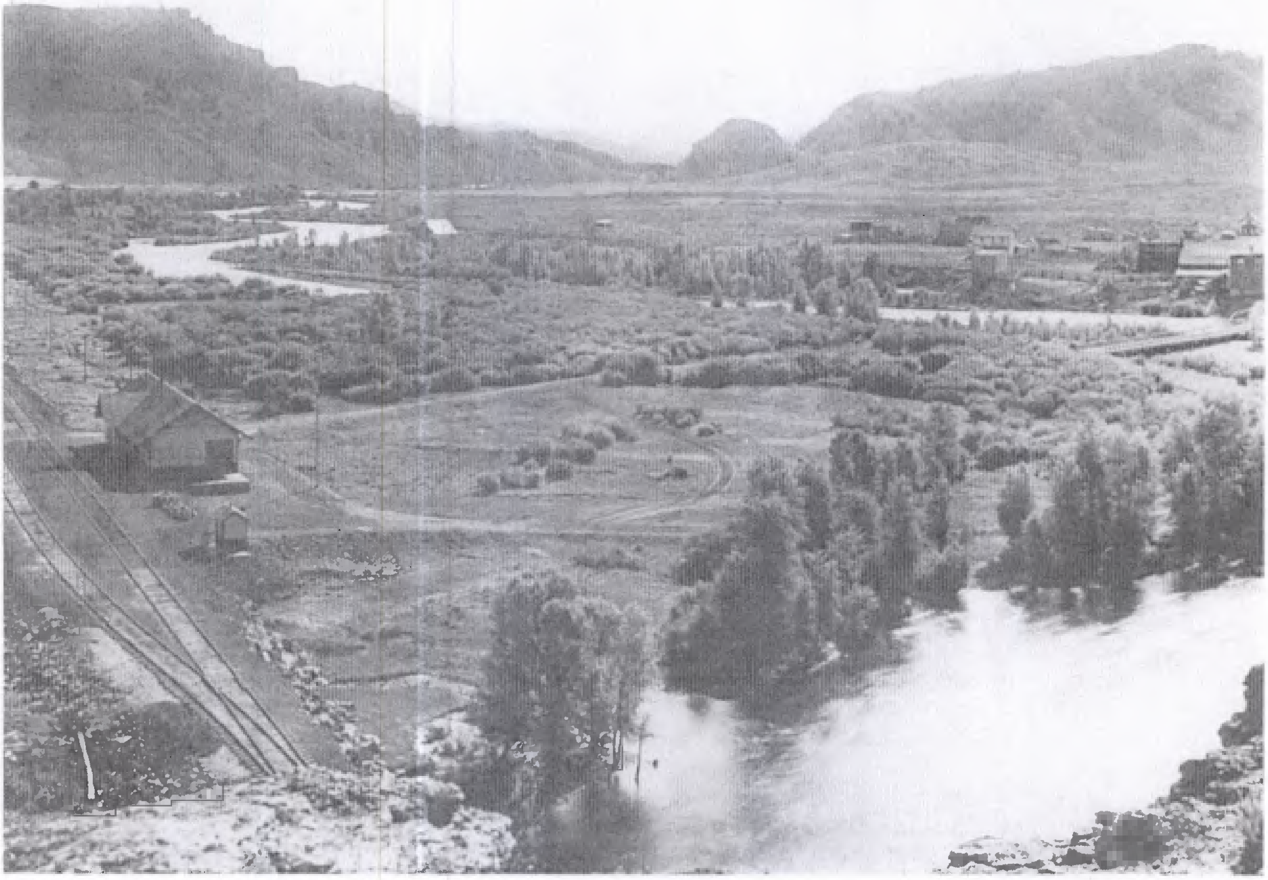

FIG. 5(b). L. C. McClure, AD 1900–06, near Hot Sulphur Springs, Colorado, on the Colorado River. Young trees are *Populus angustifolia*. (Photo courtesy of the Denver Public Library, Western History Department, Colorado.)

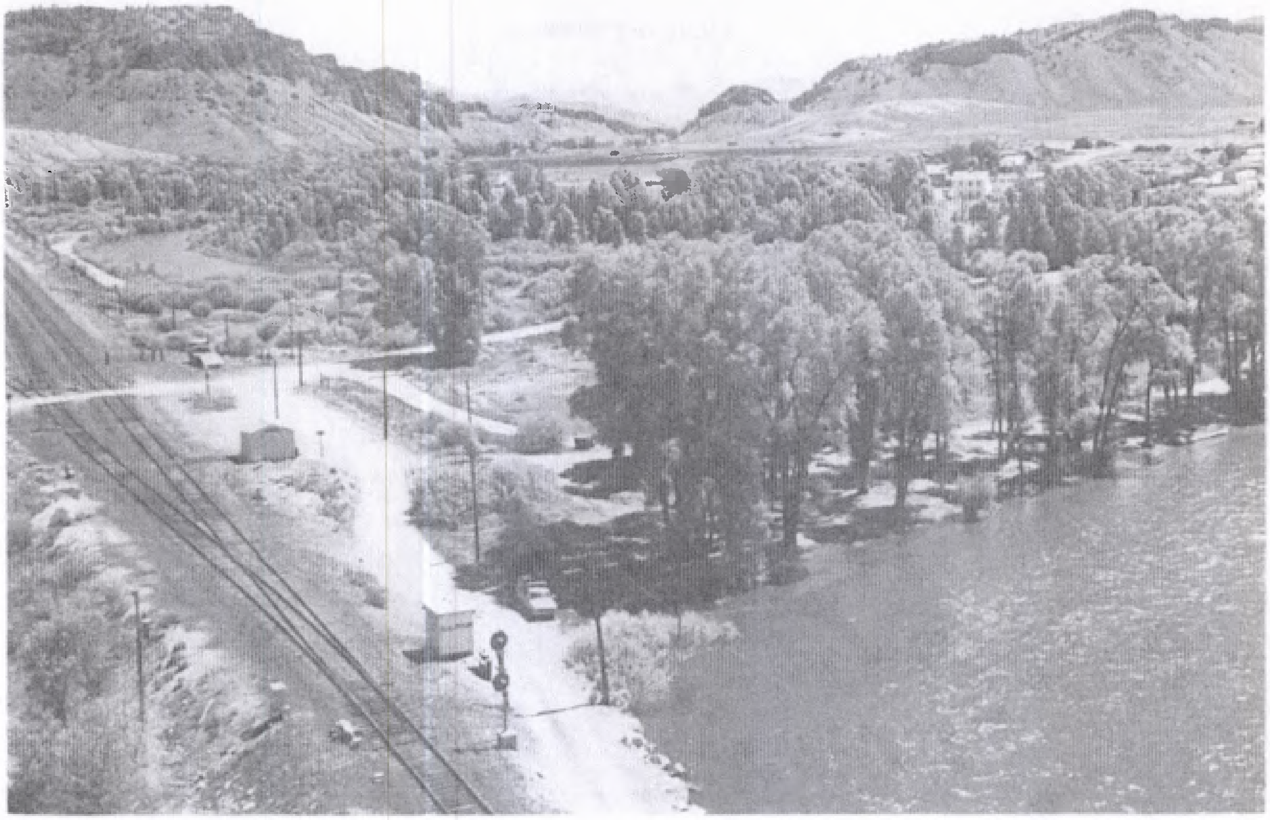

FIG. 5(c). William L. Baker, AD 1985, near Hot Sulphur Springs, Colorado, on the Colorado River. The floodplain is now dominated by *Populus angustifolia*, with scattered patches of *Salix*.

the Animas River, this may be only about once every 10–15 years. But when a stand-destructive flood does occur, climatic conditions during that single year (and perhaps the following year) may be the primary determinant of the composition and structure of the riparian vegetation for the length of the lag.

In the study area, for example, riparian forests have a turnover time (time needed to recycle all stands) of 100–150 years (a crude estimate based only on the maximum age of extant stands: Fig. 3a). Major stand-destructive floods occur about every 15 years. It may be, then, that, if 'initial-floristics' (Egler, 1954) sets future vegetation composition and structure, this structure is primarily determined during 6–10 of the 100–150 years.

Perhaps more problematic for methods that use vegetation to reconstruct climate is the additional possibility that these 6–10 years could be atypical of the decadal or century-length mean temperature, precipitation, and atmospheric circulation conditions. Moreover, in such a climate-sensitive system subject to periodic disturbances, the low frequency large-scale disturbances, such as the floods of 1941 and 1957 on the Animas River, may allow the vegetation to change rather abruptly over large areas. If so, then landscape composition and structure could be determined by climatic conditions in a few atypical years out of the 100–150 years.

However, the climate sensitivity I report here is tentative, and such climate-sensitive, disturbance-mediated communities might be unusual. Where disturbances are small and frequent, such as in some temperate zone deciduous forests, such sensitivity is likely to be absent or averaged-out on large land areas. But where species that have climatically-sensitive regeneration patterns dominate communities that are subject to low-frequency, large-scale stand-destructive disturbances, landscape structure and composition may primarily reflect the last few large disturbances and the climatic conditions during the years of, or a few years after those disturbances.

Limits of the method

I have combined several methods in order to reconstruct riparian seedling and stand-origin dynamics. The reconstruction is tentative because of several problems and assumptions. The method could be more reliable if some of these problems are solved.

First, is the problem of separating climatic effects on seedling abundance from other factors that affect abundance, including abiotic (e.g. floods) and biotic (e.g. herbivores, competitors) sources of mortality. This problem affects all reconstructions that use age structures to estimate past reproductive success. Better estimates can be obtained from annually monitored permanent plots (White, 1985).

Second, the climatic and hydrologic data used are not local, introducing some unknown bias. Required proximity to stations with long-term records may limit the applicability of the approach. Moreover, available tree-ring chronologies: (1) are also relatively sparse, (2) do not include recent years, necessitating the two-step reconstruction used here, and (3) only accounted for 40% of the variance in seedling abundance. The method relies on only a few years of seedling and climatic data, restricting the possible extent (number of variables and lags) of the regression analyses, and increasing the chance that a significant statistical relationship might be found where there is none.

Third, it is difficult to date stand-origin accurately, and yet a longer chronology of certain stand-origin and no-stand-origin years is needed in order to estimate a useful discriminant function. If stand-origin is a very rare event, then it is unlikely that a statistically adequate discriminant model can be developed.

Because of these limits, the method may be useful only for generating plausible hypotheses about the past. But, such hypotheses can be refined, if not tested, with photographic, historical, palynological, or other kinds of data. A combination of approaches may be needed to understand changes in vegetation from about 1600 to the present, a period that is remarkably unknown compared to the remainder of the Holocene.

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FACTORS CONTROLLING THE ESTABLISHMENT OF FREMONT COTTONWOOD SEEDLINGS ON THE UPPER GREEN RIVER, USA

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ABSTRACT

Declines in cottonwood (*Populus* spp.) recruitment along alluvial reaches of large rivers in arid regions of the western United States have been attributed to modified flow regimes, lack of suitable substrate, insufficient seed rain, and increased interspecific competition. We evaluated whether and how these factors were operating during 1993–1996 to influence demographics of Fremont cottonwood (*P. deltoides* Marshall subsp. *wislizenii* (Watson) Eckenwalder) along reaches of the Green and Yampa Rivers near their confluence in northwestern Colorado. We examined seedling establishment, defined as survival through three growing seasons, at three alluvial reaches that differed primarily in the level of flow regulation: a site on the unregulated Yampa, an upper Green River site regulated by Flaming Gorge Dam, and a lower Green River site below the Green–Yampa confluence. Seed rain was abundant in all sites, and led to large numbers of germinants (first-year seedlings) appearing each year at all sites. The regulated flow in the upper Green River reach restricted germination to islands and cut banks that were later inundated or eroded; no seedlings survived there. Mortality at the lower Green River site was due largely to desiccation or substrate erosion; 23% of 1993 germinants survived their first growing season, but at most 2% survived through their second. At the Yampa River site, germinants appeared on vegetated and unvegetated surfaces up to 2.5 m above base flow stage, but survived to autumn only on bare surfaces at least 1.25 m above base flow stage, and where at least 10 of the upper 40 cm of the alluvium was fine-textured. Our studies of rooting depths and the stable isotopic composition of xylem water showed that seedlings in the most favorable locations for establishment at the Yampa site do not become phreatophytic until their third or fourth growing season. Further, the results of experimental field studies examining effects of shade and competition supported the hypothesis that insufficient soil moisture, possibly in combination with insufficient light, restricts establishment to unvegetated sites. Collectively, the demographic and experimental studies suggest that, in arid regions, soil water availability is at least as important as light level in limiting establishment of Fremont cottonwood seedlings. We hypothesize that in cases where arid land rivers experience large spring stage changes, recruitment is further constrained within bare areas to those sites that contain sufficient fine-textured alluvium, saturated during the spring flood, to provide the flood-derived soil moisture normally necessary for late-summer seedling survival. Copyright © 1999 John Wiley & Sons, Ltd.

KEY WORDS: alluvial soil; Colorado; competition; cottonwood; desiccation; *Populus*; regulated river; riparian vegetation; seedling population dynamics; tamarisk; *Tamarix*; Utah

INTRODUCTION

The structure, functioning, and dynamics of floodplain ecosystems are determined in part by stream flows and fluvial processes that influence site hydrologic and geomorphic conditions, and in part by ecological processes that influence the patterns of species colonization, competition, and succession (Johnson *et al.*, 1976; Hupp and Osterkamp, 1996). Sediment erosion and deposition during periods of high flow are of particular importance because these processes both destroy and create seedbeds, thereby linking fluvial and ecological processes (Campbell and Green, 1968; Hupp and Osterkamp, 1996; Scott *et al.*, 1996).

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In many temperate and boreal regions of North America, the primary colonizers of mineral soil surfaces exposed by receding floodwaters are species of *Populus* (cottonwood) and *Salix* (willow). The ecological significance of cottonwood is especially great in arid regions of western and southwestern North America because in most areas no native replacement tree species exists (Rood and Mahoney, 1990). Our understanding of cottonwood autecology varies among the three dominant taxa present in this region, narrow-leaf cottonwood (*P. angustifolia* James), plains cottonwood (*P. deltoides* Marshall subsp. *monilifera* (Aiton) Eckenwalder), and Fremont cottonwood (*P. deltoides* Marshall subsp. *wislizenii* (Watson) Eckenwalder), with Fremont cottonwood probably being least known (nomenclature follows Weber and Whittman, 1996). It is recognized that cottonwood recruitment involves multiple factors (Rood and Mahoney, 1993; Busch and Smith, 1995), and most likely varies with geomorphic setting and channel type (Scott *et al.*, 1996; Friedman *et al.*, 1997). Recruitment processes on free flowing river systems remain incompletely understood for even the most studied species. For example, cottonwood seedling establishment has been reported to result primarily from large, relatively infrequent floods (Everitt, 1968; Scott *et al.*, 1997). However, large floods may result in stage changes greater than 2–3 m with seedlings establishing in relatively high landscape positions (Scott *et al.*, 1997). Because seedlings are intolerant of dry soils, rapid water table declines (> 4–6 mm/day) can leave seedlings far above the late summer water table and lead to seedling death (Mahoney and Rood, 1991, 1992; Segelquist *et al.*, 1993). Thus, the mechanism of seedling establishment on rivers with large stage change is unclear.

Cottonwood seedlings are reported to be shade intolerant (Read, 1958; Braatne *et al.*, 1996; Scott *et al.*, 1996). Studies of rooted stem cuttings of eastern cohorts of plains cottonwood indicate that plants can attain approximately 80 and 60% of their maximum net photosynthetic rate (P_n) in approximately 50 and 25%, respectively, of full sun (Regehr *et al.*, 1975; Bassman and Zwier, 1991). However, physiological studies of cottonwood seedlings have not been performed and thus it is unclear if cottonwood seedlings on western rivers can attain similarly high photosynthetic rates in shaded environments. The rooted cuttings were also sensitive to soil water availability, with stomatal closure and the cessation of photosynthesis at twig xylem pressure potentials (Q_{xp}) of between -1.10 and -1.25 MPa (Regehr *et al.*, 1975; Bassman and Zwier, 1991), and 80–90% loss of xylem hydraulic conductivity occurring at Q_{xp} of -1.5 to -2.0 MPa (Tyree *et al.*, 1994). It is unclear whether reduction of sunlight or reduction of soil water availability by neighbors has a greater influence on seedling survival.

The apparent correlation between flow modification of the major rivers of interior western North America and the limited cottonwood recruitment now found along them (Colorado River: Busch and Smith, 1995; Rio Grande: Howe and Knopf, 1991; Missouri River: Johnson *et al.*, 1976; Reily and Johnson, 1982; Gila River: Fenner *et al.*, 1985; Oldman River: Rood and Mahoney, 1990; Marias River: Rood and Mahoney, 1995) strongly suggests that regulation may be a causative factor (Johnson *et al.*, 1976; Williams and Wolman, 1984; Braatne *et al.*, 1996). River regulation by high dams and water diversions typically reduces both annual maximum or peak flow (Andrews, 1986; Stanford and Ward, 1991) and sediment load (Andrews, 1986, 1991), raises annual low or base flow (Williams and Wolman, 1984), and modifies the rate of flood stage decline. Resultant modifications in hydrologic and fluvial processes could potentially affect every stage in the recruitment process, from quantity and quality of seed rain to the growth and survivorship of seedlings. They could also indirectly affect the recruitment process through direct affects on herbivore or competitor populations. The widespread invasion of a competitor, tamarisk (*Tamarix ramosissima* Ledebour), into western riparian systems further complicates establishment of cause-and-effect linkages between river regulation and declines in cottonwood recruitment (Turner, 1974).

We utilized field studies conducted at paired floodplain sites along the unregulated Yampa River and regulated Green River to examine seed rain, and the requirements for Fremont cottonwood seedling establishment (defined by us to be survival through the first three growing seasons). The rivers studied are large (typical peak annual discharges of 300–500 m^3/s), have sand beds, and in their unregulated condition, feature annual stage changes of 2–3 m. The goal of this paper is to address five primary questions: (1) What are the natural patterns of seedling establishment on regulated and unregulated rivers? (2) What is the effect of shade on cottonwood seedling survival? (3) What is the effect of competition from tamarisk on cottonwood seedling survival? (4) Is cottonwood seedling survival linked to taproots reaching the late summer water table or capillary fringe? (5) Is soil texture an important determinant of cottonwood seedling survival?

THE STUDY REACHES

Our studies were conducted on floodplains of the Green and Yampa Rivers, above and below their confluence in northwestern Colorado (Figure 1). The Green River originates in the Wind River Range in west central Wyoming and flows generally southward to its confluence with the Colorado River in Utah. The Green River is regulated by two high dams: Flaming Gorge, completed in 1962, and Fontanelle, a smaller, upstream structure completed in 1964. Releases from Flaming Gorge Reservoir, which began to

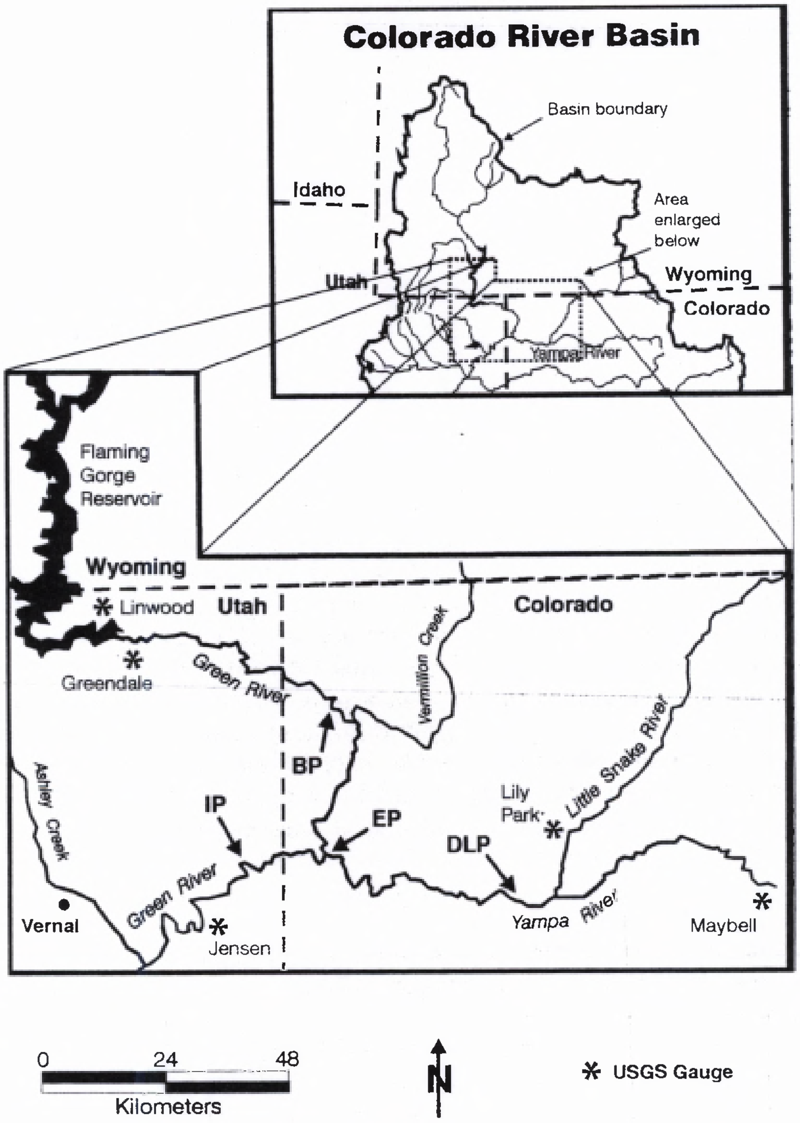

Figure 1. Locations of the three main study areas in Colorado and Utah: Island Park (IP), Deer Lodge Park (DLP), and Brown's Park (BP). Locations of USGS stream gauges used in the study are also shown, as is Echo Park (EP) at the confluence of the Yampa and Green Rivers

fill in December 1962, almost completely determine flows in the Green for 102 km, until its confluence with the Yampa River. The extent of river regulation in the Colorado River and Green River systems are reviewed by Stanford and Ward (1986) and Stanford (1993).

The Yampa River originates in the Park Range and White River Plateau in north central Colorado and is the last major tributary of the Colorado River that remains largely unregulated. There are three small headwater dams within its basin, and a total of about 10% of the annual flow is diverted for municipal or agricultural use.

Two of our three study sites, Brown's Park and Deer Lodge Park are along reaches that were quite similar in geomorphic, hydrologic, and ecological setting prior to river regulation. The Brown's Park site (BP) is in Brown's Park National Wildlife Refuge, along the highly regulated segment of the Green River, 63 km below Flaming Gorge Dam (see Figure 1). Deer Lodge Park (DLP) is on the unregulated Yampa River, 50 km above its confluence with the Green and below the last major tributary of the Yampa River, the Little Snake River. The third site, Island Park (IP) is on the Green River, 15 km below the confluence with the Yampa. The geomorphic and ecological setting at IP is similar to that of the upstream sites, but its hydrologic regime features an intermediate level of regulation. Both DLP and IP are located in Dinosaur National Monument. The elevations at DLP, BP, and IP are approximately 1705, 1630, and 1510 m, respectively. The river channel is unconfined within each study reach, meandering across thick, generally fine-textured alluvium (< 2 mm). We also worked in Echo Park (EP), at the confluence of the Yampa and Green Rivers.

Long-term discharge data for these reaches are available from USGS gauging stations (Figure 1). We used the Linwood, UT gauge (# 09225500) to represent BP flows from 1929 to 1962, when this station was inundated by the filling of Flaming Gorge Reservoir. We used data from the Greendale, UT gauge (# 09234500), located just below the dam, for 1963 to present. For DLP, we summed discharges of the Yampa River at Maybell, CO (gauge # 09251000) and the Little Snake River at Lily Park, CO (gauge # 09260000). Both of these gauges have continuous data from 1922 to present. For the combined flow of the Yampa and Green Rivers at IP, we used data from Jensen, UT (1947 to present, gauge # 09261000).

The Green and Yampa Rivers both have snowmelt driven peak flows, and their hydrographs prior to 1963 were similar. Mean annual discharges on the two rivers were 54.6 and 58.1 m^3/s, respectively, and are not significantly different. Historic Green River peak flows averaged 80% of the Yampa's, and typically occurred about 2 weeks later than the Yampa peak. There was no significant difference between the mean peak annual discharge of the Yampa at DLP for the periods 1922–1962 and 1963–1995. In contrast, mean peak annual discharge of the Green River was significantly lower during the 1963–1995 post-Flaming Gorge Dam period at both BP and IP. DLP and IP had similar peaks in 1993 (498 and 566 m^3/s, respectively) and 1995 (519 and 527 m^3/s), reflecting the large contribution of the Yampa to peak discharge of the Green at IP.

Annual flow variation (calculated as peak flow divided by low flow for a given year) averaged ~ 33 in BP and ~ 100 in DLP prior to 1963. Current Green River flow variation is approximately 5–6. The two rivers have distinctive patterns of stage dynamics (Figure 2). During 1993–1995, river stage in DLP varied by 1.8–2.9 m, and occurred during the 6–8 weeks between late May and late July or early August (Figure 2). The analogous stage decline was only ~ 0.7 m in BP where peak stage was similar in both magnitude and duration (~ 1 month) each year (Figure 2). We also regularly monitored floodplain water table depth in hand-bored wells cased with slotted PVC pipe. We related water table elevation to river stage by developing rating curves using staff gauges we installed in our study areas and United States Geological Survey (USGS) daily average discharge data.

Both the Yampa River and the pre-dam Green River carried large sediment loads. The mean annual sediment load for the Yampa River at its mouth, the Green River in Brown's Park, and the Green River at the Jensen gauge (downstream from Island Park, see Figure 1) were 1.5, 3.3, and 6.3 × 10^6 tons/year, respectively, prior to 1962. Since 1963, sediment load within the BP reach has been reduced to input from a few small tributaries. The sediment load at the Jensen gauge has been decreased by 54% due to sediment retention in Flaming Gorge Reservoir (Andrews, 1986).

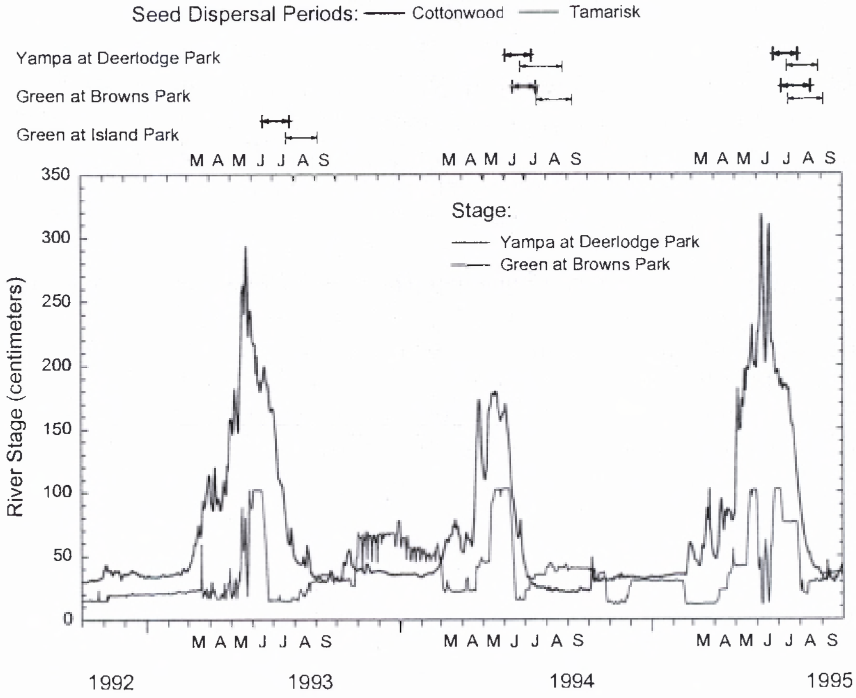

Figure 2. Daily mean stage for the period October 1993 to October 1995 for the Yampa River in Deer Lodge Park (DLP) and the Green River in Brown's Park (BP). The periods of seed rain for DLP and BP (1994 and 1995) are shown as horizontal arrows. Stage was calculated from USGS daily mean discharge data, and the rating curve generated from our stage measurements

Climatic conditions at the three sites are similar, based on daily precipitation and temperature data from US National Weather Service stations at Maybell, CO (located 20 km east of DLP), Brown's Park, CO (located ~5 km from BP), and Jensen, UT (located ~15 km southwest of IP). Long-term mean annual precipitation for Maybell, Brown's Park, and Jensen are 284, 209 and 199 mm, respectively. On the average, approximately 1/12th of the annual mean precipitation fell during each of the four growing season months (June–September). A critical dry period occurred during the summer of 1994 when less than 10 mm of rain fell during June and July ($<20\%$ of the long-term mean), and essentially no rain fell during July.

METHODS

Patterns of Fremont cottonwood and tamarisk seedling establishment

We determined the period of cottonwood and tamarisk seed dispersal by observation during 1993 (IP) and 1994 (DLP and BP). In 1995, we quantified cottonwood seed rain in BP and DLP using eight traps in each area. The traps were oriented in two lines parallel with the river and located in areas where seedlings could potential establish. Traps were 400-cm^2 boards, coated with Tanglefoot© and mounted horizontally 1 m above the soil surface. We removed seeds and reset traps every 4–15 days from early June (prior to seed release) through mid-August, by which time all capsules had opened. We determined the period of tamarisk seed dispersal in 1995 by monitoring ten tamarisk plants in the area of the seed traps in both BP and DLP.

We evaluated the causes and magnitude of mortality among natural cohorts of Fremont cottonwood seedlings by monitoring the fates of nearly 5000 seedlings contained in 139 permanent plots, 0.25 m^2 in size, distributed among the DLP, BP and IP study areas. Plots were selected to represent the full range of geomorphic and hydrologic conditions present in these study areas. Most (90) plots were established to monitor members of the 1993 cohort. We censused live seedlings within each plot periodically each summer during 1993–1995. No plot was protected from herbivores. Seedling survival was evaluated separately in each study area, with plots grouped by establishment date. We assigned cause of death into one of four possible categories: inundation, channel erosion, bank sloughing, and desiccation. Channel erosion or bank sloughing was determined by the loss of the plot substrate, desiccation by the presence of dead dry seedlings, and inundation, by dead seedlings in seasonally or semi-permanently saturated soils.

To evaluate the importance of stage decline rate and water table depth on the survival of cottonwood germinants, we established two 60-m long transects in DLP in 1995 (D95-1, and D95-2), running from the mature cottonwood forest edge across the topographic gradient of the unvegetated floodplain toward the river. These transects were located in the inside bend of meanders across sites with active sediment deposition. We placed permanent 10 × 10-cm plots at 1-m intervals along each transect and censused the live cottonwood germinants present in the plots in late July, and again in mid-September. Plot surface elevation above the late summer base flow water table and soil texture were determined by surveying and the hydrometer method, for plots ($n = 60$) containing germinants. We pooled plot data from both transects for analysis using logistic regression to model fates (death or survival) of individual germinants within each plot ($N = 774$ plants) over the monitoring period. Stepwise regression (Steinberg and Colla, 1991) was used to derive a model relating probability of death to position along the elevation gradient (variable ELEV, distance above base flow stage elevation, in centimeters), percentages of SILT and CLAY in plot surface soils (1–10 cm depth), initial plant density (JUL95), and mid-September gravimetric surface soil water content expressed as a percent (MOIST).

We tested whether cottonwood germinants rooted to the late-summer water table using morphologic (rooting depth) and topographic data (elevation above the late summer water table). We measured maximum first year rooting depths by carefully excavating 64 germinants (1995 and 1996 cohorts) from DLP sites spanning the full range of elevations and landforms where germinants had survived through early September.

Determination of xylem water sources

We directly determined the source of water used by cottonwoods from stable isotope analyses of ground water, soil water, and xylem water. Because of their greater atomic mass, water molecules containing deuterium, a stable isotope of hydrogen, are enriched in water exposed to evaporation. Thus, both unsaturated soil water and summer precipitation contain a higher relative amount of deuterium than does ground water recharged by the river, furnishing a basis for determining whole plant water sources using free water extracted from plant tissues (Flanagan and Ehleringer, 1991; Dawson 1993). We collected fully suberized stem samples from plants that were 2, 4, 8–12, 20–25, and 90+ years old in late August 1996 at DLP; age was determined by ring counts of stems sectioned just above the germination surface. No 3-year-old plants (1994 seedling cohort) occur at this site. Because stems of germinants (1996 cohort) were not yet suberized, we collected the top 5 cm of the taproot. Each sample of germinant tissue contained the taproots of 12 individuals. Unsaturated soil water was obtained from soil collected at a 10–35 cm depth at sites where plants were collected. Samples of ground water were collected by pumping from monitoring wells that were generally within 10 m of each sample location. We calculated the isotope ratio relative to that of a standard, δD, as:

$$\delta D\ (‰) = [(D/H)_{\text{sample}}/(D/H)_{\text{standard}} - 1] \times 1000,$$

using Standard Mean Ocean Water (SMOW) as our standard (Dawson, 1993). Hydrogen isotope ratios were determined by Mountain Mass Spectroscopy (Evergreen, CO), using cryogenic distillation methods with liquid nitrogen to trap water from soil and plant samples, and zinc as a catalyst in hydrogen reduction of all water samples (Ehleringer and Osmond, 1989).

The effects of competition from older cohorts on cottonwood seedling establishment

We assessed the effect of previously established cottonwoods on cottonwood germinant survivorship in a mensurative experiment using paired plots established on 36 fluvial landform features. These features, located at DLP and Echo Park (EP), represented the full range of sites where cottonwood germinants survived to mid-September during 1995 and 1996. A 1-m^2 plot containing live germinants was established at a representative location on each landform. On landforms where living or dead germinants were present both on bare soil and beneath a canopy of older cottonwoods (generally 2–15 years old), a plot was established in each area. Germinants were censused and their heights measured in early September.

We determined the surface elevation of each plot relative to the river at base flow stage, documented the underlying soil stratigraphy, and collected samples from each soil horizon for analysis of texture and water content. We determined gravimetric soil water content for each soil horizon on landforms examined in 1995, whereas both gravimetric and volumetric samples were collected during 1996 that allowed the determination of both gravimetric and volumetric water contents. Because soil samples collected in 1995 and 1996 had similar texture and gravimetric water content, the volumetric water content of 1995 samples was estimated by tabular comparison with 1996 samples. Soil matric potential for each sample was calculated from soil texture and volumetric water content using the procedures in van Genuchten *et al.* (1989).

Effects of shade on seedling establishment

Three shade experiments addressed whether a reduction of photosynthetically active radiation (PAR) would negatively and differentially affect cottonwood or tamarisk seedling survival. We shaded seedlings using screen canopies with open sides in 1993, and canopies with both screen tops and sides in 1994 and 1995. In all experiments, we measured sunlight reaching seedlings as PAR (Li-Cor Model 189) relative to that of full sun on a cloudless mid-summer day. Seedlings were grown from local seed and transplanted into the field when approximately 1 month old. The seedlings are used as phytometers (Clements, 1935) to measure the effect of shade on plants of identical age, health and stature. However, we did not control for, or measure, potential changes in air or soil temperature due to our shading; shade/temperature interactions were considered in interpretation of results.

Experiment 1. We tested for an effect of shade on the survival of cottonwood seedlings under natural field conditions using a completely randomized experimental design. We established five replicates of each of four treatments (55, 30, 17 and 4% of full sun) plus a control on 400-cm^2 plots arranged in a grid on a freshly exposed sediment bar in IP. The bar was leveled to ensure that all plots were a similar distance above the water table (~ 1 m in late summer). Twelve, 1-month-old seedlings were transplanted in a regular array in each plot in mid-July 1993, and revisited in September 1993 and in May and August 1994. We tested for a relationship between shade and the proportion of seedlings surviving to each census using logistic regression (SAS Proc GENMOD, SAS Institute, 1992).

Experiment 2. We tested for an effect of shade on cottonwood and tamarisk seedlings grown from seed *in situ* at a field site where abundant soil water was provided by sprinkler irrigation. We created 20 pairs of adjacent 400-cm^2 plots in a grid pattern on a newly exposed sediment bar in DLP and transplanted 15 cottonwood seedlings into one plot and 15 tamarisk seedlings into the other in July 1994. We randomly assigned the paired plots to generate five replicates each of three shade treatments (69, 40 and 17% of full sun) plus controls, using a completely randomized block design. All plots received water three times daily (~ 1.8 cm/day total) until mid-August, when watering was stopped. The water table was 143 cm beneath the bar surface in early September 1994. Survival in plots at the end of the watering period, and 1 month after watering ceased was determined. We analysed data as in Experiment 1.

Experiment 3. We tested for an effect of shade and intraspecific competition on naturally established cottonwood seedlings by placing shade canopies over ~ 3-week-old cottonwood germinants in DLP in late July 1995. Five replicate pairs of 400-cm^2 plots were established for each of three shade treatments (69, 40 or 17% of full sun), plus a control. We thinned one plot from each pair to a density (r) of ten seedlings/plot ($= 250$ individuals/m^2), whereas the other plot retained its original seedling density

($r = 1073$ individuals/m^2; S.D. $= 196.7$; $n = 20$). Because no location could accommodate all 40 plots, we established five sets of four plots each, one of each treatment plus a control, at different locations (LOC) within a 0.01-ha area. Plots were revisited after 1.5 months. We analysed data as in Experiment 1.

Effects of competition with tamarisk on cottonwood seedling establishment

Experiment 4. We tested the effects of an adult tamarisk overstory (2–4 m tall) on the survival of transplanted 1-month-old cottonwood seedlings. We transplanted 15 seedlings into each of fifteen 400-cm^2 plots established under tamarisk and assigned five plots to each of two treatments plus a control. Treatment A consisted of pruning the tamarisk canopy at ground level to eliminate competition for light. Treatment B consisted of canopy pruning plus trenching the plot perimeter to sever horizontal roots in the top 40 cm of soil and reduce soil water acquisition by neighboring plants. Plots were created in July 1993 and revisited in September 1993, and in May and August 1994. We tested for differences in proportions of survivors using chi-square analysis.

Experiment 5. We tested for an effect of interspecific competition from tamarisk seedlings on survival of cottonwood seedlings. The treatment consisted of transplanting 15 cottonwood seedlings (~ 1 month old) into dense beds of naturally occurring tamarisk seedlings (~ 5000 individuals/m^2), and was replicated in three plots in IP in 1993. We removed, by hand, all tamarisk seedlings in one control plot. Removal caused only slight disturbance to the soil surface and no effort was made to duplicate the soil disturbance in the treatment plots. We monitored fates of the transplanted seedlings through September 1994.

Soil stratigraphy of fluvial features supporting emergent, seedling, and established cottonwoods

We excavated trenches across each of the 36 fluvial landform features used in the analysis of cottonwood germinant survival to analyse soil stratigraphy. We used regression analysis to relate the density of germinants surviving to mid-September to the total thickness of loam-textured soil layers (sandy loam, loam and silty loam) within the rooting zone (0–45-cm depth). We also excavated a trench through an infrequently flooded terrace supporting mature Fremont cottonwood trees in order to examine soil stratigraphy and evaluate landforms on which the trees established.

RESULTS

Patterns of Fremont cottonwood and tamarisk seedling establishment

The 1993 cottonwood seed rain, which was monitored solely in IP, began in mid-June (Figure 2). In 1994, seed rain in DLP began in early June, just after the Yampa River reached peak stage, and continued through the entire period of stage decline. In 1995, seed rain in DLP began in late June (Figure 3). Seed rain began somewhat later in BP than in DLP in both 1994 and 1995 (Figures 2 and 3), but lasted a similar length of time, 4–6 weeks. The maximum mean rate of seedfall in 1995 was higher in DLP, 362 seeds/m^2/day, than that recorded in BP, 70 seeds/m^2/day (Figure 3). Seed rain generally coincided with the declining limb of the spring hydrograph at DLP and IP, but to a lesser extent at BP due to flow regulation. Seed rain in BP during 1995 began during the second stage peak of the Green River, when all river bars in BP were inundated. When stage had declined sufficiently to reveal bars (early August), cottonwood seed rain was nearly complete, although tamarisk seed dispersal was at its peak.

Tamarisk seed dispersal began after cottonwood in all sites and years (Figures 2 and 3). In 1995 tamarisk seed dispersal began in early to mid-July during the period of maximum cottonwood seed release in DLP and BP and continued until mid-September. Overlap of seed release resulted in the formation of mixed cottonwood and tamarisk seedling stands in many locations in all study areas.

During all four summers of fieldwork (1993–1996), large numbers of cottonwood germinants established on the DLP floodplain as floodwaters receded. Germinants were also common at BP and IP during those years. In BP, successful germination was restricted primarily to islands and steep cut-banks, the only areas with moist surface soils. More than 93% of the monitored 1993 cottonwood germinants at DLP and

77% of those at IP died within a few months of germination (Table I). Survivorship through the first growing season was only slightly higher at BP (88% mortality, sites pooled). Survivorship over winter 1993–1994 was high, but survivorship through the 1994 growing season was again low (0.29 for DLP, 0.12 for IP; sets pooled: Table I), which included a 5 week long mid-summer rainless period. None of the monitored members of the 1993 cohort survived through their third growing season (i.e. to September 1995) in BP, and only 4% (61 of 1251 seedlings) survived in DLP (Table I). The DLP survivors were concentrated in four plots, all of which were located on surfaces > 185 cm above river base flow stage.

The causes of seedling mortality varied among the sites. In BP, 62.5% of the seedling mortality was due to prolonged inundation during the growing season, whereas inundation caused no deaths at IP or DLP. Germinants on BP banks were killed when banks saturated by higher stage failed (18.8%), a fate uncommon at DLP (2.3%) and absent at IP, because relatively few germinants grew on banks. In DLP and IP, seedling mortality was due primarily to desiccation (51.2 and 65.4%, respectively) during the first or second growing season, or substrate erosion during high flow in the second growing season (46.5 and 34.6%, respectively).

The cohort of 1995 cottonwood germinants monitored along transects DL-1 and DL-2 at DLP emerged on sites with surface elevations that varied from 100 to 225 cm above river base flow elevation. The logistic model fit to the July-to-September survival data included soil moisture, soil texture and initial density as independent variables [Logit (probability of dying) = 3.78 + (1.33 MOIST) – (0.80 CLAY) – (0.24 SILT) – (0.03 JUL95)]. p-values for these variables were all < 0.025, and odds ratio values were all significantly different from 1.00 (MOIST, 3.8; CLAY, 0.45; SILT, 0.78; JUL95, 0.97). The overall fit of the model was satisfactory (McFadden's $\rho^2 = 0.219$). Thus, percentages of clay and silt, as well as initial

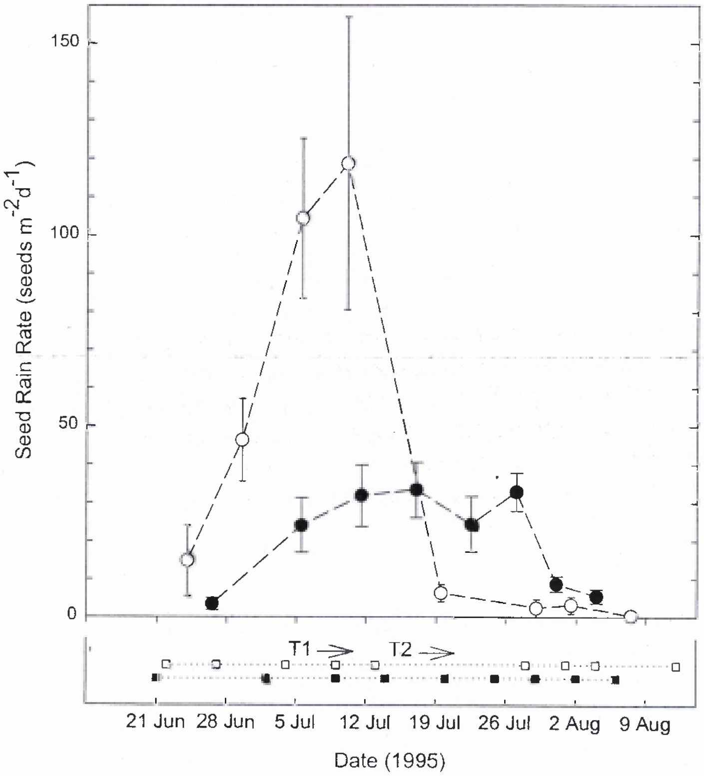

Figure 3. Density of cottonwood seed rain in Browns Park (BP, large solid circles) and Deer Lodge Park (DLP, large open circles) during 1995. Values are means of eight traps and are plotted in the middle of the period sampled; bars show ± 1 S.E. Small squares (coded as above) along the two horizontal dotted lines depict trap collection dates for each site. T1 and T2 indicate the period of tamarisk seed rain in BP and DLP, respectively

Table I. Survivorship in the 1993, 1994, and 1995 cohorts of cottonwood seedlings in Deer Lodge Park (DLP), Browns Park (BP) and Island Park (IP)

Date	DLP					BP				IP		
	1993 Cohort			1994 Cohort	1995 Cohort	1993 Cohort			1994 Cohort	1993 Cohort		
	Time 1 ($n=8$)	Time 2 ($n=8$)	Time 3 ($n=12$)	Set A ($n=12$)	Set A ($n=26$)	Site A ($n=6$)	Site B ($n=9$)	Site C ($n=6$)	Set A ($n=11$)	Time 1 ($n=30$)	Time 2 ($n=2$)	Time 3 ($n=9$)
1993												
3–8 July	151.0					71.3	76.9	55.3		196.4		
	(24.2)					(20.9)	(30.6)	(23.3)		(48.5)		
26–7 September	10.5	96.5				10.0	5.3	9.3		44.8	92.0	
	(2.1)	(21.0)				(8.5)	(2.2)	(3.4)		(20.1)	(36.0)	
1994												
18–22 May	10.5	69.5	252.0							18.7	84.0	68.9
	(2.1)	(24.1)	(64.8)							(6.4)	(32.0)	(14.3)
15 June										8.6	84.0	65.3
										(4.2)	(32.0)	(15.4)
6–7 July	0.0	45.5	174.0	339.7								
		(19.9)	(52.8)	(63.0)								
14–18 August		39.0	57.7	71.0		0.0	1.8	0.0	81.5	4.7	2.0	4.4
		(17.4)	(29.2)	(41.3)			(1.8)		(18.5)	(3.8)	(2.0)	(3.5)
1995												
19 July		0.0			707.5							
					(121.6)							
12 August					419.7		0.0		0.00	—	—	—
					(90.2)							
30 September			5.1	—	1.3							
			(2.4)		(3.6)							

Each column represents a group of seedlings from the same cohort followed through time. The uppermost value in a column is the mean count (expressed as seedlings/m^2, with standard error in parentheses) of seedlings initially present in a set of 0.25-m^2 plots (n = number of plots) established at the same time. Subsequent values in a column are the mean number of survivors in that set at the indicated date. Dates are bracketed to indicate the period during which sets were established or revisited. Note that within the 1993 cohort, sets are differentiated by both time of establishment (DLP and IP) and by site (BP).

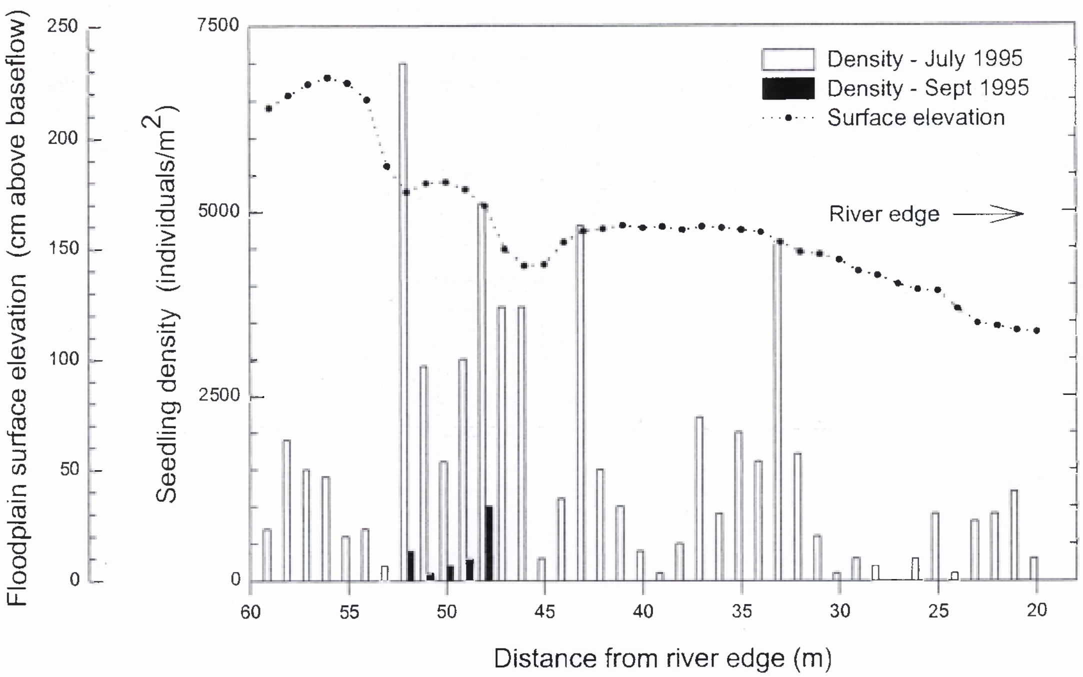

Figure 4. Densities of July germinants (open bars) and 1st-growing-season survivors (filled bars) of Fremont cottonwood seedlings along a 60-m transect, DL-1, traversing a portion of the floodplain inundated in 1995 at Deer Lodge Park. The transect was oriented perpendicular to the Yampa River, located to the right in the figure. No seedlings established at distances closer than 20 m to the river. The wavy horizontal line depicts plot surface elevation relative to river stage at base flow. Transect DL-2 featured a very similar pattern

plant density were positively associated with the proportion of germinant survival through the period. Importantly, plot elevation above ground water was not a significant determinant of survivorship probability. Germinant survival through mid-September was highest in areas 175 and 125 cm above river base flow stage along transects DL-1 and DL-2, respectively (Figure 4).

Taproot lengths of Fremont cottonwood germinants at the end of the 1995 growing season in DLP averaged 34.2 cm ($n = 64$, S.D. = 5.3). The maximum taproot length was 44.0 cm.

The stage decline rate at DLP averaged > 3 cm/day for at least a 1-month period in each of 1993, 1994, and 1995. In addition, a period of very rapid decline, > 6 cm/day for > 10 days, occurred in 1993 and 1995, and > 5 cm/day for > 14 days in 1994. Depth to the floodplain water table at DLP was tightly coupled to river stage, with the value of the regression slope close to one (e.g. Well 20: $Y = -29.267 + 1.013X$, $r^2 = 0.99$, $p = < 0.001$). Thus, the rate of ground water table decline in areas supporting germinants is nearly identical to the rate of river stage decline.

Determination of xylem water sources

There was no significant difference in the mean deuterium isotopic ratio (δD) of soil water (-91.5 ± 3.8) and sap water of either germinants (-86.7 ± 11.9) or 2-year-old seedlings (-91.5 ± 4.6) (t-tests; $p > 0.05$) (Figure 5). Germinant and 2-year-old δD sap ratios differed significantly from mean values for sap in plants > 4 years old and ground water (-114.9 ± 2.8) ($p < 0.05$). The mean ratio for stem water in plants > 4 years old was not statistically different from that for ground water ($p > 0.05$).

The effects of competition from older cohorts on seedling establishment

Germinant mortality was 100% under or immediately adjacent to older cottonwoods on bars and in backwaters. Soils beneath isolated stands of live germinants had a higher gravimetric water content than

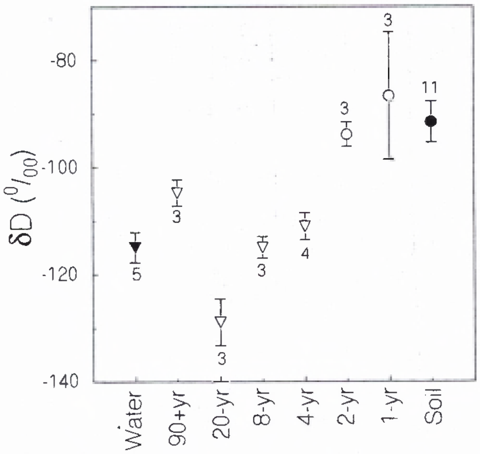

Figure 5. Isotopic ratios in stem water in cottonwood trees of various ages and in water from unsaturated soil (Soil) and from ground water (Water)

soil of similar texture collected at the same time (late August) from beneath cottonwood seedlings and saplings established in previous years (Figure 6). Coarse-textured soils (sand and loamy sand) consistently had moderately negative matric potentials and low volumetric water content, regardless of whether the sample was obtained from beneath saplings or germinants (Table II). In contrast, the matric potential and water content of sandy loam, loam and silt loam soils were significantly different beneath germinants and saplings. The highest water content occurred in fine-textured layers (sandy loam, loam, and silt loam) under germinants (Table II). Sites supporting live germinants in late summer had at least one soil layer in the rooting zone that contained plant-available water (matric potential between 0 and − 1.5 MPa), whereas plant-available water was absent in the upper 45 cm of soils under saplings.

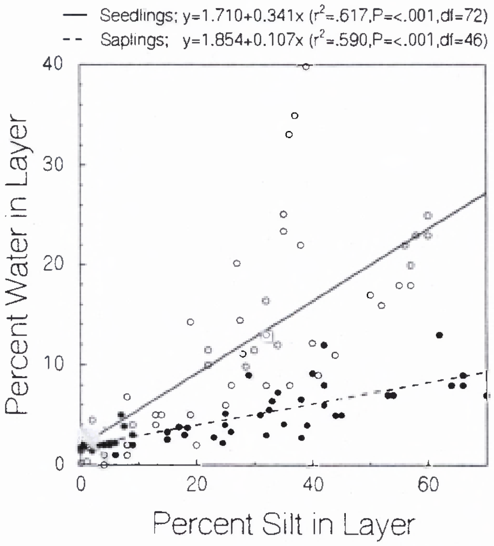

Figure 6. Regression analysis of percent gravimetric water content for each soil layer between 7- and 45-cm depth against percent silt in that layer. Open circles are for layers in plots supporting only seedlings, filled circles are for layers in plots supporting an overstory of existing woody plants

Table II. Comparison of matric potential (MPa) and volumetric water content (cm^3/cm^3) of like-textured soils under cottonwood seedlings and sapling stands

Soil texture	Under seedlings			Under saplings		
	n	Matric	Volumetric	n	Matric	Volumetric
Sand	32	−5.13 (17.46)^{a}	3.74 (1.60)^{a}	14	−8.27 (25.56)	3.44 (1.67)
Loamy sand	7	−2.76 (34.89)^{b}	5.59 (2.66)^{a}	5	−7.83 (8.59)	3.65 (1.85)
Sandy loam	20	−0.96 (2.27)^{c}	15.99 (8.66)^{c}	15	−285 (high)	5.55 (1.74)
Loam	4	−0.48 (0.31)^{c}	27.33 (4.07)^{c}	7	−538 (high)	7.27 (2.93)
Silt loam	9	−1.49 (0.62)^{c}	14.75 (1.20)^{c}	7	−1246 (high)	5.29 (2.05)

Values are means, with 1 S.D. in parentheses. Student's t-tests were used to compare matric potential and volumetric water content between seedling and sampling samples of the same soil texture.

[a] No significant difference, $p > 0.05$.

[b] Different at $p < 0.05$.

[c] Different at $p < 0.001$.

The effects of shade on intra- and interspecific competition

The probability that a transplanted cottonwood seedling would survive through the first 10 months of Experiment 1 was significantly related to the percentage of full sun (SUN) it received [logit (probability of survival) $= -2.055 + (0.0178\ \text{SUN})$; variable SUN: $\chi^2 = 6.71$, $p = 0.01$]. The shade dependence remained significant through the August 1994 census (13 months; $\chi^2 = 8.97$, $p = 0.003$).

Shading had no detectable effect on survival of Experiment 2 transplants during the ~4 week period prior to the termination of irrigation. Survivorship was 100% in nearly all plots, including four of the five plots receiving only 17% PAR. After irrigation ended, survival dropped dramatically in all plots. The lowest values were for cottonwood (Table III).

Table III. Survivorship of cottonwood seedlings in experiments involving shade treatments (replicates pooled)

Experiment	Period	Group	Survivorship (N_f/N_o)	
		(%PAR)	Cottonwood	Tamarisk
1	July 1993–May 1994	100	26/60 = 0.43	
		55	9/60 = 0.15	
		30	23/60 = 0.38	
		17	8/60 = 0.13	
		4	2/60 = 0.03	
2	June/July 1994–August 1994 (Irrigated)	100	74/75 = 0.99	58/75 = 0.77
		69	73/75 = 0.99	60/75 = 0.80
		40	75/75 = 1.00	66/75 = 0.88
		17	69/75 = 0.92	70/75 = 0.93
	Aug 1994–September 1994 (Post-irrigation)	100	20/74 = 0.27	53/58 = 0.91
		69	22/73 = 0.30	12/60 = 0.20
		40	20/75 = 0.27	42/66 = 0.63
		17	32/69 = 0.46	53/70 = 0.76
3	July 1995–September 1995	100-Thinned	17/50 = 0.34	
		100-Unthinned	14/450 = 0.03	
		69-Thinned	33/50 = 0.66	
		69-Unthinned	40/515 = 0.08	
		40-Thinned	26/50 = 0.52	
		40-Unthinned	19/497 = 0.04	
		17-Thinned	17/50 = 0.34	
		17-Unthinned	4/503 = 0.01	

Tabulated survivorship values are given as N_f/N_o, where N_f is the final, and N_o the original population size.

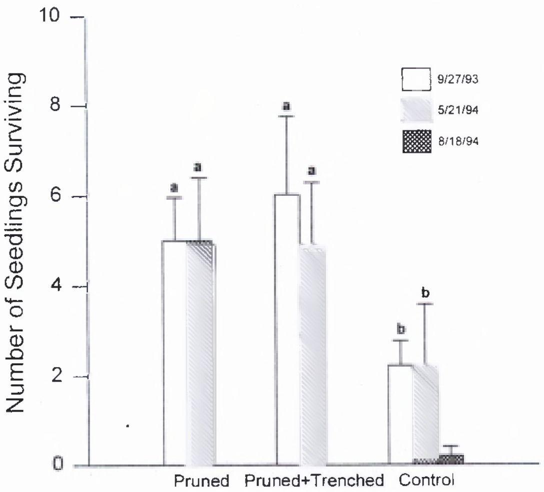

Figure 7. Mean (± 1 S.E.) number of cottonwood seedlings (out of 15 planted in July 1993) surviving under adult tamarisk in two treatments (pruned, pruned and trenched) and control. Three overlapping periods are evaluated. Means with same letter are not significantly different. Data from Experiment 5, conducted in the Island Park study area

The proportion of naturally established cottonwood seedlings surviving in unthinned plots was much lower than in thinned plots (Experiment 3; Table III); however, the number of seedlings ultimately surviving in thinned and unthinned plots was similar. The probability that a naturally growing cottonwood germinant in an unthinned plot would survive through the 6 weeks of Experiment 3 was significantly related to its location on the floodplain (categorical variable LOC), but not to the percentage of full sun (SUN) it received [logit (probability of survival) $= -2.710 + 0.0115$ SUN $- 0.438$ LOC; variable SUN: $\chi^2 = 2.1$, $p = 0.15$; variable LOC: $\chi^2 = 4.9$, $p = 0.03$]. Survivorship also appeared to be independent of shade in plots thinned to 250 seedlings/m^2 (variable SUN: $\chi^2 = 0.07$, $p = 0.79$).

Effects of tamarisk on seedling establishment

Cottonwood seedlings transplanted under adult tamarisk suffered higher mortality during their first summer than those similarly planted but with the tamarisk canopy removed (Experiment 4: $\chi^2 = 14.1$, df $= 2$, $p = 0.001$) (Figure 7). Canopy removal plus trenching did not significantly increase cottonwood seedling survival over canopy removal alone ($\chi^2 = 0.718$, $p = 0.40$). Although the higher survivorship was still evident in May 1994, the effect of canopy removal was eventually masked by desiccation during the drought of mid-summer 1994, which led to the death of all planted seedlings.

Cottonwood seedlings transplanted into dense beds of naturally established tamarisk seedlings had lower survivorship than the control group transplanted into a plot cleared of tamarisk seedlings (Experiment 5: $\chi^2 = 41.04$; $p < 0.001$). Through two summers (1993 and 1994), 11 of 15 (73.3%) of cottonwood seedlings in the control group survived, compared with only two of 45 (4.4%) in treatments.

Soil stratigraphy of fluvial features supporting cottonwoods

We found complex stratification of the underlying alluvial materials in all 36 fluvial features examined. A representative transverse cross section through an accreting braid bar, backwater, and channel complex in DLP is depicted in Figure 8. Braid bars are linear features formed on the channel margin where flow splits into multiple channels. The bar shown in Figure 8 was cigar-shaped and ~ 10 m long in 1995. Saplings (~ 10 years old) grew on the upstream end and a stand of 3-year-old seedlings (the only survivors of the 1993 cohort on the bar) occupied the middle section. At peak stage in 1995, floodwaters were more than 1 m deep in the backwater and covered the bar.

We sectioned the bar downstream of the 1993 cottonwoods, through a group of surviving germinants (1995 cohort). The sediment texture 0.5–1.0 m below the bar surface was sand (Figure 8). A mound of sandy loam sediment formed the core of the braid bar, most likely deposited where roughness, higher due to the presence of ~ 10- and 3-year-old plants, allowed fine sediments to settle out of suspension. A series of vertically accreted deposits that varied in texture between loam and sand had raised the channel side of the bar, and a series of silt loam, sandy loam, and sand deposits had raised the floor of the backwater. Surface sediments on the bar were loam. Germinants had initially grown on all three of these landforms, but they survived only on bar and backwater sediments, where loam textured layers occurred.

Germinant density on these 36 landforms was significantly related to the total thickness of loam-textured soil layers (sandy loam, loam and silty loam) within the rooting zone (0–45-cm depth). Germinants survived where loam layers > 10 cm thick occurred in the upper 45 cm of soil, such as the backwater and bar illustrated in Figure 8, whereas 100% mortality occurred in the channel areas.

A trench excavated across a relatively flat terrace supporting mature cottonwoods provided insight into the long-term fate of cottonwoods established on braid bars. Floodwaters reached the top of the terrace only four times in recent decades, in 1957, 1974, 1984, and 1997. Beneath a clay surface soil, we found two well-developed braid bars composed of a 20–30 cm thick silt loam layer, separated by a channel (Figure 9). A series of sections (slabs) taken from a cottonwood tree growing next to the trench indicated that the ~ 90-year-old tree had germinated on one of the braid bars (see right arrow on Figure 9). The germination surface was located by identifying the slab with the highest ring count (Scott *et al.*, 1997), and the lowest slab with a pith. A second cottonwood along the trench with similar morphological characteristics was not aged, but the root crown occurred at the same location on the other braid bar surface. The germination surfaces of these two trees were ~ 150–200 cm above the current late-summer water table. The trees had survived the vertical accretion of more than 1 m of sediment, including ~ 50 cm of loam, a thin bed of red sandy loam (probably derived from a flooding tributary), and 50 cm of clay sediments.

DISCUSSION

Seed rain

Seed rain was abundant in all 3 years at all study sites, and does not appear to be restricting the establishment of either Fremont cottonwood or tamarisk. Seeds were aerially dispersed across the full

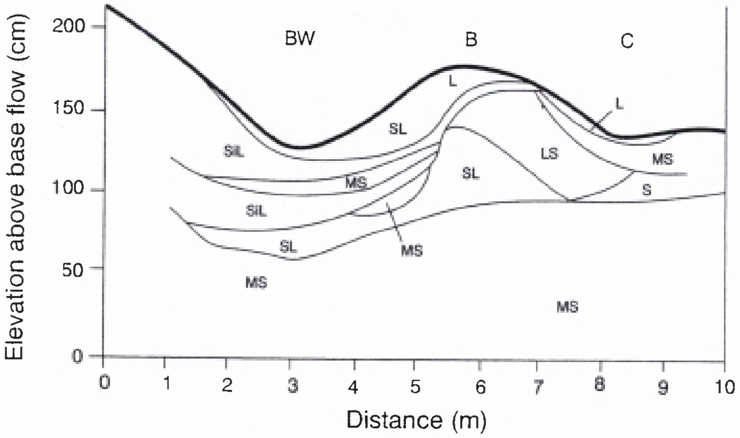

Figure 8. Transverse cross section through a braid bar (B) at Deer Lodge Park depicting sediment stratigraphy. A backwater (BW) borders the bar toward the upland, and by a channel (C) toward the river. Textures of layers are loam (L), silt loam (SiL), sandy loam (SL), medium sand (MS), and sand (S)

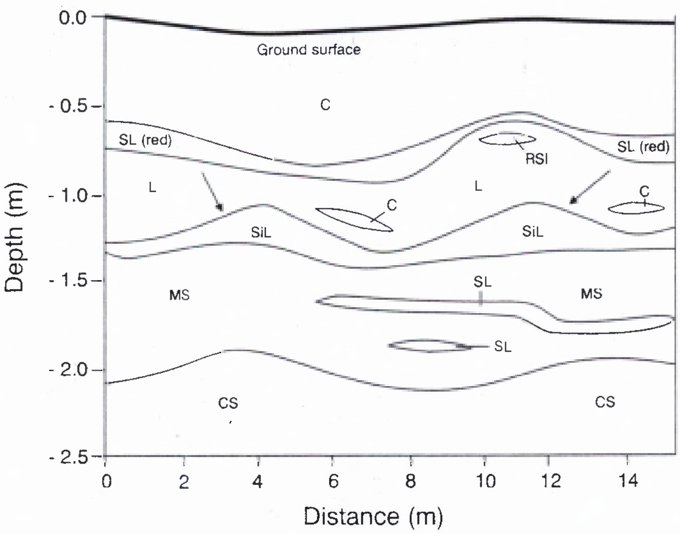

Figure 9. Stratigraphic cross section through part of a DLP terrace that currently supports mature cottonwoods. The profile was oriented perpendicular to the river channel. Soil textures of layers are clay (C), loam (L), silt loam (SiL), sandy loam (SL), medium sand (MS), and coarse sand (CS). Two cottonwoods had germinated on surfaces of well-developed braid bars, now buried, at positions marked by arrows

range of moist floodplain surfaces and elevations exposed as floodwaters receded at DLP and IP (Figure 2). The 4–5 week duration of seed dispersal we noted was similar to that reported for cottonwood along the San Pedro River in Arizona (Warren and Turner, 1975), and along the Rio Grande in New Mexico (Everitt, 1980), but slightly shorter than that reported for plains cottonwood along the Platte River, Nebraska (Johnson, 1994). The mean density of cottonwood seeds reaching the floodplain was much greater in DLP than in BP (Figure 3), a difference we attribute to the presence of dense stands of young, yet sexually mature cottonwood poles (ranging from 22 to 26 years old) at DLP. Seeds in BP are produced solely by large, old trees that are widely scattered on high floodplain surfaces. The density of seeds dispersing onto the DLP floodplain is higher than values reported for Fremont cottonwood along the Salt, Gila and San Pedro Rivers in Arizona (Horton *et al.*, 1960; Turner, 1974; Warren and Turner, 1975), but lower than values recorded for plains cottonwood along the Platte (Johnson, 1994). The majority of germinants in DLP, BP, and IP originated from aerially dispersed seed falling on moist substrate. The high densities we recorded, > 500 seedlings/m^2, have previously been associated primarily with water dispersed seed (Craig and Malanson, 1993).

Overlap in the timing of cottonwood and tamarisk seed dispersal resulted in mixed seedling beds in all study areas. However, because cottonwood seed dispersal begins earlier than tamarisk (Figure 2), the timing of peak discharge from Flaming Gorge Dam can influence the composition of seedling beds in BP: early summer peaks promote cottonwood establishment, whereas mid- to late-summer peaks promote tamarisk establishment. Fenner *et al.* (1985) and Everitt (1995) also noted the relationship of flood peak timing to seedbed composition along western US rivers.

Survival of natural seedling cohorts

Our results indicate that landscape position plays a strong role in cottonwood seedling survival. Cottonwood germinants established in large numbers in all study areas, on the wet sediments of bars, islands, backwaters, and banks, in years of low (1994) as well as high (1993 and 1995) peak discharges. Survivorship through the first growing season, however, was extremely low at DLP and IP except in previously unvegetated sites on particular landforms along the floodplain margin far from the late summer and winter channel position. Where germinants survived their first growing season in low topographic positions relative to late summer stage, they were likely to be scoured out and die as the channel bed was mobilized during the subsequent spring flood. Cottonwood seedlings that survived their first few growing seasons at DLP, EP, or IP were located on the tops and sides of unvegetated vertically accreting bars and backwaters with fine-textured soils, but not in the channels between braid bars, or on broad point bars, a location often associated with successful establishment of plains cottonwood (Bradley and Smith, 1986). The actively accreting bars and backwaters that supported 2- and 3-year-old cottonwood in DLP and IP were absent in BP. Cottonwood germinants in BP were restricted to islands and cut banks where long-term survival was improbable given the long duration of soil saturation on islands and the instability of annually sloughing vertical banks. Thick beds of *Schoenoplectus lacustris*, *Bobloschoenus pungens* and other marsh vegetation on the islands attested to their wetland rather than riparian character (Merritt, 1997) and consistently high water table. The limited range of stage change and lack of suitable unvegetated, developing fluvial landforms in BP precluded natural cottonwood seedling establishment.

Most cottonwood seedling mortality in DLP and IP was attributable to either flood scouring or desiccation. Sacchi and Price (1992) also considered soil moisture a key to *Salix lasiolepis* seedling survival at a riparian site in northern Arizona. McBride and Strahan (1984) noted that 93% of Fremont cottonwood seedlings on gravel bars along a California stream survived through summer if they were located adjacent to surface water, whereas none survived where the late summer water table depth was > 1 m.

Fremont cottonwood seedling survival was not found to be dependent upon their maintaining contact with the ground water. In DLP, IP, and EP cottonwood germinants initially established throughout a wide elevation zone, but first summer survival occurred almost exclusively at elevations > 125–250 cm above base flow ground water elevations (Figure 4). Our isotopic analyses, and excavations of seedlings, indicate that only 4 + -year-old cottonwoods have rooted to the depth of the late summer ground water table.

Soil texture and cottonwood seedling survival

Free-flowing western rivers with large (> 2 m) annual stage changes and large fine-textured suspended sediment loads, such as the Yampa, create environmental opportunities for, and place constraints on, cottonwood establishment fundamentally different from those on (1) regulated rivers with small (< 1 m) stage changes, (2) regulated or unregulated rivers with low sediment loads, or (3) river reaches with primarily coarse-textured substrates. Large annual stage changes and a highly mobile sand bed limit seedling survival to relatively stable sites in high landscape positions. These sites are typically far from the winter channel and are unaffected by river ice flows. In contrast, the bars formed along cobble and gravel bed river reaches are more stable than sand bed channels, and offer opportunities for seedling establishment close to the channel.

The mechanisms that allow Fremont cottonwoods seedlings to survive high above the late-summer water table in DLP for the 3–4 years necessary to become phreatophytic are, (1) the presence of fluvial landforms containing layers of fine-textured sediment, (2) relatively high annual river stage, even in years with average or below average peak discharge, and (3) the predictable occurrence of at least a small amount of July and August precipitation. Our rating curve (relating discharge to stage) for DLP indicates that a flow of 270 m^3/s, which occurs in 4 years out of 5 (probability of occurrence = 0.83), results in a river stage 200 cm above late summer base flow stage, a height adequate to saturate soils on most landforms supporting seedlings, even when seedlings initially establish on surfaces created during a large flood such as occurred in 1995 (peak discharge of 519 m^3/s, peak stage 277 cm above base). Peak flows less than 170 m^3/s, which still results in a stage 164 cm above base flow level, have occurred only three times since 1922: in 1934, 1954 and 1977.

The importance of fine-textured sediment is due to its capacity to store more plant-available water than sands (van Genuchten *et al.*, 1989). Soil moisture derived from spring floods and depleted by growing seedlings can only be replenished by summer precipitation. A drought during the mid-summer of 1994 resulted in the death of almost all seedlings planted in our 1993 experimental plots, as well as most natural seedlings of the 1993 and 1994 cohorts. Thus, during a seedlings first 3–4 years of life, it is susceptible to drought induced mortality, regardless of landscape position. Once a seedling roots to the late summer water table depth its probability of long-term survival becomes limited by biotic rather than abiotic factors. Although erosion may have a role in survival after the 4th summer, herbivory and other biotic factors become increasingly important (Andersen and Cooper, unpublished data).

Floodplains with primarily coarse-textured substrates have low water holding capacity, limiting germinant survival to sites where they can maintain contact with the water table as stage declines (Rood and Heinze-Milne, 1989; Mahoney and Rood, 1993; Stromberg, 1993; Braatne *et al.*, 1996). Hupp and Osterkamp (1996) suggest that along such reaches in arid and semi-arid regions the spatial pattern of germination and initial seedling establishment is influenced by river surface flows (floods), whereas ground water levels greatly influence seedling survival. On rivers with large stage changes, however, germinants growing close enough to the channel elevation to reach the water table could be under >2 m of water during most subsequent stage maxima, with a low probability of surviving sediment burial or scouring (Hosner, 1957, 1960; Warren and Turner, 1975; McBride and Strahan, 1984). Everitt (1968) and Scott *et al.* (1996, 1997) documented that plains cottonwood trees had established 2 m or higher above river base flow elevation on the northern Great Plains, but neither study provided an explanation of how seedlings could have survived there. Krasny *et al.* (1988) linked willow seedling survival and the texture of the alluvial substrate on Alaskan floodplains.

Tamarisk and cottonwood seedling competition

The timing of cottonwood and tamarisk seed dispersal overlaps, resulting in mixed-species seedbeds in many areas. We found that cottonwood seedling survival was low in dense tamarisk seedling beds. Our 1994 shade experiment in DLP indicated high survival of both cottonwood and tamarisk seedlings under conditions of high soil moisture. When supplemental watering was ceased however, cottonwood survival fell below that of tamarisk. Thus, we feel that Turner's (1974) statement that tamarisk outcompetes native vegetation must be qualified. Our results support Busch and Smith's (1995) hypothesis that tamarisk, because of its higher water use efficiency, will outcompete cottonwood when water is limiting.

Our field analyses of germinants on sites with and without older cottonwoods showed that soil water was depleted under stands of saplings relative to soils supporting only germinants (Figure 6). These results suggest that competition for water is a factor restricting Fremont cottonwood seedling establishment to sites lacking existing plants. While cottonwoods >4 years old use ground water, they also likely deplete soil water.

Shade and cottonwood seedling survival

We hypothesize that both intra- and interspecific competition effects on cottonwood seedlings are manifested primarily through competition for soil water, and secondarily for light. Our experimental studies indicate that Fremont cottonwood is more shade tolerant than previously reported (Read, 1958; Strahan, 1984; Harris, 1987; Scott *et al.*, 1996). Only the greatest reduction in PAR caused a significant reduction in seedling survival in unwatered plots, and shade had no effect on survival in watered plots (Table III). Heavy shade increased cottonwood seedling mortality in (a) unwatered plots, (b) dense plots of cottonwood seedlings, and (c) plots under adult tamarisk, all situations in which competition for soil moisture is high. Further testing of this hypothesis should include an analysis of interaction effects; shade may limit root growth and reduce a seedling's ability to acquire soil water, as has been shown for *Salix lasiolepis* (Sacchi and Price, 1992) and plains cottonwood (Shafroth *et al.*, 1995). Shade also changes soil and air temperatures that could alter water use by plants.

Removal of an overstory tamarisk canopy resulted in a large increase in 1st-year cottonwood seedling survival, as did canopy removal plus trenching (Figure 7). Both treatments increased light reaching cottonwood seedlings and reduced the transpirative area, which could have increased soil water availability to seedlings. Because we did not monitor soil water in Experiment 4 we cannot reject the hypothesis that increased water availability, rather than increased light, improved seedling survival.

Synthesis and management implications

The formation of fluvial features comprised of fine-textured sediments requires a supply of fine sediment and backwater or slackwater areas for deposition of this material to occur. Obstructions to flow, such as large woody debris, bedforms, or the stems of vegetation lead to a localized reduction in stream power and the deposition of fine-textured sediment. When exposed, these fine-textured surfaces not only provide adequate sites for germination, but also enhance survival through the first growing season due to their higher water holding capacity. Our data suggest that, in the absence of older plants, soils with a thickness of at least 10–15 cm of fine-textured layers within the top 40 cm of soil have sufficient water holding capacity to support germinants through their first summer. Where seedlings persist through the following year's flood they increase hydraulic roughness, decrease velocity and result in vertical and lateral accretion (Hadley, 1961; Smith, 1976; McBride and Strahan, 1984; Strahan, 1984; Hupp, 1992; Johnson, 1994; Friedman *et al.*, 1996; Hupp and Osterkamp, 1996) forming elongated bars that build vertically and in a downstream direction. Fresh fine-textured sediment deposited in the lee of the bar each year allows additional cohorts of cottonwood and tamarisk seedlings to establish, creating a patchy landscape with small (1–20 m^2) stands of relatively even-aged plants which decrease in age in a downstream direction.

Fluvial complexes of bars, channels between bars, and backwaters develop and vertically accrete as a unit. Eventually they are inundated by only the largest floods, which deposit fine-textured sediment, burying the landforms, leveling the topography, and creating a superficially homogenous fluvial feature, as illustrated by our high floodplain excavation (Figure 9) (Schumm and Lichty, 1963; Brice, 1964; Nadler and Schumm, 1981). In our study areas, we also found areas where seedlings have established in abandoned channels (in IP). Although fine-textured bars high above base flow stage appear to be the primary sites for seedling establishment in our study sites, establishment also occurs in other areas where fines are present.

Although the design of Flaming Gorge Dam allows for releases above power plant capacity, there is no capability to restore fine-textured sediment now trapped in the reservoir to regulated reaches of the river. Currently, Green River flows are managed primarily for endangered Colorado River fish, and annual variability (including peak flow) is essentially constant from year to year. Seed bed soils are saturated for much of the summer and are unsuitable for cottonwood establishment. Prescribed high flows in the range of 185–245 m^3/s could flood sparsely vegetated or mechanically cleared fluvial deposits that were formed by pre-dam floods. These features could provide seedling beds for recruitment events, but once cottonwood or tamarisk populates these surfaces further seedling establishment is unlikely until new, open substrates become available through tree mortality, or are artificially created. Cottonwood seedlings established by controlled floods will be dependent upon subsequent high flows during their 2nd and 3rd growing seasons to provide soil moisture until taproots reach the late summer water table. A reservoir release intended to establish cottonwood seedlings should be followed the next 2 years by flows with similar peaks. Our data also suggest that dense tamarisk thickets preclude or hinder cottonwood establishment by depleting soil moisture and creating shade. Tamarisk removal prior to a controlled flood could facilitate cottonwood seedling establishment in existing tamarisk stands.

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STREAMFLOW REQUIREMENTS FOR COTTONWOOD SEEDLING RECRUITMENT—AN INTEGRATIVE MODEL

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Abstract: This paper describes the 'recruitment box,' an integrative model that defines the stream stage patterns that enable successful establishment of riparian cottonwood seedlings. In western North America, cottonwood seed dispersal generally occurs after annual peak river flows. The receding stream exposes moist sites upon which seeds land after transport by wind and water. Germination is rapid, and initial seedling establishment is often prolific. However, the vast majority of seedlings die, primarily due to drought stress, as root growth is insufficient to maintain contact with the receding zone of moisture. Cottonwood roots grow about 0.5 to 1 cm per day or 60 to 100 cm in the first year. Along the 'losing' streams in semi-arid regions, the riparian water table is an almost horizontal extension from the stream stage. A capillary fringe exists above the water table and is often 30 to 40 cm in elevation, but can range from about 5 to 130 cm depending on substrate texture. The combination of root growth and capillary fringe define the successful recruitment band, which is usually from about 0.6 to 2 m in elevation above the late summer stream stage. Within this range, higher elevation establishment occurs (i) for the *Aigeiros* cottonwoods, *Populus deltoides,* and *P. fremontii,* which grow more rapidly than *Tacamahaca* species and occur in warmer areas with longer growing seasons; (ii) along larger rivers that are characterized by more gradual stage fluctuations; and (iii) along streams with finer substrate. The rate of stream stage decline is also critical for seedling survival and should not exceed 2.5 cm per day. The recruitment box model is consistent with dendrochronological interpretations that moderate flood events are naturally required for cottonwood recruitment. Flood events with recurrences of about 1 in 5 to 1 in 10 years often satisfy the model and provide stream stage patterns with a gradual decline through the recruitment box. The model will facilitate analyses of the reproductive ecology of riparian cottonwoods and also permit the prescription of stream stage patterns for cottonwood seedling recruitment along dammed rivers.

Key Words: cottonwoods, hydrology, modelling, *Populus,* riparian zone, seedlings

INTRODUCTION

The maintenance of riparian cottonwood populations relies on periodic recruitment to compensate for ongoing mortality. The recruitment can be through either seedlings or through clonal processes, particularly suckering (Rood et al. 1994). Seedling recruitment is probably the dominant means of replenishment for the section *Aigeiros* Duby cottonwoods, the prairie cottonwood (*Populus deltoides* Bartr. ex Marsh.) and the Fremont cottonwood (*P. fremontii* Wats.). Clonal processes are probably more common in the section *Tacamahaca* Spach. cottonwoods, the black cottonwood (*P. trichocarpa* T. & G. *ex* Hook (or *P. balsamifera* L., subsp. *trichocarpa* T. & G. *ex* Hook (Brayshaw 1965)) and the balsam poplar *(P. balsamifera* L.) (Gom 1996). The narrowleaf cottonwood (*P. angustifolia* James) may be intermediate between the other *Tacamahaca* species and the *Aigeiros* cottonwoods. Even for the *Tacamahaca* species, periodic seedling recruitment is essential since sexual recombination introduces the genetic diversity required to cope with gradual change in physical or biological conditions. Seedling recruitment is also a principal mechanism for dispersal and colonization of new islands and other recruitment sites.

One common major impact of river damming in western North America has been a reduction of cottonwood seedling recruitment (reviewed in Rood and Mahoney 1990, Braatne et al. 1996). This failure has been partially caused by the imposition of artificial patterns on stream flow (stage) in which (i) flood events are often attenuated, (ii) flow changes and par-

Table 1. Estimated flood recurrences associated with cottonwood recruitment based on dendrochronological analyses (chronological listing).

Flood Return Interval (yrs)	*Populus* Species	River	Source
5	*P. deltoides*	Milk, AB, MT	Bradley and Smith 1986
3	*P. angustifolia*[1]	Animas, CO	Baker 1990
10–15	*P. angustifolia*[2]	Animas, CO	Baker 1990
10	*P. balsamifera*	Bow, AB	Cordes 1991
3	*P. fremontii*	Rio Grande, NM	Howe and Knopf 1991
5	*P. deltoides*	Milk, AB	Reid 1991
7	*P. fremontii*	Hassayampa, AZ	Stromberg et al. 1991
10	*P. deltoides*	Red Deer, AB	Marken 1994
10	*P. fremontii*	Colorado, UT	Rood et al. 1997
9	*P. deltoides*	Missouri, MT	Scott et al. 1997
10	*P. deltoides*	Red Deer, AB	Cordes et al. 1997
5–10	*P. balsamifera*	Bow, AB	Rood et al. 1998a

[1] Seedlings.
[2] Stands.

ticularly declines can be abrupt, and (iii) insufficient flows may be delivered in mid- through late summer. These artificial patterns may prevent initial establishment of seedlings at appropriate streambank elevations and/or exaggerate drought stress, increasing mortality of the small, vulnerable seedlings. The attenuation of flooding also prevents the essential geomorphic disturbance that creates new nursery sites (Johnson et al. 1976, Rood and Mahoney 1990, 1995, Scott et al. 1997, Stromberg et al. 1997).

Fortunately, it is primarily the pattern of streamflow management rather than the presence of dams, *per se,* that determines impacts on downstream cottonwoods. With respect to cottonwood recruitment, informed stream-flow management should enable seedling recruitment and may even permit regulation of stream stage patterns to promote seedling recruitment for the conservation and restoration of the riparian cottonwood-based ecosystem. Here, we analyze the hydrologic pattern that is required for seedling recruitment of riparian cottonwoods and propose a model for assessing and predicting the impact of water-management strategies on riparian cottonwoods. This should contribute to the understanding of cottonwood reproductive ecology and also facilitate river resource management that is directed toward the conservation and restoration of riparian woodlands, particularly in semi-arid regions of western North America.

HYDROLOGIC REQUIREMENTS FOR COTTONWOOD SEEDLING RECRUITMENT

Flood Flows

Cottonwood seedling recruitment is episodic and relatively rare even along free-flowing streams. It has been repeatedly concluded that flood events enable cottonwood seedling recruitment both through geomorphic impacts and direct hydrologic patterns (Johnson et al. 1976, Rood and Mahoney 1990, Scott et al. 1996, and citations in Table 1). The flood magnitude required for cottonwood recruitment has been estimated with a dendrochronological approach in which cottonwoods are aged and correlations (or in this case, 'core-relations') are investigated between recruitment years and high stream flows. The specific aging of cottonwoods may be problematic due to ambiguous annual rings, the occurrence of flood-training and other processes that topple seedlings and saplings, heart-rot which is common in middle-aged and older trees, variable growth rates up to the height at which increment cores are taken, and other biological and methodological complexities. Despite these problems, various researchers have reached relatively similar conclusions regarding the need for moderate flood events for successful cottonwood establishment (Table 1).

Studies have consistently suggested that a 1 in 5 to 1 in 10 year flood event is associated with cottonwood recruitment (Table 1). These moderate flood events drive the erosional and depositional processes associated with the creation of barren nursery sites on meander lobes, lateral bars, and islands and also provide a pattern of stream flow and stage that is suitable for seedling establishment. Larger floods may cause massive fluvial-geomorphic change that sets the framework for cottonwood recruitment over the next years and even decades (Friedman et al. 1996, Stromberg et al. 1997, Rood et al. 1998).

Pattern of Flow

The roles of specific components of the flood hydrograph relative to seedling establishment have been proposed (Bradley and Smith 1986, Mahoney and Rood 1991b, Scott et al. 1993). Agreement with respect to components by various researchers provides some confidence in the general process and also indicates common applicability for different cottonwood species and different streams. Following our review of the literature and field and greenhouse studies, we previously developed a general model describing the hydrologic requirements for cottonwood seedling recruitment (Mahoney and Rood 1991b). We subsequently applied the general model to assess potential impacts of different flow scenarios along dammed rivers (Mahoney and Rood 1993a, 1993b). By integrating subsequent results, we are now able to quantitatively define some features relevant to the model. The resultant quantitative model describes the streambank elevation and timing of stream stage patterns that are required for successful cottonwood seedling recruitment.

A Generalized Hydrograph for Rivers in Western North America

Along many rivers in the western prairie and mountain regions of western North America, a typical hydrograph includes low flows in the early spring and rising flows that accompany spring rains and mountain snow-melt (Figure 1). Annual hydrographs are rather jagged due to precipitation events and variations in temperature, which influence the rate of snow-melt. Peak flows typically occur in early June and persist for a few days. The recession component or 'falling limb' of the hydrograph is initially very rapid and becomes more gradual as the summer proceeds. Low flows typically occur in mid- to late summer when snow-melt is complete and rainfall is often sparse. At this time, temperatures are generally maximal, creating conditions of greatest water demand. This hot, dry period in mid- through late summer is also the period of greatest irrigation demand, and thus, offstream diversion is often greatest.

Riverine and riparian ecosystems have adapted to natural stream-flow conditions. While discharge is normally reported for stream-flow analyses, interpretations relative to riparian processes are more appropriately made relative to the stream stage, which represents the water-surface elevation. River stage is the parameter measured at hydrometric gauging stations, and these data are then converted to discharges using stage-discharge ratings curves. For analyses relative to cottonwood seedling recruitment, river stage data should be used. However, unlike discharge, stream stage is site-specific because channel geometry and gradient determines the stage-discharge function. Ratings curves from gauging stations can be used to initially estimate stage patterns, but gauging sites are generally selected based on ease of access and are often at points that do not display a cross-sectional geometry that is typical of the river reach. More appropriately, analyses should involve site-specific stage-discharge determinations at meander lobes and other sites that are suitable for cottonwood seedling recruitment. Analyses should also consider variations in channel width and slope and streambank geometry along the reach.

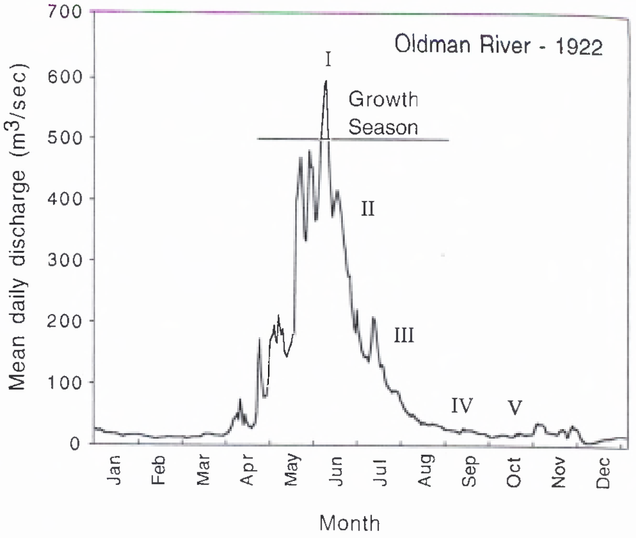

Figure 1. The daily hydrograph for the Oldman River, at Lethbridge, Alberta, for 1922, prior to the construction of major dams upstream. Roman numerals represent important components relevant to cottonwood seedlings recruitment: (I) high flows to drive geomorphological processes that create suitable moist and barren nursery sites, (II) falling flows to expose the nursery sites, (III) gradual flow decline after germination that permits the growing roots to maintain contact with the receding moisture zone, (IV) sufficient flows through the hot and dry period of mid- to late summer, and (V) sufficient flows in late summer and autumn to provide the seedlings with a favorable water balance to withstand the winter.

Despite latitudinal differences, the timing of annual peak flows is reasonably similar in the western prairie and Rocky Mountain regions of western North America (Figure 2). Southward from Alberta, Canada to New Mexico, the rivers that drain the southern and central Rocky Mountains usually peak in early June. Annual peaks that are substantially earlier or later than the normal period are generally relatively small and correspondingly less important for cottonwood seedling recruitment. The relative synchronization of the peak flows is partly explained by elevational patterns. The Rocky Mountains of Colorado are higher than those of Montana or Alberta, and this elevational increase compensates for the latitudinal gradient. However, this timing of peak flow is certainly not experienced by all western rivers. Those draining more

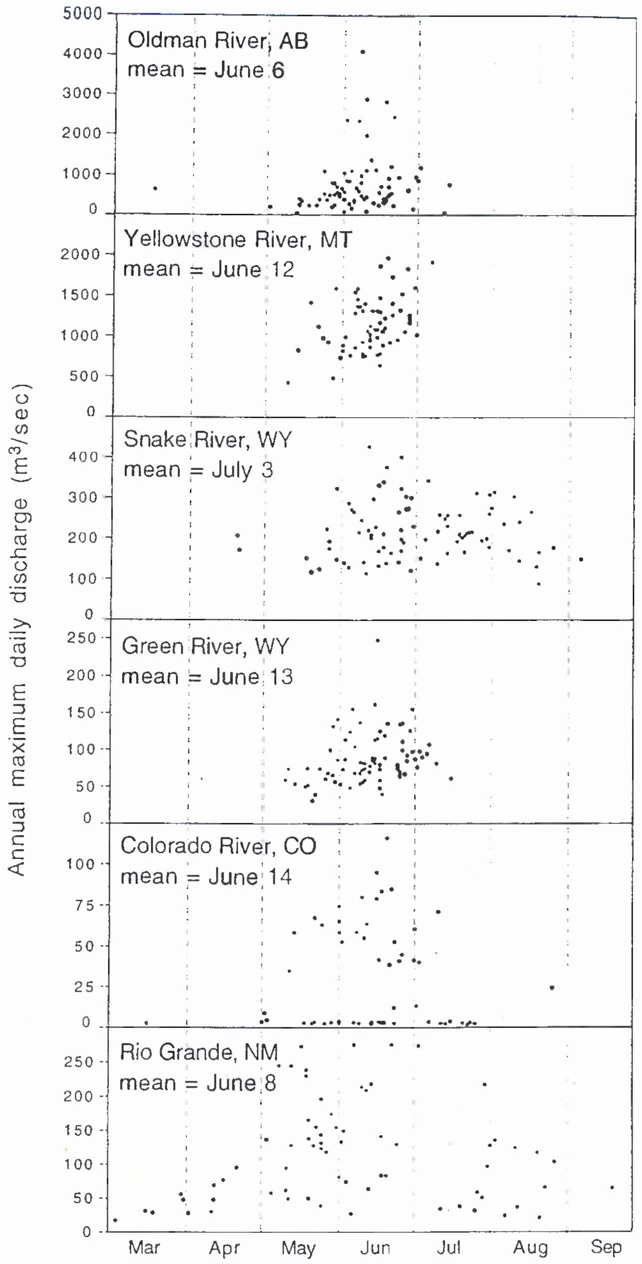

Figure 2. Dates and discharges of annual peak daily flows for six rivers draining the Rocky Mountains of western North America (north to south): the Oldman River at Lethbridge, AB (Water Survey of Canada station 05AD007; SD (standard deviation of the mean) = 17 days; median = June 7; years: 1912 to 1995); the Yellowstone River near Billings, MT (USGS station # 06214500; SD = 11; median = June 13; 1904 to 1994); the Snake River near Moran, WY (# 13011000; SD = 32; median = June 27; 1904 to 1994); the Green River near Daniel, WY (# 09191000; SD = 15; median = June 14; 1913 to 1994); the Colorado River near Granby, CO (# 09019500; SD = 26; median = June 16; 1908 to 1994); and the Rio Grande River near Taos, NM (# 08276500; SD = 48; median = May 31; 1926 to 1994). Of these rivers, the Oldman was dammed in (about) 1992, the Yellowstone remains free-flowing and the Green River is

southerly and especially southwesterly areas or lower elevations peak earlier; more northern, glacier-fed streams peak more gradually and somewhat later; and many streams in Pacific regions are more responsive to seasonal rains that are often heavy in the autumn and winter.

Patterns of Seed Release

The phenology of cottonwood flowering and seed release is partly determined by photoperiod (day length) and, hence, is relatively constant across years at a given site. However, temperature also influences development, often hastening or delaying seed release by one or two weeks. Temperature patterns also influence the duration of seed dispersal, which typically occurs over about one month. The phenology of seed release has been reviewed by Braatne et al. (1996); release tends to extend from May into July for most cottonwood species. The exception is *P. fremontii,* which occurs in warmer areas and generally releases seed earlier than the other species.

Cottonwoods are prolific seed producers, with large females producing hundreds of thousands (Kapusta 1972) or even millions of seeds (Bessy 1904). Initial viability is almost complete but declines completely over a one-to-four-week period (Braatne et al. 1996). Thus, there is no carryover seed bank from previous years, and the seeds must land on suitable sites for successful establishment. Cottonwoods have thus adopted a reproductive strategy in which many propagules are produced, but each has been provided with minimal resources, and very few survive. The limited period of seed dispersal and viability defines the period for cottonwood seedling establishment. The total period can reach about six weeks but has a more limited period of maximal seed release of about three weeks (Lee et al. 1991, Virginillo et al. 1991, Johnson 1994). Thus, a model describing stream-flow requirements for cottonwood seedling establishment begins with a temporal framework related to cottonwood phenology (Figure 3 (top)).

Seed release generally occurs after peak flows and during the falling limb of the hydrograph. This timing is appropriate since the receding stream exposes moist sites that are suitable for seedling establishment. The seeds are initially wind-dispersed and may land on the stream-side lateral or point bars. Alternately, the seeds

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free-flowing at the gauging site used. Conversely, the Snake and Colorado gauging sites are below dams and a number dams exist on the Rio Grande and its tributaries upstream from the gauging site used.

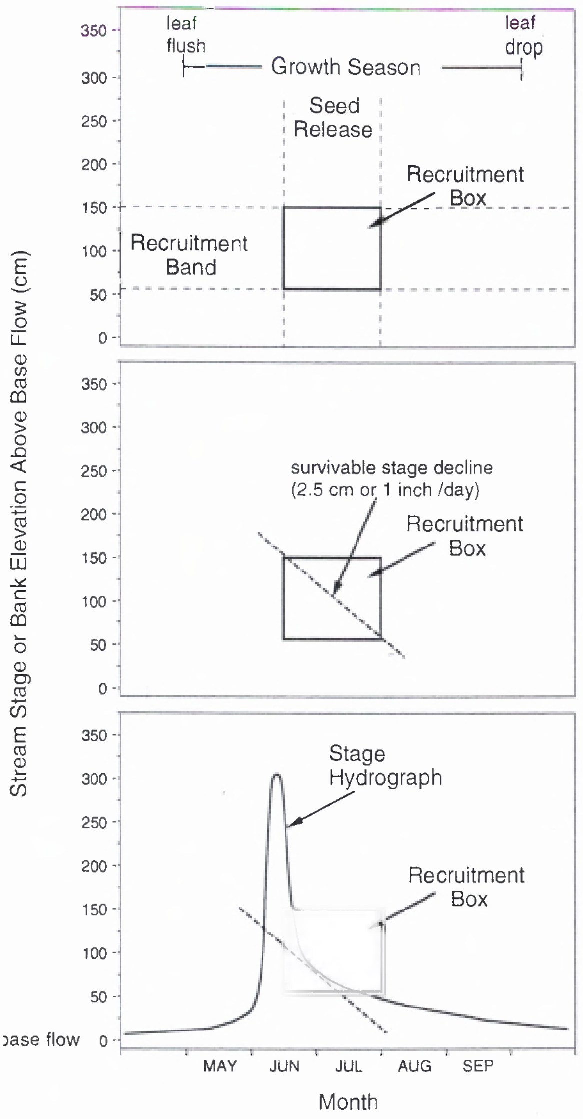

Figure 3. The 'Recruitment Box,' a zone defined in elevation and time in which riparian cottonwood seedlings are likely to become successfully established if stream flow patterns are favorable. The graphs represent phenology of components (top), survivable rate of stage decline (middle), and a hydrograph that satisfies requirements for seedling establishment (bottom).

may land on the stream and be deposited by the receding stream edge in bands along the shoreline. This combination of wind and water dispersal increases the chances that the small seeds will land on appropriate recruitment sites.

The process of seed dispersal partially explains the banding that is common in riparian woodlands (Braatne et al. 1996). Moist sites occur at specific elevations paralleling the receding stream, and thus, seedlings are more likely to survive in bands. The floating seeds deposited directly along the stream edge are also deposited in bands of constant elevation, again favoring a banded distribution. The arcuate banding is emphasized by the processes of seedling mortality and scouring. Seedlings initially established at higher elevations are likely to succumb to drought stress, and those established at low elevations are likely to be scoured away by subsequent high stream flows or ice. Thus, both seedling establishment and seedling survival tend to produce banding patterns in riparian cottonwoods.

Elevation of Successful Seedling Recruitment

As already introduced, bands of riparian cottonwood seedlings typically occur at common streambank elevations. These bands are partially a result of the moist and barren zones that are exposed during the falling limb of the hydrograph. Initially, broad bands of seedlings are established, but mortality restricts the elevational range in which seedlings survive to grow into saplings and mature trees.

The elevation of successful cottonwood seedling recruitment can be determined by (i) direct observation of seedling elevations along various streams, (ii) excavation of seedlings to determine root length and moisture depth, and (iii) physiological studies to determine root growth and establishment potential. The three methods are somewhat independent, and quantitative agreement would strengthen their collective interpretation.

Various researchers have determined recruitment elevations, although primarily for *Aigeiros* cottonwoods (Table 2). Direct comparison of the data is complicated by differences in reference elevations. As much as possible, the values in Table 2 have been converted to a common reference, with '0' representing the growing season 'base-flow,' which is the typical low flow at the end of the growing season. This conversion was particularly problematic for the Reid (1991) data due to interbasin transfers that artificially elevated summer flows for much of the period of record.

Recognizing the complexity of a common reference stage, the observed elevations across eight streams are relatively consistent in indicating that successful seedlings tended to establish at elevations from about 60 to 150 cm above the base flow. These data are limited but also suggest that cottonwoods are successfully established at slightly higher elevations along larger rivers. This conclusion would be consistent with the knowledge that larger rivers tend to have more gradual stage changes since multiple tributaries combine to produce the overall river flow. Abrupt flow fluctuations along individual tributaries are attenuated by flow patterns from other tributaries. The larger rivers also tend to have finer substrates and occur at lower elevations with longer growing seasons and warmer

Table 2. Elevation of cottonwood seedlings established along various rivers in western North America (chronological listing).

Elevation[1] (cm)	*Populus* Species	River	Source
150–180	*P. deltoides*	Little Missouri, ND	Everitt 1968
100–130	*P. deltoides*	Minnesota, MN	Noble 1979
20–100	*P. fremontii*	Dry Creek, CA	McBride and Strahan 1984
100–120	*P. deltoides*	Milk, AB	Redi 1991
60–100	*P. fremontii*	Hassayampa, AZ	Stromberg et al. 1991
40–70	*P. deltoides*	Platte, NB	Johnson 1994
60–120	*P. deltoides, P. angustifolia, P. balsamifera*	Marias, MT	Rood and Mahoney 1995 and unpublished
20–230[2]	*P. deltoides*	Missouri, MT	Scott et al. 1997
40–240[3]	*P. deltoides*	Missouri, MT	Scott et al. 1997
60–260[4]	*P. deltoides, P. angustifolia, P. balsamifera*	Oldman, AB	Rood et al. 1998b

[1] Elevation is expressed relative to base flow, which usually represents the typical low stream stage during the late summer or autumn.

[2] Seedlings.

[3] Saplings.

[4] Following an exceptional 1 in 100 year flood.

temperatures, additional physical factors that enable cottonwood establishment at higher bank elevations.

The second approach, the excavation of cottonwood seedlings along various rivers, also provided general consistency with respect to root length (Table 3). Seedlings situated close to the stream edge would be expected to have shorter roots since the depth to the moist zone would be relatively shallow. It is most useful to compare the longer root data and data from actual riparian zones rather than from artificial studies. In these cases, roots of first year seedlings were less than 1 m in length and tended to be about 60 cm long. The limited data also reveal shorter roots for the *Tacamahaca* seedlings, which would further limit the establishment elevation of these slower-growing cottonwood species.

Rates of root elongation have been measured in artificial or experimental systems, and values of about 4 to 10 mm per day have been observed (Table 3). Assuming seedling establishment in early June and a first year growth period of about 60 to 90 days, this growth rate would result in root lengths of about 60 cm. This

Table 3. First-year root growth rates for cottonwood seedlings (chronological listing).

Growth Rate	*Populus* Species	System/River	Source
Per day (mm - rounded off to 1 mm)			
6–13	*P. fremontii*	artificial	Fenner et al. 1984
13	*P. fremontii*	artificial	McBride et al. 1988
4	*P. deltoides* × *P. balsamifera*	artificial	Mahoney and Rood 1991
3	*P. angustifolia*	Oldman, AB	Virginello et al. 1991
6–8	*P. balsamifera*	upland	Peterson and Peterson 1992
4	*P. deltoides*	artificial	Segelquist et al. 1994
4–12	*P. trichocarpa*	artificial	Reed 1995
After first year (cm - rounded off to 5 cm)			
60	*P. deltoides*	S. Canadian, OK	Ware and Penfound 1949
70–165	*P. fremontii*	artificial	Fenner et al. 1984
10–60	*P. deltoides*	Milk, AB	Bradley and Smith 1986
10–15	*P. balsamifera*	Belly, AB	Reid et al. 1992
40	*P. deltoides*	artificial	Segelquist et al. 1994
15[1]	*P. trichocarpa*	Elk, BC	Rood 1995
40[1]	*P. deltoides*	Coal Ck, CO	Friedman et al. 1997

[1] Estimated from photograph.

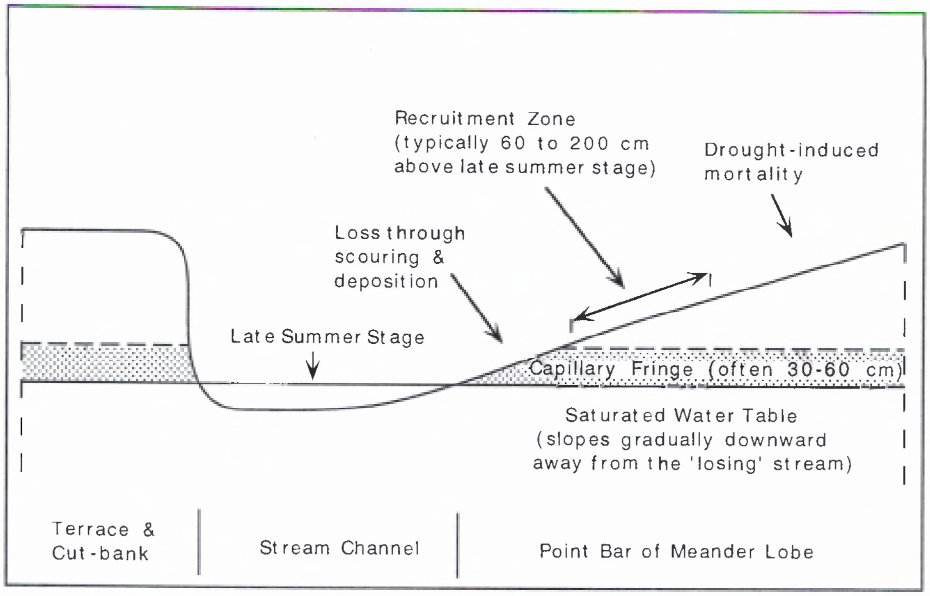

Figure 4. Cross section of a stream and riparian zone at the point bar of a meander lobe, showing the riparian water table, the capillary fringe, and the suitable band for cottonwood establishment and survival.

physiological analysis is thus consistent with the actual field measurements.

These analyses of seedling establishment elevation and seedling root growth provide relatively consistent results but also indicate that the seedlings' roots often do not reach the saturated water table. The roots would grow to about 60 cm or less in the first year, but the successful seedlings are situated from 60 to 150 cm above the late summer stream stage. The difference between root length and establishment elevation reflects the presence of an important subsurface moisture band above the water table, the capillary fringe or 'tension saturated zone.'

The Capillary Fringe

Alluvial floodplains along streams in western North America contain relatively coarse substrates consisting of sand, gravel, cobble, and boulders, along with silts and other finer materials. The collective substrates are generally relatively freely permeable, and consequently, infiltration and drainage are very rapid (Mahoney and Rood 1991, Mahoney 1996). In semi-arid regions, influent systems occur in which the streams tend to be 'losing' streams during the hot, dry period of midsummer. At this time, the riparian water table is provided with water percolating or discharging from the stream. This results in a relatively horizontal riparian water table that slopes gently downwards away from the stream edge (Kondolf et al. 1987, Rood et al. 1995, Mahoney 1996). Within the seedling recruitment zone that typically occurs within about 50 m of the stream edge, the summer riparian water table is approximately level with the stream stage, and as the stream stage recedes, the riparian water table declines correspondingly (Rood et al. 1995, Mahoney 1996).

The capillary fringe is a zone of moisture that extends above the saturated riparian water table (Figure 4). This moisture moves upwards due to water 'wicking,' resulting from adhesive and cohesive forces associated with the polarity of water and its resulting surface tension (Gordon et al. 1992). Observations of root architecture indicate that the fine cottonwood roots that are primarily responsible for water uptake especially occur in the capillary fringe. At depths below the water table, conditions are relatively anaerobic and, hence, unfavorable for root functioning. This alters a conception of phreatophytes. Rather than having drinking straw-like linkages with the saturated water table, the phreatophyte roots probably favor the moist and aerobic capillary fringe.

The extent of the capillary fringe is determined by substrate texture and ranged from about 5 cm in a mixture dominated by coarse gravel to 70 cm in medium textured sand (Mahoney and Rood 1991). Finer textured sand and silts have even greater capillary capacity. The capillary zone can be seen as a moist band above the stream stage (Rood et al. 1995), particularly if the stream site is visited in the morning before the surface is dried by sunshine and warmth. The extent of this apparent capillary fringe was associated with substrate texture along rivers in Alberta and Montana (Table 4). For coarse-textured substrates along streams that typically support *Tacamahaca* cottonwood species, the capillary fringe was typically about 20 to 40 cm. For finer-textured substrates along streams that are

Table 4. Apparent extent of the capillary fringe on point bars of meander lobes with differing substrate textures along rivers in Alberta and Montana.

River	Latitude (N)/ Longitude (W); and Date	Surface Substrate Composition[1]	*Populus* Species[2]	Apparent Capillary Fringe[3] Distance (m)	Apparent Capillary Fringe[3] Elevation (cm)
Bow, AB	50°49′/113°46′; 24.7.1996	medium cobble	*P. balsamifera*	1.1	3
	50°51′/113°36′; 24.7.1996	coarse sand, coarse gravel, medium cobble	*P. balsamifera*	3.8	39
St. Mary, AB	49°36′/112°54′; 12.6.1996	fine cobble, silt	*P. angustifolia*	1.7	12
	49°36′/112°54′; 12.6.1996	medium sand, fine cobble	*P. angustifolia, P. deltoides*	8.6	33
Oldman, AB	49°42′/112°52′; 14.8.1996	medium gravel, silt, fine cobble	*P. deltoides, P. angustifolia, P. balsamifera*	7.9	38
South Saskatchewan, AB	50°25′/110°24′; 30.6.1996	medium sand	*P. deltoides*	2.7	21
	50°02′/110°38′; 7.8.1996	fine sand, silt	*P. deltoides*	1.6	65
	50°02/110°39′; 11.8.1995	silt	*P. deltoides*	18.5	138
Missouri, MT	48°01′/110°07′; 16.7.1996	silt	*P. deltoides*	3.2	131

[1] In accordance with Gordon et al. (1992): silt: <0.06 mm; sand: 0.06 to 2 mm; gravel: 2 to 64 mm; cobble: 6 to 25 cm; boulder: >25 cm. Sand, gravel and cobble categories are split (equally) into fine, medium and coarse. Component materials are listed in descending order of abundance.

[2] Multiple species are listed in descending order of abundance.

[3] The apparent capillary fringe is the zone of moisture extending away from the stream edge, distance and elevation are relative to the stream stage.

dominated by *Aigeiros* species, the capillary fringe ranged from 30 to more than 100 cm.

The combination of the capillary fringe (Table 4) plus the root growth potential (Table 3) does result in elevation predictions consistent with the observed values in published reports (Table 2). Roots would extend downwards about 60 to 100 cm and penetrate into the capillary fringe which would range from about 50 to 100 cm above the riparian water table for most of the study streams with sandy substrates. The combination of root growth plus capillary fringe, would enable seedlings to become established up to about 200 cm above the stream's base flow. Thus, the different research approaches involving measurements of elevational position or root length plus capillary fringe, provide reasonable consistency (Figure 3 (top)).

The lower elevational limit of successful cottonwood recruitment is probably defined by erosional (physical) rather than physiological processes. Seedlings established at low elevations would be particularly prone to scouring during subsequent high stream flows or by ice (McBride and Strahan 1984, Johnson 1994, Scott et al. 1997, Rood et al. 1998b). Consequently; a lower limit of the seedling recruitment zone is probably about 60 cm above the base stage (Figure 4). Lower elevation establishment may occur if the stream flows remain low for a few years following seedling establishment. However, the prospects for survival are reduced as streambank elevation is lowered. Consequently, the typical recruitment band probably extends from about 60 to 150 cm above the base flow for coarse-textured substrates and from about 60 to 200 cm above base flow for streams with finer substrates (Figure 3 (top)). For both cases, the higher elevations are probably most applicable to larger rivers.

Survivable Rate of Stream Stage Decline

As already indicated, seedling survival through the first summer is relatively rare. The vast majority of seedlings die, primarily due to drought-stress, and those that survive probably do so because they are able to maintain a functional root contact with the receding moisture zone. Although root elongation is typically 1 cm per day or less, manipulative studies have demonstrated that many seedlings can survive water-table-decline rates of 2 to 4 cm per day (Segelquist et al. 1993, Mahoney and Rood 1991, 1992, McBride et al. 1988). The presence of a moist zone remaining temporarily above the receding water table may explain the difference between root growth rate and survivable water-table-decline rate.

For purposes of the recruitment box model, a value of about 2.5 cm per day decline in the water table is included as the maximal survivable stream stage decline rate (Figure 3 (middle)). This rate is very probably too rapid if particularly hot and dry conditions persist or if the riparian substrate is coarse. Conversely, even more rapid rates of stage decline may be survivable during periods that are cool and cloudy or if rain events occur to recharge the root zone from above.

The Cottonwood Recruitment Box Model

Following the preceding analyses, a seedling recruitment box model is proposed that outlines the timing and pattern of stream stage change that should permit seedling recruitment of cottonwoods. The stream stage should be declining to expose saturated sites for initial seedling establishment during the period of seed dispersal (mid-June). Ideally, streambanks between 0.6 and 2.0 m above the base stage should be exposed at this time. Subsequent gradual stage decline of less than 2.5 cm per day should permit seedling survival, with improved health and survival accompanying more gradual rates of stage decline.

Figure 3 (bottom) shows favorable hydrologic conditions for cottonwood seedling establishment based on the recruitment box model. The annual peak flow has passed prior to the onset of seed release, and the river stage is declining rapidly. The river-stage decline through the recruitment box exposes new areas for seedling establishment over a range of elevations. The rate of river-stage decline in the latter part of the recruitment box is favorable for cottonwood seedling establishment. Seeds germinating at the start of the period of seed release will have a low probability of survival due to high rates of river stage decline that will contribute to drought stress and mortality. Seeds germinating at the end of the seed release period will also have a low probability of survival due to mortality from ice scour and subsequent flooding.

MANAGEMENT IMPLICATIONS

Riparian cottonwood forests are rich aesthetic, environmental, and recreational resources in the semiarid regions of western North America (Braatne et al. 1996). These woodlands provide prime habitat for a range of terrestrial animals and abundant and diverse bird species and thus comprise some of North America's richest wildlife habitats (Finch and Ruggiero 1993). The riparian woodlands are linked to and benefit the adjacent riverine aquatic ecosystems by providing shade that reduces water temperature and by contributing organic matter, leaves, and woody debris that provide a basis for the aquatic food web (Wallace et al. 1997). However, although being especially valuable, the riparian woodlands are especially vulnerable to impacts of human development. These impacts include direct clearing for agriculture and domestic settlement, trampling and grazing by livestock, and influences of river-damming and diversion. The latter two major impacts, livestock and river damming, often particularly impede recruitment of the riparian trees. Many woodlands have declined due to insufficient replenishment to compensate for ongoing tree aging and mortality. The restoration of degraded woodlands and the conservation of the remaining cottonwood groves is reliant on reestablishing cottonwood recruitment that often particularly involves seedling recruitment. This integrative report reviews the hydrologic processes underlying cottonwood seedling establishment and develops the recruitment box model, a quantitative model that can provide the basis for developing instream flow prescriptions for cottonwood conservation and restoration.

The recruitment box model also contributes to the understanding of cottonwood reproductive ecology. The hydrologically-based model partially explains why moderate and large flood events directly enable cottonwood recruitment, whereas smaller flood events are often insufficient for cottonwood replenishment. Although smaller peaks moisten the suitable recruitment zone, the falling limb of the hydrograph is very rapid after the peak flow, and thus, the rate of stage decline is too abrupt for seedlings to retain root contact with the descending moist zone. In contrast, with moderate flood events, the peak is well above the recruitment box, and the rapidly falling portion of the falling limb of the hydrograph occurs while the hydrograph stage is above the recruitment zone. As the hydrograph descends into the recruitment box, the rate of stage decline will have slowed to a rate that is gradual enough that the seedlings can maintain root contact.

This analysis also provides a management opportunity with respect to cottonwood recruitment. If the rate of stage decline can be artificially managed as a gradual stage recession, it should be possible to promote cottonwood seedling recruitment. It should also be possible to deliver a stage pattern satisfying the recruitment box model, even without a major flood event. Such a strategy will only succeed if suitable recruitment sites exist; geomorphological disturbance and the creation of recruitment sites is one reason major flood events are required to ensure long term cottonwood forest survival.

The present integrative model is built on established principles of hydrology and physiology and should be applicable for a range of cottonwood species and for various streams, large and small. The quantitative coefficients with respect to the timing of seed release, suitable elevation, and survivable rate of stage decline will undoubtedly undergo some refinement and some specific fine-tuning for different stream systems (Shafroth et al. 1998). However, the principles of hydrology and physiology are universal, and thus, it is likely that the 'recruitment box' will be applicable across a range of streams. Although developed with data from western North American rivers, the model is likely to be broadly applicable because riparian woodlands in semi-arid regions of North America, Africa, and Europe share common conditions (Hughes 1994).

It is also likely that the recruitment box model will be applicable across plant species and even genera. For example, an artificial hydrologic pattern that closely followed the recruitment box model resulted in a major cottonwood recruitment event along the Truckee River, downstream of Reno, Nevada, USA (Gourley, pers comm). In addition to the establishment of *P. fremontii* seedlings, abundant willows (*Salix exigua* Nutt.) were also established and, regrettably but not surprisingly, a few Russian olive (*Elaeagnus angustifolia* L.) and tamarisk (*Tamarix chinensis* Lour.) seedlings were also established. Riparian cottonwoods provide the foundation for the riparian woodland ecosystems across western North America, and the fate of these rich ecosystems follows the fate of the cottonwoods. The health and abundance of other riparian plants, especially willows, that are influenced by similar hydrologic characteristics will most closely follow the fate of the cottonwoods. Some differences do exist across species with respect to the timing of seed dispersal and the tolerance of flooding and water-table-decline rate, and these differences may be used to favor recruitment of native cottonwoods and willows over exotic species such as tamarisk or Russian olive (Shafroth et al. 1995).

The cottonwood recruitment box model has been successfully applied to dammed rivers in Alberta and Nevada. In another paper in the present issue, we describe a case study of the Oldman River, Alberta, in which dams were operated to deliver a gradual stage recession after a major natural flood, and this permitted extensive cottonwood seedling recruitment (Rood et al. 1998b). Along the Truckee River through Nevada, artificial flow regulation directed towards the recovery of an endangered fish coincidentally provided a stream stage pattern that satisfied the cottonwood recruitment box model and this permitted an extensive cottonwood seedling recruitment event (Gourley, pers comm). Subsequently, dams in the Truckee River basin were deliberately managed to deliver a stream stage pattern that satisfied the cottonwood recruitment box model and the optimistic results from that novel project will be described in subsequent reports. The successful implementation of instream flows developed with the recruitment box model provide some validation of the model and also provide some optimism for the conservation and partial restoration of riparian cottonwood forests.

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Fluvial process and the establishment of bottomland trees

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Abstract

The effects of river regulation on bottomland tree communities in western North America have generated substantial concern because of the important habitat and aesthetic values of these communities. Consideration of such effects in water management decisions has been hampered by the apparent variability of responses of bottomland tree communities to flow alteration. When the relation between streamflow and tree establishment is placed in a geomorphic context, however, much of that variability is explained, and prediction of changes in the tree community is improved.

The relation between streamflow and establishment of bottomland trees is conditioned by the dominant fluvial process or processes acting along a stream. For successful establishment, cottonwoods, poplars, and willows require bare, moist surfaces protected from disturbance. Channel narrowing, channel meandering, and flood deposition promote different spatial and temporal patterns of establishment. During channel narrowing, the site requirements are met on portions of the bed abandoned by the stream, and establishment is associated with a period of low flow lasting one to several years. During channel meandering, the requirements are met on point bars following moderate or higher peak flows. Following flood deposition, the requirements are met on flood deposits high above the channel bed. Flood deposition can occur along most streams, but where a channel is constrained by a narrow valley, this process may be the only mechanism that can produce a bare, moist surface high enough to be safe from future disturbance. Because of differences in local bedrock, tributary influence, or geologic history, two nearby reaches of the same stream may be dominated by different fluvial processes and have different spatial and temporal patterns of trees. We illustrate this phenomenon with examples from forests of plains cottonwood (*Populus deltoides* ssp. *monilifera*) along meandering and constrained reaches of the Missouri River in Montana.

1. Introduction

The first woody plants to dominate bare, wet sediment along streams often demonstrate rapid growth, intolerance of shade, tolerance of nutrient scarcity and burial, release of large numbers of seeds following peak flows, and lack of seed dormancy (Sigafoos, 1964; White, 1979; Hupp, 1992). In the more arid regions of the northern hemisphere, the dominant plants in this group are members of the family Salicaceae, including cottonwoods and poplars (*Populus*) and willows (*Salix*). Bottomland forests provide important habitat structure for wildlife, especially where bottomlands are the only locations in the landscape wet enough to support trees (Brinson et al., 1981).

A focus of our work is to understand how spatial and temporal patterns of bottomland cottonwoods, poplars, and willows are influenced by the flow regime. These patterns are determined to a large extent by flow during the establishment phase (Stromberg et al., 1991; Scott et al., 1993). The relation between flow and establishment, however, varies from site to site. Along one stream cottonwoods may establish following high flows, whereas along another they establish during low flows. The thesis of our paper is that this variation results from differences in the fluvial-geomorphic proc-

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esses that form surfaces suitable for establishment.

Several studies have addressed the relation between flow and establishment of cottonwoods, poplars, and willows in the context of a single fluvial process (Everitt, 1968; Nanson and Beach, 1977; Bradley and Smith, 1986; Hupp, 1992; Johnson, 1994; Friedman et al., 1996). In this paper, we synthesize these studies and provide an example of how different dominant fluvial processes produce different relations between flow and patterns of cottonwoods on different reaches of the same river.

The conditions associated with successful establishment of bottomland cottonwoods, poplars, and willows are well understood. An abundant crop of wind- and water-dispersed seeds is released early each summer in association with peak flow (Densmore and Zasada, 1983; Fenner et al., 1985). The seeds can germinate immediately, but lose germinability under field conditions within a few weeks (Moss, 1938; Ware and Penfound, 1949; Densmore and Zasada, 1983). Freshly deposited alluvium typically provides ideal substrate for germination and establishment. Because they are intolerant of shade and germinate poorly in plant litter, cottonwoods, poplars, and willows are incapable of becoming established from seed under an existing stand of trees (Johnson et al., 1976) or herbs (Friedman, 1993). This trait often leads to even-aged stands. Young seedlings require a continuously moist substrate during at least the first week of growth (Moss, 1938). Root growth during the first month is slow (Burns and Honkala, 1990), but later in the first growing season seedlings of some species are able to extend a taproot deep enough to survive declines in the water table of as much as 1 m (Fenner et al., 1984; Segelquist et al., 1993). Therefore, the vulnerability of these plants to dry conditions decreases rapidly with age (McLeod and McPherson, 1973; Sacchi and Price, 1992). Bottomland cottonwoods, poplars, and willows are tolerant of burial and able to sprout from stems or roots (Nanson and Beach, 1977; Krasny et al., 1988). Extensive mortality of young plants, however, has been reported as a result of floods (Zimmerman, 1969) and ice scour (Johnson, 1994).

In summary, successful establishment from seed occurs only in channel positions that are moist, bare, and protected from removal by subsequent disturbance (Sigafoos, 1964; Everitt, 1968; Noble, 1979; Bradley and Smith, 1986; Stromberg et al., 1991; Sacchi and Price, 1992; Johnson, 1994). In humid regions vegetation is dense and grows rapidly, and as a result the need for a bare surface is more restrictive than the moisture requirement (Johnson, 1965). The reverse is true in arid regions (Zimmerman, 1969; Friedman, 1993). Some bottomland cottonwoods, poplars, and willows are capable of forming root sprouts. Where this mode of reproduction is important, formation of new stems may not be restricted to bare, moist surfaces, and the rate of lateral root growth may influence the timing of colonization of new areas.

2. Geomorphic processes and tree establishment

A suitable environment for establishment of cottonwoods, poplars, and willows can be produced by many fluvial processes, but we concentrate on three processes — narrowing, meandering, and flood deposition (Table 1). These processes are complex and the distinctions among them are sometimes arbitrary. Nevertheless, the three processes produce different spatial and temporal patterns of trees and different relations between flow regime and establishment. Our goal is to develop the ability to predict how changes in river management will affect bottomland forests.

2.1. *Narrowing*

In this paper, channel narrowing refers to abandonment by the stream of a portion of former channel bed. Thus, we include establishment of trees and shrubs in a former channel following avulsion. Establishment by channel narrowing, important in streams subject to large fluctuations in width, occurs more in braided streams than in meandering streams (Schumm, 1969), and more in arid regions than in humid regions (Wolman and Gerson, 1978).

Channel narrowing can occur as a response to flood-induced widening (Schumm and Lichty, 1963; Burkham, 1972; Osterkamp and Costa, 1987), climate change (Schumm, 1969; Gottesfeld and Johnson Gottesfeld, 1990), construction of upstream dams (Williams and Wolman, 1984), changes in land management (Nadler and Schumm, 1981), introduction of exotic bottomland plant species (Nevins, 1969; Graf, 1978), or as part of a cyclic, autogenic process (Patton and Schumm, 1981; Nanson, 1986). The

Table 1
Geomorphic processes associated with cottonwood establishment

Geomorphic process	Flow	Landform	Cottonwood community patterns
Narrowing	One to several years of flow below that which is necessary to rework channel bed	Channelbed	· Spatial patterns variable · Usually not even-aged stands · Establishment surface at relatively low elevation of former channel bed
Meandering	Frequent moderate flows	Point bars	· Moderate number of even-aged stands, arranged in narrow arcuate bands · Strong left-bank, right-bank asymmetry in distribution corresponding to meander pattern · Flood training of stems common · Establishment surface of mature trees often well below current ground surface and near channel bed elevation
Flood deposition and erosion	Infrequent high flows	Flooddeposits	· Linear stands · Small number of even-aged stands · Establishment coincident with floods · Little flood training of stems · Establishment surface of mature trees near current ground surface and well above channel bed elevation

immediate cause of narrowing is usually a period of one to several years of flows lower than that necessary to rework the entire channel bed. This allows establishment of vegetation on the channel bed. The newly established vegetation promotes deposition of fine sediment (Osterkamp and Costa, 1987) and increases resistance to erosion (Smith, 1976), thus stabilizing the channel at a narrower width.

The magnitude of flow necessary to produce channel narrowing depends upon antecedent conditions. After flood-induced widening, a stream is generally not competent to keep the entire bed free of vegetation. In this situation narrowing can occur under a wide range of low to moderate flows as has been observed on the Cimarron River in Kansas, the Gila River in Arizona, and Plum Creek in Colorado (Schumm and Lichty, 1963; Burkham, 1972; Osterkamp and Costa, 1987). Where the channel is closer to an equilibrium width, narrowing may occur only as a response to one to several years of exceptionally low peak flows. Thus, narrowing of the South Platte River in Colorado was associated with low flows during the 1930's (Nadler and Schumm, 1981).

Populations of cottonwoods, poplars, and willows established during channel narrowing are usually not strictly even-aged (Friedman, 1993); individuals in a stand may have been established at any time within a period of several years of relatively low flow. Stands usually have an irregular shape, of which the greatest dimension, or axis, is generally parallel to the direction of flow. Where narrowing occurs rapidly, young individuals are inundated infrequently and are usually not flood-trained (bent downstream into a decumbent position). The germination point of trees and shrubs established during channel narrowing is at the elevation of the channel bed at the time the surface was abandoned by the stream. This elevation may be different from the present bed-level because the process of channel narrowing sometimes involves bed-level changes (Friedman et al., 1996).

Most published examples of channel narrowing have involved the process discussed above. Channel narrowing, however, does not always involve establishment of vegetation on the channel bed. Channel narrowing can occur by lateral deposition at channel islands (Schumm and Lichty, 1963; Osterkamp and Costa, 1987) or at the channel bank (Nadler and Schumm, 1981). Where this process is important, establishment from seed will take place at higher elevations than the channel bed, as occurs along meandering channels. In addition, in the case of gradual narrowing by lateral deposition along an already vegetated surface, establishment of new individuals from root sprouts or sprouts from decumbent stems is likely to be important.

2.2. Meandering

Meandering streams are characterized by low width-to-depth ratios and progressive channel movement. The process of meandering is most important along low-gradient streams with low discharge variability and sediment load dominated by suspended sediment (Schumm, 1969). Infrequent events can have long-lasting effects on the geometry of meandering streams, especially in arid and semiarid regions (Schumm and Lichty, 1963; Burkham, 1972; Wolman and Gerson, 1978). Most of the sediment deposition on point bars, however, is carried out by moderate flows with recurrence intervals less than 5 years (Wolman and Miller, 1960). Forests produced as a result of meandering generally take the form of a series of parallel, arcuate bands of even-aged trees. These bands develop on point bars, and are, therefore, parallel to the direction of flow at the time they were established (Everitt, 1968; Nanson and Beach, 1977; Noble, 1979). On the point-bar side of the channel, the age of bands increases with distance from the channel. Stands on the cutbank side are older and not necessarily parallel to the present direction of flow. Because establishment is on a surface subject to frequent deposition, young stems may be repeatedly flood-trained (Everitt, 1968). The establishment surface of an adult tree is at the elevation of a young point bar — typically below the present flood plain, but above the channel bed. In some cases extensive flood-training may make it difficult to locate precisely the original root flare of a tree (Everitt, 1968).

Along a meandering stream, progressive movement of the channel protects trees and shrubs on former point bars from flood disturbance. This results in the preservation of a large number of bands on the flood plain. If a band is not removed by erosion, the cottonwoods, poplars, and willows are eventually replaced by shade-tolerant woody species (Weaver, 1960; Johnson et al., 1976; Nanson and Beach, 1977) or by grassland (Hefley, 1937; Lindauer, 1983).

Along the Little Missouri River in North Dakota, Everitt (1968) found establishment of plains cottonwood (*Populus deltoides* ssp. *monilifera*) seedlings at about 2 m above the low-water level. Adult trees occurred on surfaces as high as 5 m above low water. When trees were excavated, the establishment surface was found to be at approximately the elevation now occupied by seedlings. Cottonwoods were arranged in arcuate bands, and the stems in each band at ground level were generally even-aged. Because of extensive damage caused by flood-training, it was often impossible to find or date the establishment point.

On the Milk River in Alberta and Montana, Bradley and Smith (1986) counted rings in cores of plains cottonwood trees and found that establishment took place at approximately 5-year intervals, when flows of 2-year recurrence interval or greater occurred during the period of seed release. Cottonwood trees were arranged in parallel, arcuate bands, each spanning a range of ages of one to a few years. No consistent pattern of tree presence occurred relative to flood-plain ridges and swales. Seedlings were established approximately 0.5 m above the channel bed and then experienced 0.5 to 2 m of sediment deposition during flood-plain development.

On the Beatton River in British Columbia, establishment of balsam poplar (*Populus balsamifera*) occurred on the tops of scroll bars (Hickin and Nanson, 1975; Nanson and Beach, 1977). These bars were formed on average once every 27 years, but the periodicity varied from one bar to the next depending on the local rate of channel migration (Hickin and Nanson, 1975). Poplars became established on bars that had exceeded approximate bankfull stage. Subsequent deposition of sediment then buried the establishment surface by about 2.5 m (Nanson and Beach, 1977). Seasonality of individual flows was probably relatively unimportant in this case because establishment was not from seed but from root sprouts. As the scroll bars grew laterally, new stems were added on the streamward side. Therefore, the ages of stems on an individual scroll bar encompassed several years.

2.3. Flood deposition

Flood deposition and erosion occur along most streams, but are especially important for cottonwood establishment where lateral channel movement is constrained by a narrow valley. Because the channel is not moving, the only locations that are safe from subsequent scouring are those at high elevations. Only the greatest flows produce bare, moist substrate at these high elevations. Therefore, along a constrained channel trees occur in a small number of even-aged groups. The germination point of individuals is at a high elevation relative to the channel bed and close to the present ground surface. Flood-training is rare because the high establishment surface is rarely inundated.

For several reasons, the oldest trees along a constrained channel do not always date to the greatest recent discharge. First, the area of bare surface generated by flood deposition or erosion is a function not only of discharge but also of sediment load, type and age of pre-existing vegetation, local channel geometry, and flow history. Second, a bare surface will not support establishment unless it is moist during the time of seed viability. Flow timing, flow duration, subsequent precipitation, and sediment particle size may also be important. Finally, trees are susceptible to removal by subsequent floods, drought, fire, grazing, or competition from other plants.

Along the Animas River, a montane stream in western Colorado, establishment of narrow-leaf cottonwood (*Populus angustifolia*) occurred about once every 10 years, when peak snowmelt flows of recurrence interval over 3.6 years coincided with cool, wet weather (Baker, 1990). This combination of events produced the locations necessary for establishment — bare, moist surfaces high enough to be safe from future scouring. Because seedlings need cool moist conditions in the first growing season, high spring flows did not always result in cottonwood establishment.

Stromberg et al. (1991) observed successful recruitment of Fremont cottonwood (*Populus fremontii*) and Goodding willow (*Salix gooddingii*) about every 12 years along the Hassayampa River in Arizona. Flows with a recurrence interval of at least 7 years appeared to be necessary to create suitable bare surfaces. In this system, peak flows usually occurred months after the March through May period of seed release. As a result establishment took place 1 to 3 years after the year of peak flow and appeared to depend on moisture from precipitation. In the two cases just described, the river valley was wide enough to allow movement of the channel. This protected established trees from flood disturbance and explains the relatively large number of age classes observed.

Floods can cause tree establishment either directly, through the process of flood deposition, or indirectly, by initiating an episode of channel narrowing. For example, along a sandbed stream in the Great Plains, deposits left on low terraces by a catastrophic flood in 1965 were too high, and, therefore, too dry, to allow establishment of cottonwood from seed; however, the flood widened the stream, and during subsequent decades of narrowing, extensive establishment occurred at or near the elevation of the channel bed (Friedman et al., 1996).

3. Case example from the Missouri River in Montana, USA

The fluvial processes previously discussed can act alone or in combination. Where the dominant process changes along a stream, patterns of trees may change accordingly. We examined patterns of cottonwood (*Populus deltoides* ssp. *monilifera*) establishment within a post-glacial section of the upper Missouri River in Montana, USA (Fig. 1), where the river is variously constrained by a narrow valley (Lemke et al., 1965).

We present data from two sites within the post-glacial section (Fig. 1). At Site A, 153.3 km downstream of Fort Benton, Montana, lateral migration is prevented by the narrow valley (Fig. 2A and Fig. 3). At Site B, 237.5 km downstream of Fort Benton, the valley is wider and some meandering occurs (Fig. 2B and Fig. 4). In 1992, a transect was surveyed perpendicular to the channel at each site. Distinct fluvial surfaces along the transect were noted and the nearest four to ten trees on each surface downstream of the transect were selected for sampling. We excavated these trees to the root flare and sectioned and aged the stem above, below, and at the root flare. For trees larger than 60-cm diameter, we extracted cores instead of stem sections. We cross-dated all trees at a site to identify false or missing rings (Phipps, 1985).

Flow records were obtained from the United States Geological Survey gages at Fort Benton and Landusky, upstream and downstream, respectively, of our study sites (Fig. 1). Because patterns of discharge at these two gages are similar, only data from Fort Benton are presented here. Canyon Ferry Dam, approximately 220 km upstream of Fort Benton (Fig. 1), has been in operation since 1953. The dam, however, has limited storage capacity, and several unregulated tributaries enter the Missouri River between the dam and the study area.

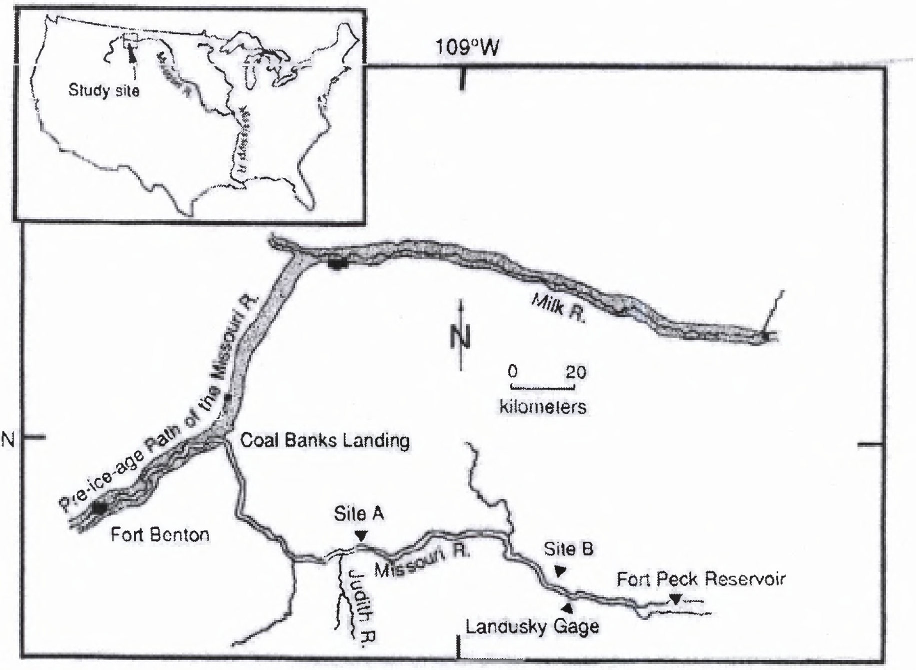

Fig. 1. Map of the study reach on the Missouri River, Montana. The stippled area represents the pre-Illinoian channel of the Missouri River (redrawn after Lemke et al., 1965).

As a result, the reduction in peak flows caused by Canyon Ferry Dam is small in this part of the river.

At Site A, where a narrow valley (0.4 km) limits channel meandering, we found a narrow single band of trees at a high position adjacent to the valley wall (Fig. 2A and Fig. 3). These trees became established at an elevation of 3 m above the low-water stage (measured at a discharge of approximately 115 m^3/s), on a layer of coarse sand apparently deposited by the flood of 1927 (Fig. 3); none of these trees were flood-trained (Fig. 5). Three of four sampled trees dated to the year following a flood of 1500 m^3/s in 1927, and the fourth tree was established in the second year following the flood (Fig. 6). The only other cottonwoods present were seedlings (individuals less than 1 m tall) established during the last two growing seasons at elevations less than 1.5 m above the low-water surface. Such seedlings, present along much of the study reach, are not likely to survive future high flows. Others researchers have reported that cottonwood seedlings occupying low-channel positions are prone to flood-related mortality from scour, burial, and inundation (McBride and Strahan, 1984; Asplund and Gooch, 1988; Stromberg et al., 1991).

At Site B the point-bar and cut-bank characteristics of a meandering channel were associated with several arcuate bands of cottonwoods distributed across a relatively broad bottomland (1.2 km) (Fig. 2B and Fig. 4). We sampled trees in the three bands closest to the channel. The band adjacent to the channel consisted of seedlings established in 1991 and 1992. Trees sampled on the other two bands included 15 individuals established up to two years after flows of 1400 to 2000 m^3/s in 1964, 1978, and 1981 (Fig. 6); the 1978 flood was recorded at the Landusky gage, following breakup of an ice jam between Fort Benton and Landusky (Fig. 1). Four other trees were apparently established following lesser flows from 1968 to 1970 (Fig. 6). The root flares of all sampled trees were within 2 m of the low-water surface and at or below the elevation occupied by seedlings at this cross-section (Fig. 4). These trees had experienced 0.5 to 1.0 m of sediment accretion since establishment (Fig. 4) and most stems were flood-trained (Fig. 7).

In summary, the frequency of cottonwood establishment in the post-glacial section of the Missouri River is determined by the locally dominant fluvial processes. Where lateral movement of the channel is prevented by

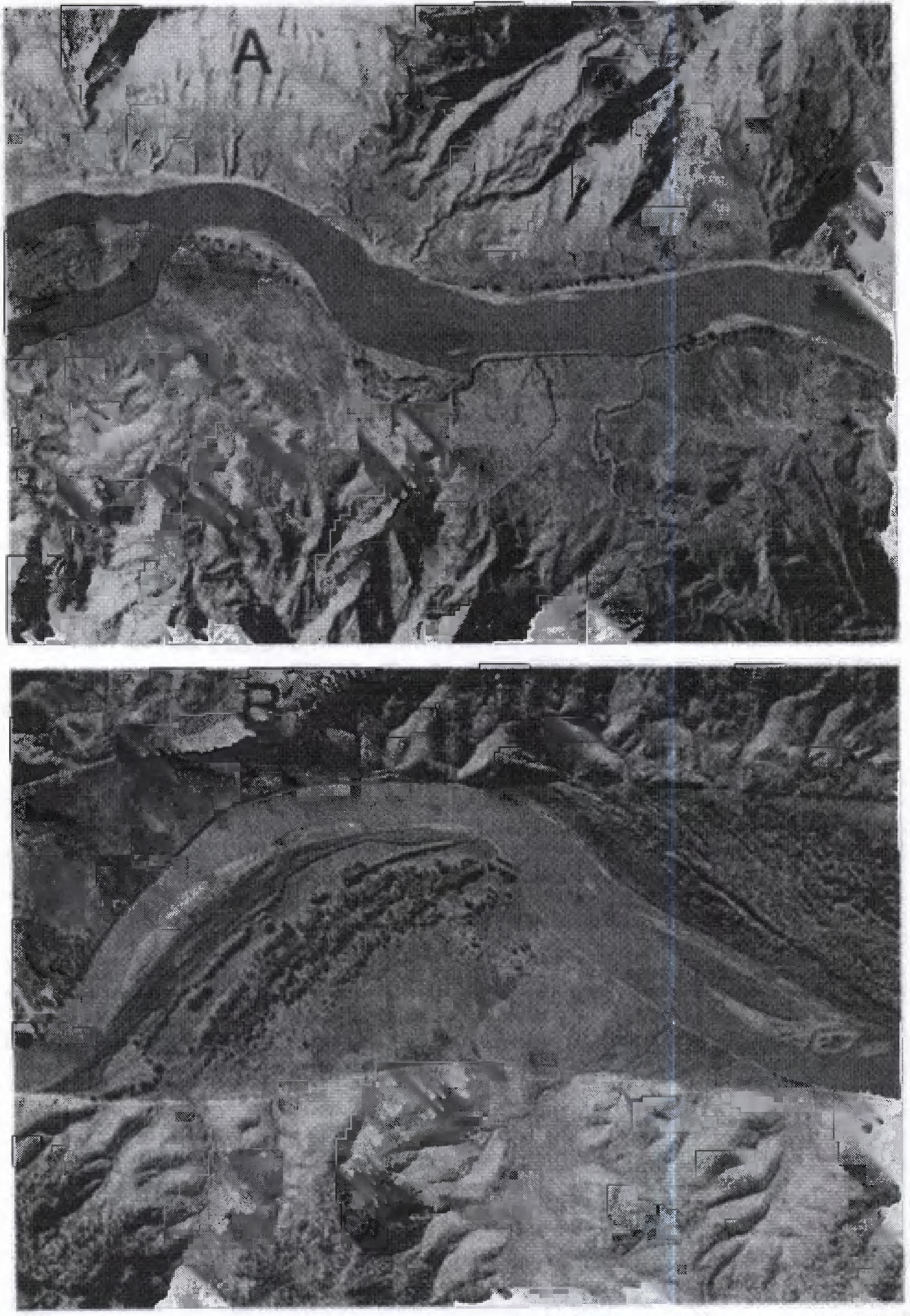

Fig. 2. Aerial photographs of (A) the constrained channel at Site A with associated narrow band of trees, and (B) the less constrained, meandering channel at Site B with a broad zone of bottomland trees arranged in arcuate bands.

a narrow valley, mature cottonwoods are few and largely restricted to narrow, elevated deposits of infrequent floods. On the other hand, in a less constrained reach cottonwood establishment occurs more frequently and at relatively low elevations. These conclusions are supported by preliminary examination of

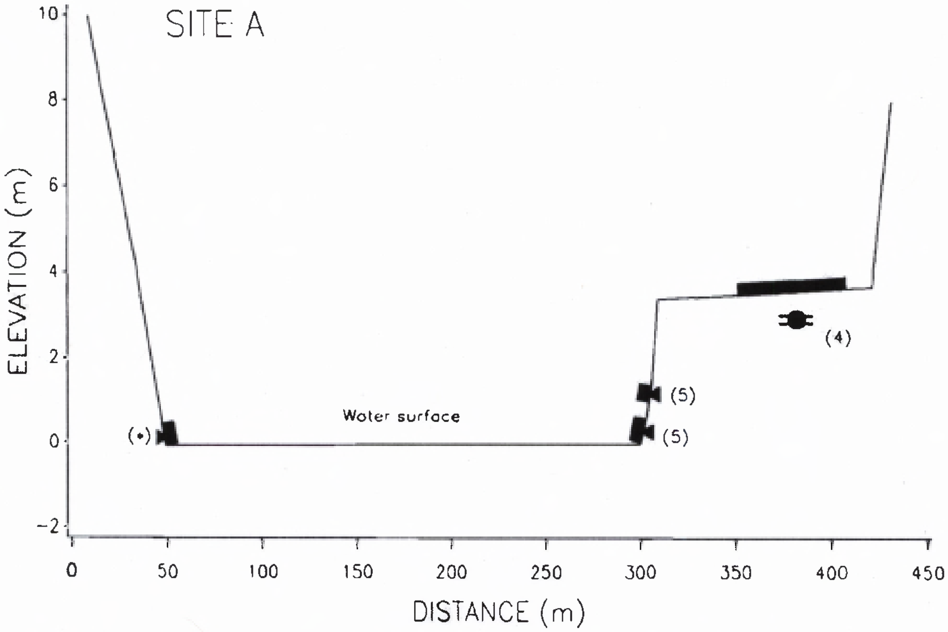

Fig. 3. Cross-section at Site A, Missouri River, Montana. Surfaces occupied by cottonwood are marked by thick bars. Triangles are seedlings and circles are trees. Bars attached to circles show the range of root-flare elevations. All seedlings had root flares within 10 cm of the present surface. The number of trees aged on a surface is given in parentheses. The asterisk indicates a surface on which seedlings were surveyed but not aged.

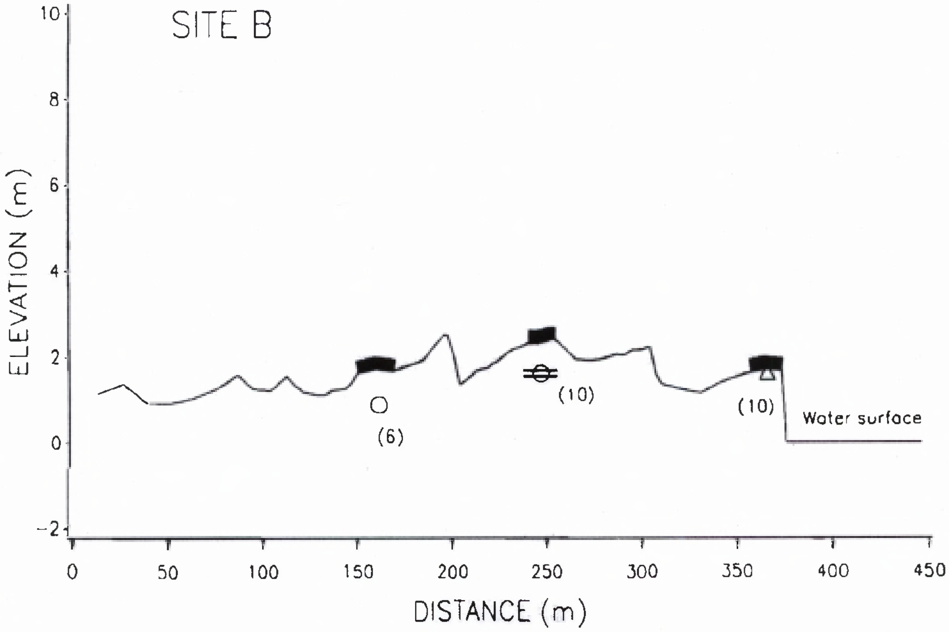

Fig. 4. Cross-section at Site B, Missouri River, Montana. Surfaces occupied by cottonwood are marked by thick bars. Triangles are seedlings and circles are trees. The number of trees aged on a surface is given in parentheses. Bars attached to circles show the range of root-flare elevations. On the surface at 160 m six trees were aged, but depth to root flare was measured for only one. All seedlings had root flares within 10 cm of the present surface.

Fig. 5. Photograph of an excavated cottonwood tree on a flood deposit along a narrow, highly constrained reach of the Missouri River.

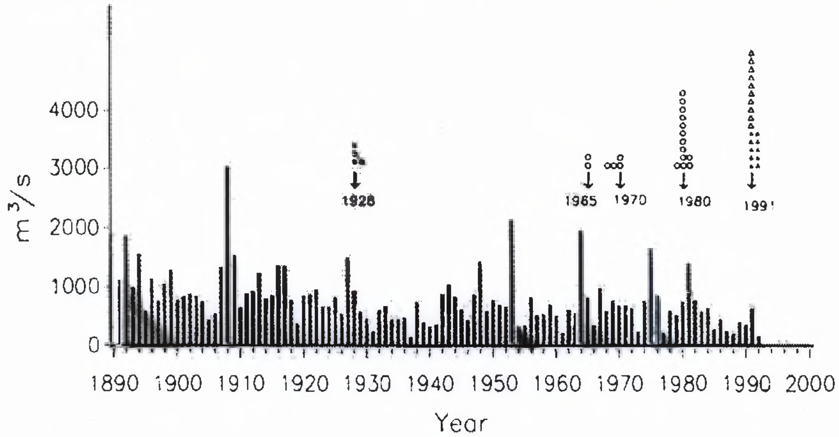

Fig. 6. Years of cottonwood establishment along the Missouri River, Montana, and peak mean daily discharge at the Fort Benton gage. Each circle or triangle indicates the establishment date of one cottonwood. Closed symbols are from Site A and open symbols are from Site B. Circles are trees and triangles are seedlings.

results from eight additional cross-sections examined along the Missouri River, Montana, in 1992 and 1993.

4. Discussion

Impacts of water development and river regulation on bottomland tree communities in western North America have generated substantial concern because of the important habitat and aesthetic values of these communities. Consideration of these impacts in water management decisions has been hampered by variability of responses of bottomland tree communities to flow alteration. Placing the relation of flow to vegetation in the appropriate geomorphic context helps explain this

Fig. 7. Photograph of an excavated, flood-trained stem from a meandering reach of the Missouri River. Note the prostrated, buried stem from which a new stem has arisen.

variability and may improve prediction of the effects of proposed flow alterations on bottomland vegetation.

Where meandering is the dominant fluvial process, a reduction in peak annual flows could decrease the rate of meandering, leading to decreased establishment. This phenomenon has been observed downstream of several dams in North America (Johnson, 1992; Bradley and Smith, 1986; Rood and Mahoney, 1990). On the other hand, reduction of peak flows in a braided stream could lead to narrowing and a one-time pulse of establishment during a period of low flow. After this pulse, additional establishment would occur infrequently, at higher elevations, and following higher flows. Thus, the extensive cottonwood forests that have developed during channel narrowing along the Platte and North Platte Rivers in Nebraska and along the South Platte and Arkansas Rivers in Colorado in the 1900s may be transient features. As the trees of these forests die they will probably be replaced by shade-tolerant tree species in relatively humid regions (Johnson, 1994), and by shrubland and grassland in more arid regions, where shade-tolerant bottomland trees do not occur.

If management of a stream prevented lateral migration of a formerly meandering channel, then the dominant fluvial process could shift from meandering to flood deposition and erosion. In other words, the discharge necessary for establishment could increase, because saplings on point bars would no longer be protected by lateral migration of the channel.

In this paper we have described a reach of the upper Missouri River in which sections of constrained channel alternate with sections where lateral migration occurs. In the former situation establishment occurs only at high flows, but in the latter situation establishment occurs at both moderate and high flows. Therefore, the constrained reaches would be more likely to exhibit cottonwood forest decline following construction of a dam that decreased the magnitude of flows with a recurrence interval of ten years or greater.

A better appreciation of the relevant geomorphic processes can help establish appropriate management objectives for bottomland forests. Often environmental objectives are formulated in terms of protecting the current situation from degradation. Bottomland cottonwood, poplar, and willow, however, are disturbance-dependent pioneer species. The current locations and extents of these bottomland forests do not always represent reasonable management objectives. Over the long-term, the natural extent and distribution of bottomland trees are limited by the geomorphic processes creating suitable establishment locations, and existing stands may be relicts of the geomorphic processes associated with a former flow regime. In the case of channel narrowing following a reduction in peak flows, extensive cottonwood and willow woodland is a transient response representative of neither the old nor the new flow regime.

Even in an unregulated situation, establishment along some constrained streams may occur only once in several decades. Bottomland cottonwoods, poplars, and willows do not live more than one or occasionally two centuries (Burns and Honkala, 1990). Thus, punctuated age distributions and large changes in densities from one decade to the next are the norm, and are not necessarily the result of human influence. Furthermore, the frequency of floods has varied naturally in some areas over the last several centuries (Webb et al., 1991; Knox, 1993). This has led to large changes in abundance of trees along streams where regeneration occurs on flood deposits (Baker, 1990) and along some streams in arid and semiarid regions prone to flood-related fluctuations in width (Schumm and Lichty, 1963; Burkham, 1972).

Quantifying many of the differences we have identified in the relations between flow and bottomland forests (Table 1) depends on accurate determination of the date and elevation of tree establishment. These data cannot be obtained without excavating the original root flare. Along the Missouri River, we have found that trees are often many years older below ground than above ground. The number of extra years below ground varies considerably from tree to tree within sites because it is influenced by factors such as flood injury and beaver attack. In this situation a core taken above the ground surface is a misleading indicator of the age of a tree.

We have emphasized the importance of establishment in determining patterns of woody plants and further have focused on how stream discharge operates through different geomorphic processes to produce suitable establishment surfaces. Discharge, however, is not an infallible predictor of the bottomland disturbance necessary for establishment. Along some streams ice jams during relatively low flow can result in inundation of areas otherwise rarely flooded (Butler, 1979). Slumps, debris flows, and tributary alluvial fans may provide bare, moist surfaces for establishment independently of discharge. Such surfaces are often high above the channel, and can provide important safe havens during destructive floods (Osterkamp and Costa, 1987).

Cottonwoods, poplars, and willows do not always establish when suitable locations are present. One reason is the absence of viable seeds. Abundant seeds of these species are produced almost every year and they can be transported large distances by air or water. Seeds, however, are produced during a period of a few weeks, usually in early summer, and remain germinable only for a few weeks more. Floods occurring outside of the seed dispersal period may not lead to establishment, especially in arid regions where moisture provided by flood water is critical. Similarly, dams that delay the occurrence of peak flows can decrease establishment opportunities (Fenner et al., 1985). Grazing and trampling by cattle can also prevent establishment (Kauffman et al., 1983).

Adult mortality also influences the pattern of bottomland trees and shrubs. Geomorphic processes that create new establishment opportunities may also remove existing adults; such processes include flood scouring (Yanosky, 1982), cutbank erosion of a meandering river, ice impact (Sigafoos, 1964), fire (Nanson and Beach, 1977), drought (Albertson and Weaver, 1945), ground-water pumping (Stromberg et al., 1992), and beaver damage (Bradley and Smith, 1986), as well as timber harvest and land clearing. These factors dominate patterns of some populations, but in most cases the underlying pattern determined through establishment is still clear.

5. Conclusions

Establishment of bottomland cottonwoods, poplars, and willows from seed occurs almost exclusively on bare, moist surfaces protected from disturbance. These conditions can be produced by several different fluvial processes, including narrowing, meandering, and flood deposition. These processes are associated with different flows and produce different spatial and temporal patterns of trees. Because of the importance of bottomland forests as habitat, managers need to be able to predict how a flood-plain landscape would be affected by a change in flow regime. Such predictions require an understanding of the locally dominant fluvial processes.

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Kristen C Guerriero/DNV/SOL/DOI@SOL

09/28/2009 09:31 AM

To Roy Smith/COSO/CO/BLM/DOI@BLM@DOI

cc

bcc

Subject Re: Donala Opposition - updated file

Roy,

I don't think we ever received the formal request on this one (it doesn't matter as far as for filing purposes but I wanted to let you know). Also, can you send me the verification info on it or scan it and send it? I never heard from Jim Dubois again so I think that means that he never heard from the other agencies.

Thanks.

Kristen Guerriero, Attorney
Office of the Solicitor, Rocky Mountain Region
Department of the Interior
755 Parfet Street, Suite 151
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DOI - Stewardship for America With Integrity and Excellence

Roy Smith/COSO/CO/BLM/DOI@BLM

Roy Smith/COSO/CO/BLM/DOI@BLM

08/20/2009 03:54 PM

To Kristen C Guerriero/DNV/SOL/DOI@SOL

cc

Subject Donala Opposition - updated file

[attachment "Donala Opposition.doc" deleted by Kristen C Guerriero/DNV/SOL/DOI]

Ecological Applications, 7(2), 1997, pp. 677–690

FLOOD DEPENDENCY OF COTTONWOOD ESTABLISHMENT ALONG THE MISSOURI RIVER, MONTANA, USA

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Abstract. Flow variability plays a central role in structuring the physical environment of riverine ecosystems. However, natural variability in flows along many rivers has been modified by water management activities. We quantified the relationship between flow and establishment of the dominant tree (plains cottonwood, *Populus deltoides* subsp. *monilifera*) along one of the least hydrologically altered alluvial reaches of the Missouri River: Coal Banks Landing to Landusky, Montana. Our purpose was to refine our understanding of how local fluvial geomorphic processes condition the relationship between flow regime and cottonwood recruitment. We determined date and elevation of tree establishment and related this information to historical peak stage and discharge over a 112-yr hydrologic record. Of the excavated trees, 72% were established in the year of a flow >1400 m^3/s (recurrence interval of 9.3 yr) or in the following 2 yr. Flows of this magnitude or greater create the necessary bare, moist establishment sites at an elevation high enough to allow cottonwoods to survive subsequent floods and ice jams. Almost all cottonwoods that have survived the most recent flood (1978) were established >1.2 m above the lower limit of perennial vegetation (active channel shelf). Most younger individuals were established between 0 and 1.2 m, and are unlikely to survive over the long term. Protection of riparian cottonwood forest along this National Wild and Scenic section of the Missouri River depends upon maintaining the historical magnitude, frequency, and duration of floods >1400 m^3/s. Here, a relatively narrow valley constrains lateral channel movement that could otherwise facilitate cottonwood recruitment at lower flows. Effective management of flows to promote or maintain cottonwood recruitment requires an understanding of locally dominant fluvial geomorphic processes.

Key words: bottomland; dendrogeomorphology; disturbance; flood; Missouri River; Montana; patch dynamics; Populus deltoides; *riparian ecosystems; seedling establishment.*

INTRODUCTION

Variation in streamflow is central in structuring the physical environment of riverine ecosystems and in determining community composition of lotic and riparian environments (Hupp and Osterkamp 1985, Poff and Ward 1989). Flow regime influences species abundance by determining the spatial and temporal occurrence of suitable habitat patches (Bain et al. 1988, Johnson 1992, Auble et al. 1994, Poff and Allen 1995). Although extreme flow variation can eliminate species (Zimmerman 1969, Bain et al. 1988), floods or droughts are necessary for the persistence of some species of fish (Meffe 1984) and plants (Nilsson et al. 1991, Friedman et al. 1996).

The early successional woody plants that dominate newly formed surfaces along streams typically demonstrate rapid growth, intolerance of shade, tolerance of nutrient scarcity and sediment accretion, high seed production, seed release associated with peak flows, and lack of seed dormancy (Sigafoos 1964, White 1979, Hupp 1992). In more arid regions of the northern hemisphere, this functional group is dominated by members of the Salicaceae, including cottonwood (*Populus* spp.). More complete understanding of the relationship between flow regime and the spatial and temporal patterns of riparian tree establishment would allow water managers to maintain or adjust flows to sustain populations of this riparian forest species. Such efforts are complicated, however, because the response of riparian vegetation to changes in flow varies as a function of geomorphic setting (Malanson 1993, Hughes 1994). When the relation between flow and riparian vegetation establishment is placed in a geomorphic context, much of the observed variability in vegetation response is explained and management prescriptions are clarified (Johnson 1993, Hughes 1994, Scott et al. 1996).

Establishment of cottonwood seedlings is generally restricted to bare, moist sites protected from intense physical disturbance (Bradley and Smith 1986, Friedman et al. 1995). For species that reproduce vegetatively, such as *P. balsamifera* (Nanson and Beach 1977), establishment of new stems may not be as tightly restricted to bare, moist surfaces. However, root or shoot sprouts are relatively uncommon in plains cottonwood (*Populus deltoides* subsp. *monilifera*), and appear to be primarily limited to shoot suckering from flood-trained stems (Rood et al. 1994).

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TABLE 1. Fluvial processes producing sites suitable for cottonwood establishment.†

Fluvial process	Flow	Landform	Community patterns
Narrowing	one to several years of flow below that necessary to rework channel bed	channel bed	spatial patterns variable; usually not even-aged stands; establishment surface at relatively low elevation of former channel bed
Meandering	frequent moderate flows	point bars	moderate number of even-aged stands, arranged in narrow, arcuate bands; strong left-bank, right-bank asymmetry in ages corresponding to meander pattern; flood training of stems common; establishment surface of mature trees often well below present ground surface and near channel bed elevation
Flood deposition	infrequent high flows	flood deposits	small number of linear, even-aged stands; flood training of stems rare; establishment surface of mature trees near present ground surface and well above channel bed elevation

† Based on Scott et al. 1996.

Three fluvial geomorphic processes are important in producing sites suitable for establishment of cottonwoods from seed: channel narrowing, channel meandering, and flood deposition (Table 1; Scott et al. 1996). At a site, these processes may act alone or in combination; their relative importance depends upon geologic and climatic factors, including flow variability, sediment load, and stream gradient.

The process of channel narrowing involves stream abandonment of a portion of the former channel bed. This includes reduction in width of a single channel or loss of flow in one or more channels of a multiple-channel stream. Although narrowing can occur along any stream, it is most important along braided channels typified by a high width : depth ratio and large areas of channel bed exposed for much of the growing season (Friedman et al. 1997). These conditions are maintained by high flow variability, high gradient, and a sediment load dominated by sand and gravel; such coarse sediment must be transported along the bed and forms highly erodible banks (Osterkamp 1978). Channel narrowing can occur in response to flood-induced widening (Schumm and Lichty 1963, Osterkamp and Costa 1987, Friedman et al. 1996), climate change (Schumm 1969), construction of upstream dams (Williams and Wolman 1984), establishment of exotic bottomland plant species (Graf 1978), or as part of a cyclic, autogenic process (Patton and Schumm 1981). Narrowing occurs during a period of relatively low flow, when stream power is insufficient to rework the entire channel bed. Exposed portions of the bed are ideal sites for establishment of vegetation, including cottonwood. This vegetation promotes deposition of fine sediment (Osterkamp and Costa 1987) and increases resistance to erosion (Smith 1976), thus stabilizing the channel at a narrower width. Cottonwood trees established during an episode of channel narrowing are often not even-aged, since establishment could occur at any time within the period of relatively low flow (Friedman et al. 1996). Stands usually have an irregular shape, with the longest axis parallel to the direction of flow. The establishment point of trees is low, at the elevation of the channel bed at the time the surface was abandoned by the stream (Friedman et al. 1996).

Meandering channels are generally characterized by low flow variability, low gradient, low width : depth ratio, and a sediment load dominated by silt and clay. During the process of meandering, cutbanks on the outside of channel bends erode outward and downstream, while the sediment removed is deposited downstream in point bars on the inside of bends. Most of this channel movement is produced by moderately high flows with recurrence intervals of <5 yr (Wolman and Miller 1960). Conditions suitable for establishment occur on portions of the point bar that are sufficiently moist and safe from riverine disturbance (Bradley and Smith 1986). Sediment accretion and movement of the channel away from the point bar protect vegetation from flood disturbance and ice scour. Stands produced by channel meandering typically exhibit arcuate bands of even-aged trees oriented parallel to the flow at the time of establishment (Everitt 1968, Noble 1979). These bands form relatively frequently, and each band occupies a small portion of the floodplain. The establishment point of these trees is at the moderate elevation of the point bar: above the channel bed but below the surface of the flood plain (Everitt 1968, Bradley and Smith 1986).

Floods can produce tree establishment by creating bare, moist deposits high enough above the channel bed to minimize future flow- or ice-related disturbance. Trees established on flood deposits along constrained channels occur as even-aged stands oriented along the direction of flood flow. The establishment point is high relative to the channel bed, and close to the present floodplain surface (Table 1). Flood deposition should be particularly important for tree establishment where channel movement is constrained by a narrow valley (Scott et al. 1996). Because the channel is relatively immobile, the only positions safe from flow-related disturbances are on relatively high surfaces. Only the largest flows would be capable of producing bare, moist alluvial deposits at these elevations. Floods can induce tree establishment directly through the process of sediment deposition, or indirectly by initiating a process of channel narrowing.

Because channel meandering is accomplished in small increments by relatively frequent flow, the area occupied by an individual cohort is a small portion of the bottomland, and forest area and age structure can be relatively stable over time (Everitt 1968, Bradley and Smith 1986, Hughes 1994). In contrast, where flood deposition is the dominant mode of establishment, cohorts may be widely spaced in time, and forest area and age structure may, likewise, vary widely. Episodes of channel narrowing lasting for decades and separated by ≥50 yr can also lead to highly variable or punctuated age structures (Schumm and Lichty 1963, Hughes 1994, Friedman et al. 1997). These different modes of cottonwood establishment can be distinguished by examination of the elevation and year of establishment (Friedman et al. 1996; J. C. Stromberg et al., *personal communication*).

The dominant fluvial processes acting along a river control the response of riparian vegetation to flow alteration. Dam management characteristically decreases downstream sediment loads and peak flows, thereby reducing stream power and the movement of sediments along the channel bed. This can lead to channel narrowing and a temporary increase in riparian vegetation, as cottonwood and other early successional species become established on formerly active channel surfaces. Channel narrowing with forest recruitment resulting from flow alteration is most pronounced along formerly wide, shallow, braided channels and has been reported along the Rio Grande (Williams and Wolman 1984), Arkansas (Williams and Wolman 1984), South Platte (Nadler and Schumm 1981, Johnson 1994), Republican (Northrop 1965, Williams and Wolman 1984), North Platte and Platte Rivers (Johnson 1994). Along meandering channels, which have a low width : depth ratio, the primary effect of diminished peak flows and sediment loads is not narrowing, but a reduction in the meandering rate resulting from the river's decreased capacity to erode and deposit sediments. This decreases the formation of establishment sites and, thus, reduces the recruitment of cottonwood and other early successional species (Scott et al. 1996, Friedman et al. 1997). Such responses have been reported along the Missouri (Johnson et al. 1976, Johnson 1992), Milk (Bradley and Smith 1986), Marias (Rood and Mahoney 1995), and Bighorn Rivers (Akashi 1988). Along channels where lateral movement is constrained by a narrow valley or by channel stabilization, flood deposition may be the only process that produces cottonwood establishment high enough to survive the effects of future damage from ice and floods (Scott et al. 1996). Thus, reductions in peak flows along a constrained channel may curtail cottonwood recruitment. In summary, management of flows to promote cottonwood recruitment requires an understanding of the locally dominant fluvial geomorphic processes.

The objective of this research was to refine our understanding of how local fluvial geomorphic processes condition the relationship between flow regime and cottonwood recruitment along the National Wild and Scenic reach of the Missouri River in Montana. A narrow valley constrains the channel throughout much of this section of river, suggesting that the dominant fluvial geomorphic process controlling cottonwood establishment is flood deposition. If so, the reproduction of cottonwoods should occur primarily at high elevations following infrequent large flows (Table 1). In previous analyses of cottonwood population age structure, trees have been dated by coring the stem above the ground surface. This approach can underestimate the age of the tree and provides no information on the elevation of establishment; this information is critical for determining the fluvial processes that created the establishment surface. To more precisely measure the age and elevation of establishment, we excavated trees and sampled them at the root collar. This approach has been used to date changes in channel morphology (Hereford 1984, Hupp 1992, Friedman et al. 1996) and to estimate sedimentation rates (Nanson and Beach 1977).

STUDY AREA

The Missouri River, formed by the confluence of the Jefferson, Madison, and Gallatin Rivers in southwestern Montana, flows north to Great Falls and then trends northeast and east through central Montana. Before the Pleistocene, the river flowed north and east into Hudson Bay. Pre-Wisconsinan continental glaciation diverted drainage southward into the Mississippi River (Wayne et al. 1991). The modern course of the Missouri River from Coal Banks Landing to the confluence with the Milk River, downstream of Fort Peck Reservoir (Fig. 1), corresponds roughly to the Late Illinoian ice margin (Wayne et al. 1991). Our study reach is the upstream 172 km of this postglacial channel extending from Coal Banks Landing to Landusky (Fig. 1). This comparatively young section of river is constrained by a narrow valley and exhibits low sinuosity. Comparison with detailed maps prepared by the Missouri River Commission between 1892 and 1895 indicates that little channel migration has occurred in this reach in the last 100 yr. In contrast, relatively high sinuosities, wide valleys, and more rapid channel migration are typical for the Missouri River upstream of Coal Banks Landing and downstream of the Milk River confluence.

The Missouri River in Montana is a snowmelt-dominated river, with peak flows occurring in spring, usu-

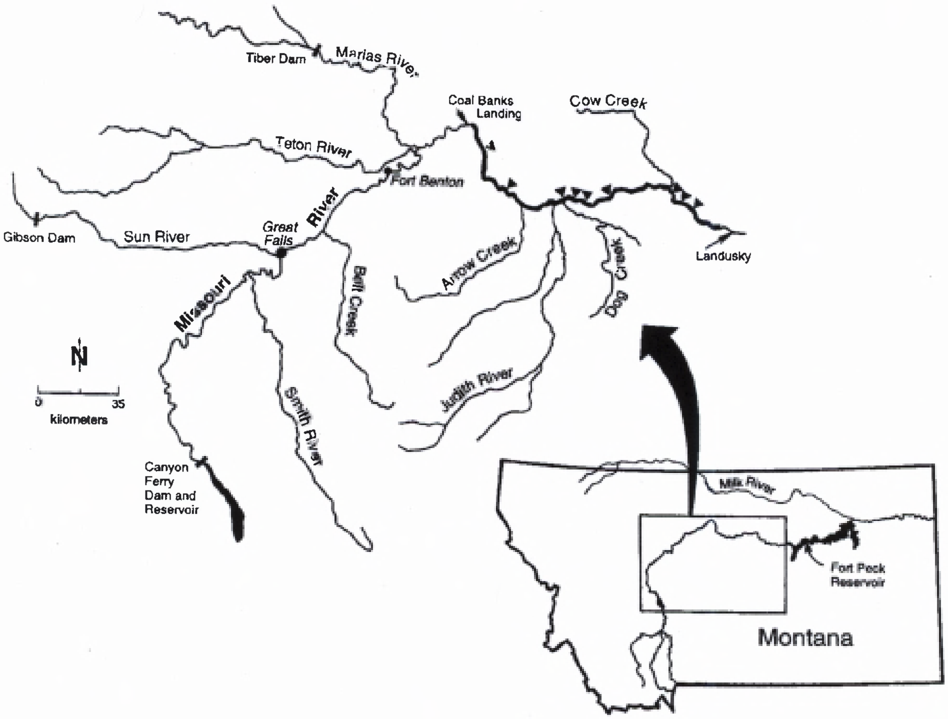

FIG. 1. Location of the study reach along the Missouri River, Montana. Study sites are indicated by triangles.

ally during late May or early June, and low flows occurring in late fall and winter. At the Fort Benton gage (U.S. Geological Survey gage 06090800), the Missouri River drains an area of 64 100 km^2 and has a mean annual discharge of 219 m^3/s (EarthInfo 1994). Flows on this portion of the river are influenced by irrigation withdrawals and a number of upstream dams, principally Canyon Ferry (Fig. 1; Ramey et al. 1993). Many unregulated tributaries join the Missouri River below Canyon Ferry, including the Smith, Teton, and Judith Rivers and Belt, Arrow, Dog, and Cow Creeks (Fig. 1). The cumulative upstream reservoir storage is $\approx$51% of the annual flow at Fort Benton and $\approx$43% at Landusky (Ramey et al. 1993). Unregulated tributaries, the limited storage capacity, and the operation of dams for irrigation and hydropower, as well as flood control, all limit the influence of reservoir operations on peak flows. As a result, the study reach (Fig. 1) is the least hydrologically altered alluvial portion of the Missouri River. Below Landusky (Fig. 1), backwaters from Fort Peck Reservoir influence both hydrology and vegetation.

The dominant riparian tree species along the study reach is plains cottonwood, *Populus deltoides* subsp. *monilifera*. Also present are *Acer negundo, Fraxinus pennsylvanica,* and *Salix amygdaloides.* The shrub community includes *Salix lutea, S. exigua, Symphoricarpos occidentalis, Rosa woodsii, Cornus stolonifera,* and *Prunus virginiana.* Within the study reach, where lateral channel movement is constrained, the cottonwood forest consists of discontinuous, often single-ranked stands of trees. In more geomorphically active locations, such as tributary junctions and channel islands, cottonwood stands and alluvial surfaces are wider. Upstream of the study area, the meandering preglacial river channel is associated with a broad floodplain and more extensive cottonwood stands (Hansen 1989).

The journals of the Lewis and Clark expedition (1804–1806; Coues 1893) indicate that cottonwood stands in the study area were spatially restricted before European settlement of the region. For example, in the constrained reach above Cow Creek (Fig. 1), they note that "there is, however, no timber on either side of the river, except a few pines on the hills." At a location above Arrow Creek, they state "There is now no timber on the hills, and only a few scattering cottonwood, ash, box elder, and willows along the water." In contrast, above Coal Banks Landing, where the river meanders within the broad preglacial valley, they reported that its "timber increases in quantity, the low grounds become more level and extensive," and they "came-to for the night in a handsome, low cottonwood plain on the south." Water management is not the only human activity that has affected riparian cottonwood forests. Native Americans used cottonwoods for fuel and forage for horses, which were introduced to North America in the 1500s (Winship 1904). From 1860 to 1890, there was widespread timber cutting for steamboat fuel along the Missouri River in Montana (Hansen 1989), and cattle grazing has occurred along portions of the study reach since the turn of the century. Nevertheless, within the study area, cottonwoods now occur in small, scattered stands similar to those described in 1805. Cottonwoods along this reach of the Missouri River are considered important regional nesting habitat for Bald Eagles and migratory bird species (R. Hazlewood, *personal communication*). Between Fort Benton and Landusky (Fig. 1), the river has been designated Wild and Scenic; the historical significance of the river and the scenic qualities of the cottonwood forests are central to this designation.

METHODS

Nine sites were selected to represent the range of geomorphic conditions that occur within the study reach, including channel islands, back channels, and small tributaries. The sites were identified by number of river kilometers (RK) downstream of Fort Benton, Montana (RK 90.4, 117.3, 144.4, 152.1, 153.2, 157.7, 209.2, 211.1, and 218.0: Fig. 1), as shown on maps of the Wild and Scenic River (Government Printing Office 1990). We avoided sites dominated by trees of >1 m diameter at breast height (dbh), assuming that many trees of this size predate the period of hydrologic record that began in 1891. Also, in order to minimize the complicating effects of tributary hydrology, we avoided sampling the relatively young populations at major tributary junctions.

At each site, a transect was established perpendicular to the channel. Distinct topographic surfaces along the transect were noted and surveyed. Elevations were determined relative to the lowest extent of perennial emergent vegetation, i.e., the active channel shelf of Osterkamp and Hedman (1982). Four size classes of cottonwoods were defined: seedling (0–1 m tall); sapling (1 m tall to 10 cm in diameter); pole (10–30 cm in diameter); and tree (>30 cm in diameter). On each surface, four stems in each size class, if available, were selected for determination of establishment date and elevation.

We estimated densities of cottonwoods on each surface by counting individuals by size class in rectangular quadrats downstream of the transect. The width of each quadrat was the width of the respective surface along the transect, and the downstream length was a distance from the transect sufficient to record at least 10 individuals of each size. Quadrat widths ranged from 1.5 m for a narrow surface with seedlings to 112 m for a high bench with poles and trees. Quadrat lengths parallel to the channel ranged from 1 to 108 m. We sampled the sites in October 1992 and from April to July 1993 (excluding seedlings that germinated in 1993).

Relating the origin of cottonwood stands to specific flows requires precise dating of individual stems. This can be difficult with cottonwood for two reasons. First, the early years of growth are often well below the present ground surface because of sedimentation (Everitt 1968). Second, cottonwood has diffuse-porous wood and can exhibit false or missing rings. In order to find the oldest wood on the tree, we excavated each stem with hand shovels and sectioned or cored it above, below, and at the apparent point of establishment as indicated by the flared root collar (Sigafoos 1964). We also sampled each stem at the ground surface to gauge the improvement in age determination provided by tree excavation. In seven cases, we were not able to obtain accurate ages at the ground surface, and excluded these trees from analyses comparing ground and establishment ages.

We photographed and sketched each excavated stem, indicating the apparent establishment surface, its distance below the present ground surface, and the positions of the slabs (or cores) removed from the stem. In addition, we recorded the sediment stratigraphy associated with each excavated stem, noting the depth and texture of each stratum. Finally, we collected samples of flood or ice scars found on trees near our cross sections.

All stem sections, cores, and scar samples were returned to the laboratory and air-dried. Cores were mounted on wooden blocks (Phipps 1985), and all slabs and cores were sanded with progressively finer sandpapers to a median particle size of 15 μm (600 grit). Ring number and width were recorded using a University Model incremental measuring machine (obtained from Curt Zahn, formerly of Fred C. Henson Company) and the TRIMS (Version 1.2) software system from Madera Software. Each core or slab was interpreted by at least two readers.

We detected and accounted for both false and partial rings (i.e., rings that were not continuous around the stem circumference). False rings were generally identifiable by an incomplete transition between early- and late-wood vessels through some portion of the stem. Where possible, false and missing rings were confirmed by cross dating (Stokes and Smiley 1968) both within and between trees. However, cross dating was reliable only after approximately the first 30 yr of growth. Presumably, for younger trees, effects of shading and local soil conditions obscured the hydrologic and climatic influences on annual growth increment (Stromberg and Patten 1996).

Flow records for three U.S. Geological Survey gaging stations on the main stem of the Missouri River were obtained from CD-ROM (EarthInfo 1994). Most of our analyses were based on the Fort Benton gage (06090800) at the upstream end of the study reach, because of its long period of record. The currently accepted period of record starts in water year 1891. We also used records for water years 1881 to 1890 (U.S. Geological Survey 1922), and estimated maximum daily discharge for water year 1890 from incomplete records for that year. Although these earlier records ex-

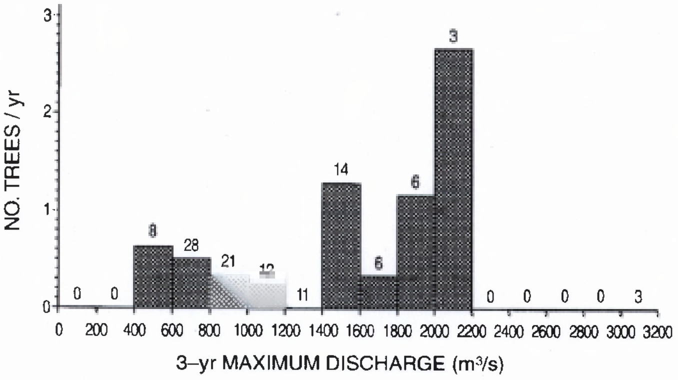

FIG. 2. Frequency distribution of mean rate of tree establishment vs. 3-yr maximum discharge. Mean rate of tree establishment equals no. trees established in years with 3-yr maximum discharge in the given range, divided by no. years in that range. The 3-yr maximum discharge is the maximum daily discharge of the given year and two preceding years. The number of years in each range of 3-yr maximum discharge is given above the bars.

clude winter months and are less accurate, we judged that they would be acceptable for identification of flood years.

We used least squares linear regressions to examine the following relations: (1) age at establishment surface vs. age at ground surface; (2) age at establishment surface vs. burial depth; and (3) age vs. dbh. We compared flood hydrographs from establishment and non-establishment years using the Fort Benton USGS gage records for the period 1891–1992. The analyses, based on water year (1 October to 30 September), examined growing-season flow volume (1 May through 30 September), minimum and maximum values for highest mean daily flow by date, and recession limb characteristics of total days with flow >1400 m³/s, 1050 m³/s, and 700 m³/s.

We determined whether the channel had downcut within the study reach by comparing the relation between stage and peak instantaneous discharge at the Fort Benton gage for the pre- and post-dam periods; stages associated with ice jams were excluded from this analysis. If significant downcutting had occurred, we would expect a downward shift in the stage–discharge relationship with lower stages associated with given discharges. To identify ice-related events not reflected in the Fort Benton gage, we used the Landusky gage (061152; 1934–1992) at the downstream end of the study reach.

We evaluated the significance of the association between high flows and cottonwood establishment by comparing our data to expectations from a null hypothesis that individuals were independently and randomly established over time. In the null hypothesis, all individuals have an equal chance of being established in any year, regardless of the flow in that year. Seedling establishment can occur 1–3 yr following a flood on bare, alluvial deposits (J. Stromberg and M. Merigliano, *personal communication*). In addition, age underestimates may result from failure to detect small, annual increments in the first 1–2 yr of growth. Therefore, we defined a suitable establishment year as the year of a flood ($\geq$1400 m³/sec) or the following two years. Using the binomial distribution, we calculated the probability that the observed proportion of individuals established in suitable years could have occurred by chance alone (Snedecor and Cochran 1980).

If four stems of all size classes present had been dated from all surfaces at all sites, there would have been a total of 216 dated stems; we dated 157. Failure to date stems resulted from: (1) the presence of large trees, especially those likely to predate the hydrologic record; (2) failure to recognize a second size class within an apparently even-aged stand; and (3) occurrence of heartrot. Four of the dated stems were excluded from the data set because they were identified as sprouts from buried roots or stems. Because of variability in the incidence of undated stems, dated stems do not perfectly represent riparian forest on a per-unit-area basis. To investigate the influence of undated stems, we created and analyzed an alternative data set, in which each dated stem was replaced by the area of forest it represented and was normalized across sites in units of hectares of forest established in a given year per kilometer of river.

RESULTS

Temporal patterns of establishment

Establishment of plains cottonwood along this reach of the Missouri River was strongly associated with floods exceeding 1400 m³/s (Fig. 2). Of 64 saplings, poles, and trees that were established during the period of record at Fort Benton, 35 (55%) dated to years in which flow exceeded 1400 m³/s (recurrence interval of 9.3 yr) or to the two years following these flood years (Fig. 3A and C). This large proportion of cottonwoods dating to the 32 flood and postflood years in the 112-yr record was inconsistent with the null hypothesis that all years had an equal likelihood of producing cottonwoods regardless of flow ($P = 1.1 \times 10^{-5}$).

An additional 11 saplings, poles, and trees were established from 1978 to 1980, following an ice jam that occurred between the Fort Benton gage and the study reach in March 1978 (Fig. 3A). This ice jam produced the highest stage of record at Landusky. When the jam released, the Landusky gage recorded an instantaneous

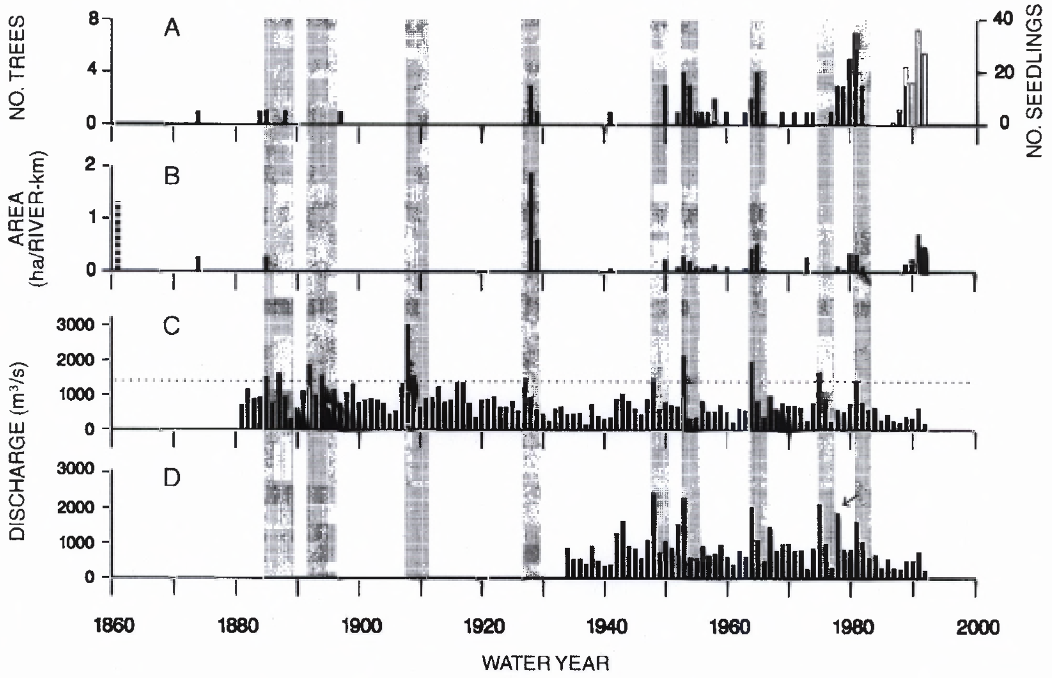

FIG. 3. (A) Number of sampled cottonwood trees and seedlings established in each year along the Missouri River, Montana. Solid bars represent tree, sapling, and pole size classes. Open bars represent seedling size class, with a different scale. (B) Area established in a given year per kilometer of river, based on weighting sampled cottonwoods (all size classes combined) by forest area. The dashed bar at 1861 represents the area occupied by older trees that could not be aged. (C) Maximum daily discharge for each water year at Fort Benton, Montana. The dotted line indicates a discharge of 1400 m³/s. Shaded vertical sections are years with maximum discharge >1400 m³/s and the two following years. (D) Maximum daily discharge for each water year at Landusky gage. The ice-related stage at Landusky in 1978 is indicated with an arrow.

discharge of 3060 m³/s, the third highest discharge of record (Fig. 3D). Considering 1978 as a flood year, there were 35 flood or postflood years out of a total of 112, and 46 of 64 cottonwoods (72%) established in these years (Fig. 3A).

When stems were weighted by the area of riparian forest they represent, the relative importance of individual years was changed, but the relation between flood years and establishment remained strong. During the 112-yr flow record, 62% of the sampled cottonwood forest area was established in the 32 years (29% of all years) that were associated with flows >1400 m³/s (Fig. 3B). Including the ice-related high stage of 1978, 68% of the cottonwood forest area was established in 31% of the years.

Eighteen of 64 sampled trees, poles, and saplings (28%) and all of the 88 seedlings exhibited no relation between establishment and high discharge. Seedlings dated to all years since the ice jam of 1986, and most postdated the lesser ice jam of 1989 (Fig. 3A).

During the 102-yr period of the published USGS record (1891–1992), there were 10 years in which flows exceeded 1400 m³/s. Five of these flood years were associated with establishment of sampled trees and five were not; we found no clear or consistent differences between the hydrographs in terms of growing-season volume, maximum daily discharge, flood duration, date of peak, or rate of recession following the peak. This analysis was not extended to the flood years of 1885 and 1887 (Fig. 3A), because daily flow data prior to 1891 were incomplete and, therefore, less precise.

The highest flows almost always occurred during the ice-free period, but the highest stages usually occurred during ice jams (Fig. 4). A similar pattern has been observed along the Turtle River in North Dakota (Harrison and Reid 1967). Most flood scars collected were produced by ice jams rather than ice-free floods. Two or more of the 21 collected scars dated to each of four years: 1978, 1979, 1986, and 1989 (Fig. 4). These were the four years of highest ice-related stage at Landusky since 1972. Only one scar dated to a year (1953) of discharge >1400 m³/s at Fort Benton (Fig. 4). In almost all cases, the wound generating the scar tissue occurred between growth rings, indicating that the tree was dormant at the time of the event. Although ice jams were more likely than ice-free floods to produce scars on pre-existing trees, ice-free floods were more likely to produce establishment of new trees. The only ice jam clearly associated with cottonwood establishment was that of 1978. Unlike most other ice jams, this event resulted in high discharge (Fig. 4).

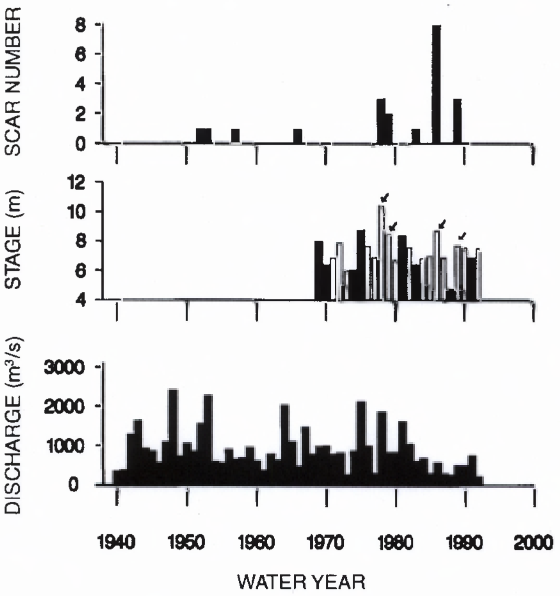

FIG. 4. Dates of injury (as indicated by scar tissue) for trees along the Missouri River, Montana, in relation to peak stage and maximum daily discharge at Landusky. Dark bars indicate ice-free stages. Open bars indicate high stages in the presence of ice. Stages in years that produced two or more sampled scars are indicated by arrows.

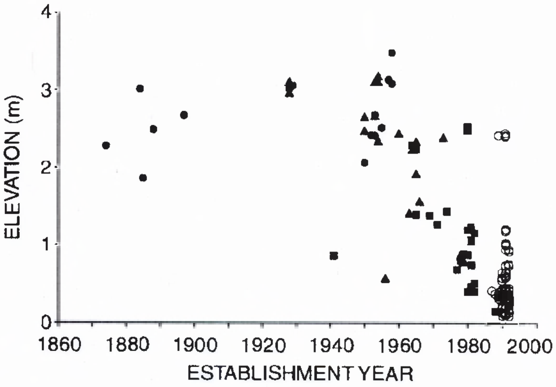

FIG. 5. Elevation of establishment surface and year of establishment for sampled cottonwoods. Size classes are represented as trees (●), poles (▲), saplings (■), and seedlings (○).

Spatial patterns of establishment

Cottonwood age is strongly related to elevation of the establishment surface (Fig. 5). Thirty-seven of 40 cottonwoods (98%) that predated 1978 were established between 1.2 and 3.4 m above the lower limit of perennial vegetation. In contrast, 21 of the 25 cottonwoods larger than seedlings (84%) postdating the ice-related high flow of 1978 were established below 1.2 m. The root flares of excavated poles and trees were typically associated with relatively coarse alluvial deposits of gravel or sand. However, across-site variance in stratigraphic sequences and depths was high, indicating a spatially complex depositional environment throughout the study reach.

Nonflood cottonwoods were established across a range of elevations and sites. Five trees were established at elevations between 2.7 and 3.1 m at two sites. These trees occurred on surfaces where nearby stems dated to flood years. At another site, four nonflood poles and saplings were established in a former back channel at elevations between 1.2 and 1.4 m. Six nonflood poles and saplings were established at elevations between 0.15 and 0.8 m on depositional surfaces at the downstream end of an island and the inside of a channel bend. Eighty-four of 88 seedlings (95%) were established at elevations below 1.2 m and 60 (68%) were established below 0.5 m (Fig. 5).

Temporal changes in the elevation of establishment did not appear to be related to changes in channel bed elevation. Plots of stage at peak instantaneous discharge for pre- and post-dam periods at the Fort Benton gage showed no downward shift in the stage–discharge relation, and indicated that the channel has not downcut in the post-dam (Canyon Ferry) period (Fig. 6).

Stem size structure and distribution

All size classes were present at only two of the nine sites (RK 144.4 and RK 218.0). Trees were absent at RK 152.1. Poles were absent at three sites and saplings were absent at five of the nine sites. Seedlings were not found at RK 90.4, where high water on the day of sampling may have obscured seedlings in low positions. Seedlings occurred on both banks (and both island edges) at all sites except for RK 90.4 and RK 209.2. Trees, poles, saplings, and seedlings occupied areas of 3.9, 2.3, 2.0, and 1.6 ha/river-km. Most surfaces had a single size class; where two size classes occupied the same surface, they were usually similarly aged poles and trees. Nonzero stem densities averaged across surfaces were 212 stems/ha ($n = 8$) for trees,

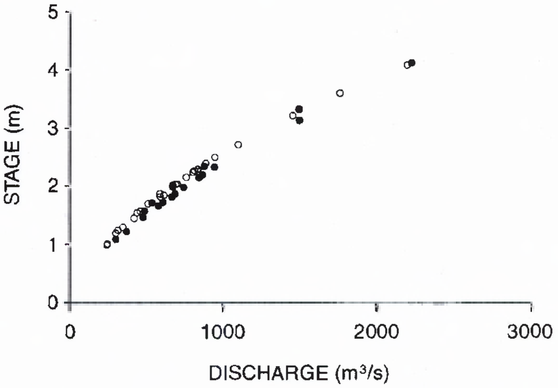

FIG. 6. Peak stage in relation to peak instantaneous discharge at Fort Benton, Montana, before and after presence of the Canyon Ferry Dam. Closed circles are water years before 1954; open circles are after 1954. Years in which peak stage was associated with ice jams are excluded.

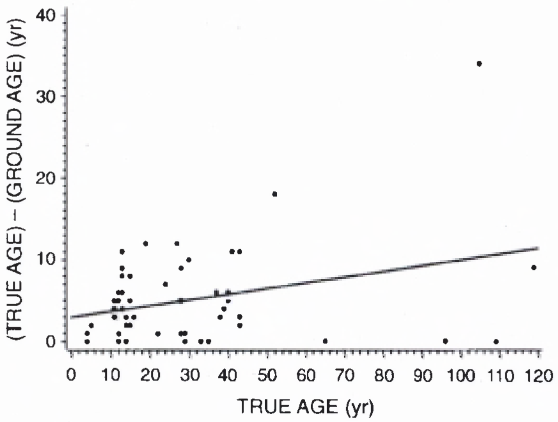

FIG. 7. The difference between true age and age at the ground surface vs. true age for cottonwood trees harvested along the Missouri River, Montana. The plotted line equation is $y = 2.97 + 0.070x$ ($F_{1,55} = 6.28$, $P = 0.02$, $r^2 = 0.10$, $n = 57$).

299 stems/ha ($n = 6$) for poles, 1428 stems/ha ($n = 4$) for saplings, and 16 217 stems/ha ($n = 8$) for seedlings.

Sources of error in dating cottonwood stems

Cottonwoods dated from 1862 to 1992. The difference in age between the establishment surface and the ground surface was 0–18 yr ($\bar{X} = 4.8$ yr, $n = 29$) for saplings, 0–12 yr ($\bar{X} = 4.3$ yr, $n = 18$) for poles, and 0–34 yr ($\bar{X} = 7.1$ yr, $n = 10$) for trees. All sampled seedlings were established within ≈ 2 cm of the present ground surface, and no difference in age between establishment and ground surfaces was observed. A linear regression of difference in age on true age was significant ($P = 0.02$, $n = 57$), but explained only 10% of the variance (Fig. 7). Differences in age were also significantly ($P = 0.02$, $n = 57$) related to depth of burial, but the relationship explained $<10\%$ of the variance. There was a highly significant relationship ($P = 0.0001$) between dbh and age at the establishment surface for saplings, poles, and trees (Fig. 8). However, the dispersion of points ($r^2 = 0.80$) and displacement from the origin limit the utility of this relationship for predicting age from size.

DISCUSSION

Fluvial processes and cottonwood establishment

Patterns of cottonwood establishment and survival within the study reach support the conclusion that successful recruitment of trees along constrained alluvial channels occurs following infrequent floods on elevated flood deposits. A significant majority of the trees, poles, and saplings was established in years when flows exceeded 1400 m^3/s (recurrence interval of 9.3 yr), or in the following 2 yr. Cottonwoods that survived the most recent ice-related flood (1978) were established ≥ 1.2 m above the lower limit of perennial vegetation. In contrast, saplings and seedlings that postdate 1978 were established between 0 and 1.2 m; most seedlings were established below 0.5 m.

The nearly ubiquitous occurrence of seedlings on bare, moist surfaces near the water's edge strongly suggests that the sparse pattern of older size classes cannot be explained by a shortage of seed. The strong correlation between cottonwood age and elevation of the establishment surface (Fig. 5) could be explained by recent channel degradation and associated changes in river stage (Hereford 1984) resulting from dam construction (Williams and Wolman 1984). However, our stage and discharge analysis shows that such channel degradation has not taken place in the study reach (Fig. 6). Thus, observed patterns of cottonwood establishment and survival indicate that, in most years, seedlings germinate on low, bare surfaces created by localized scour and deposition associated with winter ice or spring flows. However, these stems are unlikely to survive future ice jams and high discharges. Long-term survival is usually possible only for seedlings established on the higher bare, moist sites produced by extreme floods (Scott et al. 1996, Johnson 1994), or in protected depositional microsites like the downstream end of islands or the inside of large channel bends.

Although the instantaneous peak stage in most years is associated with ice jams, and most tree scars result from ice damage, cottonwood establishment is more closely associated with late-spring floods (Fig. 3). This may be because the large volume of water in a flood transports more sediment than the relatively low volume resulting from release of an ice jam. As a consequence, floods deposit a more spatially extensive, bare, alluvial surface necessary for cottonwood estab-

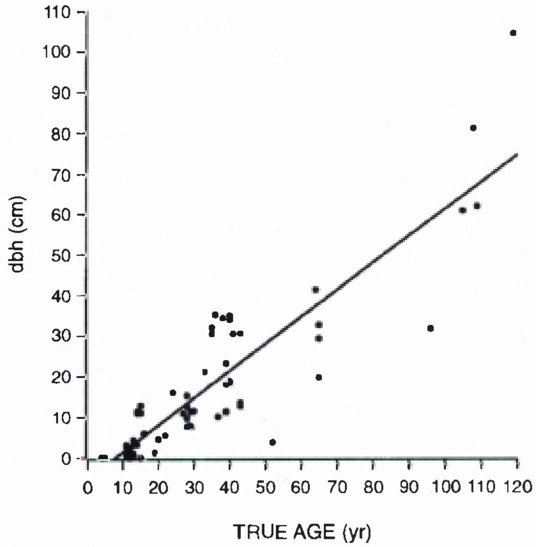

FIG. 8. Diameter at breast height (dbh) vs. true age for cottonwood trees along the Missouri River, Montana. The equation of the plotted line is $y = -5.35 + 0.67x$ ($F_{1,63} = 244$, $P = 0.0001$, $r^2 = 0.80$, $n = 65$).

lishment than do ice jams. Another important difference is associated with the timing of these events relative to the seed dispersal period for cottonwoods; typically, ice jams occur between January and March, well before seed release, whereas flood peaks occur during, or immediately before, the period of seed dispersal in late May through June. The association of peak and recession flows with seed release can be an important element of successful cottonwood establishment (Read 1958, Fenner et al. 1985, Mahoney and Rood 1993, Scott et al. 1993, Stromberg et al. 1993). Although ice jams seldom enable establishment, they can be an important cause of mortality, especially for smaller stems in relatively low channel positions (Fig. 3A; Johnson 1994).

Of the 12 floods with discharge >1400 m^3/s at Fort Benton, only seven (1885, 1887, 1927, 1948, 1953, 1964, and 1981) resulted in cottonwood establishment in the year of the flood or in the two following years (Fig. 3). We detected no establishment following the floods of 1892, 1894, 1908, 1909, and 1975. Several factors could explain the absence of apparent establishment following these five floods. The first is our relatively small sample; there may be unsampled cottonwoods in the study area that date to these floods. A second factor could be subtle differences in the shape of the flood hydrograph. However, we observed no clear or consistent differences between the flood years that produced sampled trees and those that did not. A third factor is scouring by subsequent floods or ice jams. For example, the ice jam of 1978 may have removed young trees that had become established on surfaces deposited by the flood of 1975. Similarly, the flood of record in 1908 may have removed young trees established following the floods of 1892 and 1894. Other possible explanations include droughts (Albertson and Weaver 1945, Baker 1990), climate-related failures of the seed crop, or periods of intense grazing by livestock. The most interesting apparent failure of establishment occurred following the flood of record at Fort Benton in the period 1908–1911 (Fig. 3). It is possible that the high flows of 1907–1909 destabilized existing vegetation and initiated a period of widening. Such postflood widening has been observed elsewhere (Schumm and Lichty 1963, Osterkamp and Costa 1987). Alternatively, widespread cottonwood reproduction following cessation of cutting for steamboat operation may have resulted in extensive recruitment in the 1890s, thereby preempting sites that might otherwise have been occupied following the 1908 flood.

The study area has been grazed by livestock since the 1800s. We observed many seedlings that had been damaged by grazing. Recent reproduction of cottonwood seems to be more abundant at sites where cattle are excluded. It seems likely that grazing has decreased cottonwood establishment and survival. However, this effect has not obscured the significant relationship between cottonwood establishment and flood years. Construction and long-term monitoring of livestock exclosures would help to determine the importance of grazing within the study reach.

Apparent establishment in the two years following a flood year could be an artifact resulting from failure to discern small, inner rings or to locate the precise point of establishment. Alternatively, if these trees are dated precisely, they indicate that survival of seedlings along the study reach is not always dependent upon the moisture left in a flood deposit by the flood. Similar age distributions of adult *Populus* spp. in Idaho have been attributed to establishment from seed 1–3 yr following a flood (M. Merigliano, *personal communication*). In Arizona, limited establishment in the 2nd yr following a flood was facilitated by high soil moisture on new fluvial surfaces located near the water table (J. C. Stromberg et al., *personal communication*). The best way to determine whether establishment in the study reach occurs in years following a flood year would be to monitor seedling establishment in permanent plots following floods (cf., Johnson 1994).

Although the majority of cottonwood trees, poles, and saplings was established at high elevations following floods, ≈30% of the sampled stems were not. Therefore, although floods have a dominant influence on cottonwood establishment along this section of the Missouri River, other factors also produce bare, moist sites suitable for seedling establishment. Such factors could include tributary floods, local slope failures, and cultivation. A few trees became established in nonflood years at low-to-moderate elevations in sites protected from floods and ice. Finally, it is possible that some dated stems were undetected sprouts from stems or roots; such sprouts may not have as strong a dependence on bare, moist substrate as do seedlings.

Nevertheless, the relationship between infrequent, large floods and cottonwood regeneration observed along this constrained channel reach of the Missouri River is clear, and is consistent with results of other recent studies that describe the importance of low-frequency, high-magnitude floods in the establishment of riparian trees (Friedman et al. 1996; J. C. Stromberg et al., *personal communication*). Flood deposition can facilitate establishment along a broad array of stream types by enabling germination at elevations that are infrequently flooded. Long-term cottonwood establishment along some nonmeandering stream types is associated with infrequent large floods with recurrence intervals of 30–50 yr (Hughes 1994). Along the section of the Missouri River examined in this study, a narrow valley severely restricts channel movement. Physical disturbance by ice and higher flows removes almost all seedlings established at lower elevations. As a result, establishment of tree-sized cottonwoods occurs chiefly on high-elevation fluvial surfaces created by floods with recurrence intervals >9 yr.

To dig or not to dig

In previous studies relating dates of establishment of riparian cottonwood trees to flow, investigators have dated cores taken above ground (Everitt 1968, Bradley and Smith 1986, Baker 1990, Howe and Knopf 1991). Our results demonstrate that dating cottonwoods at the ground surface can underestimate the age of a tree by as much as 34 yr, with a mean underestimate of 5.1 yr. The error introduced by sampling above ground could falsely strengthen or weaken a relationship between high flow and establishment. Microsite differences in environment or herbivory can cause different apparent rates of growth in buried portions of a stem. As a result, two trees established following the same flood may have widely different ages at the present ground surface. On the other hand, two trees established in different years may have the same age at the present ground surface if they were cut back to ground level in the same year by a flood or by beaver. In this study, if trees had been aged at the ground surface instead of the establishment surface, no significant relationship between floods and establishment would have been detected. In upland and riparian forests, attempts have been made to correct for the age discrepancy between the establishment surface and the point from which a core sample is taken by estimating the years necessary to grow to this height (Henry and Swan 1974, Stromberg et al. 1991). Although we found a significant correlation between depth of the establishment surface and the age underestimate at the ground surface, a low r^2 suggests that depth of burial is an unreliable predictor of the age difference between the ground and establishment surface. We recognize that, in some situations, the error introduced by coring at or above the ground surface is not as large as at our study area, and that this level of error is acceptable for some objectives. However, excavation is required in any study that depends on precise dates of establishment for riparian trees.

Excavation of trees to the establishment surface decreases by as much as an order of magnitude the number of trees that can be sampled per unit time. In this study, excavation time for trees ranged from two to 16 person–hours. However, information about the elevation and precise date of establishment is important for distinguishing between different modes of establishment. For example, without such data, the correlation between age and elevation observed at this site could be explained by accretion: cottonwoods established at low elevations survive over the long term as a series of moderate high flows raise the occupied surfaces without removing the trees. Such a process is typical of meandering and narrowing streams, where sediment accretion and progressive channel movement away from growing trees protects even those established at low elevations (Everitt 1968, Nanson and Beach 1977, Bradley and Smith 1986, Scott et al. 1996, Friedman et al. 1997). If this process were common along the study reach, there would be many trees that had established outside of extreme flood years (Fig. 3), and there would be many old trees with low elevations of establishment (Fig. 5). Outside of the constrained postglacial reach of the river, the valley is wider and the presence of point bars containing arcuate, even-sized bands of cottonwoods indicates that meandering is an important process (Everitt 1968, Noble 1979, Bradley and Smith 1986). In these areas, we would expect that establishment would occur more frequently and that the elevation of establishment would be relatively low (Scott et al. 1996).

Hydrologic alteration

Ramey et al. (1993) used recorded daily changes in reservoir storage to reconstruct what flows would have occurred at Fort Benton without dams. Comparison of this derived record with the actual flow since 1954 indicates that dams have decreased the magnitude of flows >1400 m^3/s by 14–23%, but have not decreased the actual number of flow events >1400 m^3/s (Ramey et al. 1993). Operation of the dams has decreased the expected frequency of flows necessary for cottonwood establishment, but the decrease in flows >1400 m^3/s has not yet been expressed in the short post-dam record. On alluvial rivers, channel degradation is sometimes observed downstream of dams as a result of sediment removal by the dam (Williams and Wolman 1984). We observed no evidence of degradation within the study reach (Fig. 6).

Classification of cottonwood stands in the study reach by size class (Hansen 1989) shows a relative scarcity of smaller, and presumably younger, trees within a portion of the study reach, implying a future decrease in the area of mature trees. Hansen (1989) interprets this apparent shortage as an impact of upstream dams. However, results of the present study indicate that cottonwood reproduction has been highly episodic; therefore, size class ratios at one point in time may not be a reliable predictor of future trends. Furthermore, dams have not yet altered the observed number of flows exceeding 1400 m^3/s in the 38 yr since Canyon Ferry was completed. Therefore, if the present scarcity of young trees does represent the beginning of a long-term decline in forest area, the present level of flow regulation is unlikely to be the principal cause.

Management implications

By demonstrating the dependency of riparian cottonwood establishment and survival on floods, this study supports the central role of floods in structuring large riverine ecosystems (Welcomme 1979, Junk et al. 1989, Power et al. 1995). On the Missouri River, high flows in late May and June have been shown to stimulate spawning migrations of shovelnose sturgeon (*Scaphirhynchus platorynchus* Rafinesque) and paddlefish (*Polyodon spathula*) (Berg 1981). Flood flows also are important in creating and maintaining geomorphic features such as side channels or back channels, sandbars, chutes, and pools that serve as essential habitat for native terrestrial and aquatic species, including the endangered pallid sturgeon (*Scaphirhynchus albus*), the sturgeon chub (*Macrhybopsis gelida*), sicklefin chub (*Macrhybopsis meeki*), blue sucker (*Cycleptus elongatus*), and paddlefish (Hesse et al. 1993). Cottonwood is a dominant tree species along rivers and streams throughout arid and semiarid regions of North America, and provides structural habitat for a diversity of wildlife species (Brinson et al. 1981). Therefore, identifying flows associated with the maintenance of cottonwood forests is consistent with management efforts emphasizing preservation of processes that support a diversity of riparian species (Nilsson 1992, Sparks 1995).

Complex interactions among flow regime, channel processes, and vegetation life history traits contribute to considerable apparent variability in the response of riparian vegetation to flow alteration (Pettis 1980, Johnson 1994). This apparent variability constrains the effectiveness of traditional vegetation analyses in assessing and predicting future change. Consideration of riparian vegetation in water management decisions must be balanced against competing needs for limited water and operational mandates such as flood control and power generation. In this context, flow prescriptions for cottonwoods benefit from specification of flows that maximize potential recruitment (Hughes 1994). By placing relations between flow and cottonwood establishment in a geomorphic context (Table 1), some of the observed variability of response can be explained and predictions can be improved. Demonstration of the primacy of flood deposition processes in the establishment and persistence of riparian cottonwoods within this constrained reach of the Missouri River provides a sharp focus for management prescriptions aimed at maintaining riparian cottonwoods. Protecting the frequency, timing, and duration of flows >1400 m^3/s throughout this reach is central to maintaining the current abundance and distribution of much of its cottonwood forest.

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WOODY RIPARIAN VEGETATION RESPONSE TO DIFFERENT ALLUVIAL WATER TABLE REGIMES

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ABSTRACT.—Woody riparian vegetation in western North American riparian ecosystems is commonly dependent on alluvial groundwater. Various natural and anthropogenic mechanisms can cause groundwater declines that stress riparian vegetation, but little quantitative information exists on the nature of plant response to different magnitudes, rates, and durations of groundwater decline. We observed groundwater dynamics and the response of *Populus fremontii*, *Salix gooddingii*, and *Tamarix ramosissima* saplings at 3 sites between 1995 and 1997 along the Bill Williams River, Arizona. At a site where the lowest observed groundwater level in 1996 (–1.97 m) was 1.11 m lower than that in 1995 (–0.86 m), 92–100% of *Populus* and *Salix* saplings died, whereas 0–13% of *Tamarix* stems died. A site with greater absolute water table depths in 1996 (–2.55 m), but less change from the 1995 condition (0.55 m), showed less *Populus* and *Salix* mortality and increased basal area. Excavations of sapling roots suggest that root distribution is related to groundwater history. Therefore, a decline in water table relative to the condition under which roots developed may strand plant roots where they cannot obtain sufficient moisture. Plant response is likely mediated by other factors such as soil texture and stratigraphy, availability of precipitation-derived soil moisture, physiological and morphological adaptations to water stress, and tree age. An understanding of the relationships between water table declines and plant response may enable land and water managers to avoid activities that are likely to stress desirable riparian vegetation.

Key words: groundwater, riparian habitat, Populus, Salix, Tamarix, *Arizona, root distribution.*

Although surface water flows and associated fluvial processes exert strong influences on woody riparian establishment in arid and semiarid regions (Stromberg et al. 1993, Scott et al. 1996), the alluvial groundwater and associated capillary fringe and unsaturated zone are water sources upon which many riparian plants rely for most of the year (Busch et al. 1992, Kolb et al. 1997, Snyder et al. 1998). The importance of alluvial groundwater is pronounced in intermittent or ephemeral streams and in regions with little precipitation, such as the southwestern United States (Robinson 1958, Snyder et al. 1998). The need for high water tables (often <1.5 m from the ground surface) for successful seedling establishment of woody riparian plants has been observed at numerous sites (Mahoney and Rood 1998) and experimentally demonstrated for *Populus* (Mahoney and Rood 1991, 1992, Segelquist et al. 1993). In addition, mature riparian trees and shrubs are often associated with water tables <3 m deep (Stromberg et al. 1996).

Floodplain water tables can fluctuate considerably over time, resulting from a variety of natural and anthropogenic phenomena. Natural variability in stream flow and evapotranspiration can result in intra- and interannual changes in alluvial water tables. Fluvial processes such as channel incision or bed aggradation may also cause groundwater regimes to change. Human activities such as groundwater pumping, surface flow diversion, or in-stream sand and gravel mining may lead to declines in riparian water tables (Groeneveld and Griepentrog 1985, Stromberg et al. 1992, Stromberg and Patten 1996, Kondolf 1997).

Water table declines can reduce riparian plant growth and potentially lead to mortality (Scott et al. 1999). Declines in alluvial water tables also may change the distribution and abundance of different riparian plant associations, which tend to thrive under different groundwater conditions (Bryan 1928, Stromberg et al. 1996). Of particular research and management interest are conditions influencing the relative abundance of dominant woody floodplain species, including native *Populus* and *Salix* spp. and exotic *Tamarix* spp. *Populus* and *Salix* require relatively shallow groundwater and are sensitive to drought associated with groundwater declines (Busch et al. 1992,

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Tyree et al. 1994, Smith et al. 1998, Scott et al. 1999). *Tamarix* is reported to be more tolerant of water stress than *Populus* or *Salix* (Busch and Smith 1995, Cleverly et al. 1997, Devitt et al. 1997, Smith et al. 1998), and therefore it should be able to survive where water tables are relatively deep. There are also likely critical water table depths beyond which given sized individuals of a given species cannot survive (Graf 1982).

Despite the importance of alluvial water table conditions to riparian vegetation, little is known about how established plants respond to different magnitudes, rates, and durations of groundwater decline. Quantifying plant response to changing water table conditions may result in identification of stress or mortality thresholds and hence aid efforts to manage land use and stream flow in ways that minimize impacts to groundwater and promote survival of desirable riparian species. Few studies in western riparian ecosystems have reported a plant response to measured water table declines (Condra 1944, Judd et al. 1971, Stromberg et al. 1992, Devitt et al. 1997, Scott et al. 1999). The objective of our study was to add to this sparse database by quantifying the response of 3 woody riparian species to different water table dynamics and to clarify factors that are likely to be important in determining plant response. We examined growth and survival of saplings of *Populus fremontii*, *Salix goodingii*, and *Tamarix ramosissima* at 3 sites with different groundwater regimes over a 3-yr period along the Bill Williams River in western Arizona.

STUDY AREA

The Bill Williams River drains approximately 13,700 km^2, with headwaters in the Central Highlands region of central Arizona at approximately 1830 m, and downstream reaches in the Sonoran Basin and Range Province in west central Arizona. Beginning at the confluence of the Big Sandy and Santa Maria rivers, the Bill Williams River flows for approximately 70 km. The upstream-most 6.5 km now consists of waters impounded behind Alamo Dam, which was completed in 1968. Downstream of the dam the Bill Williams River flows 63 km to its confluence with the Colorado River (now Lake Havasu) at an elevation of 137 m. Variation in the depth of alluvium results in a mix of reaches with perennial and seasonally intermittent flow. Average annual precipitation along the river ranges from approximately 22 cm near Alamo Dam (National Climatic Data Center stations; Alamo Dam 6ESE and Alamo Dam) to 13 cm near the Colorado River (National Climatic Data Center station; Parker 6NE). Mean annual flow in the Bill Williams River is approximately 3.5 m^3 s^{-1} (1941–1996; U.S. Geological Survey Gaging Station #09426000). Flow regulation by Alamo Dam has dramatically reduced flood peaks and in recent years has increased low flows (Shafroth et al. 1998). Riparian vegetation along the Bill Williams River is dominated by several woody species common to low-elevation southwestern riparian ecosystems, including *Populus fremontii* S. Watson (Fremont cottonwood), *Salix gooddingii* Ball (Goodding willow), *Tamarix ramosissima* Ledebour (saltcedar), *Baccharis salicifolia* (R. & P.) Pers. (seep willow), and *Prosopis* spp. (mesquite).

METHODS

In April 1995 we selected 8 sites along the Bill Williams River as part of a larger study (Shafroth et al. 1998). The sites were subjectively selected to represent a range of geomorphologic and vegetative conditions. For the present study we examined 3 of these sites (BW1, BW5, BW7). At each site a cross-valley transect was established perpendicular to the stream channel, and different patches of vegetation were identified along the transect based on a combination of overstory dominance and geomorphologic setting. For this study we examined patches that contained seedlings and saplings of *Populus*, *Salix*, and *Tamarix* that became established between 1993 and 1995 (age determined by counts of annual rings; Shafroth et al. 1998). Seedling patches were those containing plants that became established in 1995, saplings in 1993–94. The number of seedling and sapling patches per transect was variable and included 2 patches along BW1 and 4 patches along BW5 and BW7. Within each patch we randomly located a 5 × 20-m quadrat and in January 1996 measured the diameter of all saplings in the quadrat. During summer 1996, wilting, chlorosis, and apparent shoot mortality of woody plants were observed at 1 of the sites (BW5). To quantify the response, we resampled stem densities in the 2 sapling quadrats at BW5 in October

1996. In December 1997 these sapling quadrats were again resampled and 2 quadrats containing 1995 cohorts were also sampled. In December 1997 quadrats with plants of the same age as those at BW5 were also resampled at 2 other sites (BW1, BW7) that had groundwater dynamics different from those at BW5. At each site a representative *Populus fremontii* sapling was excavated in December 1997, its root distribution sketched, and the soil stratigraphy of the excavated pit described.

Sandpoint wells were installed at each site in April 1995 and used to measure the depth to groundwater approximately monthly through October 1997. To obtain relative elevations of the quadrats and monitoring wells, we surveyed the topography of each transect in January 1996. Soil samples were collected from 2 depths at each quadrat: 0–30 cm and 30–60 cm below ground surface. The proportion of each sample in 5 particle size classes was determined by (1) visual estimation in the field for particles >2 cm median dimension, (2) sieving for particles >2 mm and <2 cm, and (3) hydrometer method for sand, silt, and clay (Day 1965). Electrical conductivity (dS m^{-1}) of the filtered solution from a 1:1 soil:water slurry was determined with a Beckman Instruments conductivity probe.

Groundwater level measurements were summarized as follows: measured depths through time, maximum depth to the water table for each year, and difference between the deepest water table level in 1995 and deepest levels in 1996 and 1997. Changes in stem density and basal area between January 1996 and December 1997 were calculated and expressed as percentages of the January 1996 measurements. To assess correlations between plant response and groundwater level change, we conducted simple linear regression analysis with change in stem density and basal area for both *Populus/Salix* and *Tamarix* as dependent variables and change in groundwater level as the independent variable.

RESULTS

At site BW1 the water table had regular intra-annual fluctuations, with observed differences between annual high and low water tables ranging from 1.51 to 2.10 m (Fig. 1a). The maximum depth to water where saplings at BW1 survived was –2.91 m. The lowest water table levels in 1996 (–2.55) and 1997 (–2.91) were 0.44 and 0.80 m deeper than the lowest water table level in 1995. Soil texture at BW1 ranged from strata containing principally coarse and medium sands to strata with large quantities of organic material and silt (Fig. 1b). Electrical conductivity ranged from 0.7 to 1.6 dS m^{-1}. At BW1 the 1997 rooting depth was approximately –1.40 m, where a flare of roots spread atop a soil layer rich in organic material and silt (Fig. 1b). Coarse roots also occurred at other locations throughout the soil column. Because of large fluctuations in the water table, most roots were inundated for part of the year and were well above the water table at other times.

At BW1 *Populus* and *Salix* sapling densities declined 88–89% between January 1996 and December 1997. However, basal area of these species increased 110–160% over the same period. *Tamarix* stem density at BW1 decreased 50%, while its basal area increased 16%. In December 1997 the mean ± $s_{\bar{x}}$ density of *Populus/Salix* and *Tamarix* was 70 ± 55 and 28 ± 23 stems 100 m^{-2}, respectively ($n = 2$). The mean ± $s_{\bar{x}}$ basal area was 3.46 ± 2.64 cm^2 100 m^{-2} for *Populus/Salix* and 3.23 ± 3.07 cm^2 100 m^{-2} for *Tamarix* ($n = 2$).

At site BW5 the water table was relatively high and stable throughout 1995 (ca –0.80 m), but the lowest water tables in 1996 and 1997 were 1.11 and 2.28 m deeper than in 1995 (Fig. 2a). Quadrats containing saplings at this site were 1.55–1.97 m and 2.72–3.14 m above the lowest water table in 1996 and 1997, respectively. Soils at BW5 primarily comprised sands and secondarily gravels (Fig. 2b); electrical conductivity ranged from 0.3 to 1.5 dS m^{-1}. At BW5 the excavated sapling was rooted to a depth of –0.65 m in 1997, and the majority of root biomass was distributed between –0.45 and –0.60 m (Fig. 2b), or 0.14–0.41 m above the high water tables observed between 1995 and 1997.

Populus and *Salix* saplings at BW5 experienced a 92–100% reduction in stem density between January and October 1996. By December 1997 no *Populus* or *Salix* individuals were alive in the quadrats, and only scattered, older trees survived in the transect vicinity. In the 2 sapling quadrats at BW5, *Tamarix* stem density declined 0–13% by October 1996. By December 1997 stem density in 1 quadrat increased by 105%, while in the other it

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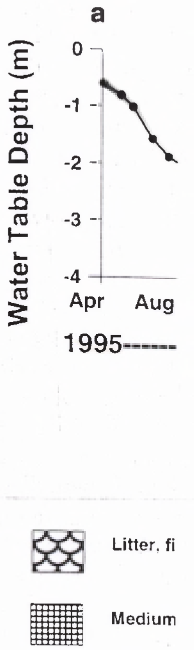

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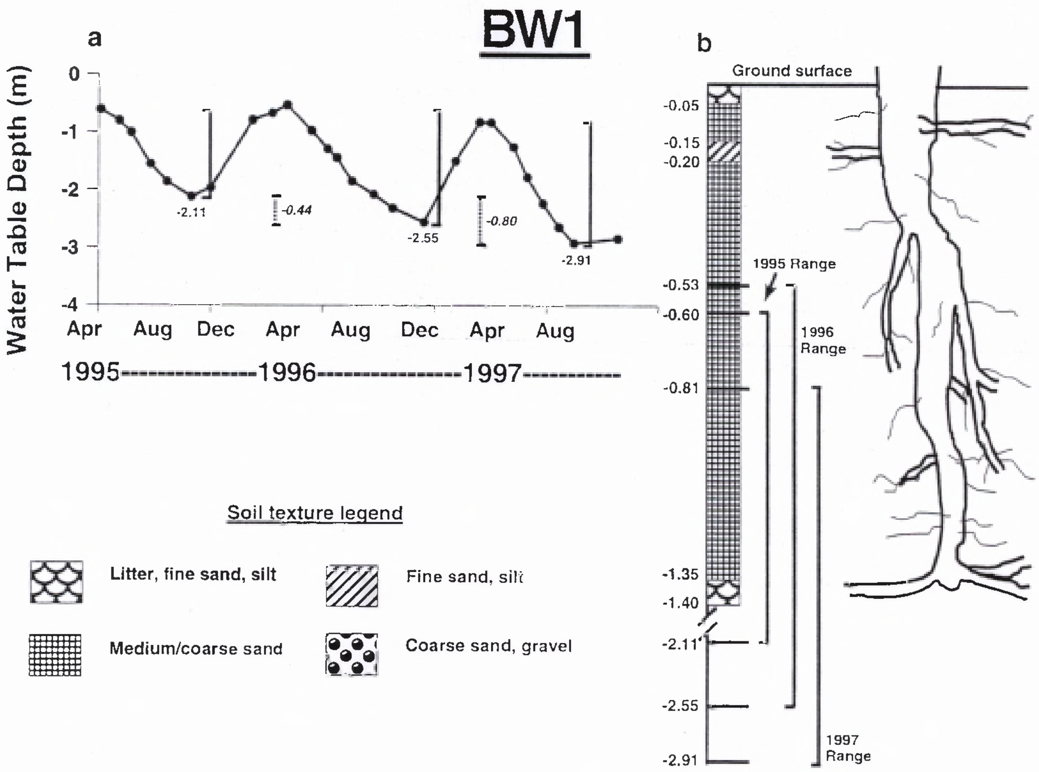


Fig. 1. Groundwater dynamics and *Populus fremontii* sapling root architecture at site BW1, Bill Williams River, Arizona: **a**, BW1 water table levels, measured approximately monthly from April 1995 through October 1997. Solid vertical bars depict annual water table level range, with lowest observed water table depth noted below the bar. Hashed vertical bars depict water table decline, defined as the difference between lowest observed water table depth in 1995 and lowest observed in 1996 and 1997. **b**, Root architecture of a *Populus fremontii* sapling at site BW1. Annual water table level range is shown for years 1995–1997. Also shown is the soil profile where the sapling was excavated.

decreased to 48% of the January 1996 level. Basal area of *Tamarix* in 1997 increased 300% in 1 quadrat and decreased 33% in the other, though the absolute changes were small. By December 1997 only *Tamarix* survived at relatively low stem densities and basal area. Its mean ± $s_{\bar{x}}$ density was 55 ± 39 stems 100 m^{-2}, and mean ± $s_{\bar{x}}$ basal area was 0.57 ± 0.48 cm^2 100 m^{-2} (n = 4).

The water table at site BW7 was high and stable throughout the study period (ca –0.40 m), except for a decline of 0.66 m in June and July 1997 (Fig. 3a). Even with this drop, the water table was relatively high and was only 0.44 m lower than the lowest water table in 1995 (–0.38 m) and no more than 0.82 m below the ground surface of a quadrat containing saplings. Soil texture at BW7 was the coarsest, with the proportion of gravel almost equal to that of sand in most samples. Soil electrical conductivity ranged from 0.2 to 0.5 dS m^{-1}. At BW7 roots were much shallower, reaching a depth of only –0.20 m (Fig. 3b), always within 0.12 m of the annual high water table level. Where excavated, these roots were of large diameter and had spread laterally.

At BW7 only *Salix* and *Tamarix* were present in the sapling quadrats. Stem density of *Salix* decreased 57%, while *Tamarix* stem density varied from a 48% decrease to a 400% increase. *Salix* basal area increased 201%, while *Tamarix* basal area increased 43–78%. The December 1997 mean ± $s_{\bar{x}}$ density of *Salix* and *Tamarix* was 27 ± 18 and 176 ± 83 stems 100 m^{-2}, respectively (n = 4). For *Salix* the mean ± $s_{\bar{x}}$ basal area was 10.58 ± 4.94 cm^2 100 m^{-2} and for *Tamarix* it was 2.87 ± 1.14 cm^2 100 m^{-2}.

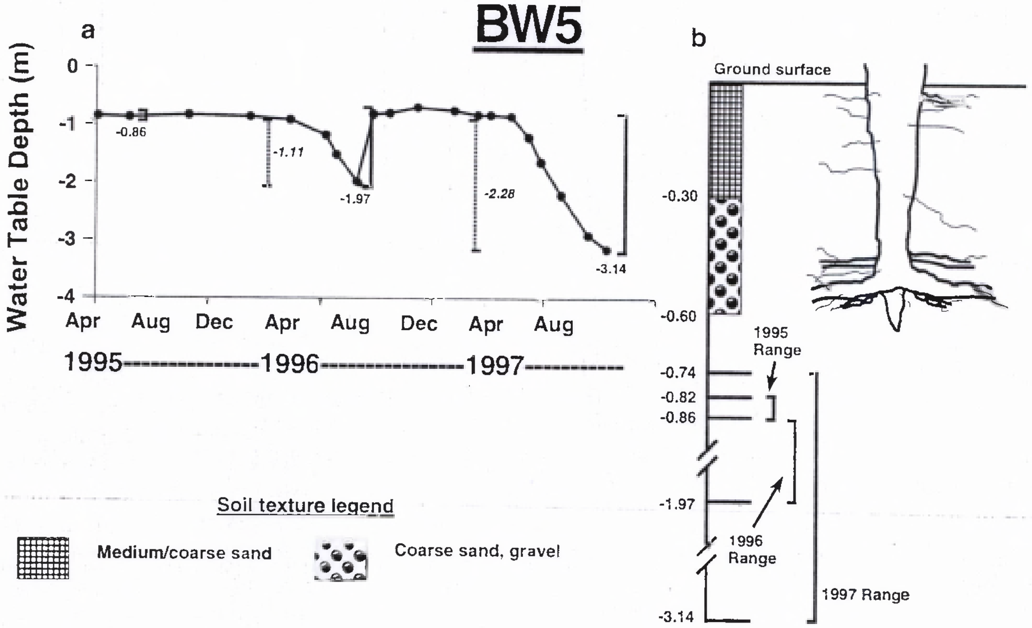


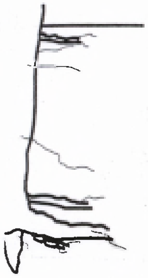
Fig. 2. Groundwater dynamics and *Populus fremontii* sapling root architecture at site BW5, Bill Williams River, Arizona. Details of a and **b** are as described in Figure 1.

Change in stem density between sampling dates decreased in linear fashion with the change in water table depth (defined as the maximum annual decline from the lowest water table level observed in 1995) for *Populus* and *Salix* (Fig. 4a, $r^2 = 0.65$, $P = 0.05$, df error = 4), but not for *Tamarix* (Fig. 4c, $r^2 = 0.04$, $P = 0.74$, df error = 3). Stem density of *Populus* and *Salix* decreased in all sampled quadrats (Fig. 4a), whereas *Tamarix* stem density increased in some quadrats (Fig. 4c). Change in basal area was also negatively correlated with change in water table depth for *Populus* and *Salix* (Fig. 4b, $r^2 = 0.99$, $P < .01$, df error = 4), but not for *Tamarix* (Fig. 4d, $r^2 = 0.12$, $P = 0.56$, df error = 3). Basal area of *Populus* and *Salix* increased between January 1996 and December 1997, except at BW5 where all plants died (Fig. 4b). Basal area of *Tamarix* increased in 4 of 5 measured quadrats between January 1996 and December 1997 (Fig. 4d).

DISCUSSION

Almost complete mortality of *Populus* and *Salix* saplings was observed following a groundwater decline of 1.11 m (from lowest level in 1995 to lowest level in 1996) in soils composed largely of sand and gravel, and complete mortality followed a decline of 2.28 m in the subsequent year (from lowest level in 1995 to lowest level in 1997; site BW5). Where groundwater declines were smaller, decreases in *Populus* and *Salix* density were smaller and basal area increased. In contrast to *Populus* and *Salix*, some *Tamarix* individuals survived under all conditions and basal area increased in 80% of the measured quadrats. Decreases in stem density are typical as a stand of young trees ages and, except where complete mortality is observed, should be interpreted in conjunction with basal area measurements. For example, where plots were subjected to a groundwater change of 0.44–0.80 m, *Populus* and *Salix* density decreased 52–89% but basal area *increased* 200–300% (Figs. 4a, 4c).

These results are consistent with previous studies that documented lethal effects of groundwater declines on *Populus*, but not on *Tamarix*. Scott et al. (1999) observed high mortality of mature *Populus deltoides* ssp. *monilifera* trees in eastern Colorado following a sustained groundwater decline of 1.12 m, and reduced branch growth where water tables declined by 0.47 m. Condra (1944) reported mortality of shallow-rooted *Populus*, *Fraxinus*,



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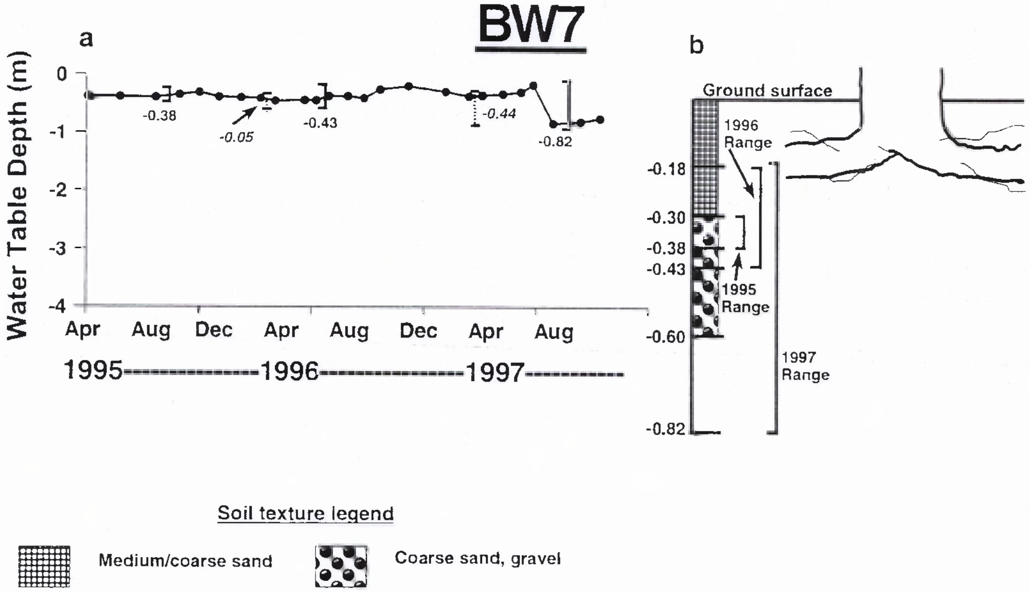

Fig. 3. Groundwater dynamics and *Populus fremontii* sapling root architecture at site BW7, Bill Williams River, Arizona. Details of a and b are as described in Figure 1.

and *Acer negundo* trees along the Platte River following water table declines of 0.61–0.91 m in coarse soils. Two-year-old *Tamarix* survived a water table decline (0.9 m) that stranded roots above moist soil for 30 d; roots resumed growth immediately following rewetting (Devitt et al. 1997). Differential survival of *Tamarix* vs. *Populus/Salix* at site BW5 corroborates reports that greater tolerance of water stress can lead to *Tamarix* dominance on relatively dry, riparian sites (Smith et al. 1998, Stromberg 1998).

Results of this study suggest the importance of *change* in groundwater depth relative to a previous condition or pattern as opposed to the absolute depth to the water table. For example, saplings at site BW1 survived where the depth to the alluvial water table was −2.91 m and their basal area increased, whereas almost no saplings at site BW5 survived at water table depths of −1.55 to −1.97 m (1996), and none survived where water table depths were −2.72 to −3.14 m (1997). By contrast, the change in water table was 1.11 m (1996) and 2.38 m (1997) at BW5 vs. 0.48 m (1996) and 0.8 m (1997) at BW1. Water content of *Tamarix* cladophylls did not vary on plants growing at sites with different depths to the water table in New Mexico (range of ca 1–3 m; Wilkinson 1972). However, studies of *Prosopis velutina* in southwestern riparian ecosystems suggest that the absolute water table depth may effectively determine the expression of various physiological and morphological traits (Stromberg et al. 1992). At 2 sites along the Bill Williams River, Busch and Smith (1995) reported that leaf number, leaf area, specific leaf area, and stem elongation of *Populus fremontii* were greater at the site with relatively high and stable water tables.

We propose that the importance of change from a previous groundwater depth is due to the influence of groundwater history on root architecture. Root architecture has been shown to be a function of soil moisture conditions and water table depth in *Populus* and *Salix* in Nebraska (Sprackling and Read 1979) and *Tamarix* in Arizona (Gary 1963). At site BW1, where relatively large fluctuations in groundwater levels are the norm, *Populus* saplings were rooted relatively deeply, with a somewhat broad depth distribution of coarse roots. At sites BW5 and BW7, roots were distributed largely in a flare above, but near, the annual high water table, suggesting that water tables were stable in the early years of plant growth. When groundwater levels dropped in 1996 and

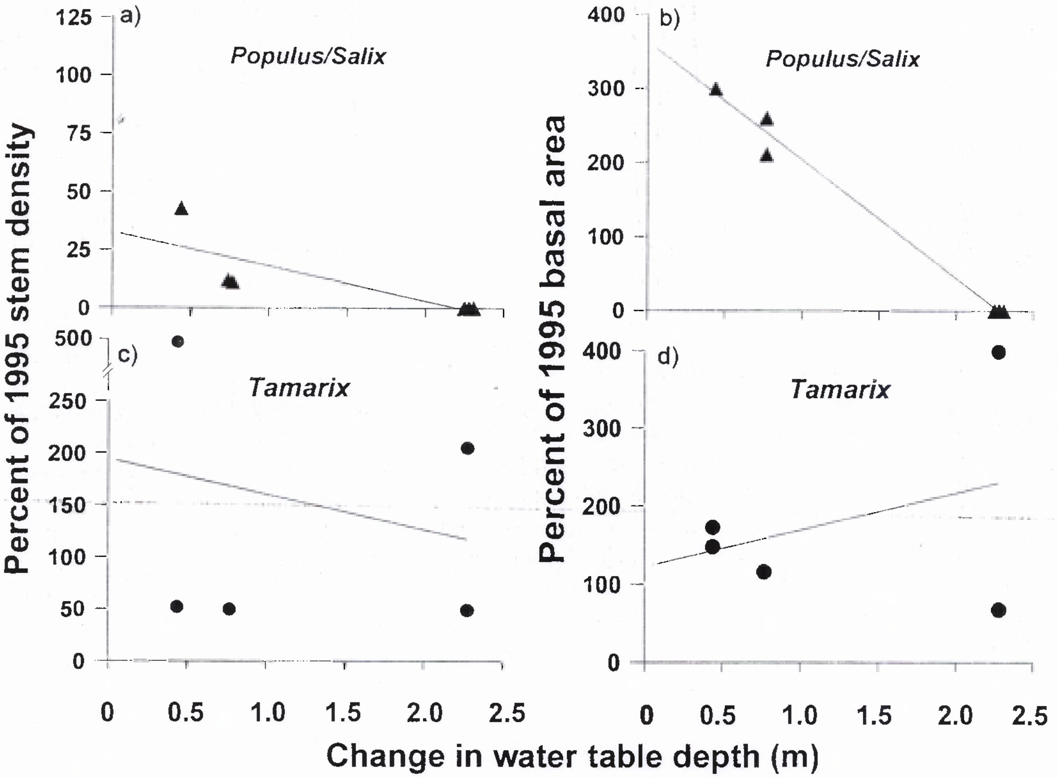

Fig. 4. Change in stem density and basal area of stands of saplings as a function of change in annual low water table level. Lines are from linear regression analysis: **a**, stem density of *Populus* and *Salix*; density change = 32.8–14.9* (water table change; $r^2 = 0.65$, $P = 0.05$, df error = 4); **b**, basal area of *Populus* and *Salix*; basal area change = 362.6–159.2* (water table change; $r^2 = 0.99$, $P < .01$, df error = 4); **c**, stem density of *Tamarix*; density change = 194.0–33.9* (water table change; $r^2 = 0.04$, $P = 0.74$, df error = 3); **d**, basal area of *Tamarix*; basal area change = 122.5 + 46.8 (water table change; $r^2 = 0.12$, $P = 0.56$, df error = 3).

1997 at BW5, roots apparently were stranded well above the water table, resulting in shock to the plants.

Plant response to water table level change is mediated by soil water retention, which is largely a function of soil texture and stratigraphy. Trees growing in finer-textured soils may survive greater water table changes than trees growing in coarser soils (Condra 1944). Cooper et al. (1999) have noted the importance of fine-textured soils for the survival of *Populus* seedlings that have not yet tapped the alluvial water table. Stratification of the soil profile may result in retention of significant quantities of water where a finer-textured layer lies above a coarse layer (Brady 1990). This effect may explain how saplings at site BW1 survived with their deepest roots more than 1.5 m above the lowest water table, as many of these roots are located at a layer of fine sediments and organic matter which likely retains excess water even when the water table has dropped to a lower level (Fig. 1). Water retained above a clay lens at a site in the Carmel River valley, California, apparently enabled trees to maintain relatively vigorous growth, despite a groundwater change in excess of 2.5 m (J.G. Williams personal communication; Fig. 5). Relatively little water can be retained in coarser soils found at BW5, which likely contributed to mortality observed there. Textural differences alone do not determine water availability, however, and better estimates can be obtained with measures of soil water potential.

Species differences in morphological and physiological above- and belowground adjustments to reduced soil moisture should result

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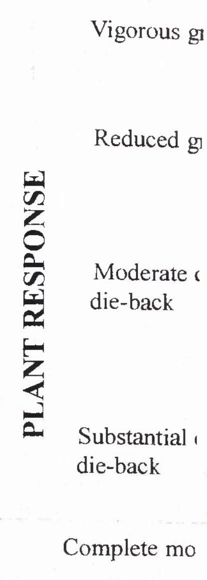

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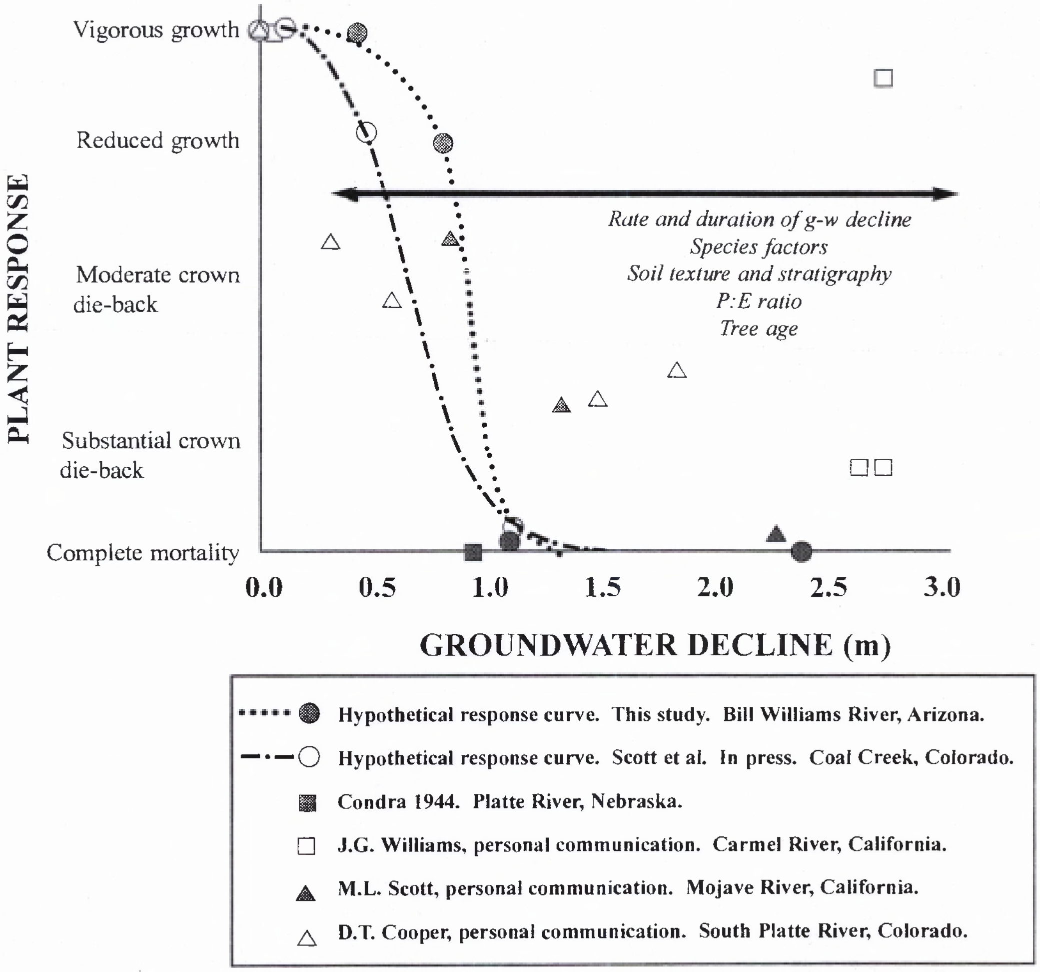

Fig. 5. Conceptual model of woody riparian plant response to water table decline. Plant response (y-axis) scale is semi-quantitative and represents a gradient of growth and morphological responses. Position of plotted points on y-axis is estimated. Groundwater decline (x-axis) refers to a change in groundwater from a previous, presumably consistent, condition or dynamic. All plotted points are responses of either *Populus* or *Salix* spp. Lines are hypothetical response curves for data from this study and another. In this conceptual model hypothetical response curves would shift position along the x-axis and their slopes could be altered, depending on different combinations of groundwater decline rate and duration, species, soil texture, precipitation:evaporation ratio, and tree age.

in differential survival or growth following a groundwater decline. At site BW5, some *Tamarix* individuals survived and increased in size, whereas all *Populus* and *Salix* died. Devitt et al. (1997) reported *Tamarix* survival following a depth and duration of water table decline similar to that observed at BW5. *Tamarix* has been shown to have greater water-use efficiency than *Populus* or *Salix* and can maintain high rates of photosynthesis at relatively low water potentials (Busch and Smith 1995, Cleverly et al. 1997), whereas *Populus* is vulnerable to cavitation at relatively high water potentials (Tyree et al. 1994). Additionally, whereas *Populus* and *Salix* may reduce leaf area in response to dry conditions (Smith et al. 1991, Busch and Smith 1995), *Tamarix* can maintain high leaf areas under these conditions (Sala et al. 1996, Cleverly et al. 1997). The ability of plants to grow new roots to respond to groundwater declines is not well understood but would likely be effective only where water table changes are gradual (Groeneveld and Griepentrog 1985, Mahoney and Rood 1991, Segelquist et al. 1993).

Species differences in dependence on groundwater may influence response to water table declines. Plants that rely on precipitation-derived soil water for some of their water supply (facultative phreatophytes) may experience a reduction only in leaf area or crown volume in some situations that are lethal to plants that must maintain root contact with the groundwater or capillary fringe (obligate phreatophytes). Similarly, facultative phreatophytes should be able to survive a given water table decline for a longer duration than obligate phreatophytes. There appears to be mixed evidence in the literature for the phreatophytic status of *Populus*, *Salix*, and *Tamarix*. There is some evidence that *Tamarix* is a facultative phreatophyte (Busch et al. 1992), although it has been observed to use only groundwater where this was readily available (McQueen and Miller 1972). *Populus fremontii* on the Bill Williams River has been shown to be dependent on groundwater (Busch et al. 1992), though it may be considered a facultative phreatophyte when including the full range of its growing sites (McQueen and Miller 1972, Snyder et al. 1998). *Salix gooddingii* has been reported to be an obligate phreatophyte (McQueen and Miller 1972, Busch et al. 1992), although it is apparently more drought tolerant than *P. fremontii* (Busch and Smith 1995).

Climatic variables such as precipitation, temperature, and humidity will also influence plant response to water table decline. The degree to which plants use precipitation-derived soil water depends in part on reliability and quantity of precipitation and is therefore probably more common in regions or at elevations with higher precipitation. Detrimental effects of water table declines may be mitigated where precipitation occurs and plants have roots near the surface. Climatic factors are also important determinants of transpirational demand (via temperature, humidity). Consequently, in especially hot and dry settings such as low-elevation sites in western Arizona, the lethal duration of water table decline of a given magnitude is likely to be much shorter than at sites where plants can utilize precipitation and where lower temperatures and more humid conditions result in lower transpirational demand.

CONCLUSIONS

The impact of a particular water table decline depends on several interacting factors that influence both water uptake and water demand. These factors include magnitude of groundwater decline relative to the pre-decline distribution of roots, rate of decline, duration of decline, ability of soil to retain water following the decline, ability of the plant to grow new roots to adjust to lowered water table, ability of the plant to adjust water demand (e.g., via physiological and morphological adaptations), plant age and size, transpirational demand, and importance of other sources of water (e.g., precipitation) to the overall plant water supply. We synthesize these variables into a conceptual model of woody riparian plant response to water table decline in Figure 5. We have drawn hypothetical response curves for our data and another study (Scott et al. 1999) that span the plant response range from vigorous growth to complete mortality. The basic shape of these curves may apply to other situations and species, but the position on the *x*-axis and the slope of the response curves may vary depending upon the particular combination of rate and duration of groundwater decline, species attributes, soil texture and stratigraphy, climate and tree age (Fig. 5).

Future research incorporating more of the variables discussed above would provide a better understanding of how particular magnitudes, rates, and durations of alluvial groundwater decline will influence woody riparian vegetation in arid and semiarid regions. Such research could have important management implications. For example, on the Bill Williams River, flows from Alamo Dam upstream of our sites could be managed to promote survival of desirable species. This could be accomplished by intentionally varying flows in early years following an establishment event to promote deeper root growth and hence less vulnerability to lower water tables during inevitable dry periods. Another stream flow management option would be to release a mid- to late-summer pulse to resaturate the soil column and raise water tables. Such summer pulses commonly occurred prior to the construction of Alamo Dam in association with monsoonal

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precipitation, but they have been virtually eliminated since completion of the dam. Other human activities that impact alluvial water table levels throughout western North America such as groundwater pumping and sand and gravel mining could be managed to ensure that water tables do not fall at rates and magnitudes likely to kill existing stands of riparian vegetation.

ACKNOWLEDGMENTS

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RIPARIAN VEGETATION RESPONSE TO ALTERED DISTURBANCE AND STRESS REGIMES

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Abstract. River damming and flow regulation can alter disturbance and stress regimes that structure riparian ecosystems. We studied the Bill Williams River in western Arizona, USA, to understand dam-induced changes in channel width and in the areal extent, structure, species composition, and dynamics of woody riparian vegetation. We conducted parallel studies along a reference system, the Santa Maria River, an unregulated major tributary of the Bill Williams River. Flood magnitude on the Bill Williams River has been dramatically reduced since the closure of Alamo Dam in 1968: the 10-yr recurrence interval flood in the pre-dam era was 1397 m^3/s vs. 148 m^3/s post-dam. Post-dam average annual flows were higher due to increased precipitation in a few years, but increases in post-dam May–September flows are largely attributable to dam operation. An analysis of a time series of aerial photographs showed that channels along the Bill Williams River narrowed an average of 111 m (71%) between 1953 and 1987, with most narrowing occurring after dam closure. Multiple regression analysis revealed significant relationships among flood power, summer flows, intermittency (independent variables), and channel width (dependent variable). The pattern of channel width change along the unregulated Santa Maria River was different, with less narrowing between 1953 and 1987 and considerable widening between 1987 and 1992. Woody vegetation along the Bill Williams River was denser than that along the Santa Maria River (27 737 stems/ha vs. 7559 stems/ha, $P = 0.005$), though basal areas were similar (14.3 m^2/ha vs. 10.7 m^2/ha, $P = 0.42$). Patches dominated by the exotic *Tamarix ramosissima* were marginally ($P = 0.05$) more abundant along the Bill Williams River than along the Santa Maria River, whereas the abundance of patches dominated by the native *Populus fremontii* or *Salix gooddingii* was similar across rivers ($P = 0.30$). Relative to *Populus* and *Salix*, *Tamarix* dominates floodplain vegetation along the Bill Williams River ($P < 0.0001$). Most stands of the dominant pioneer trees on both rivers became established in the 1970s and 1980s. Recent seedling establishment occurred in wider bands along the Santa Maria River (15.3 m wide vs. 5.4 m wide on the Bill Williams River, $P = 0.0009$), likely due to larger floods and associated seedbed formation along the Santa Maria River. Seedling survival rates were generally higher along the Bill Williams River, perhaps due to higher summer flows.

Key words: channel narrowing; disturbance; plant invasion; Populus; *riparian vegetation;* Salix; *seedling establishment; species composition; streamflow regulation; stress;* Tamarix; *vegetation structure.*

INTRODUCTION

Physical disturbance and environmental stress play central roles in determining the spatial and temporal dynamics of a variety of plant communities (Grime 1979, White 1979, Pickett and White 1985, Osmond et al. 1987). The principal disturbance and stresses influencing riparian vegetation in arid and semiarid regions are associated with streamflow. Disturbance by large floods influences the establishment (Stromberg et al. 1991, Hughes 1994, Scott et al. 1997), mortality (Schumm and Lichty 1963, Stromberg et al. 1997), and patch structure (Salo et al. 1986, Friedman et al. 1996) of riparian vegetation. Drought stress associated with periods of low flow influences plant survival (Albertson and Weaver 1947, Stromberg and Patten 1992, Rood et al. 1995), growth (Reily and Johnson 1982, Stromberg and Patten 1991), and species composition (Zimmerman 1969, Busch and Smith 1995, Stromberg et al. 1996).

Dams often have profound effects on patterns of streamflow (Dynesius and Nilsson 1994, Graf 1999), thereby changing disturbance and stress regimes. These effects can be especially pronounced in arid and semiarid settings where natural flow is highly variable (Davies et al. 1994) and reservoir storage capacity is large (Graf 1999). Responses of riparian vegetation to dam-induced flow changes have been studied in some semiarid systems (cf. Williams and Wolman 1984, Friedman et al. 1998), but questions remain regarding the timing

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and nature of response and the resulting areal extent, structure, species composition, and dynamics of vegetation. Studies of channel and vegetation changes downstream of dams can reveal impacts of dams on physical and biological systems and can further our knowledge of general relationships between streamflow and riparian vegetation and the effects of altered disturbance and stress regimes on native and exotic plant populations (D'Antonio et al. 1999). These insights may improve management and restoration of downstream ecosystems (Stanford et al. 1996, Poff et al. 1997).

The effects of dams on the areal extent of downstream vegetation and the character of stream channels vary among rivers, reflecting complex interactions between regulated flows and the fluvial geomorphic setting (Petts 1979, Williams and Wolman 1984, Johnson 1998). Along braided channels, a reduction in flood magnitude and associated disturbance effects often cause channel narrowing and an increase in riparian vegetation that colonizes the former channel bed (Williams and Wolman 1984, Johnson 1994, Friedman et al. 1996, 1998). Along meandering channels, reductions in flood magnitude may result in reduction of both channel migration and pioneer species recruitment (Johnson et al. 1976, Bradley and Smith 1986, Friedman et al. 1998).

The rate and nature of channel and vegetation response to flow regulation should differ between perennial and intermittent or ephemeral reaches, though these nonperennial systems have not been well studied. Ephemeral and intermittent streams and reaches are characterized by higher flow variability (Davies et al. 1994) and deeper and more variable water tables than perennial counterparts (Stromberg 1998*a*, Shafroth et al. 2000), both of which tend to retard vegetation development (Zimmerman 1969, Stromberg 1998*a*). In a dry climate, annual or seasonal reductions in streamflow resulting from flow regulation can similarly reduce the areal extent of riparian vegetation (Stromberg and Patten 1992, Rood et al. 1995). Conversely, flow increases from reservoirs during normally dry seasons can increase the extent of riparian vegetation (Nadler and Schumm 1981).

Effects of dams on the extent, survival, and growth of vegetation should be reflected in within-patch structural metrics such as stem density and basal area. Vegetation structure can have important feedbacks, influencing future susceptibility to disturbance. For example, high-density vegetation is more resistant to flow than low-density vegetation, resulting in decreased flow velocities and increased sedimentation, both of which may reduce the disturbance effects of future floods. Dense vegetation and the accumulation of litter have been implicated in promoting fire in southwestern U.S. riparian ecosystems (Busch 1995). Finally, changes in vegetation structure associated with dams are likely to affect wildlife use, especially in arid and semiarid riparian forests (Ohmart and Anderson 1982, Saab 1999).

Alteration of disturbance and stress regimes may influence the species composition of plant communities. Of particular interest in riparian systems of the southwestern United States is the abundance of the exotic shrub *Tamarix ramosissima* relative to native trees in the genera *Populus* and *Salix*. The widespread establishment of *Tamarix* in western North American riparian ecosystems has been attributed, in part, to flow regulation (Everitt 1998, Smith et al. 1998). Altered timing of flood events may favor *Tamarix* recruitment because it has a longer period of seed dispersal and seed viability than the native *Populus* and *Salix* spp. with which it competes (Warren and Turner 1975, Shafroth et al. 1998). Some authors have suggested that *Tamarix* is relatively intolerant of flood disturbance and extended inundation (Gladwin and Roelle 1998, Stromberg 1998*a*, but see Warren and Turner 1975) and therefore may be more abundant along regulated rivers. Compared to the native *Populus* and *Salix*, *Tamarix* is more salt tolerant (Jackson et al. 1990) and more tolerant of low soil moisture conditions (Busch and Smith 1995, Stromberg 1998*a*, Shafroth et al. 2000), which sometimes are formed by flow regulation. Few studies, however, have compared *Tamarix* populations along regulated and unregulated portions of river systems (Merritt and Cooper 2000); therefore, inferences regarding the role of flow regulation on the invasion process are weak.

Disturbance strongly influences forest stand dynamics (White 1979, Johnson 1992). The distribution of riparian forests of various successional stages often reflects the spatial and temporal variation of past flood events, as flooding tends to reset the successional cycle and promote the establishment of pioneer species (Salo et al. 1986, Stromberg 1998*a*). Changes within existing stands of riparian vegetation are strongly influenced by abiotic changes associated with overbank flooding and floodplain sedimentation (Johnson et al. 1976, Salo et al. 1986, Boggs and Weaver 1994), processes that are frequently disrupted as a consequence of flow regulation. Shifts toward later seral stages are a typical response to flood reduction (Johnson et al. 1976, Johnson 1992).

The central objective of our research was to quantify riparian vegetation and stream channel responses to altered disturbance and stress regimes resulting from dam construction and operation. In particular, we sought to determine whether changes in channel width and in the extent, structure, species composition, and dynamics of native and exotic woody riparian vegetation were related to dam-induced streamflow changes. We studied these responses along the dammed Bill Williams River, a major tributary of the lower Colorado River in western Arizona, USA. We conducted parallel studies along a reference system, the unregulated Santa Maria River, a major tributary of the Bill Williams

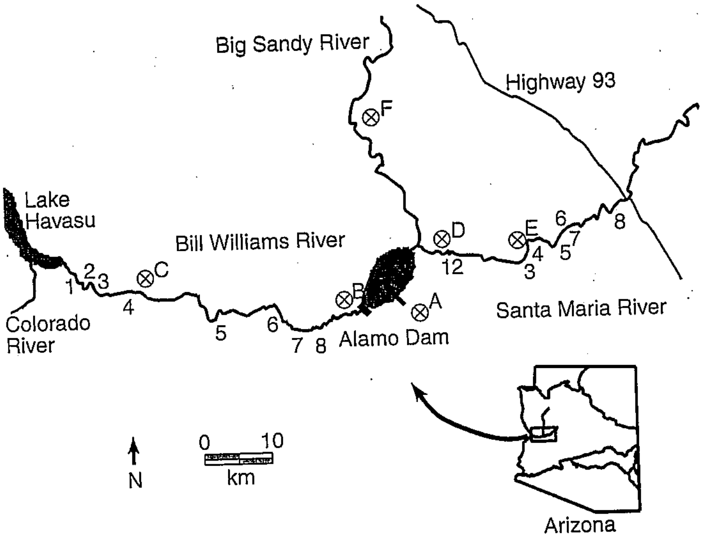

FIG. 1. Map of the Bill Williams and Santa Maria rivers, study area (Arizona, USA). Numbers along the rivers indicate study transect locations; ⊗ symols indicate locations of six former or currently operating USGS stream gages used in this study: (A) #09426000, Bill Williams River near Alamo, Arizona, 1940–1968; (B) #09426000, Bill Williams River below Alamo Dam, Arizona, 1968–present; (C) #09426500, Bill Williams River at Planet, Arizona, 1928–1941; (D) #09425500, Santa Maria River near Alamo, Arizona, 1939–1966; (E) #09424900, Santa Maria River near Bagdad, Arizona, 1967–1985, 1989–present; (F) #09424450, Big Sandy River near Wikieup, Arizona, 1966–present.

River. While we examined all woody vegetation, we focused our work on the dominant floodplain species *Populus fremontii, Salix gooddingii,* and *Tamarix ramosissima.*

Study area

The Bill Williams River drains ~13 700 km^2 in west-central Arizona, with headwaters in the central highlands of Arizona at ~1829 m and downstream reaches in the basin and range landscape of the northern Sonoran Desert. Principal tributaries are the Big Sandy and Santa Maria rivers (Fig. 1). The Santa Maria River drains ~3937 km^2, and the Big Sandy River drains ~7278 km^2 (Patterson and Somers 1966, Garrett and Gellenbeck 1991). Flow in the Bill Williams and Santa Maria rivers results principally from frontal winter rain events combined with small amounts of snow at the highest elevations, convectional monsoonal rain, which falls in late summer and early fall, and occasional tropical storms (Ely et al. 1994). Average annual precipitation in the watershed ranges from ~45 cm in the headwaters to 22 cm near Alamo Dam (National Climatic Data Center station Alamo Dam 6ESE and Alamo Dam) to 13 cm near the Colorado River (National Climatic Data Center station Parker 6NE).

Riparian vegetation along the Bill Williams and Santa Maria rivers is dominated by several woody species common to low elevation southwestern riparian ecosystems, including *Populus fremontii* S. Watson (Fremont cottonwood), *Salix gooddingii* Ball (Goodding willow), *Tamarix ramosissima* Ledebour (salt cedar), *Baccharis salicifolia* (R. & P.) Pers. (seep willow), *Prosopis* spp. (mesquite), *Tessaria sericea* (Nutt.) Coville (arrowweed), and *Hymenoclea monogyra* Torr. and Gray (burro-brush). Sonoran desertscrub dominates the uplands adjacent to the study area.

The Bill Williams River extends ~61.5 km, its upstreammost 6.5 km now consisting of water impounded behind Alamo Dam, a flood control structure that was completed in 1968 and has a reservoir storage capacity of ~1233 × 10^6 m^3. Downstream of the dam, the Bill Williams River flows 55 km with a gradient of 0.002–0.004 to its confluence with the Colorado River (Lake Havasu) at an elevation of 137 m (Fig. 1). The Bill Williams River passes through canyons interspersed with alluvial basins, including the 9.5 km long Planet Basin, a significant hydrological control on flows in the 17.7 km of river between the basin and the confluence with the Colorado River. No perennial tributaries enter the Bill Williams River downstream of Alamo Dam. Channel bed and floodplain sediments are dominated by coarse particles (81%), primarily sand (67%), and are generally low in electrical conductivity (1.0 dS/m; Shafroth 1999). Flows of 35 m^3/s and larger readily transport the poorly consolidated sand.

The study segment of the Santa Maria River extended ~42 km, from the Arizona State Highway 93 bridge crossing (elevation ~539 m above sea level [asl]) downstream to the confluence with the Big Sandy River (elevation ~341 m asl; Fig. 1). In the study segment the Santa Maria River flows through a 24-km canyon and then into a broad basin just downstream of the USGS stream gage #09424900 (Santa Maria River near Bagdad; Fig. 1). This basin extends 7 km before the valley becomes slightly more constrained for its final 11 km. No perennial tributaries enter our study segment. Channel bed and floodplain sediments are dominated by coarse particles (82%), primarily sand (59%), and are generally low in electrical conductivity (~0.5 dS/m; Shafroth 1999).

Human use is minimal in both river corridors. Although extensive alfalfa farming and associated groundwater pumping occurred within the Planet Basin historically and as recently as the early 1990s, agriculture is currently limited to a single cotton farm along a 2-km reach of the Bill Williams River. On the Bill

TABLE 1. Date, scale, location, and source of aerial photographs interpreted for this study.

Date	Scale	River	Source
July 1953	1:20 000	Bill Williams River, Santa Maria River	Soil Conservation Service
August 1964	1:34 000	Bill Williams River, Santa Maria River	U.S. Geological Survey
August 1976	1:12 000	Bill Williams River	U.S. Army Corps of Engineers
September 1976	1:24 000	Santa Maria River	Bureau of Land Management
August 1987†	1:4800	Bill Williams River, Santa Maria River	Bureau of Land Management
March 1988‡	1:7920	Bill Williams River	U.S. Fish & Wildlife Service
September 1992	1:40 000	Bill Williams River, Santa Maria River	National Aerial Photography Program
October 1996	1:4800	Bill Williams River	U.S. Army Corps of Engineers

† Photography from 1987 covered six of the Bill Williams River reaches and both of the Santa Maria River reaches.

‡ Photography from 1988 covered the two Bill Williams reaches not covered in 1987.

Williams River, cattle graze only a small area within the Planet Basin. Limited winter cattle grazing occurs along part of the Santa Maria. Feral burros are present throughout the study area, but their grazing and browsing impacts appear to be minor.

METHODS

Surface water hydrology

We used records of surface water discharge (peak instantaneous flow, average daily flow) from six U.S. Geological Survey gaging stations to summarize flood flows and average flows for periods of record before and after the completion of Alamo Dam, on both the Santa Maria and Bill Williams rivers (Fig. 1). To evaluate the effect of Alamo Dam on peak and average seasonal (October–April, May–September) flows, we compared the differences in flow between the Santa Maria (Control) and Bill Williams (Impact) rivers during the pre-dam period (Before) to those from the post-dam period (After) using *t* tests (Before-After-Control-Impact design, Stewart-Oaten et al. 1986, 1992). Because differences in streamflow between the rivers should be multiplicative (based on watershed area), we $\log_{10}$ transformed the values before conducting statistical analyses. In the rare case when flow was zero, we set the flow value to 0.001 m^3/s to enable the log transformation. We excluded the period during dam construction (March 1965–July 1968) from the analyses.

We also estimated what flow conditions would have been on the Bill Williams River in the absence of Alamo Dam using stream gages on the two principal upstream tributaries, the Big Sandy and Santa Maria rivers. We calculated the annual peak as the largest summed instantaneous flows from the Big Sandy River and the Santa Maria River for a given day within each water year. We summed the daily flows on the Big Sandy River and the Santa Maria River to estimate mean flow on the Bill Williams River. No flow data are available for the Santa Maria River for the years 1986–1988. To estimate May–September flows for these years, we developed a linear regression between mean daily flows on the Big Sandy River and those on the Santa Maria River using the years 1966–1985 and 1989–1996 (Santa Maria River May–September mean flow [in cubic meters per second] $=-0.11 + 0.94 \times$ Big Sandy May–September mean flow [in cubic meters per second]; $n = 27$, $R^2 = 0.73$, $P < 0.0001$).

Channel width and vegetation extent

We interpreted a time series of aerial photographs to quantify channel width and the areal extent, structure, and species composition of woody vegetation along the Bill Williams River. We delineated 13 cover types on mylar overlays of eight reaches (total of 29 river km) along the Bill Williams River on photographs from the years 1953 (pre-dam), 1964 (pre-dam), 1976, 1987/1988, and 1996 using a Bausch and Lomb 240 stereoscope (Bausch and Lomb, Rochester, New York, USA). We excluded the 9.5 km narrow canyon immediately downstream of Alamo Dam, the Planet Basin (9.5 km), and the 4.5 km reach immediately upstream of the confluence with the Colorado River in Lake Havasu.

Photograph dates for two Santa Maria River reaches (total of 8.2 river km) were 1953, 1964, 1976, 1987, and 1992 (Table 1). The two reaches were located within the first 10 km upstream of the confluence with the Big Sandy River. On the Santa Maria River, our analysis was limited to estimation of channel area due to the photography scale in 1992 and lack of complete sets of stereo pairs for some years. On both rivers, we distinguished reaches based on differences in valley morphology (canyon vs. alluvial basin) and seasonality of low flows (perennial vs. intermittent).

To minimize error from lens and flight angle distortion, we only interpreted features in the center of the photo (~19 × 19 cm of 23 × 23 cm). Qualitative error checking suggested that interpretation error (e.g., inaccurate delineation of patches, pen width vs. photo scale) and processing error (transfer from mylar to ARCINFO) were minor and unbiased.

The 13 cover types were hierarchical in nature; most could be collapsed into a single, combined cover type (Table 2). The combined cover types were discernable on all photos, whereas the individual cover types were only discernable on the finer scaled photos. The different geomorphic surfaces associated with cover types were based on elevation (relative to the thalweg), as visible on the aerial photography, and included (from

TABLE 2. Cover types delineated on aerial photography of the Bill Williams River, Arizona, USA, 1953–1996.

Combined cover type	Description
Channel	1) Low flow channel, including vegetated channel margins and islands. 2) Essentially bare sediment (<2% vegetated) within low floodplain.
Sparse floodplain vegetation	1) Low floodplain surface. Total cover >2% with juvenile woody plants dominant. 2) Woody vegetation on floodplain surface. Total cover 2–50%, with *Populus* and/or *Salix* dominant and other woody species subdominant. 3) Woody vegetation on floodplain surface. Total cover 2–50%, with *Tamarix* dominant and other woody species subdominant.
Dense floodplain vegetation	1) Woody vegetation on floodplain surface. Total cover >50%, with *Populus* and/or *Salix* dominant and other woody species subdominant. 2) Woody vegetation on floodplain surface. Total cover >50%, with *Tamarix* dominant and other woody subdominant.
Sparse terrace vegetation	1) Woody vegetation on high floodplain or terrace. Total cover 2–50% with *Prosopis* dominant. 2) Woody vegetation on high floodplain or terrace. Total cover 2–50% with xeric riparian shrub species (e.g., *Hymenoclea monogyra, Tessaria sericea, Atriplex* sp., *Lycium* sp.) dominant.
Dense terrace vegetation	1) Woody vegetation on high floodplain or terrace. Total cover >50% with *Prosopsis* dominant. 2) Woody vegetation on high floodplain or terrace. Total cover >50% with xeric riparian shrub species (e.g., *Hymenoclea monogyra, Tessaria sericea, Atriplex* sp., *Lycium* sp.) dominant.
Bare or cultivated terrace	1) Essentially bare sediment (<2% vegetated) on high floodplain or terrace. 2) Cultivated land.

Note: "Combined cover types" were visible on all sets of aerial photographs and were created by combining cover types that occurred on similar surfaces and with the same range of total cover, but without particular species identified.

lowest to highest relative elevation) channels, floodplains, and terraces.

To obtain digital images we scanned the mylar overlays using a UMAX Astra 1200S scanner (UMAX, Fremont, California, USA) at a resolution of 600 dpi. We transferred the digital images to ARCINFO version 7.1.1 (Environmental Systems Research Institute, Redlands, California, USA), assigned a cover type to each delineated polygon, and calculated the area of cover types. We conducted paired t tests on the difference in the average pre-dam vs. post-dam proportions for each of the seven combined cover types.

We determined average channel width for every reach-year. First, we estimated the photographic scale within each reach-year by comparing the total reach area to the same region on a 1:24 000 U.S. Geological Survey 7.5 min topographic map. We then calculated the area (in square meters) of the reach occupied by the "channel" combined cover type (Table 2) and divided this area by the stream length (in meters) through the reach to obtain channel width (in meters).

To assess the relationship between channel width and flood flows (disturbance) and summer flows (drought stress), we conducted a multiple regression analysis relating channel width to three independent variables: maximum flood power, summer low flow, and seasonal intermittency. To meet the assumption of homoscedasticity, we $\log_{10}$ transformed the dependent variable, channel width. We used SAS version 8.01 for this and all other statistical analyses (SAS 1999), except where specified. We applied the regression coefficients to the reconstructed values of flood power and low flow frequency under unregulated conditions (Fig. 5) to estimate channel width in the absence of Alamo Dam.

We determined maximum total flood power (Ω) within five years of the date of each photo for each reach using the equation: $\Omega = \rho g Q S$ in watts per meter, where ρ is the density of water in kilograms per cubic meter, g the acceleration due to gravity in meters per square second, Q the maximum instantaneous discharge within 5 yr of the photograph date, and S the dimensionless energy slope for which we substituted the bed slope measured on 1:24 000 topographic maps. Flow values for the upstream-most six reaches were determined from USGS gage #09426000, (Alamo gage, Fig. 1). Gaging records indicate that peak flows are somewhat attenuated downstream of Planet Basin. Therefore, we developed a linear regression between a former gage just downstream of Planet Basin (gage #09426500) and the Alamo gage to estimate the peak flow values for the study reaches downstream of Planet Basin: flow at Planet Basin (in cubic meters per second) = −2.136 + 0.86 × (flow at Alamo [in cubic meters per second]); $n = 350$, $R^2 = 0.96$, $P < 0.0001$.

We used average flow from 1 May to 30 September in the regression model because riparian vegetation in the Sonoran Desert typically exhibits symptoms of drought stress during these months. Because there is some reach-to-reach variation in low flow, the final independent variable in the regression model was a binary classification of each reach as either intermittent or perennial, which we determined based on the presence or absence of flow on those aerial photo dates that were taken during low flows and on our knowledge of this factor from numerous site visits during the years 1995–1997.

Vegetation structure and species composition

To address the effects of Alamo Dam on vegetation structure and species composition, we sampled woody vegetation along 16 relocatable transects, 8 on the Bill Williams River and 8 on the Santa Maria River (Fig. 1). We chose the transects to represent typical geomorphic (e.g., bottomland morphology, particle sizes), hydrologic (e.g., perennial vs. intermittent flow), and vegetative conditions present along the rivers. We excluded sites that had obviously been cultivated in recent decades.

We sampled transects on the Bill Williams River between January and March of 1996 and on the Santa Maria River between September 1996 and April 1997. Each transect was oriented perpendicular to the low flow channel and extended from valley wall to valley wall. We subdivided transects into patches: homogeneous areas based on overstory vegetation composition and geomorphic landform. We identified to species and measured the diameter of every woody stem (near the ground surface) in 5 × 20 m rectangular quadrats (long axis parallel to the active river channel) randomly located within each patch (227 quadrats; 117 on the Bill Williams River and 110 on the Santa Maria River). If a patch covered >50 m of a transect, we randomly placed and sampled a second quadrat. We calculated basal area (in square meters per hectare) and stem density (number of stems per hectare) of live and dead stems of all woody species in each quadrat and classified quadrats and associated patches into patch types based on the species with the largest basal area.

We calculated the live and dead basal area and stem density per hectare of each transect by summing the values for all patches within a transect. We compared the transect-scale basal area and stem density between rivers using *t* tests. We also tested for basal area and stem density differences between rivers within four patch types: (1) dominated by *Populus* or *Salix,* (2) dominated by *Tamarix,* (3) dominated by *Prosopis* spp., and (4) dominated by xeric shrubs (e.g., *Tessaria, Hymenoclea, Lycium*). Finally, we tested for between-river differences in the proportion of transect occupied by these four patch types.

Vegetation dynamics

Age structure.—To address the effect of Alamo Dam on age structure of pioneer riparian forests,we aged most patches dominated by *Populus, Salix,* or *Tamarix.* In mixed-species stands we aged individuals from more than one species. We collected cores and/or stem cross-sections from enough trees within a patch to yield at least three samples that were aged with reasonable confidence (±2 yr). We excavated saplings and poles to ensure that we obtained a sample from the oldest portion of the stem. For multiple-stemmed *Tamarix* individuals, we excavated deep enough to obtain a sample below the surficial cluster of multiple stems. In the laboratory, we sanded the cores and stem cross-sections to 400 (*Tamarix*) or 600 grit (*Populus* and *Salix*) and determined a minimum age of each sample by counting the annual growth rings under a microscope. Stand age, by species, was estimated as the age of the oldest sample within a patch. On the Bill Williams River, we obtained minimum stand ages of *Populus* in 17, *Salix* in 20, and *Tamarix* in 30 patches. On the Santa Maria River we obtained minimum stand ages of *Populus* in 10, *Salix* in 8, and *Tamarix* in 16 patches.

Seral species recruitment.—To examine effects of flow regulation on the recruitment of later successional species in pioneer forests (e.g., *Prosopis* spp., *Acacia gregii*) we compared, between rivers, the proportion of patches classified as *Tamarix, Salix,* or *Populus* that contained later successional species. We tested for differences in proportions using Fisher's exact test on the 2 × 2 contingency table of later successional species vs. river. To test whether there was a greater density of later successional species in older aged stands, we conducted simple linear regression of the successional species density vs. stand age.

Seedling establishment.—To assess differences between rivers in the width of establishment zones, we compared the width of patches containing woody pioneer seedlings (of any species) in September 1995 using a *t* test. To assess differences between rivers in the spatial distribution of seedling patches, we compared the horizontal distance from plots to the thalweg for all plots containing woody pioneer seedlings (of any species) in September 1995 using a *t* test and also examined the coefficient of variation in distance to thalweg associated with each river.

To assess seedling survival over time, we counted the number of woody seedlings, by species, in September or October 1995, 1996, and 1997, in permanent 1 × 2 m quadrats, nested within the 5 × 20 m quadrats that were sampled for vegetation structure and species composition. We compared seedling survival between rivers and within species for the periods 1995–1996 and 1995–1997 using multi-response permutation procedures (MRPP), a distribution-free statistical analysis that can test for differences even when the data contain a large number of zero values, as our survival data did (Biondini et al. 1988).

RESULTS

Surface water hydrology

Flood flows.—Pre-dam peak flows on the Bill Williams River were larger than those on the Santa Maria River, consistent with differences in watershed area (Fig. 2). Alamo Dam has dramatically reduced the magnitude of peak flows on the Bill Williams River (Table 3, Fig. 2), and in the post-dam era, peak instantaneous

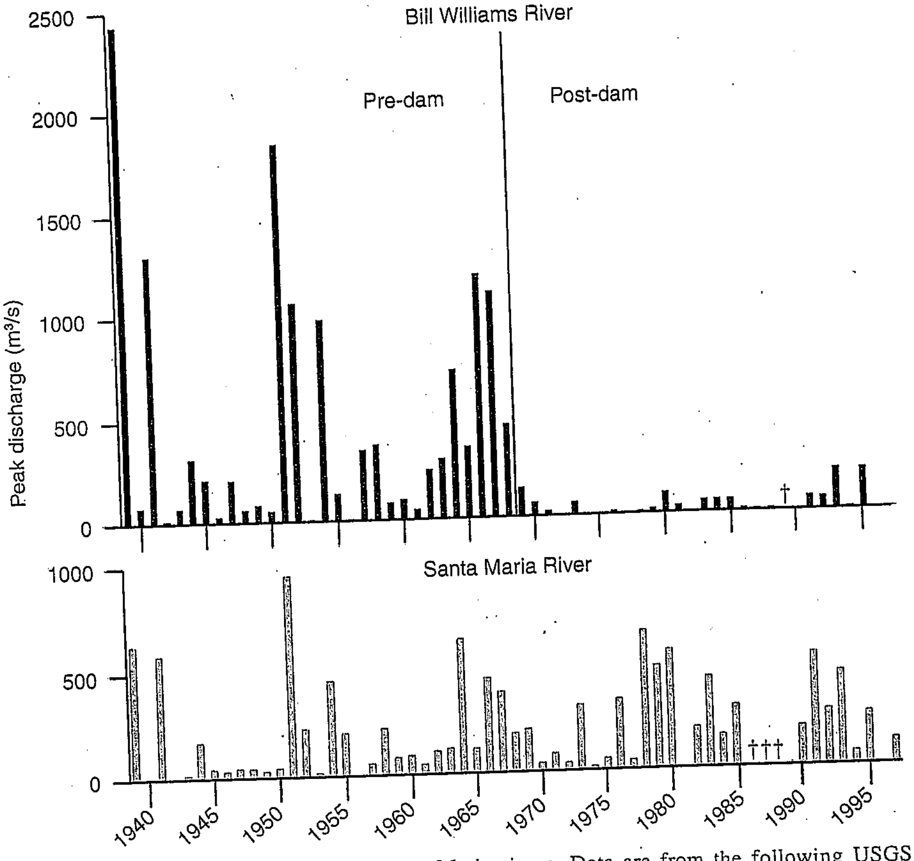

FIG. 2. Annual flood series, Bill Williams and Santa Maria rivers. Data are from the following USGS stream gages: #09426000, Bill Williams River near Alamo, Arizona, 1939–1968; #09426000, Bill Williams River below Alamo Dam, Arizona, 1969–1997; #09425500, Santa Maria River near Alamo, Arizona, 1939–1966; #09424900, Santa Maria River near Bagdad, Arizona, 1967–1985, 1989–1997. Alamo Dam was constructed between March 1965 and July 1968.

†Years when data were not collected.

flows on the Santa Maria River have generally exceeded those on the Bill Williams River (Fig. 2).

Average flows.—The mean annual flow in the post-dam era was considerably higher than pre-dam (4.4 vs. 2.6 m³/s), reflecting the strong effect of a few particularly wet years in the late 1970s and early 1990s. Increases in summer flows (May–September) can be partially attributed to the operation of Alamo Dam (Fig. 3, Table 3, Fig. 5b), whereas winter and spring flows (October–April) have risen due to precipitation increases in the post-dam era (Fig. 3, Table 3).

Channel width and vegetation extent

Channel width.—Channels along the Bill Williams River narrowed an average of 111 m (71%) between 1953 and 1987–1988, after which some minor widening occurred (Fig. 4a, b). Channel width in 1953 and the pattern of narrowing differed somewhat between intermittent and perennial reaches, with channels in intermittent reaches tending to be wider (Fig. 4a, b). The channel of the Santa Maria River narrowed between 1953 and 1976 on both reaches, then widened slightly

TABLE 3. Effect of Alamo Dam on annual peak and seasonal mean flows on the Bill Williams River, Arizona (mean ± 1 SE).

Streamflow variable	Pre-dam difference	Post-dam difference	df	t	P
Peak instantaneous flow (m³/s)	238.1 ± 81.5	−183.9 ± 36.7	28.3	−4.65	<0.0001
Average flow, October–April (m³/s)	2.3 ± 1.0	2.5 ± 1.4	25.9	0.94	0.36
Average flow, May–September (m³/s)	0.5 ± 0.1	2.3 ± 1.0	26.6	2.43	0.02

Notes: We used t tests to compared pre- vs. post-dam flow differences between rivers (i.e., flow on the Bill Williams River minus flow on the Santa Maria River). In all cases degrees of freedom were adjusted using the Satterthwaite (1946) method to account for unequal variances. Reported differences were calculated from the raw data. The t tests were conducted on $\log_{10}$-transformed data.

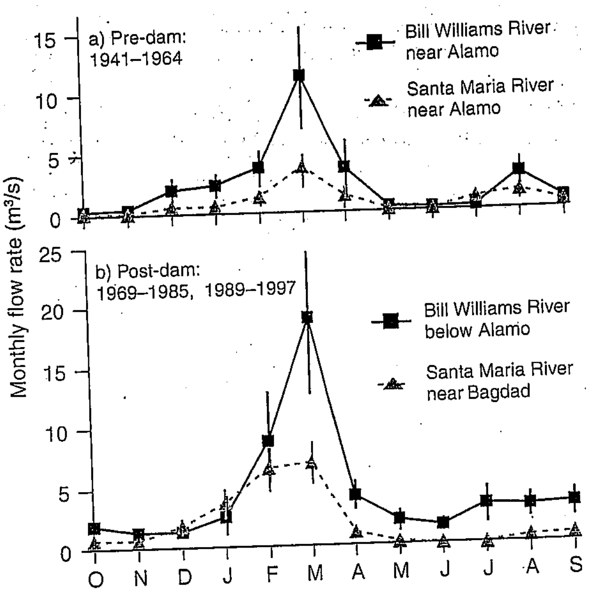

FIG. 3. Monthly flow comparisons, Bill Williams and Santa Maria rivers, Arizona (means ± 1 SE). Keys refer to names of USGS gaging stations where data were obtained (see Fig. 1). Data from the period of dam construction (March 1965–July 1968) are excluded, as are water years 1986–1988 when data were not collected on the Santa Maria River.

on one between 1976 and 1987, and widened markedly on both reaches between 1987 and 1992 (Fig. 4c).

Flood power on the Bill Williams River was highest in the pre-1953 photograph interval (average of 50.7 W/m), the result of a peak flow of 1843 m^3/s in August 1951 (Fig. 5a). Flood power did not exceed 10 W/m for any of the other intervals. Flood power on the Santa Maria River was similar to that on the Bill Williams for the pre-1953 and 1964 intervals but was higher than the Bill Williams for the pre-1976, 1987, and 1992 intervals (Fig. 5a).

On the Bill Williams River, average May–September flow was <1.5 m^3/s during the 5 yr preceding the 1953, 1964, and 1976 photographs and >2.5 m^3/s during the 5 yr preceding the 1987/1988 and 1996 photographs (Fig. 5b). On the Santa Maria River, average May–September flows were always lower than those on the Bill Williams River, but this difference was especially pronounced in the 5-yr intervals preceding the 1987 and 1992 photographs (Fig. 5b).

The multiple regression model containing the independent variables flood power, May–September average flow, and intermittency explained 57% of the variation in log$_{10}$ channel width on the Bill Williams River and was the model with the lowest value of Mallow's Cp statistic. The coefficients for the three independent variables were all statistically significant, and the signs of the coefficients indicate that channels were wider when flood power was higher, average summer flows were lower, and where flow was intermittent (Table 4).

Post-dam channels under unregulated conditions (predicted by the regression model) would have been much wider than those observed (Fig. 4a, b), due to high flood power values associated with reconstructed peak flows in 1976 (1005 m^3/s), 1983 (796 m^3/s), and 1993 (2389 m^3/s; Fig. 5a), and reconstructed May–September flows that were $<50\%$ of actual flows in the 5 yr preceding the 1987/1988 and 1996 photographs (Fig. 5b).

Vegetation extent.—Between 1953 and 1996, the total area of floodplain vegetation in our eight study reaches on the Bill Williams River increased 61%, from 315 to 509 ha. Terrace vegetation increased 23%, from 542 to 667 ha, over the same time period. Comparisons of the average values within the pre- and post-dam periods indicate that the proportion of the bottomland occupied by channel was significantly less in the post-dam era, while the proportion of dense floodplain vegetation was marginally greater (Table 5).

Vegetation structure and species composition

Field sampling.—The per-transect live basal areas of 14.3 ± 3.7 m^2/ha (mean ± 1 SE) on the Bill Williams

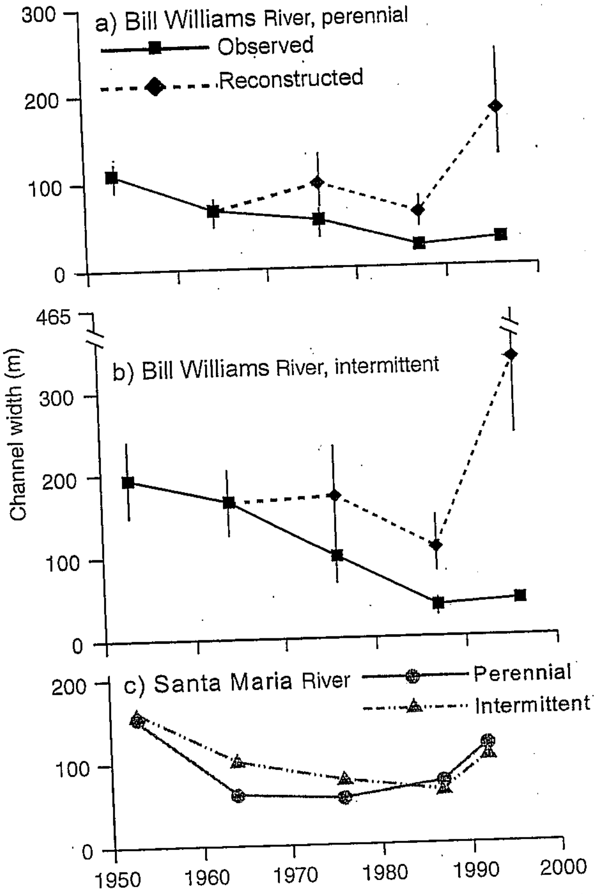

FIG. 4. Observed and reconstructed (predicted) change in channel width through time (means ± 1 SE). For the Bill Williams River, $n = 4$ for perennial and intermittent reaches; for the Santa Maria River, $n = 1$ for perennial and intermittent reaches. Alamo Dam was constructed between March 1965 and July 1968.

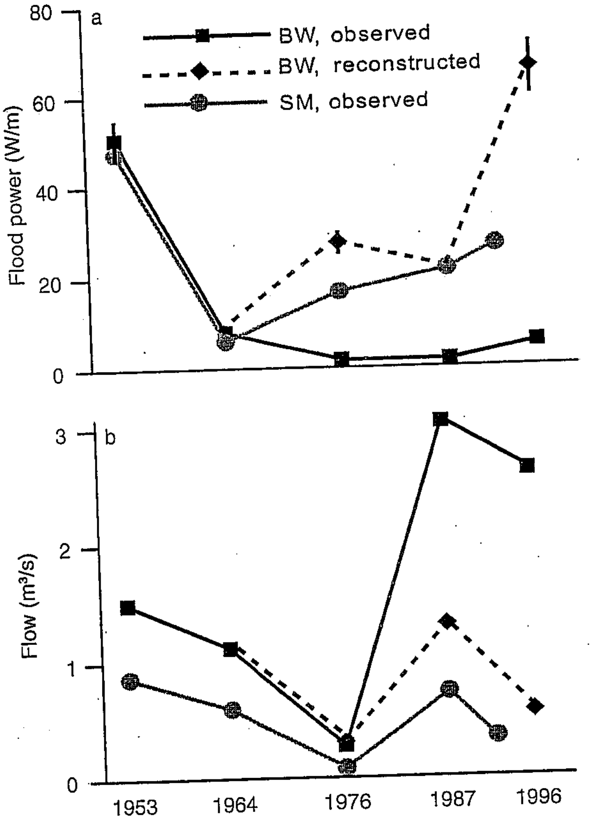

FIG. 5. Values for independent regression variables, Bill Williams (BW) and Santa Maria (SM) rivers, Arizona. (a) Maximum stream power in five years preceding aerial photograph data (means ± 1 SE, where given). (b) Mean flow from May to September in five years preceding aerial photograph date. Alamo Dam was constructed between March 1965 and July 1968.

River and 10.7 ± 2.4 on the Santa Maria River were not significantly different (n = 8, t = 0.8, P = 0.42). On the Bill Williams River, live basal area was concentrated on surfaces at relatively low positions within the bottomland (12.5 ± 4.0 m²/ha on surfaces <3 m above the thalweg vs. 1.8 ± 0.5 m²/ha on surfaces >3 m above the thalweg; n = 8, t = 2.68, P = 0.03). On the Santa Maria River, live basal area was distributed relatively evenly (4.1 ± 1.6 m²/ha on surfaces <3 m above the thalweg vs. 6.5 ± 2.1 m²/ha on surfaces >3 m above the thalweg; n = 8, t = 0.91, P = 0.38). Dead basal area on the Bill Williams River (5.6 ± 0.8 m²/ha) was greater than on the Santa Maria River (1.1 ± 0.2 m²/ha; n = 8, t = 5.6, P = 0.0004).

Stem densities were greater along the Bill Williams River transects (27 737 ± 5124 live stems/ha) than along the Santa Maria River transects (7559 ± 1882 live stems/ha; n = 8, t = 3.7, P = 0.005). The difference in live stem density was most pronounced on high surfaces (low surfaces, Bill Williams River = 14 839 ± 5118 stems/ha; Santa Maria River = 5816 ± 1971 stems/ha; n = 8, t = 1.64, P = 0.13; high surfaces, Bill Williams River = 12 898 ± 4576 stems/ha, Santa Maria River = 1743 ± 708 stems/ha; n = 8, t = 2.4, P = 0.04). Dead stem density was greater on the Bill Williams River (33 725 ± 8682 stems/ha) than on the Santa Maria (3593 ± 1291 stems/ha; n = 8, t = 3.4, P = 0.01).

Live basal area on both rivers tended to be highest in stands of *Populus* and *Salix*, and live stem densities were highest in xeric shrub patches (Table 6). Basal area was higher within *Populus/Salix* and *Tamarix* patches along the Bill Williams River than along the Santa Maria River, and *Tamarix* stands were also denser along the Bill Williams River (Table 6).

Patches dominated by *Tamarix* or xeric shrubs occupied proportionally more of the transects on the Bill Williams River than on the Santa Maria River (Table 6). The relative abundance of *Tamarix* (i.e., proportion of *Tamarix* : *Populus/Salix*) was also greater on the Bill Williams River (n = 8 transects, t = 2.59, P = 0.02). *Prosopis* spp. woodlands were more extensive along the Santa Maria River transects, while *Salix*- and *Populus*-dominated patches occupied similar proportions of the transects along both rivers (Table 6).

Aerial photography.—The proportion of *Tamarix*-dominated floodplain was significantly greater than *Populus/Salix*-dominated floodplain on the 1996 aerial photographs of the Bill Williams River (Fig. 6a; n = 8 reaches, t = −5.63, P < 0.0001). *Prosopis* spp. stands dominated terrace vegetation relative to xeric shrub communities (Fig. 6b; n = 8, t = 4.63, P = 0.0004). Floodplain vegetation with a dense canopy cover was more abundant than that with a sparse canopy cover in perennial but not intermittent reaches (Fig. 6a; perennial, n = 4, t = 3.13, P = 0.02; intermittent, n = 4, t = −2.36, P = 0.93). On terraces, canopy cover density did not differ as a function of perenniality (Fig. 6b; perennial, n = 4, t = 1.11, P = 0.31; intermittent, n = 4, t = −2.36, P = 0.06).

Vegetation dynamics

Age structure.—Only 6 of the 44 stands of pioneer tree species along the Bill Williams River that we aged pre-dated Alamo Dam. The oldest *Tamarix* dated to

TABLE 4. Results of multiple regression analysis.

Dependent variable	Independent variable	Parameter estimate	P
$\log_{10}$ (Channel width)	flood power	0.008	0.0001
	summer flow	−0.152	0.0004
	intermittency	0.229	0.0052

Notes: Number of observations = 40, error df = 36, model r^2 = 0.57, model P < 0.0001. The dependent variable is the $\log_{10}$ of the channel width, which was measured within eight reaches on aerial photographs. "Flood power" is the maximum stream power in the 5 yr preceding a photograph; "summer flow" is the mean May–September flow in the 5 yr preceding a photograph; and "intermittency" refers to whether a reach has seasonally intermittent or perennial flow.

TABLE 5. Change in the proportion of the bottomland occupied by seven cover types, pre- vs. post-dam, Bill Williams River, Arizona.

Cover type	Pre-dam Mean	Pre-dam SE	Post-dam Mean	Post-dam SE	t	P	Adjusted P
Channel	0.29	0.05	0.11	0.02	4.90	*0.002*	*0.01*
Small floodplain vegetation	0.08	0.02	0.06	0.02	0.74	0.48	0.99
Sparse floodplain vegetation	0.10	0.03	0.09	0.01	−0.31	0.77	0.99
Dense floodplain vegetation	0.09	0.03	0.20	0.07	2.35	*0.05*	0.31
Sparse terrace vegetation	0.24	0.07	0.27	0.06	0.85	0.44	0.98
Dense terrace vegetation	0.13	0.04	0.17	0.04	2.16	0.06	0.36
Cultivated/barren terrace	0.07	0.03	0.09	0.03	2.19	0.07	0.38

Notes: The mean and SE are those of the proportion of the bottomland occupied by each cover type. Paired t-test analysis was used to test the difference between the mean pre-dam (1953, 1964) and mean post-dam (1976, 1987–1988, 1996) proportions of the cover types. $N = 8$. See Table 2 for more detailed descriptions of cover types. Adjusted P values were calculated using the Sidak method for multiple tests: $1 - (1 - P)^n$, where P is the raw P value and n is the number of tests (7). Values in italic type are significant at the $P < 0.05$ level.

1959, and the oldest *Populus* to 1910. Few stands became established in the first 6 yr following the construction of Alamo Dam (1969–1974), but many became established later (Fig. 7a). Between 1975 and 1989, many *Tamarix* cohorts recruited relative to *Salix* and *Populus*. In the early 1990s more *Salix* and *Populus* stands became established than *Tamarix*. On the Santa Maria River, fewer stands originated prior to the mid-1970s than on the Bill Williams River (Fig. 7b). From the mid-1970s to the mid-1980s, more new stands were composed of *Populus* or *Salix* than *Tamarix* (Fig. 7b).

Seral species recruitment.—Seral species were more frequently present in the understory of stands dominated by *Populus*, *Salix*, or *Tamarix* along the Bill Williams River than along the Santa Maria River (Bill Williams River, 17 of 46 stands; Santa Maria River, 7 of 44 stands; Fisher's exact test $P = 0.03$). There was not a significant linear relationship between stand age (independent variable) and later successional species density (dependent variable; model $R^2 = 0.02$, $n = 24$, $P = 0.49$). In all but one stand, *Prosopis* was the only late successional genus present.

Seedling establishment.—Patches containing new woody pioneer seedlings in September 1995 were wider on the Santa Maria River (15.3 ± 2.7 m, $n = 35$) than on the Bill Williams River (5.4 ± 0.6 m, $n = 22$; $t = -3.6$, $P = 0.0009$; Fig. 8). Because of higher survivorship, the average width of these seedling patches was greater on the Bill Williams River by 1997 (Fig. 8). The distance from woody pioneer seedling patches to the thalweg in September 1995 did not differ between rivers (Bill Williams River, 80.6 ± 29.9 m, $n = 22$; Santa Maria River, 66.9 ± 16.3 m, $n = 35$; $t = 0.4$, $P = 0.69$). The coefficient of variation on the Bill Williams River was slightly higher (1.73) than on the Santa Maria River (1.44).

First-year seedling densities (September 1995) of all species were higher on the Bill Williams River than on the Santa Maria River (Fig. 9). *Tamarix* densities were the highest after 1 and 2 yr on both rivers, but numbers of surviving *Tamarix* in October 1997 were comparable to other species. On the Bill Williams River, some seedlings of all species survived, and, except for *Salix*, occurred at average densities >1.3 seedlings/m² in Oc-

TABLE 6. Extent and structure of four woody riparian vegetation patch types along the Bill Williams and Santa Maria rivers (means ± 1 SE).

Variable	Patch type	Bill Williams River	Santa Maria River	n	t	P	Adjusted P
Basal area (m²/ha)	*Populus/Salix*	45.3 ± 7.1	24.1 ± 6.1	13, 28	2.08	*0.04*	0.15
	Tamarix	23.9 ± 3.7	7.5 ± 2.3	33, 16	3.73	*0.0005*	*0.002*
	Prosopis	13.6 ± 3.9	10.5 ± 3.0	7, 22	−0.55	0.59	0.97
	Xeric shrub	8.9 ± 1.5	5.7 ± 2.5	25, 13	1.14	0.26	0.70
Stem density (1000 stems/ha)	*Populus/Salix*	21.3 ± 7.4	16.1 ± 3.9	13, 28	0.70	0.49	0.93
	Tamarix	25.1 ± 3.9	13.7 ± 2.2	33, 16	2.56	*0.01*	*0.04*
	Prosopis	26.7 ± 9.6	4.5 ± 1.2	7, 22	2.29	0.06	0.22
	Xeric shrub	59.8 ± 12.0	41.7 ± 19.1	25, 13	0.84	0.41	0.88
Extent (percentage of transect)	*Populus/Salix*	6.5 ± 2.5	1.6 ± 0.8	8, 8	−1.11	0.30	0.76
	Tamarix	30.6 ± 9.5	7.4 ± 2.3	8, 8	2.36	*0.05*	0.19
	Prosopis	5.0 ± 2.3	34.2 ± 8.3	8, 8	−3.38	*0.009*	*0.04*
	Xeric shrub	33.2 ± 8.1	10.7 ± 3.4	8, 8	2.55	*0.03*	0.11

Notes: The first value in the n column refers to the number of patches along the Bill Williams River, the second to those along the Santa Maria River. We used t tests to test for differences between rivers. Adjusted P values were calculated using the Sidak method for multiple tests: $1 - (1 - P)^n$, where P is the raw P value and n is the number of tests (4). Values in italic type are significant at the $P < 0.05$ level.

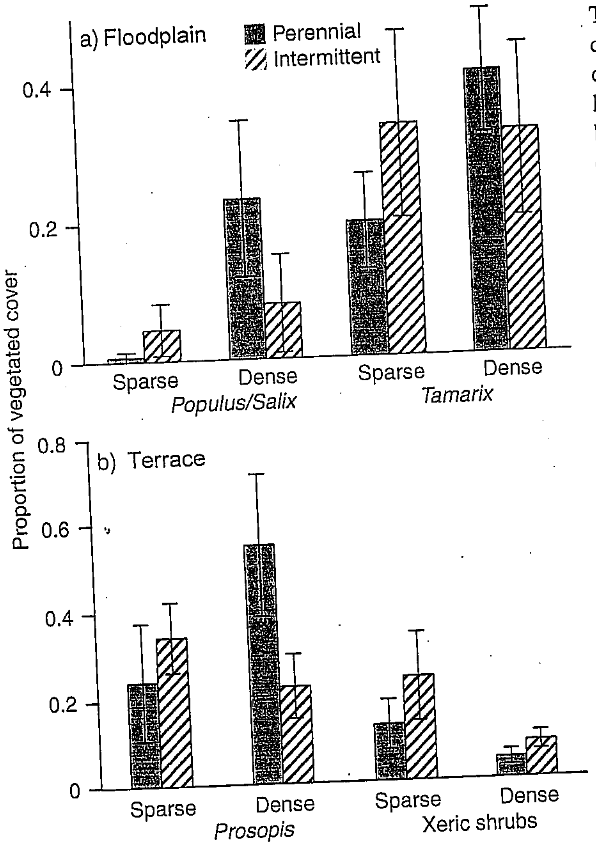

FIG. 6. Proportion of (a) floodplain and (b) terrace vegetation occupied by different cover types in 1996, Bill Williams River, Arizona (means ± 1 SE). "Sparse" cover types were characterized by 2–50% total cover, whereas "dense" cover types were characterized by >50% cover. Data are from aerial photograph interpretation. For perennial and intermittent reaches, $n = 4$.

tober 1997 (Fig. 9). On the Santa Maria River, by October 1997 there were no surviving *Populus* or *Tessaria* seedlings in the quadrats, and densities of *Baccharis*, *Salix*, and *Tamarix* were all <1 seedling/m^2 (Fig. 9). Survival rates differed between rivers for *Salix* and *Baccharis* for 1995–1996 and for *Baccharis* for 1995–1997 (Fig. 9).

DISCUSSION

Channel width and vegetation extent

Flow regulation associated with the construction and operation of Alamo Dam has had profound effects on flood disturbance and drought stress regimes along the Bill Williams River. As a response to these changes, stream channels have narrowed dramatically, and the areal extent of riparian vegetation has increased. This general pattern has been observed along other braided, sand-bed rivers in arid and semiarid western North America and has been attributed most often to decreased flood magnitude (Schumm and Lichty 1963, Burkham 1972, Johnson 1994, Friedman et al. 1996). Typically, the narrowing process is accomplished by a combination of vegetation establishment on former channel and sediment deposition, which may be enhanced by the increased hydraulic roughness provided by the vegetation. Extensive riparian forest can form during periods with relatively small floods and low flows that are high enough to sustain tree growth. Historically, extensive forest development along the Bill Williams River was likely short-lived as many trees were eliminated by frequent, large floods. For example, channels were wide and vegetation sparse in the 1953 aerial photographs that were taken following discharges of 1843 and 1064 m^3/s in 1951 and 1952 (Fig. 2). A period of narrowing occurred between 1953 and 1964. We speculate that the channel widened in 1966 and 1967 in response to flows of 1186 and 1101 m^3/s and then narrowed slightly in early post-dam years, before extensive narrowing in the late 1970s and 1980s.

Our results also point to the importance of increased summer discharge in promoting vegetation establishment and channel narrowing along the Bill Williams River, an aspect of flow regulation that has received less attention in the literature than flood alteration (Nadler and Schumm 1981). In arid environments, riparian plant survival and growth are highly dependent on moisture supplements provided by streamflow and associated high water tables (Zimmerman 1969). The extent of riparian vegetation growth may be naturally limited by episodic or seasonal drought (Albertson and

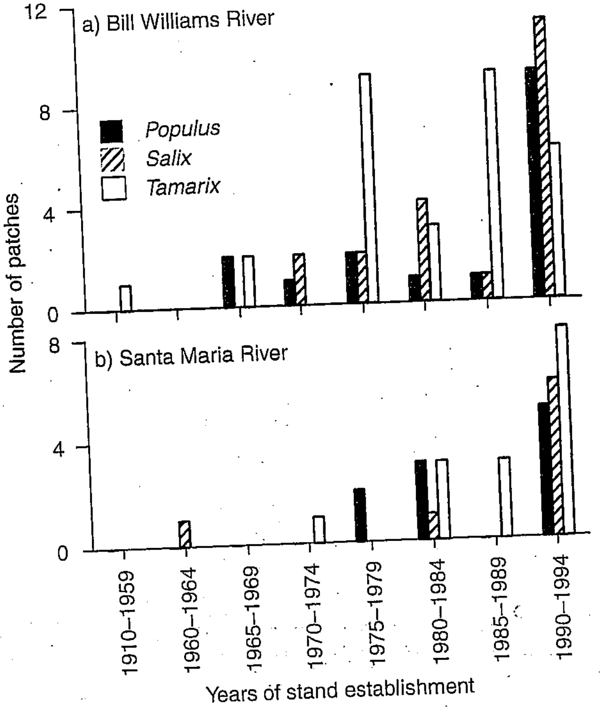

FIG. 7. Age distribution of three dominant tree species within floodplain vegetation patches at study transects along the Bill Williams and Santa Maria rivers, Arizona.

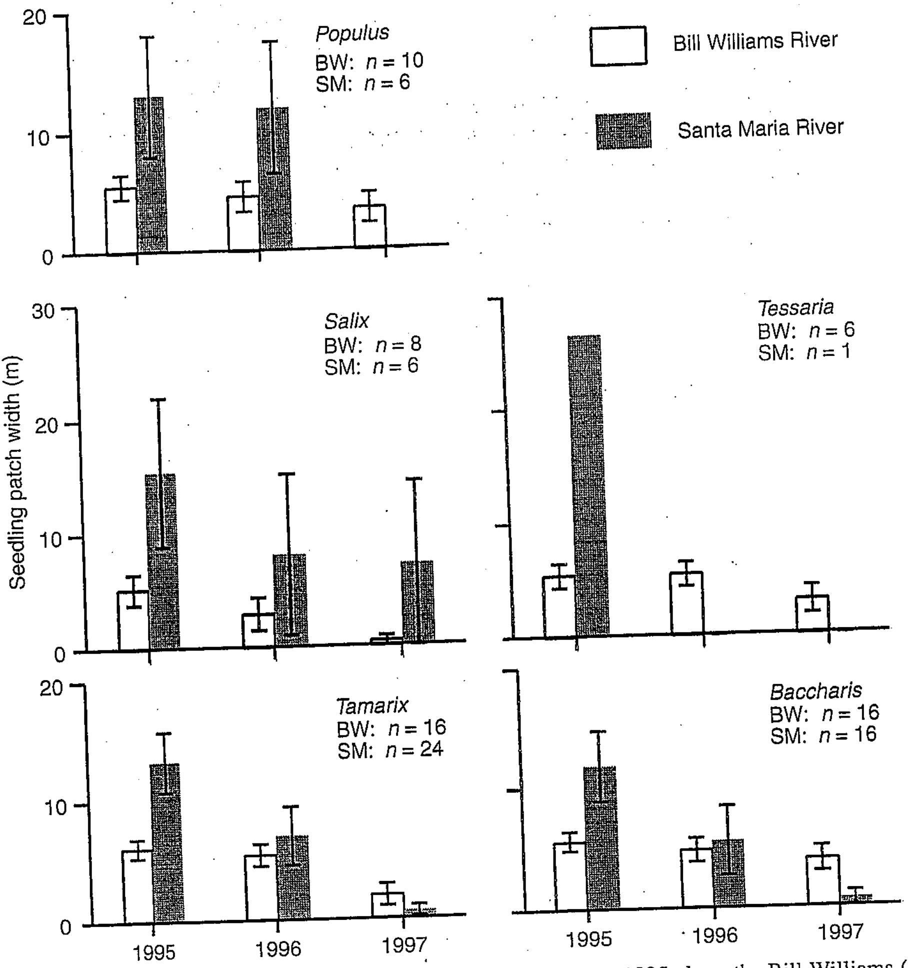

FIG. 8. Width of patches containing five woody species that germinated in 1995 along the Bill Williams (BW) and Santa Maria (SM) rivers, Arizona (means ± 1 SE). Mean values for all years are calculated as the total patch width containing live seedlings divided by the total number of patches containing seedlings in October 1995, which is noted within each panel.

Weaver 1947, Stromberg 1993) or by spatial variation in the extent of perennial flow or magnitude of low flows (Rood et al. 1995). On the Bill Williams River, the extremely low flows in the early 1970s apparently associated with reservoir filling may explain why the channel had not narrowed considerably by 1976. Since 1976, however, summer flows have been higher, dampening or eliminating seasonal and annual drought, and "perennializing" formerly intermittent portions of the stream, thereby permitting the establishment and growth of woody vegetation on former channels. Increased average summer flows during the last two decades have been a function of higher base flows. Future research should explore the effects of periodic summer flood pulses on soil moisture, groundwater levels, and associated plant vigor. Further, quantifying the relationship between releases from Alamo Dam and flow within different reaches, especially those downstream from Planet Basin, would clarify the influence of summer releases on riparian vegetation.

A surge in tree recruitment along the Bill Williams River in the post-dam environment was corroborated by our stand age data (Fig. 7). Most stands along the Santa Maria River also established during the 1970s and 1980s, a period when regional weather patterns resulted in streamflow conditions favorable for riparian vegetation establishment (Stromberg 1998*a*). Nevertheless, decreased flooding and increased summer flows associated with Alamo Dam led to more pronounced channel narrowing and a larger expansion of pioneer trees on the Bill Williams River than on the unregulated Santa Maria River. Predictions of wider channels in the absence of flow regulation (Fig. 4a, b) further highlight dam-related changes on the Bill Williams River.

Vegetation structure and species composition

The pre-dam riparian vegetation along the Bill Williams River consisted of fewer, smaller, and more open stands of floodplain vegetation than that of the post-dam era. The increase in *Tamarix* along the post-dam river has produced shorter, shrubbier woodlands that are relatively dense compared to those on the unreg-

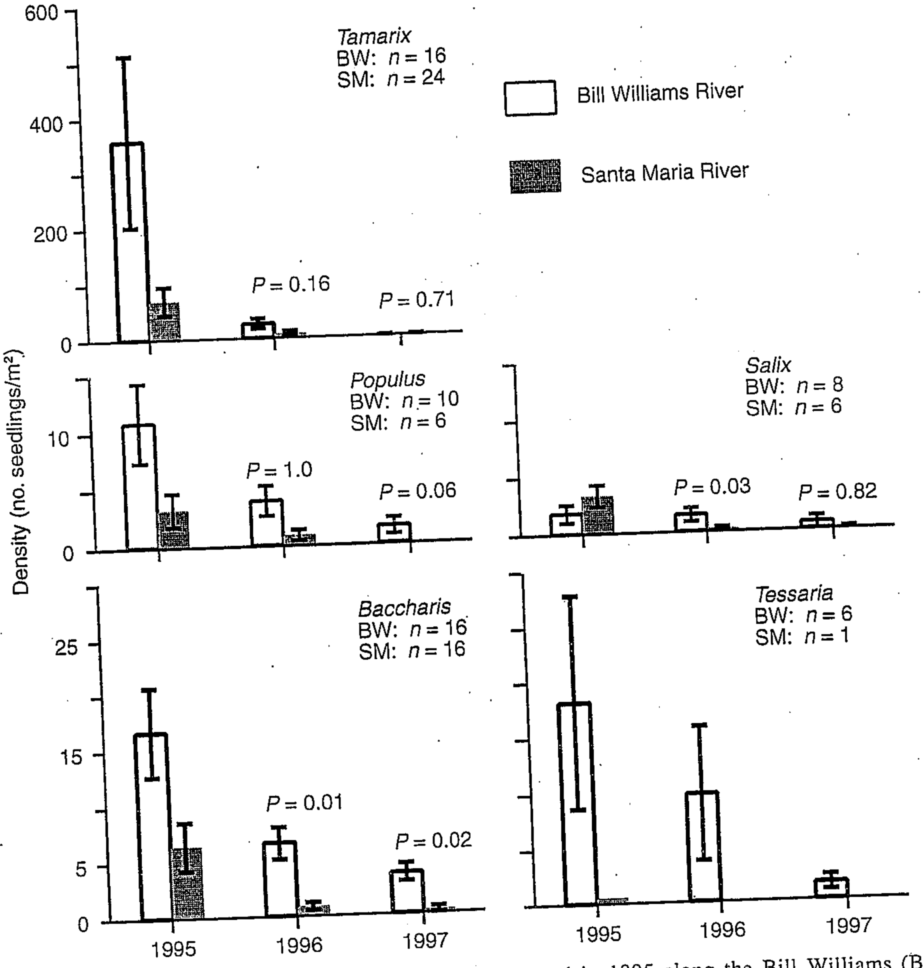

FIG. 9. Density of seedlings of five woody species that germinated in 1995 along the Bill Williams (BW) and Santa Maria (SM) rivers, Arizona (means ± 1 SE). Note scale difference for *Tamarix*. *P* values are noted above bars from 1996 and 1997 and are based on a multi-response permutation procedure comparing the survival rates between 1995 and 1996 and between 1995 and 1997, respectively. No statistical test was conducted on *Tessaria* because of the small sample size on the Santa Maria River.

ulated Santa Maria River. The average basal area in *Populus*/*Salix* stands along the Bill Williams River was somewhat higher than that reported for other deciduous floodplain forest types in North America (Brinson 1990), perhaps due, in part, to the relatively small quadrat size we used. Stem densities in our study were notably higher than those in other floodplain forests (Brinson 1990), due to the prevalence of shrubs. Relative to *Populus* and *Tamarix* woodlands of the unregulated San Pedro River in Arizona, basal area and stem density values on the Santa Maria River were slightly lower while those on the Bill Williams River were higher (Stromberg 1998*b*).

Our results suggest that *Tamarix* was present in relatively low densities prior to flow regulation on the Bill Williams River and that flow regulation facilitated its expansion. In other examples of *Tamarix* invasion into post-dam southwestern riparian ecosystems, *Tamarix* introduction and flow regulation occurred within 1–2 decades of each other (e.g., Robinson 1965, Graf 1982), making the effects of flow regulation and the species' invasive ability difficult to separate. In the case of the Bill Williams River, *Tamarix* seed had been available from the lower Colorado River since the 1920s (Ohmart et al. 1977); yet extensive stands apparently did not exist before the completion of Alamo Dam.

The abundance of *Tamarix* on the Bill Williams River likely resulted from its opportunistic colonization of large areas of bare substrate following dam construction (Everitt 1998), its resistance to mortality factors such as drought and fire (Busch 1995, Smith et al. 1998), and from the absence of other mortality agents such as large magnitude floods and herbivory (DeLoach 1997). Finally, the contemporary relative abundance of *Tamarix* could have been influenced by mortality of *Populus* that resulted from prolonged inundation between 1978 and 1980 (Hunter et al. 1987); however, our interpretations of aerial photography before and after this event did not reveal lasting compositional shifts except near the confluence with the Colorado River.

Some flow-related factors that may favor *Tamarix* do not appear to be important in the case of the Bill Williams River. For example, there was not a change in flood timing to periods when *Tamarix* seed would be more abundant than *Populus* or *Salix* (cf. Shafroth et al. 1998); winter "floods" predominated in the post-dam era (Shafroth 1999). The timing of peak flows alone may not indicate the timing of flow recession and availability of bare, moist sediment, though. For example, in the late 1970s and early 1980s, higher low flows after the seed dispersal period of *Populus* and *Salix* may have permitted *Tamarix* establishment. *Tamarix* establishment was correlated with winter floods and high winter flows along the San Pedro River, Arizona (Stromberg 1998*a*). Finally, although *Tamarix* is known to be more salt tolerant than either *Populus* or *Salix,* the floodplain soil electrical conductivity levels observed at our study sites were generally too low to affect relative survival rates of *Tamarix, Populus,* or *Salix* (Jackson et al. 1990, Shafroth et al. 1998).

Periodic fires have also affected riparian forest composition along the Bill Williams River. Fire tends to kill *Populus,* whereas *Tamarix, Tessaria,* and to a lesser extent *Salix* are able to resprout (Busch and Smith 1993, Busch 1995). *Tamarix* may perpetuate fire disturbance due to the large quantity of standing dead stems it produces and its highly combustible, multiple-stemmed form (Ohmart and Anderson 1982). Altered disturbance regimes are a product of invasive species in other ecosystems (Mack and D'Antonio 1998). Flow regulation indirectly promotes fire in riparian ecosystems because dead, combustible vegetation tends to accumulate without floods that transport and export this material and promote its decomposition (Ellis et al. 1998). On terraces, fire favors the xeric shrub *Tessaria sericea* over *Prosopis* spp. (Busch 1995).

Vegetation dynamics

Seral species recruitment.—Flow regulation has been shown to alter succession in riparian ecosystems (Johnson et al. 1976, Bravard et al. 1986, Johnson 1992). *Prosopis* colonizes the understory of *Populus fremontii* forests in Arizona (Stromberg et al. 1997, Stromberg 1998*b*), but other successional trajectories have not been well described. Even less is known of successional pathways in *Tamarix* stands, largely because *Tamarix* generally has not occupied sites on this continent long enough to senesce. In the Grand Canyon, stands of *Tamarix* that colonized the Colorado River bottomland following the construction of Glen Canyon Dam are beginning to senesce and are being replaced by a mix of upland and clonal riparian species (Stevens 1989). On the San Pedro River in southeastern Arizona, densities of later successional species were similar in *Tamarix* and *Populus* stands, but the relationship to stand age differed, with a tendency for higher densities in older *Populus* stands and no apparent stand age-related pattern in *Tamarix* stands (Stromberg 1998*b*). On the Bill Williams River, we speculate that former floodplain areas that are not reworked by the river will continue to be colonized by typical terrace taxa such as *Prosopis, Tessaria,* and *Atriplex.* The rate of colonization of *Prosopis* may be slowed by the lack of summer overbank floods and associated seed scarification and burial (Stromberg et al. 1991); however, our results did not reveal greater recruitment of *Prosopis* along the unregulated Santa Maria River.

Seedling establishment.—Our seedling establishment results suggest that differences in flood magnitudes and summer flows between the Bill Williams and Santa Maria rivers produce different seedling establishment patterns. Smaller floods on the Bill Williams River created less bare substrate suitable for pioneer seedling germination than on the Santa Maria River (Fig. 8). Initial seedling densities were higher on the Bill Williams River, perhaps because of the larger seed rain associated with the dense floodplain vegetation. Seedling survival was generally higher on the Bill Williams River, likely a result of more stable low flows and associated alluvial groundwater levels, and perhaps lack of subsequent floods (Fig. 9; Shafroth et al. 1998). In the pre-dam era, there was a greater tendency for multiple flood peaks in a year and more late summer (monsoonal) floods (Shafroth 1999), either of which might remove seedlings (Stromberg et al. 1991).

System dynamics.—Flow regulation may cause a shift in channel and riparian vegetation from a pre-regulation dynamic through a transient response phase to a new dynamic equilibrium (Petts 1987, Johnson 1997, 1998). We suggest that channels and vegetation along the Bill Williams River exhibited nonequilibrium dynamics prior to the construction of Alamo Dam, because the recurrence interval of destructive floods or fatal drought (~10 yr) was much shorter than the generation time of the dominant trees (~100 yr; Pickett 1980). During the first 20 yr following dam construction, vegetation colonized former channels and grew rapidly, representing a transient response to reduced flood disturbance and drought stress. As the stands of pioneer vegetation age and are replaced by seral species, a new, dynamic equilibrium may be reached, with a larger proportion of the bottomland occupied by relatively stable and xeric late seral communities (Merritt and Cooper 2000).

The relative importance of factors controlling a new dynamic equilibrium may change. Now that vegetation has established on many floodplain surfaces, larger floods may be required to widen channels because of increased bank stability and greater resistance of mature vegetation to flood damage. As stands of existing vegetation senesce, bank resistance and surface roughness may decrease, effectively increasing the erosive potential of a particular magnitude flow (Johnson 1997). Further, the future may be characterized by changes in driving variables, with fire increasing in importance and streamflow-driven disturbance and drought stress regimes decreasing in importance.

Streamflow management implications

Streamflow is increasingly being managed to effect the restoration of riparian plant communities (Scott et al. 1997, Rood et al. 1998) and other riverine ecosystems (Stanford et al. 1996, Poff et al. 1997). The dense riparian vegetation along the Bill Williams River is of regional importance because it is considered the best remaining example of this type of habitat in the highly degraded lower Colorado River system (Hunter et al. 1987). Thus, despite evidence that its abundance is largely attributable to regulated streamflow conditions, maintaining this regionally unique habitat is a priority for most land and water managers, including the U.S. Army Corps of Engineers, the agency that operates Alamo Dam. We suggest prospects and limits for managing vegetation via streamflow management. The maximum flow release of ~200 m³/s from Alamo Dam limits the potential creation of areas suitable for establishment of new riparian vegetation. However, following releases of the maximum controlled discharge in 1993 and 1995, some areas of channel, seedlings, and saplings were created (Shafroth et al. 1998), and *Populus* and *Salix* now dominate many of these cohorts (Fig. 7a; P. B. Shafroth, *personal observation*). If a management goal were to expand regeneration of pioneer trees, mechanical clearing of selected stands of woody vegetation prior to a managed flow release could be effective (Taylor et al. 1999). If increasing the proportion of *Populus* and *Salix* were a management goal, then releases may be timed and controlled in a manner to favor the establishment of these species over *Tamarix* (Shafroth et al. 1998). Augmenting the supply of *Populus* seed may provide it a competitive edge in mixed, *Tamarix*/*Populus* seedling patches (Sher et al. 2000).

Management of summer flows also will have an important effect on future vegetation along the Bill Williams River. Higher summer flow releases should ensure maintenance of existing vegetation while promoting relatively vigorous growth and perhaps slightly expanded vegetated areas within intermittent reaches. Higher summer flows may maintain existing ratios of *Populus*/*Salix* to *Tamarix*, whereas lower summer flows could increase the proportion of *Tamarix* and to a lesser extent *Salix* (Busch and Smith 1995, Shafroth et al. 2000).

The above flow management considerations have certain limitations. In the long term, managed flows are unlikely to maintain current quantities of *Populus* and *Salix* in the Bill Williams River bottomland, as many areas will likely succeed to later seral stages or be eliminated by fire. Controlled streamflows, however, can be used to promote periodic regeneration and continued survival of pioneer vegetation in a portion of the bottomland. The ability to manage vegetation through controlled flow releases would benefit from further study of streamflow–vegetation interactions, including the influences of monsoonal floods and different multiyear flow sequences (Hooke 1996), as well as implementation of experimental flow releases in conjunction with well-planned, interdisciplinary research and monitoring (Molles et al. 1998, Schmidt et al. 1998).

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INSTREAM FLOW MODELS FOR MIXED DECIDUOUS RIPARIAN VEGETATION WITHIN A SEMIARID REGION

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ABSTRACT

Empirical evidence from a semiarid watershed of the southwestern United States (Verde River basin, Arizona) indicated that abundance and species richness of mixed deciduous riparian forests varied in a curvilinear and quantifiable fashion as a function of stream flow parameters. Three indicators of riparian abundance—foliage area, stem basal area and stand width—increased most significantly with growing season flow volume, a surrogate indicator of riparian water availability. Tree species richness varied in a bell curve fashion with flood size, with the greatest richness occurring at streams with intermediate flood magnitudes. These instream flow models have management implications for riparian habitats. They suggest that flow volume (and the related attributes of water-table recharge and floodplain soil wetting) is the primary factor regulating riparian vegetation abundance in the Verde River watershed, and provide a first approximation of the extent of riparian loss expected from flow diversion or other types of flow reduction.

KEY WORDS Riparian vegetation Instream flow Flow reduction Semiarid region Arizona

INTRODUCTION

The importance of hydrology to arid land riparian vegetation has long been recognized. Zimmerman (1969) stated that: 'Drainage area, geology, and flow regimen are probably the three most important controls in the distribution of valley-floor vegetation' in the arid south-west of the USA. Recent studies have begun to quantitatively assess the influence of such factors on the composition of semiarid riparian vegetation. In the semiarid regions of Colorado, drainage basin variables (e.g. area and length), channel width and elevation were identified as primary factors related to the composition of riparian vegetation (Baker, 1989). Elevation, stream gradient, stream bearing, valley cross-sectional area and floodplain width have been identified as primary regulators of the composition of riparian vegetation in semiarid Arizona and New Mexico (Larkin, 1987; Szaro, 1989). These studies did not directly assess the role of stream discharge on riparian vegetation, but they imply its importance, as many geomorphic factors, including drainage basin area and channel width, are correlated with discharge (Dingman, 1984). Baker (1989) examined the role of stream discharge in more detail and found that drainage basin variables which were correlated with 'low frequency' aspects of the hydrological regime (e.g. flood flows) were more strongly related to vegetation composition than were drainage basin variables associated with 'high frequency' aspects of the hydrological regime (e.g. base flows).

Fewer studies have focused on factors related to the abundance (e.g. cover, biomass), rather than composition, of arid land riparian vegetation. Water availability is undoubtedly a primary factor limiting riparian abundance in semiarid regions. Many arid land streams are water-limited on an annual or seasonal basis because discharge has such a high degree of temporal flux (Graf, 1982; Poff and Ward, 1989). Small changes in discharge and in riparian water availability should thus produce measurable changes in the abundance of riparian vegetation. Few studies have attempted to quantify this relationship. Evapotranspiration models have been used to estimate the water needs of riparian vegetation stands of varying size (O'Keefe and Davies, 1991), but these models are not very sensitive to changes in water availability because riparian evapotranspiration rates are temporally fairly variable (e.g. Van Hylckama, 1963). Other techniques that

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directly relate the riparian vegetation response to surface flow volume involve dendroecological assessment of the instream flow needs of riparian trees. These site-specific methods have shown that stream discharge is significantly correlated with riparian tree growth and vigour, and thus indirectly with riparian tree abundance, in arid as well as mesic settings (Reily and Johnson, 1982; Stromberg and Patten, 1990; 1991). A region-specific approach adopted by Taylor (1982) indicated that riparian stand width and other community characteristics could be modelled as functions of stream discharge. This approach was facilitated by the abundance of gauged streams in the semiarid California eastern Sierra Nevada and is based on the assumption that stream discharge is a strong correlate of riparian water availability (e.g. of water-table depth). Taylor's model had high significance and was designed for use in predicting the effects of flow diversion on riparian communities within the eastern Sierra Nevada alluvial stream type. Similar models have not been developed for other regions and the robustness of the technique in other areas is unknown.

There is a growing need to understand relationships between hydrological variables and riparian vegetation response (i.e. instream flow relationships) and, as an important extension, to predict the ecological effects of altered flow regimes. Riparian ecosystems in arid and mesic regions alike are under continuing pressure from water development activities including flow diversion, groundwater pumping, interbasin water transfers, 'vegetation conversion', and flood suppression (Brown and Fogel, 1987; Harris *et al.*, 1987; Décamps, 1988; Hughes, 1990; Medina, 1990; Rood and Mahoney, 1990; Howe and Knopf, 1991; Stromberg *et al.*, 1992; Stromberg and Patten, 1992a). For example, water use models for the Verde River in central Arizona project a flow reduction of up to 25 hm^3 per year by the year 2025 (Moore, 1989). The objective of this study was to develop models relating riparian vegetation abundance and species richness to stream discharge for mixed deciduous riparian forests of the semiarid Verde River watershed in central Arizona.

STUDY AREA

The Verde River is one of the primary tributaries of the Gila River, draining a watershed of 17 218 km^2 in central Arizona (Figure 1). The Verde River watershed lies in the Central Mountains physiographic province, a transition zone between the Basin and Range province to the south-west and the uplifted Colorado Plateau to the north-east. The watershed is semiarid and has an average annual rainfall of about 30 cm.

The mid-elevation zone (*ca.* 900–1500 m) of the Verde River watershed was selected as the study area because it has a relatively high number of gauged streams within one riparian forest type (mixed broadleaf series of Interior riparian deciduous forests; Brown, 1982). Ten stream sites were selected within this zone to encompass a wide range of flow volumes. The sites included Verde River main stem sites and first-order or second-order tributaries. All were perennial stream sites except Red Tank Draw, Rattlesnake Canyon, Williamson Valley Wash, and Dry Beaver Creek. The median annual flow volume at the stream sites ranged from 4 to 338 hm^3 per year and the mean annual flow volume ranged from 6 to *ca.* 378 hm^3 per year (Table I). Instantaneous flow-rates of the 50 year return flood ranged from 68 to 2894 m^3/s. The watershed area ranged from a low of 49 km^2 to more than 12 000 km^2.

The riparian zones were vegetated by mixtures of 15 tree species (Table II). The lowest elevation site (Verde River, Camp Verde) was dominated largely by *Populus fremontii* but also supported other riparian species. Stream channel substrates ranged from sand and gravel (e.g. Verde River sites) to boulders (e.g. Red Tank Draw). The valley type ranged from wide alluvial valleys (e.g. Verde River-Camp Verde) to narrower U-shaped valleys. The stream gradient ranged from 0.02 to 0.07 m/m. Study reaches were approximately 500 m in length and were within 6 km of a stream gauge, in areas with the least amount of human disturbance and where the floodplain was least constrained by canyon walls. Nevertheless, most of the riparian areas were disturbed to some extent by cattle or recreationists and thus may not be representative of pristine riparian systems.

METHODS

The research approach involved relating riparian vegetation abundance and species richness data to watershed size and long-term stream discharge data (i.e. median and mean annual flow volume, mean flow

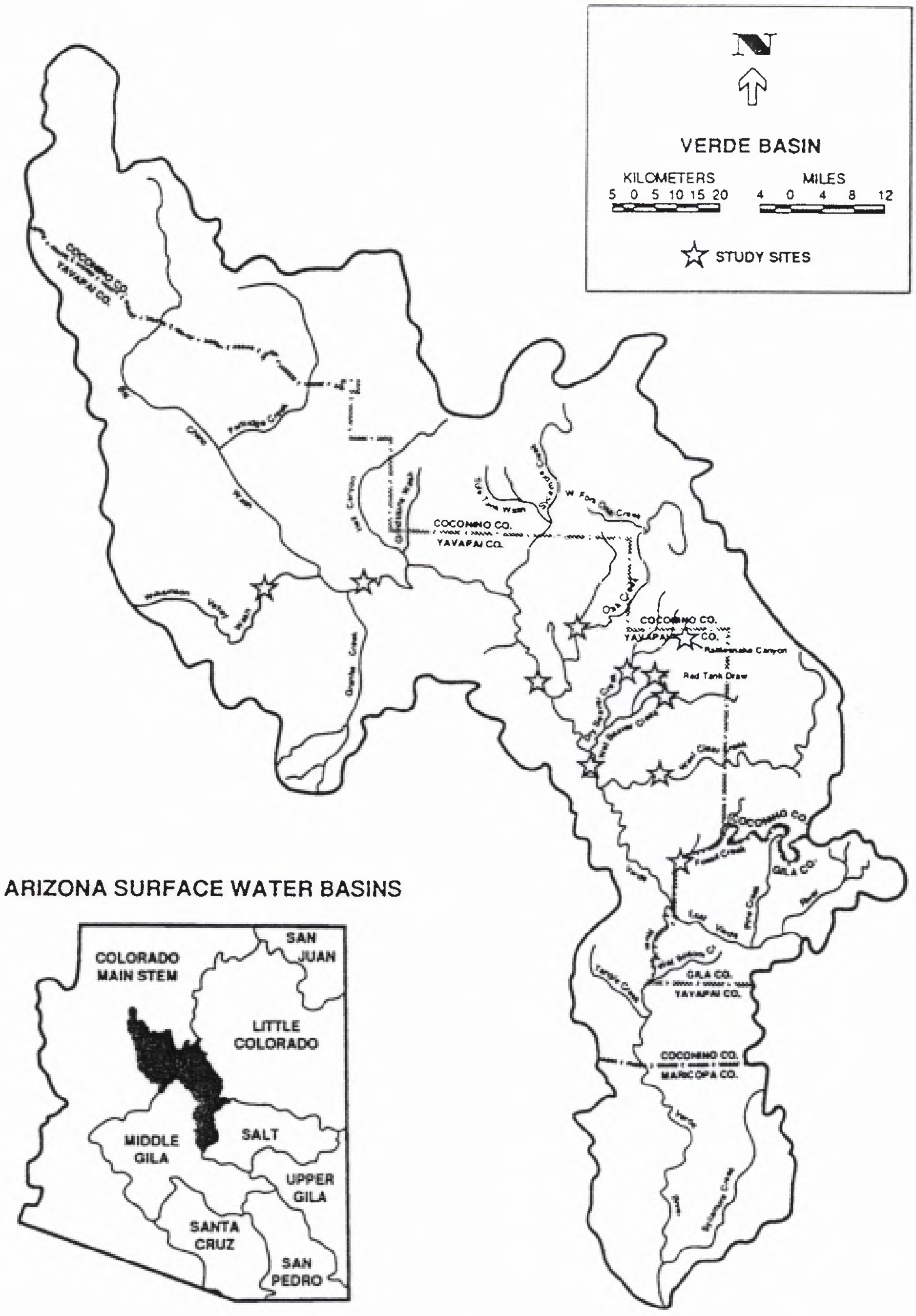

Figure 1. Location of study sites within the Verde River watershed of central Arizona

volume during the April–September season and the maximum annual flow-rate) obtained from United States Geological Survey records. The stream sites had different record lengths because of differences in dates of installation or inactivation of the gauge stations, and thus flow values were based on different spans of years. All but one encompassed at least 20 years of record. The maximum annual flow-rate data sets were used to estimate flow-rates of 10, 25, 50 and 100 year return floods, using a software program that uses log Pearson type III distributions to determine flood frequencies.

Table I. Discharge data for Verde River watershed study sites

Stream site	Elevation (m)	Watershed area (km^2)	Median annual flow (hm^3)	Mean annual flow (hm^3)	Mean seasonal flow (hm^3)	50 year return flow (m^3/s)
Red Tank Draw	1195	49	4·1	6·5	1·5	101
Rattlesnake Canyon	1484	64	5.3	8·0	2·1	68
Williamson Valley Wash	1358	255	5·5	14·0	2·2	246
Verde River—Paulden	1255	5550	25·9	37·2	13·6	359
Wet Beaver Creek	1255	287	27·7	31·5	9·8	209
Dry Beaver Creek	1126	368	32·2	41·4	9·0	412
West Clear Creek	1106	624	45·4	59·8	16·4	432
Oak Creek—Cornville	1058	919	67·0	69·3	24·5	697
Verde River—Clarkdale	1073	8130	143·0	171·5	49·1	1065
Verde River—Camp Verde	876	12 100	338·0	378·0	90·7	2894

Table II. Basal area (m^2/ha) of Verde River watershed riparian tree species by stream discharge class. Values are means and standard deviations for two to three streams per discharge class

			Median annual discharge class (hm^3)			
Scientific name	Common name	Family	3-6	26-32	39·67	143-322
*Tamarix pentandra**	Salt cedar	Tamaricaceae	0·0 ± 0·0	0·0 ± 0·0	0·0 ± 0·0	2·2 ± 2·2
Populus frémontii	Frêmont cottonwood	Salicaceae	0·8 ± 0·6	5·5 ± 6·4	8·3 ± 3·6	12·8 ± 5·5
Salix spp.†	Willow	Salicaceae	0·9 ± 0·7	0·7 ± 0·9	1·2 ± 0·2	0·7 ± 2·7
Prosopis velutina	Velvet mesquite	Leguminosae	<0·1	0·1 ± 0·1	1·3 ± 1·0	0·4 ± 0·4
Fraxinus pennsylvanica ssp. *velutina*	Velvet ash	Oleaceae	2·9 ± 19	1·7 ± 1·6	3·7 ± 0·9	0·1 ± 0·1
Platanus wrightii	Arizona sycamore	Plantanaceae	2·3 ± 17	7·5 ± 6·4	7·7 ± 4·1	<0·1
Acer negundo	Box elder	Aceraceae	0·9 ± 13	0·1 ± 0·1	0·1 ± 0·1	0·3 ± 0·3
Chilopsis linearis	Desert willow	Bignoniaceae	0·0 ± 0·0	0·7 ± 0·9	0·0 ± 0·0	<0·1
Alnus oblongifolia	Arizona alder	Betulaceau	0·0 ± 0·0	3·2 ± 4·6	4·3 ± 2·4	0·0 ± 0·0
Juniperus deppeana	Alligator juniper	Cupressaceae	0·1 ± 0·1	1·0 ± 0·4	2·9 ± 2·6	0·0 ± 0·0
Celtis reticulata	Net left hackberry	Ulmaceae	<0·1	0·8 ± 1·1	0·2 ± 0·1	0·0 ± 0·0
Juglans major	Arizona walnut	Juglandaceae	1·4 ± 1·9	0·1 ± 0·2	0·1 ± 0·1	0·0 ± 0·0
Sapindus saponaria var. *drummondii*	Western soapberry	Sapindaceae	<0·1	0·0 ± 0·0	<0·1	0·0 ± 0·0
Quercus spp.	Oak	Fagaceae	0·1 ± 0·1	0·3 ± 0·4	0·0 ± 0·0	0·0 ± 0·0

*Species names follow Lehr (1978).
†Includes *S. gooddingii* and *S. bonplandiana*.

Riparian abundance was determined by measuring the following descriptors in the summer of 1991: (1) the width of the riparian stand, measured at five random points; (2) the foliage area (leaf area index), measured at 50 random points with a LICOR 2000 plant canopy analyser in the early morning or under shaded sky conditions to minimize errors (Welles, 1990); and (3) woody plant basal area, measured in ten 100 m^2 quadrats randomly located within the riparian zone. Foliage area and stand basal area values were converted to values per linear unit (m) of river length by multiplying the riparian stand width by the average values for each variable as measured in the riparian floodplain. Tree species richness was measured in the same ten quadrats and is expressed as species number per 0·1 ha.

Univariate models relating these riparian descriptors to stream flow parameters, watershed area and elevation were developed with non-linear regression analysis. Models with the highest degree of significance were used to predict the response of a hypothetical Verde River watershed riparian zone to decreased flow volume. Additionally, general trends in abundance of individual tree species with flow volume were summarized by calculating the mean basal area per species (expressed in this instance as m^2/ha of floodplain) in each of four stream discharge classes.

RESULTS

Three descriptors of riparian vegetation abundance—foliage area per unit stream length, basal area per unit stream length, and riparian stand width—varied with high significance as functions of the mean seasonal flow volume and mean and median annual flow volume, and to a lesser extent with flood flow magnitudes (Table III). Relationships between the riparian descriptors and the flow variables were curvilinear. Foliage area, basal area and stand width increased sharply over the low range of flows and then tapered at high flow volumes (i.e. > 150 hm^3/year) (Figures 2-4). Watershed area and elevation explained less of the variance in riparian response than did the flow parameters.

Tree species richness was less significantly related to discharge parameters than were the other riparian descriptors. Tree species was most significantly correlated with flood flow rate, with the 50 and 100 year return flow variables each explaining 63% of the variation in species richness. Species richness increased as the 50 year flood increased to *ca.* 1500 m^3/s, but then decreased for the largest stream site (Figure 5).

Several tree species were present along streams falling within all four discharge classes: *Acer negundo*, *Fraxinus velutina*, *Platanus wrightii*, *Populus fremontii*, *Prosopis velutina* and *Salix gooddingii* (Table II). Of these, only *P. fremontii* had the greatest basal area in the highest stream discharge class. Another large group

Table III. R^2 values between abiotic parameters and riparian vegetation descriptors, for Verde River watershed stream sites

	Mean seasonal flow	Mean annual flow	Median annual flow	10 year return flow	25 year return flow	50 year return flow	100 year return flow	Water shed area	Elevation
Foliage area	0·98*	0·97*	0·96*	0·94*	0·94*	0·94*	0·94*	0·79*	0·82*
Basal area	0·93*	0·88*	0·89*	0·87*	0·88*	0·88*	0·88*	0·57*	0·68*
Riparian stand width	0·98*	0·97*	0·97*	0·93*	0·93*	0·93*	0·93*	0·75*	0·76*
Tree species richness	0·43	0·56*	0·50	0·59*	0·62*	0·63*	0·63*	0·43	0·45

*$p < 0.01$; df = 9.

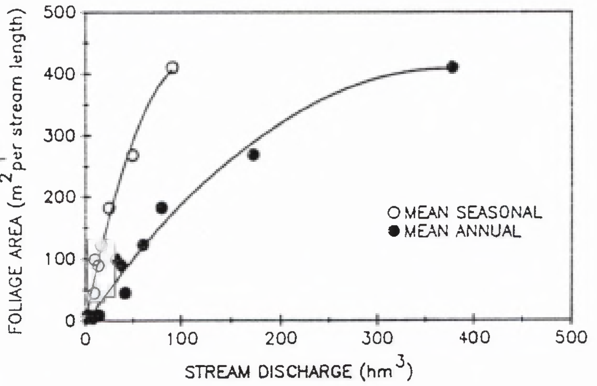

Figure 2. Foliage area (per unit of stream length) as function of mean seasonal (April-September) and annual stream discharge for stream sites in the Verde River watershed. Regression equations are: $y = -2.23 + 7.60x - 0.0034x^2$; df = 9; $r^2 = 0.98$; $p < 0.01$ (seasonal); and $y = -3.97 + 2.21x - 0.0029x^2$; df = 9; $r^2 = \cdot 0.97$; $p < 0.01$ (annual)

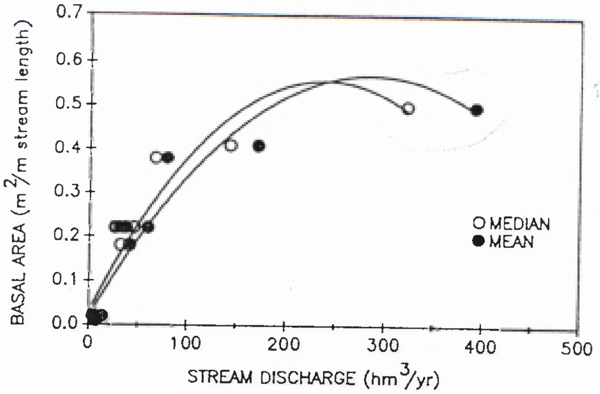

Figure 3. Woody species basal area (per unit of stream length) as functions of median and mean annual stream discharge for stream sites in the Verde River watershed. Regression equations are: $y = 0{\cdot}041 + 0{\cdot}0045x - 9{\cdot}36 \times 10^{-6}x^2$; df = 9; $r^2 0{\cdot}89$; $p < 0{\cdot}01$ (median); and $y = 0{\cdot}027 + 0{\cdot}0039x - 7{\cdot}12 \times 10^{-6}x^2$; df = 9; $r^2 = 0{\cdot}88$; $p < 0{\cdot}01$ (mean)

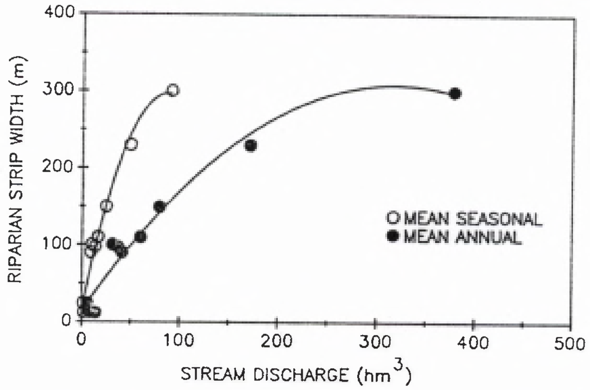

Figure 4. Riparian stand width as function of mean seasonal (April-September) and annual stream discharge for stream sites in the Verde River watershed. Regression equations are: $y = 15{\cdot}1 + 6{\cdot}45x - 0{\cdot}0037x^2$; df = 9; $r^2 = 0{\cdot}98$; $p < 0{\cdot}01$ (seasonal); and $y = 13{\cdot}61 + 1{\cdot}85x - 0{\cdot}0029x^2$; df = 9; $r^2 = 0{\cdot}97$; $p < 0{\cdot}01$ (annual)

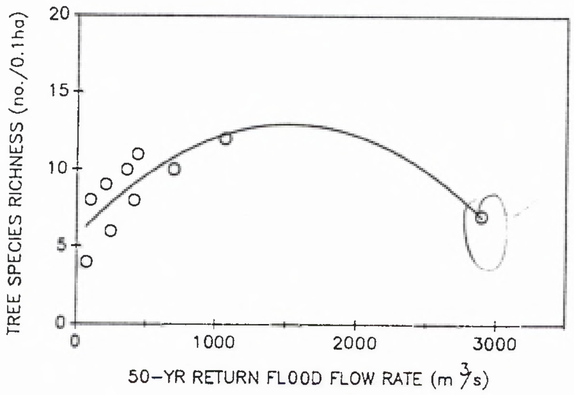

Figure 5. Woody plant species richness (per 0·1 ha) as a function of flow-rate of the 50 year return flood for stream sites in the Verde River watershed. The regression equation is: $y = 5{\cdot}62 + 0{\cdot}0096x - 3{\cdot}16 \times 10^{-6}x^2$; df = 9; $r^2 = 0{\cdot}63$; $p < 0{\cdot}01$

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of tree species was present only along streams in the three smallest discharge classes: *Celtis reticulata*, *Juglans major*, *Juniperus deppeana*, *Quercus* spp. and *Sapindus saponaria*. *Alnus oblongifolia* was unique in occurring only along mid-size streams.

DISCUSSION

This study supports the idea that riparian vegetation abundance in semiarid regions varies in a continual and quantifiable fashion as a function of stream flow volume and, in particular, with growing season flow volume. Three indicators of riparian abundance—foliage area, stem basal area and riparian stand width—increased in a curvilinear fashion with flow volume within the mixed deciduous forest type of the Verde River watershed. These findings parallel those for alluvial streams within the Californian eastern Sierra Nevada (Taylor, 1982) and suggest that vegetation abundance instream flow models are robust instream flow techniques within watersheds.

The instream flow models developed for the Verde River watershed differed in some ways from those developed by Taylor (1982). For example, the riparian stand width increased more sharply over the low range of annual stream flows (from 3 to 30 hm^3) for the Verde River watershed, although the slope of the discharge-stand width curve 'flattened' substantially for high flow streams (those $>100\ hm^3$) in both regions. Discharge explained a much higher percentage of the variance in stand width within the Verde River watershed ($>90\%$) than in the eastern Sierra Nevada (44%). This may be because the Sierra Nevada study sites encompassed a wider geographical area as well as a greater geomorphic diversity. Indeed, incorporation of elevation, stream gradient and an index of channel incision increased the variance explained by discharge alone to 67% in multiple regression analysis of the Sierra Nevada data set (Taylor, 1982).

Two related primary factors—hydrology and geomorphology—may account for the observed increase in riparian abundance with increasing stream size within the Verde River watershed. As stream flow increases, so too does the elevation of the riparian water-table, the width of the riparian zone within which the water-table is accessible by riparian tree roots, and the extent of localized recharge of stream water into floodplain soils (Standford and Ward 1988; Busch *et al.*, 1992). There is growing evidence that the riparian water-table is a primary water source for many riparian trees (Dawson and Ehleringer, 1991; Busch *et al.*, 1992). Given the semiarid setting of the study streams, it is to be expected that increased water availability in the riparian floodplain allows for a greater vegetation biomass. The vegetation decline that occurs in dewatered or partially dewatered arid region streams attests to the strong effect water limitation can have on riparian vegetation (Stine *et al.*, 1984; Smith *et al.*, 1991).

Interactive effects of flood flows must also be considered. Small streams in arid regions often are 'flashier' than are large streams, in the sense that floods of a given return interval on the small streams generally have a larger size relative to the mean daily and annual flows. The combination of destructive high peak flows in conjunction with low mean annual flows may serve to reduce the vegetative cover on small streams.

An alternative hypothesis is that geomorphical features rather than hydrological features regulate riparian abundance within the Verde River watershed. As stream flow increases, so too does the magnitude of the 'low frequency' hydrological events, i.e. flood flows, albeit in a non-linear fashion. Flood flows in some systems play a major part in 'shaping' valley floors and in physically delimiting floodplains from adjacent uplands, by variously scouring or depositing alluvial sediment (Gregory *et al.*, 1991; Hill *et al.*, 1991). Larger streams thus might be expected to have a greater areal extent of sites suitable for the establishment of riparian vegetation. However, certain valley types (e.g. wide alluvial fan types) are not dependent on flood flows for the maintenance of their geomorphology, whereas in others the valley floor has been shaped by non-fluvial historical events such as glaciers or faults (Lotspeich, 1980; Hill *et al.*, 1991). Most of the study sites in the Verde River watershed were in wide valleys or in alluvial fan type areas where the riparian floodplain border showed no appreciably sharp difference in topography (e.g. land surface height above the channel bed) from the adjacent upland. This lends support to the idea that riparian vegetation abundance was limited by water availability rather than by geomorphological factors.

At least two hypotheses can explain patterns in riverine plant species diversity. Some have predicted that vegetational diversity should increase with distance downstream (and thus with river size) as occurs for fish species (Horwitz, 1978) because larger streams provide more 'riparian niches' in terms of inundation frequency, moisture availability, or other variables. Others, however, have predicted that species diversity should be at a maximum in the midreaches because such areas have the greatest spatio-temporal diversity and intermediate levels of disturbance (Vannote *et al.*, 1980; Ward and Stanford, 1983; Sousa, 1984). Empirical studies have shown that neither theory holds true in all circumstances. Taylor (1982) found a continual increase in species diversity with increasing flow volume, with flow explaining 61 % of the variance in diversity. Nilsson *et al.* (1989), however, found a higher total species richness on intermediate flow reaches, consistent with the theory that species diversity is maximized by the spatio-temporal heterogeneity resulting from intermediate levels of disturbance. The pattern of tree species richness in this study provides limited support for this latter hypothesis. Tree species richness was more strongly related to maximum discharge than to other flow variables, and initially increased with maximum flood size, but then decreased for the largest stream site in the Verde River watershed. Beyond a certain threshold of disturbance, floodplain sediments may be reworked by fluvial processes so often that only pioneer species (e.g. *Populus fremontii*) can survive before subsequent destruction by flood waters. This interpretation is limited by the small sample size (one data point) of Verde River watershed sites with very large flood magnitudes, but is substantiated by studies of other western riparian systems (Mills, 1991). Low diversity is also to be expected at the other end of the disturbance spectrum, as evidenced by diversity declines on regulated streams where flooding has been suppressed or altered (Johnson *et al.*, 1976; Furness and Breen, 1980).

MANAGEMENT IMPLICATIONS

Data in this study suggest that flow volume (and related attributes of water-table recharge and floodplain soil wetting) are the primary factors regulating riparian vegetation abundance in the Verde River watershed and similar semiarid areas. Instream models such as those presented in this paper thus provide a first approximation of the extent of riparian loss expected from flow reduction and could be used to estimate the loss of riparian habitat expected from upstream flow diversion, groundwater pumping, or other types of flow reduction. For example, if the mean seasonal flows decrease from 20 to 10 hm^3, the instream flow models predict that the foliage area would decrease from *ca.* 150 to 75 m^2/m, resulting in a 50 % loss of foliar riparian habitat. Or returning to the water use models for the Verde River (Moore, 1989), projected flow reductions of 25 hm^3 per year for reaches with a present mean annual flow of 100 hm^3 would be expected to result in decreases in riparian strip width from *ca.* 165 to 130 m and in foliage area from *ca.* 190 to 150 m^2/m. The greatest decreases in vegetation would be expected on smaller streams, given that the vegetation abundance increased most rapidly with stream discharge over the lower range of stream sizes (e.g. those with a mean discharge of less than 150 h^3/year). This decrease in vegetation would in turn lead to decreases in the densities of birds and other animals, the abundance of which is correlated with riparian biomass (Mills *et al.*, 1991). These data highlight the importance of protecting all sources of riparian water-table recharge, including surface run-off which recharges floodplain aquifers during higher flow periods as well as basin fill aquifers that may recharge floodplain aquifers during baseflow conditions (Gilbert *et al.*, 1990).

The ability of such models to predict riparian loss has not been tested and is based on the assumption that 'space-for-time' substitutions are valid. True validation of the models would require a time series approach of monitoring riparian abundance on streams undergoing flow reduction. Taylor (1982), for example, did sample dewatered streams, and found vegetational 'relaxation' in the sense that less vegetation was present than expected based on historical flows. It must be borne in mind that such 'relaxation' is not immediate. Time lags of the order of years to decades may occur as the riparian ecosystem adjusts to a new set of flow conditions. This is because tree mortality on partially dewatered streams often occurs episodically during periodic low flows years, and because individuals within a stand may vary in their tolerance to drought stress (Petts, 1985; Stromberg and Patten, 1992b). Some trees may thus survive in a stressed condition for many years.

Although admittedly simplistic, these abundance-discharge models could be refined to account for changes in critical hydrological components other than the mean or median flow volume. These refinements should include the magnitude and duration of low or no flow periods, the importance of which is indicated by the loss of riparian vegetation along diverted streams which have had increases in the ratio of mean to minimum flow and in the duration of low flow periods (Stromberg and Patten, 1992b). Flood flows of a given magnitude, frequency and seasonal timing are also important because of their roles in influencing species diversity patterns and in creating opportunities for riparian recruitment. For example, many riparian tree species in the arid south-west of the USA are evolutionarily adapted to germinate after high spring flows, which occur as a result of snowmelt and run-off from winter rains, whereas others germinate after high summer flows, which are driven by monsoonal summer rains (Stromberg *et al.*, 1991). Disruptions in the normal timing and magnitude of flood peaks would thus be expected to decrease recruitment frequency and the abundance of native riparian vegetation. Indeed, such decreases have been observed in some below-dam riparian systems (Fenner *et al.*, 1985; Rood and Mahoney, 1990).

Modelling of changes in individual species abundance in response to changing stream discharge would be equally challenging. Much site-specific research has been conducted on relationships between tree distribution and hydrological variables in mesic regions (e.g. Bell 1974; Nixon *et al.*, 1977; Frangi and Lugo, 1985; Hupp and Osterkamp, 1985; Pautou and Décamps, 1985), and relationships between tree species abundance and water-table depth or soil moisture are beginning to be quantified for the arid south-west of the USA (Richter, 1992; Stromberg *et al.*, 1992; in press). Hydrological modelling of changes in water availability across the floodplain as a function of stream discharge, and ecological modelling of species response to these changes also has been attempted in some mesic regions (Franz and Bazzaz, 1977; Phipps 1979; Pearlstein *et al.*, 1985). Such approaches show promise for riparian ecosystems in the arid south-west of the USA.

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