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ESTABLISHMENT OF WOODY RIPARIAN VEGETATION IN RELATION TO ANNUAL PATTERNS OF STREAMFLOW, BILL WILLIAMS RIVER, ARIZONA

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Abstract: Previous studies have revealed the close coupling of components of annual streamflow hydrographs and the germination and establishment of *Populus* species. Key hydrograph components include the timing and magnitude of flood peaks, the rate of decline of the recession limb, and the magnitude of base flows. In this paper, we retrospectively examine establishment of four woody riparian species along the Bill Williams River, Arizona, USA, in the context of annual patterns of streamflow for the years 1993–1995. The four species examined were the native *Populus fremontii, Salix gooddingii,* and *Baccharis salicifolia* and the exotic *Tamarix ramosissima.* We modeled locations suitable for germination of each species along eight study transects by combining historic discharge data, calculated stage-discharge relationships, and seed-dispersal timing observations. This germination model was a highly significant predictor of seedling establishment. Where germination was predicted to occur, we compared values of several environmental variables in quadrats where we observed successful establishment with quadrats where establishment was unsuccessful. The basal area of mature woody vegetation, the maximum annual depth to ground water, and the maximum rate of water-table decline were the variables that best discriminated between quadrats with and without seedlings. The results of this study suggest that the basic components of models that relate establishment of *Populus* spp. to annual patterns of streamflow may also be applicable to other woody riparian species. Reach-to-reach variation in stage-discharge relationships can influence model parameters, however, and should be considered if results such as ours are to be used in efforts to prescribe reservoir releases to promote establishment of native riparian vegetation.

Key Words: seedling establishment, *Populus, Salix, Tamarix, Baccharis,* streamflow, water table, Arizona

INTRODUCTION

Western North American riparian forests dominated by species of the genus *Populus* have received considerable attention from researchers and land managers in recent decades, largely because of their value to wildlife (Brinson et al. 1981, Ohmart and Anderson 1982) and also because the frequency of recruitment of new *Populus* cohorts has diminished along many western rivers (Johnson et al. 1976, Bradley and Smith 1986, Ohmart et al. 1988, Rood and Mahoney 1990, Johnson 1992, Rood et al. 1995). Research has led to a relatively thorough understanding of the germination and first-year establishment requirements of *Populus* species (for recent reviews c.f., Braatne et al. 1996, Friedman et al. 1997, Mahoney and Rood 1998). A number of studies have related components of the reproductive cycle of *Populus* species to floodplain site conditions produced and maintained by streamflow and associated fluvial processes (Scott et al. 1996 and references therein). In particular, components of the annual pattern of streamflow, or annual hydrograph, are associated with specific stages of *Populus* seedling emergence and growth: flood flows that precede *Populus* seed dispersal produce suitable germination sites (Stromberg et al. 1991, Scott et al. 1997); flow recessions following a peak expose germination sites and promote seedling root elongation (Mahoney and Rood 1991, 1992, Segelquist et al. 1993); and base flows supply soil moisture to meet summer and winter seedling water demand. These relationships between the annual pattern of streamflow and *Populus* establishment have been "packaged" in conceptual and quantitative models (Bradley and Smith 1986, Mahoney

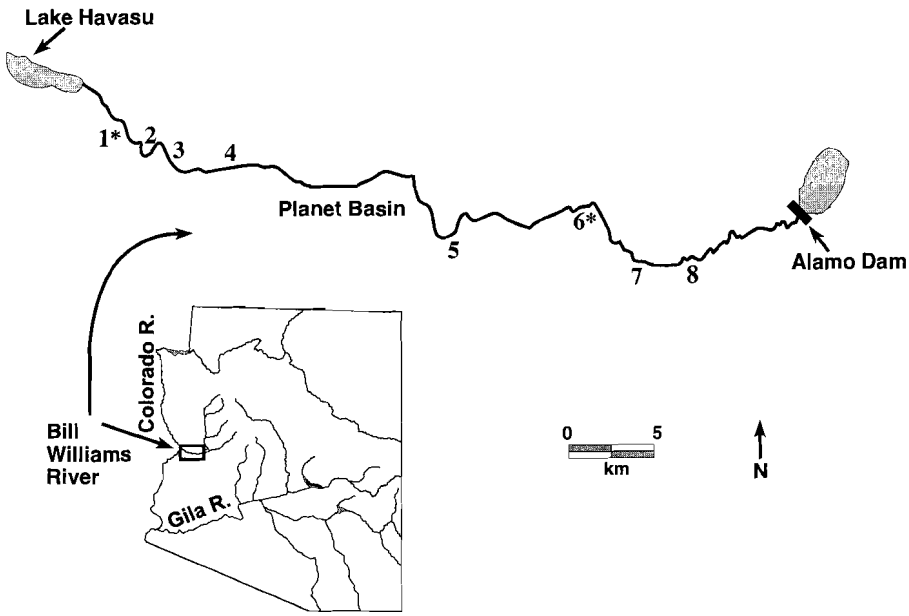

Figure 1. Map of Bill Williams River study area. Numbers along the river are study transect sites. Sites with an asterix are locations where seed dispersal phenology was observed.

and Rood 1993a, Scott et al. 1993, Mahoney and Rood 1998).

Recognition of the links between components of a natural annual hydrograph and the regeneration of *Populus* spp. supports current evidence that "naturalized" flow regimes may facilitate regulated river restoration (Sparks 1995, Stanford et al. 1996, Poff et al. 1997, Schmidt et al. 1998). Thus, models relating streamflow to *Populus* establishment are potentially useful tools in guiding flow prescriptions downstream from dams. For example, the Recruitment Box model (Mahoney and Rood 1993a, Mahoney and Rood 1998), was explicitly used to prescribe managed flows in the Truckee River, Nevada, USA (Christensen 1996) and the Oldman River, Alberta, Canada (Rood et al. 1998) that resulted in abundant *Populus* regeneration. In this paper, we focus on the flow-regulated Bill Williams River in western Arizona where the U.S. Army Corps of Engineers has recommended changes in the operations of Alamo Dam based partially on requirements of desirable woody plants, including *Populus fremontii* S. Watson (U.S. Army Corps of Engineers 1996).

In 1993 and 1995, abundant precipitation and consequent rising reservoir levels behind Alamo Dam resulted in the release of the maximum possible controlled discharge. These large releases and the subsequent recession flows and low flows provided an excellent opportunity to study patterns of woody plant recruitment in relation to the pattern of reservoir releases. In 1994, reservoir releases were low and relatively constant, providing a different set of conditions for study. In this paper, we place surface and groundwater measurements from 1993–1995 within the framework provided by existing *Populus* establishment models to predict recruitment locations of *Populus fremontii* and three other woody riparian species. We then compare these predictions to observed recruitment locations and examine establishment patterns relative to a suite of factors that are known to influence woody riparian seedling establishment.

In this study, we are testing existing models while extending the conditions to which they have normally been applied in two ways. First, we are testing the applicability of models principally generated for a single genus in the semi-arid northern Great Plains to multiple species in the arid Sonoran desert. By doing this, we hope to reveal some generalities of existing models and perhaps identify important species-specific differences. Second, whereas previous discussions and applications of the models have used estimates of river stage and ground-water-level changes over the year at a single reach or cross-section, we examine multiple reaches, representing a range of conditions.

STUDY AREA

The Bill Williams River drains approximately 13700 km^2 in west-central Arizona, USA, with headwaters in the Central Highlands region at approximately 1829 m and downstream reaches in the Sonoran Basin and Range province (Rivers West, Inc. 1990; Figure 1). Principal tributaries are the Big Sandy River, Santa Maria River, Burro Creek, and Date Creek, all of

which join within about 24 km of each other at an elevation of approximately 370 m. The Bill Williams River extends approximately 69.5 km, its upstream-most 6.5 km now consisting of impounded waters in Alamo Lake behind Alamo Dam. Downstream from the dam, the Bill Williams River flows 63 km to its confluence with the Colorado River (Lake Havasu) at an elevation of 137 m. Along its course to the Colorado River, the Bill Williams River passes through canyons it has carved through the Rawhide and Buckskin Mountains, interspersed with alluvial basins including the 9.5 km long Planet Basin, a significant hydrologic control on low flows in the 17.7 km downstream of the basin (Harshman and Maddock 1993). No perennial tributaries enter the Bill Williams River downstream from Alamo Dam. Hydrologic and geomorphic characteristics differ among river reaches, resulting from variation in factors such as valley width, channel geometry, bedrock depth, and woody vegetation density.

Average annual precipitation in the basin ranges from approximately 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). From high to low elevation, upland vegetation in the watershed grades from montane conifer forest to semidesert grassland and interior chaparral to Sonoran desertscrub, the latter of which dominates the landscape adjacent to the Bill Williams River study area (Brown 1982). Riparian vegetation along the Bill Williams River is dominated by several woody species common to low elevation southwestern riparian ecosystems, including *Populus fremontii* (Fremont cottonwood), *Salix gooddingii* Ball (Goodding willow), *Tamarix ramosissima* Ledebour (saltcedar), *Baccharis salicifolia* (R. & P.) Pers. (seep willow), and *Prosopis* spp. (mesquite).

Flow in the Bill Williams River results principally from frontal winter rain events combined with small amounts of snow at the highest elevations, convectional monsoon rain that falls in late summer and early fall, and occasional tropical storms (House and Hirschboeck 1995). Variation both between and within years is great, as in many arid-region rivers (Davies et al. 1994). Between 1941 and 1996, annual flow volumes averaged approximately 5.6×10^7 m^3 and ranged from 9.2×10^5 to 4.3×10^8 m^3 (U.S. Geological Survey Gage 09426000). Since 1968, flow in the Bill Williams River has been regulated by Alamo Dam, which was constructed principally for flood control. Several flow attributes have changed since dam closure, including an order-of-magnitude reduction in peak flows. During the 28 years from 1941–1968 in which reliable pre-dam data are available, median, mean, and maximum annual peak flows were 416, 223, and 1843 m^3 s^{-1} respectively, versus 44, 18, and 198 m^3 s^{-1} during the 28 post-dam years from 1969 to 1996 (U.S. Geological Survey Gage 09426000). Less reliable estimates of high flow events prior to 1941 indicate at least 8 years between 1891 and 1940 with peaks greater than 1980 m^3 s^{-1} (Patterson and Somers 1966, Garret and Gellenbeck 1989). The effect of the dam on high flows is underscored by the fact that post-dam average annual flow volume was 66% greater than pre-dam, reflecting several extremely wet years in the late 1970s, early 1980s, and early 1990s. Low flows have been altered as well, with post-dam releases including periods of low flow much higher than pre-dam conditions, as well as extended periods with zero flow, which was never documented in the pre-dam record.

The Bill Williams River corridor receives little human use. Although extensive alfalfa farming occurred within the Planet Basin historically and as recently as the early 1990s, agriculture is currently limited to a single cotton farm on an alluvial surface that is not inundated by the maximum controlled discharge from Alamo Dam. There is no cattle grazing except for a small area within the Planet Basin. Feral burros are present throughout the study area, but their grazing and browsing impacts appear to be small. Off-road vehicle traffic within the bottomland is minimal.

METHODS

Seed Dispersal

Recruitment of four common woody pioneer species was examined: *Populus fremontii, Salix gooddingii, Tamarix ramosissima,* and *Baccharis salicifolia.* The timing of seed dispersal was observed at 2–3 week intervals at two study transects between 7 February and 13 June 1997 and approximately one month intervals between 13 June and 9 October 1997. One site was approximately 5 km upstream of the confluence with the Colorado River at an elevation of 140 m, while the other site was approximately 40 km upstream at an elevation of 230 m (Figure 1). These observations were used to estimate the beginning and end dates of seed dispersal for each species. *Tamarix* and *Baccharis* had not finished dispersing seed by 9 October; therefore, we used published observations from similar systems to estimate the seed dispersal termination dates for these species (Horton et al. 1960, Warren and Turner 1975).

Vegetation and Physical Variable Sampling

Eight transects, perpendicular to the low flow channel and extending from valley wall to valley wall, were

established in June 1995. Four of the transects were located in a segment of the river between Alamo Dam and Planet Basin, and four were located downstream from Planet Basin (Figure 1). The transects were selected to represent different reaches and hence show variation in geomorphologic and hydrologic characteristics.

At each transect, permanent quadrats were randomly located within different patch types, identified based on a combination of overstory vegetation composition and geomorphic setting (112 quadrats total). The topography of each transect and the elevation of each quadrat and shallow ground-water observation well (see below) were surveyed in January and February 1996. Presence or absence of seedlings that became established in 1995 was noted in 5×20 m quadrats in October 1995, and saplings were noted in January and February 1996. Where saplings were present, five individuals of each species were excavated, a stem cross-section was collected at the estimated germination point, and the depth of sediment deposition was noted. In the laboratory, we sanded the stem cross-sections to 400 grit and determined the year of establishment of the excavated saplings by counting the annual growth rings under a microscope (Scott et al. 1997).

Because germination and establishment of pioneer riparian species has been shown to occur preferentially on bare, competition-free sites, the abundance of woody and herbaceous plants and light availability were measured at each quadrat. Diameter of all woody stems was measured at ca. 15 cm above the ground surface in the 5×20 m quadrats in January and February 1996, and basal areas were calculated. Cover of herbaceous vegetation was measured in the 1×2 m quadrats in March 1996. Photosynthetically active radiation (μmol s^{-1} m^{-2}) was measured approximately 50 cm above the herbaceous vegetation plots using a LI-COR LI-189 Quantum Meter on cloudless days in June 1997. Five measurements were averaged and converted to percent of full sunlight based on full sun measurements taken before and after measurements at quadrats.

At every quadrat, bulk soil samples were taken from two depths (0–30 cm and 30–60 cm), and the distribution of particle sizes in five classes was determined: > 2 cm (boulders, cobbles, coarse gravel), 2 mm–2 cm (gravel), 0.05 mm–2 mm (sand), 0.002 mm–0.05 mm (silt), < 0.002 mm (clay). The volume of particles > 2 cm was estimated visually in the field, gravel content was determined by sieving and weighing, and percentages of sand, silt, and clay were determined using the hydrometer method (Day 1965). For each soil sample, electrical conductivity (ds m^{-1}) of a filtered 1:1 soil:water slurry was measured with a conductivity probe.

Records of reservoir releases from Alamo Dam for years 1993–1996 were obtained from the U.S. Army Corps of Engineers, Los Angeles District. We did not use records from the U. S. Geological Survey gage immediately downstream from the dam because of damage sustained at the gage during high releases in 1993 and 1995. Low flows (defined here as < 3 m^3 s^{-1}) at each of the cross-sections are known to differ from Alamo Dam releases due to spatial variability in influent ("losing") and effluent ("gaining") conditions. For the sites in the upstream segment (transects 5–8), we estimated these differences based on synoptic discharge measurements of low flows from three dates in 1988 and 1994 (Bureau of Land Management, Lake Havasu Field Office, unpublished data). For transects 1–4, we estimated low flows based on synoptic discharge measurements (Rivers West, Inc. 1990) and records from two U.S. Geological Survey gages in this segment (Gage 09426620 and 09426500). These low flow discharges were used in lieu of Alamo Dam releases in our estimates of water-surface elevations on particular dates (see below).

We manually installed ground-water observation wells at seven of the eight transects to monitor water levels. Boulder-dominated alluvium on the eighth transect prevented installation of a well; however, because this transect is closest to Alamo Dam and contains very coarse alluvium, we assumed its water-table level is well-represented by the river stage associated with actual reservoir releases. Water levels in wells were usually measured once per month during 1995 and 1996. To estimate water-table levels for 1993, we simply used river-stage levels at each transect (see below) because releases were fairly high throughout the growing season. To estimate water-table levels for 1994, we used data collected in 1996. Reservoir releases during the growing season in 1994 and 1996 were nearly identical, and antecedent conditions were similar also, as both 1993 and 1995 were years with large releases.

Water-surface elevations during the study period were estimated through the use of hydraulic modeling at each of the cross-sections. We used Manning's equation to estimate stage-discharge relationships based on inputs of slope and surface roughness values (Manning's n) (Grant et al. 1992). We estimated slope from topographic maps (1:24,000) and Manning's n values from published sources (Arcement and Schneider 1989). At each cross-section, the model was calibrated using one observed high flow and one observed low flow. Final simulations were accurate to within 10 cm of the observed values.

Germination Model

For the years 1993, 1994, and 1995, we modeled areas suitable for germination by estimating the zone

containing moist surface soil at the time of seed dispersal for each of the four species at each cross-section. The upper elevation of the zone (relative to the stream thalweg) was estimated as the highest river stage during the period of seed dispersal for a given species. The lower limit was the river stage associated with the final day of seed dispersal. If the elevation of a quadrat was within the range of moist soil during the period of seed dispersal, then germination was predicted to occur. We tested the strength of this germination model as a predictor of seedling establishment using Fisher's exact test of independence (2-tailed) on the 2×2 contingency tables for each species (PROC FREQ, SAS Ver. 6.12). This test was not possible for the 1994 data because of insufficient row and column totals in the contingency tables.

Analysis of Quadrats Where Germination Model Predicted Seedling Presence

The above germination model does not include a number of factors known to influence seedling establishment and early survival, such as the degree to which a quadrat was bare and free from competition, the rate of river stage or water-table decline, the degree of inundation and potential scour by high flows, maximum water-table depth, soil salinity, and soil texture. We used our measures of light, woody basal area, and herbaceous cover to evaluate the degree that a quadrat was bare and free from competition. River stages, rates of water decline, and maximum water-table depth were determined from the hydraulic models and water-table measurements. The maximum rate of water-table decline was calculated as the difference between a quadrat's elevation and the river stage at the end of the spring flow recession divided by the number of days it took to complete this drawdown plus seven days. The seven-day lag was added to account for downstream flow attenuation and bank storage. The calculated maximum drawdown period ranged from 8 to 21 days in 1993 and from 7 to 15 days in 1995. The average soil electrical conductivity in the top 60 cm was used as a measure of salinity. The percentage of silt and clay in the upper 30 cm was determined from the particle-size analysis.

For those quadrats where the model predicted that germination would occur, we tested for differences in the above variables between quadrats where seedling establishment did or did not occur using multiple t-tests (PROC TTEST, SAS Ver. 6.12). For the 1993 and 1995 data, we examined seven variables and therefore used Bonferroni-adjusted significance levels of 0.0071 and 0.0143 (α/# tests; α=0.05, 0.1). We did not conduct these tests for the 1994 cohort because of extremely small sample sizes. In addition, we examined correlations between these variables across all of our plots.

Site Variability

Based on the results of the germination model and the analyses of other factors that may influence seedling establishment, we examined site variability in three variables that were influential in our study: the area containing moist soil at the time of seed dispersal and the basal area and depth to ground water at plots within the moist soil zone. To describe the area containing moist soil, we summarized the river stage and wetted perimeter associated with the 1993 peak flow of 198 $m^3 s^{-1}$ at all eight cross-sections. Within this wetted perimeter, we calculated composite measures of depth to ground water and basal area based on the values for these variables sampled in each patch and weighted by the percent of the wetted perimeter occupied by each patch. In addition, we calculated the width of the bottomland occupied by patches in which seedlings that became established from 1993 to 1995 were present or dominant.

RESULTS

Seed Dispersal

Populus fremontii dispersed seed from approximately 19 February to 13 April at the downstream phenology observation site (Figure 2) and from approximately 26 February to 27 April at the upstream site. *Salix gooddingii* began releasing seed by 22 March at the downstream site and by 29 March at the upstream site. At both sites, one *Salix* tree continued to disperse seed through 20 June. Dispersal of *Tamarix* seed began by 29 March at the downstream site and by 6 April at the upstream site. By 9 October, three of the eight observation trees at the downstream site continued to disperse small quantities of seed, but none of the upstream observation trees were dispersing seed. The seed-release period of *Baccharis salicifolia* did not vary among the two sites, with the first observed dispersal on March 22 and complete termination by June 1. A second flowering period was observed, with some *Baccharis* bearing unopened flower heads on 16 July and some dispersal occurring by 15 August at both sites. On 9 October, flowering and dispersal continued at both sites (Figure 2). Given the relatively small variation in dispersal timing across our sites relative to the inter-annual and intra-population variation that is known to occur at least in *Populus,* we used conservative estimates of seed-dispersal periods in the germination model for the four species and applied these to all eight cross-sections. The dispersal periods used

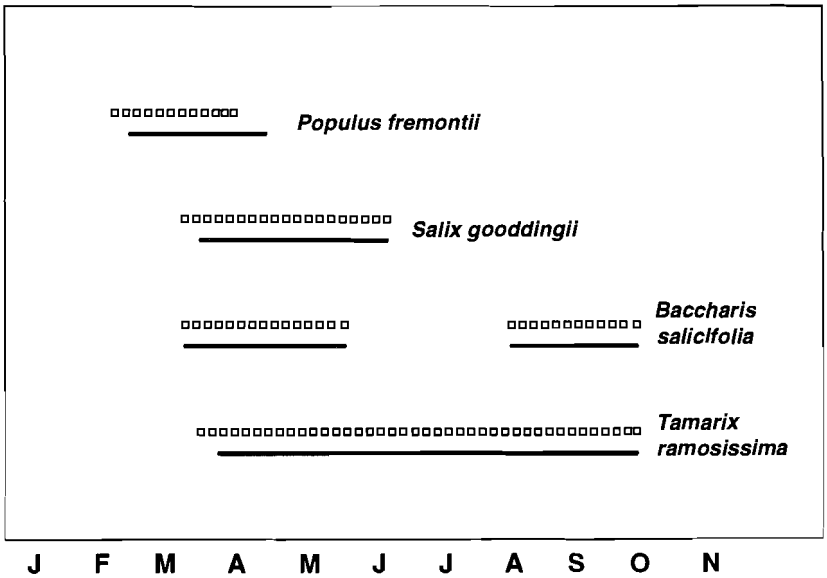

Figure 2. Seed-dispersal periods of four woody pioneer species at two sites along the Bill Williams River, Arizona. Lines span the period of dispersal. The site represented by the upper line of open squares is at 140 m asl, and the site represented by the lower black line is at 230 m asl.

in the germination model were 15 February–30 April (*Populus*), 15 March–15 June (*Salix*), and 15 March–15 October (*Tamarix* and *Baccharis*).

Physical Variables

Reservoir releases during the study period were variable and included periods of high releases in both 1993 and 1995 (Figure 3). In 1993, a period of high flow in mid-January was in the range of 60 to 70 $m^3 s^{-1}$ for about three weeks before rising to a mid-February peak of 145 $m^3 s^{-1}$ and then an annual peak of 198 $m^3 s^{-1}$ in late March, which was the maximum possible controlled release. In early April, flow receded gradually from 21 $m^3 s^{-1}$ to 11 $m^3 s^{-1}$, where they essentially remained through late May. Flow in June through September averaged approximately 7 $m^3 s^{-1}$, except for a brief spike of 28 $m^3 s^{-1}$ in September, before declining to 5 $m^3 s^{-1}$ in October. After October 1993, low flow was rather constant, at either 1.1 or 0.7 $m^3 s^{-1}$ through February 1995. Heavy rains in the Bill Williams River watershed in 1995 resulted in high lake levels and, again, the maximum possible controlled release was implemented, with peaks of 189 and 186 $m^3 s^{-1}$ in mid-February and early March. In contrast to 1993, the recession from high to low releases was very rapid in 1995, and flow was reduced to 1.1 $m^3 s^{-1}$ within a week of the early March peak. Releases remained in the 0.7 to 1.1 $m^3 s^{-1}$ range for the duration of the study period.

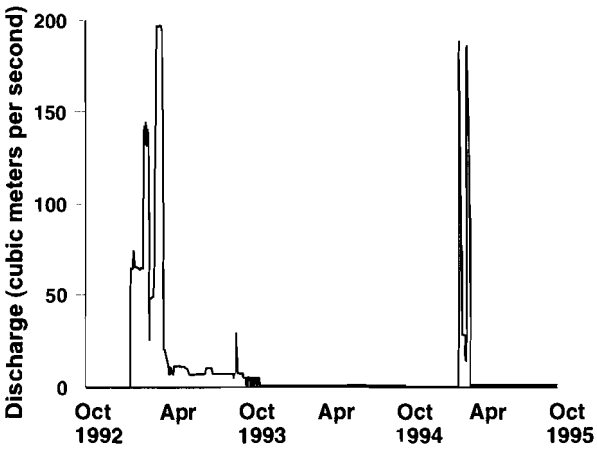

Figure 3. Discharge from Alamo Dam to the Bill Williams River from October 1992 through December 1995. Discharge values were obtained from records of the U.S. Army Corps of Engineers.

Alluvial sediments in the channel and floodplain are dominated by sand, with a smaller percentage of gravels and cobbles. Sites in more upstream reaches contain greater percentages of gravels and cobbles. Sediments on terraces and older floodplain surfaces often have relatively high silt and clay percentages (>50%). Sharp discontinuities in soil profiles (e.g., silt/clay lenses between sand layers) were extremely uncommon, occurring only in approximately 2% of the samples. Soil electrical conductivity values were generally less than 1 ds m^{-1}, with some exceptions.

Germination Model

The germination model was a highly significant and accurate predictor of where seedlings became estab-

Table 1. Proportions of quadrats containing seedlings or saplings in quadrats predicted to support germination or no germination. Predictions were based on the germination model described in the text. Observations of seedling establishment were made in Jan.–Feb. 1996.

Year	Model Prediction	Proportion of quadrats with seedlings			
		Populus	*Salix*	*Tamarix*	*Baccharis*
1993	Germination	7/37**	7/42**	4/43	8/43**
	No germination	3/75	2/70	3/69	3/69
1994	Germination	0/0♦	0/3♦	0/3♦	0/3♦
	No germination	3/112	3/109	3/109	7/109
1995	Germination	14/70***	13/46**	19/48***	20/48***
	No germination	1/42	1/66	0/64	1/64

** $P < 0.05$, Fisher's exact test of independence between predicted germination and observed establishment.
*** $P < 0.01$, Fisher's exact test of independence between predicted germination and observed establishment.
♦ Statistical test not conducted because of insufficient row and column totals.

lished in both 1993 and 1995 (Table 1). For all species in quadrats where germination was predicted to be absent, seedlings (germinated in 1995) or saplings (germinated in 1993) were, in fact, absent approximately 95% of the time. In quadrats where germination was predicted to be present, seedlings or saplings were actually present between 9 and 19% for the 1993 cohort, 0% for the 1994 cohort, and 20–42% for the 1995 cohort (Table 1).

We observed very few quadrats with seedlings that became established in 1994, rendering impossible statistical comparisons parallel to those presented for the 1993 and 1995 cohorts. In 1994, flow releases were relatively constant and low, and the area containing moist soil at the time of seed germination for all species only occurred immediately adjacent to low flow channels. The few quadrats that did contain 1994-established seedlings were uniformly above the predicted moist soil zone, suggesting that the hydraulic model was not as accurate for 1994 flows.

For all years and species, seedlings were actually present but predicted to be absent 30 times (i.e., "false negatives," Table 1). For 1993 and 1995, the modeled moist soil zone tended to be slightly higher than the establishment elevation of the false negatives (1993, mean ± stdev = 0.11 ± 0.24m, n=11; 1995, mean ± stdev = 0.10 ± 0.12m, n=3). For 1994, the modeled germination zone was always lower than the establishment elevation of the false negatives, usually by > 0.5m (1994, mean ± stdev = −0.58 ± 0.19m, n=16).

Analysis of Quadrats Where Germination Model Predicted Seedling Presence

For those quadrats where germination was predicted to occur by the germination model, we observed significant differences between quadrats with and without established seedlings in several of the variables that may be associated with seedling mortality. These analyses were not conducted for the 1994 cohort because of insufficient sample sizes. Establishment tended to occur in quadrats where basal area was low. For the 1993 cohort, basal area was significantly different in quadrats with vs. without seedlings for *Salix* and *Tamarix* (Table 2), and for the 1995 cohort, quadrats with seedlings had significantly lower basal areas for three of the four species (Table 3). In all but one case, the average light value was greater in quadrats with seedlings (Tables 2 and 3), and this difference was statistically significant for *Salix* in 1995. Herbaceous cover was significantly greater in quadrats where *Populus* became established in 1995, and averages were higher in plots containing seedlings for the other three species (Table 3).

For all but one species-year, the maximum rate of water-table decline during the first growing season (i.e., 1993 and 1995) was greater where seedlings were absent, and this difference was statistically significant between quadrats with and without seedlings for all species in 1995. The average maximum first-year rates of water-table decline for quadrats with saplings that germinated in 1993 ranged from 1.2 cm d^{-1} (*Tamarix*) to 4.4 cm d^{-1} (*Populus*), with individual quadrats containing maxima ranging from 2.3 cm d^{-1} (*Tamarix*) to 6.1 cm d^{-1} (*Populus, Salix, Tamarix*). For seedlings that germinated in 1995, the maximum first-year water-table-decline rates ranged from 2.8 cm d^{-1} (*Salix*) to 4.2 cm d^{-1} (*Baccharis;* Table 3). The most rapid estimated rate of water-table decline for a single quadrat where seedlings became established in 1995 was 16.0 cm d^{-1}.

The average maximum water-table levels in the first growing season were shallower in quadrats with versus those without saplings established in 1993 (sampled in 1996), but these differences were not statistically significant (Table 2). In 1993, cohorts of *Populus, Salix,*

Table 2. Average ± standard error values of variables that may influence establishment of woody riparian species in quadrats where seedling presence was predicted based on the modeled presence of moist surface soil in 1993. Within each species, two sets of values are presented: one for quadrats where seedlings were present and one where seedlings were absent. Observations of seedling establishment were made in Jan.–Feb. 1996.

	Populus present	*Populus* absent	*Salix* present	*Salix* absent	*Tamarix* present	*Tamarix* absent	*Baccharis* present	*Baccharis* absent
Number of plots	7	30	7	35	4	39	8	35
Basal Area (m^2/hectare)	9.7 ± 3.5	20.3 ± 4.3	6.2 ± 2.1	18.1 ± 3.9*	2.5 ± 1.5	17.1 ± 3.5**	14.5 ± 8.1	16.0 ± 3.6
Light (% full sun)	61.5 ± 14.2	50.5 ± 7.7	64.6 ± 12.5	56.2 ± 7.3	85.0 ± 12.8	53.5 ± 6.7	54.1 ± 14.8	57.0 ± 7.1
1993 Max. Rate of Water Table Decline (cm/d)	4.4 ± 0.8	4.1 ± 0.4	3.1 ± 0.8	3.9 ± 0.4	1.2 ± 0.4	3.9 ± 0.4	3.3 ± 0.6	3.7 ± 0.4
1993 Max. Water Table Depth (m)	0.82 ± 0.16	1.05 ± 0.08	0.82 ± 0.16	0.98 ± 0.09	0.44 ± 0.09	0.98 ± 0.08	0.83 ± 0.15	0.96 ± 0.09
1993 Max. Flow Depth (m)	0.02 ± 0.02	0.01 ± 0.01	0.02 ± 0.02	0.05 ± 0.02	0.09 ± 0.06	0.05 ± 0.02	0.02 ± 0.02	0.06 ± 0.02
1994 Max. Water Table Depth (m)	1.58 ± 0.14	1.88 ± 0.16	1.44 ± 0.22	1.87 ± 0.15	1.24 ± 0.34	1.82 ± 0.14	2.18 ± 0.33	1.67 ± 0.14
1995 Max. Flow Depth (m)	0.68 ± 0.12	0.54 ± 0.06	0.68 ± 0.12	0.62 ± 0.07	0.98 ± 0.16	0.62 ± 0.07	0.67 ± 0.09	0.65 ± 0.08

** Significant difference between quadrats where seedlings were present vs. absent based on t-test and Bonferroni-adjusted significance level of 0.0071.
* Significant difference between quadrats where seedlings were present vs. absent based on t-test and Bonferroni-adjusted significance level of 0.0143.

Tamarix, and *Baccharis* became established on sites that were from 2 to 175, 2 to 175, 20 to 175, and 2 to 144 cm above the estimated low water level, respectively. The estimated maximum water-table levels in 1994 were considerably deeper than in 1993; however, for no species was this variable significantly different for those sites with or without successful establishment. Established *Populus* and *Tamarix* occurred on sites with second-year (1994) estimated maximum water-table depths of 293 cm; *Salix* on sites up to 202 cm; and *Baccharis* on sites up to 381 cm. For the 1995 cohorts, the maximum depth to water table in quadrats with and without establishment was significantly different for all species except *Baccharis* (Table 3). Seedlings of all species became established at elevations as low as 5 cm above the low water table, and high elevations were 121, 78, 130, and 275 cm respectively for *Populus, Salix, Tamarix,* and *Baccharis.*

The depth of inundation by post-germination high flows was not significantly different between sites where seedlings were present vs. absent. Some 1993-established seedlings survived inundation depths of up to 42 cm during the 28 $m^3 s^{-1}$ flow in September 1993 and 135 cm during the peak flows in the spring of 1995.

Mean soil EC values showed a slight tendency to be higher in plots where seedlings were absent, and this difference was significant for *Salix.* The maximum soil EC in a quadrat where a 1995-established seedling was present was 2.6 ds m^{-1}, whereas several plots with greater values (3.2–4.4 ds m^{-1}) did not contain seedlings. The amount of silt and clay in the top 30 cm of soil tended to be greater in plots without seedlings, and this difference was significant for *Salix* (Table 3).

Several of the variables that we compared between plots with and without seedlings were significantly correlated with one another (Table 4). The correlation analysis was conducted for all plots, not only those predicted to support germination. Hydrologic variables such as rate of stage decline, depth to water table and inundation depth, which are all strongly dependent on relative elevation, displayed the strongest correlations. The percent cover of herbaceous vegetation was significantly correlated with these three hydrologic variables as well, suggesting that greater herbaceous cover tended to occur at lower, wetter positions along the cross-sections. Basal area was negatively correlated with light levels and positively correlated with the percentage of silt and clay in the surface soil. Accordingly, silt and clay percentage was negatively correlated with light. Soil EC displayed a strong positive correlation with silt and clay percentage (Table 4).

Site Variability

We observed considerable variability across sites in several of the variables important for seed germination

Table 3. Average ± standard error values of variables that may influence establishment of woody riparian species in quadrats where seedling presence was predicted based on the modeled presence of moist surface soil in 1995. Within each species, two sets of values are presented: one for quadrats where seedlings were present and one where seedlings were absent. Observations of seedling establishment were made in Jan.–Feb. 1996.

	Populus present	*Populus* absent	*Salix* present	*Salix* absent	*Tamarix* present	*Tamarix* absent	*Baccharis* present	*Baccharis* absent
Number of plots	14	56	13	33	19	29	20	28
Basal Area (m^2/hectare)	6.5 ± 6.5	19.6 ± 3.1	0.2 ± 0.2	21.5 ± 4.9**	0.5 ± 0.5	24.2 ± 5.4**	2.9 ± 1.5	23.3 ± 5.7**
Light (% full sun)	65.6 ± 10.2	51.3 ± 5.7	88.8 ± 3.9	46.0 ± 7.3**	71.9 ± 8.1	48.7 ± 8.0	66.0 ± 8.0	52.1 ± 8.4
Herbaceous Cover (%)	27.4 ± 5.6	6.0 ± 1.7**	24.2 ± 5.8	10.9 ± 3.1	23.2 ± 4.8	11.4 ± 4.3	18.2 ± 4.8	14.6 ± 4.5
Max. Rate of Water Table Decline (cm/d)	2.9 ± 0.4	12.1 ± 0.7**	2.8 ± 0.7	9.1 ± 0.8**	3.5 ± 0.8	9.4 ± 0.8**	4.4 ± 0.8	8.9 ± 0.9**
Max. Depth to Water Table (m)	0.23 ± 0.08	1.48 ± 0.11**	0.21 ± 0.05	1.24 ± 0.16**	0.26 ± 0.07	1.36 ± 0.17**	0.67 ± 0.20	1.10 ± 0.17
Soil Electrical Conductivity (ds/m)	0.8 ± 0.2	0.9 ± 0.1	0.6 ± 0.1	1.1 ± 0.2*	0.8 ± 0.2	1.0 ± 0.2	0.7 ± 0.1	1.1 ± 0.2
Silt and Clay in Surface Soil (%)	11.1 ± 5.8	17.5 ± 2.8	4.6 ± 0.6	19.7 ± 4.4**	11.9 ± 4.8	19.3 ± 4.6	9.1 ± 3.3	21.5 ± 5.0

** Significant difference between quadrats where seedlings were present vs. absent based on t-test and Bonferroni-adjusted significance level of 0.0071.
* Significant difference between quadrats where seedlings were present vs. absent based on t-test and Bonferroni-adjusted significance level of 0.0143.

and seedling establishment. Differences in cross-sectional morphology and channel roughness resulted in variation in high river stages and wetted perimeters associated with the peak discharge of 198 $m^2 s^{-1}$. Transect 1 peaked at 3.35 m above the thalweg, whereas the peak stage at transect 7 was less than half as high at 1.64 m (Figure 4A). The wetted perimeter of cross-sections at 198 $m^2 s^{-1}$ varied from a high of 390 m at transect 1 to a low of 81 m at transect 8 (Figure 4B). Maximum depth to water at a site also displayed considerable site-to-site variation, with some sites maintaining relatively shallow water tables consistently across years (e.g., transects 4 and 7), while water tables at other sites were deeper and more variable across years (e.g., transects 1, 5, and 8; Figure 4C). Basal area values within the transect area wetted by the 198 $m^2 s^{-1}$ flow were highest in the downstream segment, where they ranged from an average of 14.0 to 42.5 $m^2 ha^{-1}$. In the upstream segment, basal areas of the wetted zone were much lower, ranging from 0.2 to 4.9 $m^2 ha^{-1}$ (Figure 4D). Patches in which seedlings and saplings that became established from 1993 to 1995 were present occupied 8.4 to 88 m of transect, and patches in which these cohorts were dominant occupied 8.4 to 46.3 m. Along five of the transects, all patches containing these cohorts were dominated by them, whereas three of the transects also contained patches where seedlings were present but not dominant (Figure 4E).

DISCUSSION

Relationship of Results to Existing Models and Previous Studies

We examined seedling establishment of four woody riparian species across a range of sites, and related seedling presence or absence to variables that have previously been shown to affect establishment of *Populus* spp. in western North American riparian ecosystems. Under the conditions that we observed, the central components of existing models of *Populus* establishment were generally applicable not only to *Populus fremontii* but also to other woody riparian species. Our germination model, which combined water-surface levels and seed-dispersal phenology, was a strong predictor of which sites supported or did not support seedling establishment. This model is similar to one component of the Recruitment Box model in that germination locations are determined largely by the coincidence of seed availability and the availability of moist soil (Mahoney and Rood 1998). Previous research has combined hydraulic models, historical streamflow data, and information on seed-dispersal phenology to compare sites predicted to be appropriate for germi-

Table 4. Correlation matrix for several abiotic and biotic variables that may influence seedling establishment. Values are Pearson correlation coefficients. Correlations were determined for data from all study quadrats (n = 112).

	1995 Drawdown	1995 Depth to H2O	1995 Inund. Depth	Basal Area	Herb Cover	Light	Soil EC	Silt & Clay
1995 Drawdown	1.00							
1995 Depth to Water	0.85*	1.00						
1995 Inundation Depth	−0.79*	−0.72*	1.00					
Basal Area	0.12	0.20	−0.12	1.00				
Herb Cover	−0.51*	−0.48*	0.50*	−0.20	1.00			
Light	−0.09	−0.13	0.01	−0.62*	0.15	1.00		
Soil Electrical Cond.	0.18	0.19	−0.12	0.27	−0.06	−0.28	1.00	
Silt and Clay	0.21	0.26	−0.16	0.36*	−0.17	−0.33*	0.63*	1.00

* Correlation significantly different from zero based on Bonferroni-adjusted significance level of 0.0018.

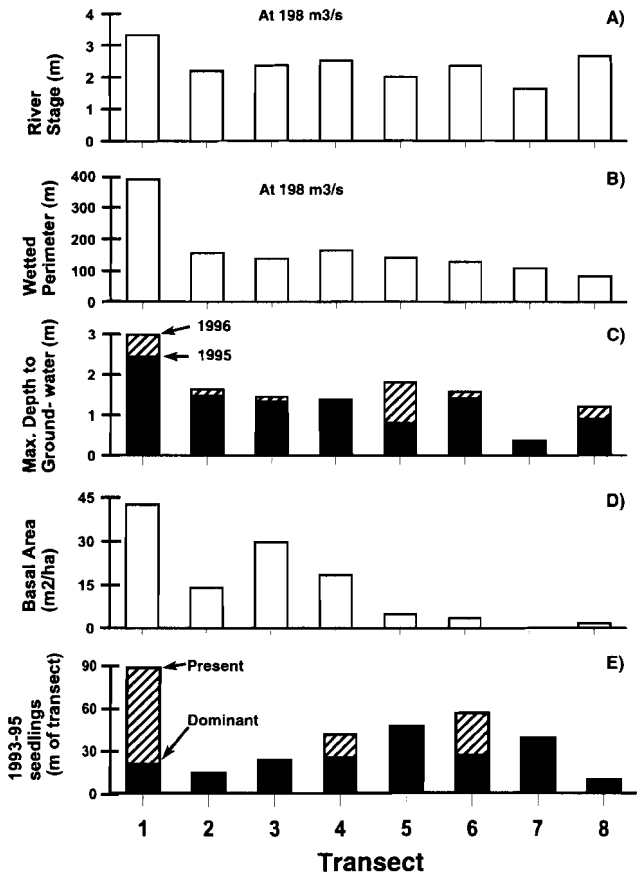

Figure 4. Site variation in variables important for woody seedling establishment: A) river stage (m) above stream thalweg at flow of 198 $m^3 s^{-1}$; B) wetted perimeter (m) at flow of 198 $m^3 s^{-1}$; C) average depth to ground water (m) in 1995 (solid bars) and 1996 (striped bars) within zone wetted by flow of 198 $m^3 s^{-1}$; D) average basal area ($m^2 ha^{-1}$) within zone wetted by flow of 198 $m^3 s^{-1}$; E) distance along transect occupied by patches in which 1993–95 seedlings/saplings were dominant (solid bars) and present (striped bars).

nation and safe from future high flows, with sites where establishment actually occurred (Auble et al. 1997, Auble and Scott 1998).

Other studies have noted the influence of the rate of river stage or water-table decline following germination on seedling establishment (McBride et al. 1988, Mahoney and Rood 1991, 1992, Segelquist et al. 1993). In the Recruitment Box model, Mahoney and Rood (1998) estimate 2.5 cm d^{-1} as a generalized maximum rate of water-table decline, which is similar to our observed maximum rates of decline where seedlings survived for both the 1993 (average 1.2–4.4 cm d^{-1}) and 1995 cohorts (average 2.8–4.2 cm d^{-1}). In experimental studies of *Populus* spp., growth was reduced, but plants survived under declines up to 10 cm d^{-1} (Mahoney and Rood 1991, 1992). Comparisons of specific rates are difficult because different reported drawdown values were averaged over different periods of time, affecting different species growing in different soils under different climatic conditions. Although precipitation during a period of rapid drawdown may permit survival, less than 1 cm of rain fell in our study area during the four months following the steep flow recession in late March 1993 (National Climatic Data Center stations Alamo Dam 6ESE, and Parker 6NE). Therefore, we speculate that seedlings exposed to somewhat rapid rates of decline were likely using water retained in the soil above the water table. In 1995, discharge and associated stages declined more rapidly (185.7 $m^3 s^{-1}$ to 1.1 $m^3 s^{-1}$ for *Populus* or 56.6 $m^3 s^{-1}$ to 1.1 $m^3 s^{-1}$ for the other species in 8–15 days), which likely desiccated germinants and resulted in a significant difference in decline rates between plots where seedlings did and did not become established (Table 3).

A variable related to *Populus* seedling establishment that is easier to interpret across studies than maximum rate of water-level decline is the elevation above the annual low water level. This value integrates two po-

tentially important causes of seedling mortality: 1) removal by future high flows and 2) desiccation due to low soil moisture associated with deep water tables. Based on a synthesis of previous *Populus* studies, the Recruitment Box model includes a successful seedling recruitment zone of 60–150 cm above the annual low water level, which is a compromise between the above two sources of mortality—that is, an elevational range the low end of which is high enough to be protected from frequent high flows that can scour seedlings and the high end of which is low enough to avoid desiccation.

For the 1995 cohort, the maximum depth to water table effectively separated plots with seedlings from those without seedlings for three of four species. In previous studies, *Populus* spp. have been observed to become established anywhere from 20 to 260 cm above the annual low water level (c.f., Mahoney and Rood 1998); however, seedlings at lower elevations may be vulnerable to removal by future high flows. At the end of the first growing season, most of the woody seedlings in our study became established within this range (Tables 2 and 3).

Removal of germinants or seedlings by high flow events subsequent to germination or establishment can be an important cause of seedling mortality in western riparian ecosystems (Stromberg et al. 1991, Stromberg et al. 1993, Stromberg et al. 1997, Auble and Scott 1998, Friedman and Auble 1999). We used depth of flow to estimate the potential for seedling removal. Removal of 1993-established seedlings by high flows in late 1993 (ca. 28 $m^3 s^{-1}$) and in early 1995 (ca. 189 $m^3 s^{-1}$) was apparently not a primary cause of mortality at the quadrat scale in our study. The apparent inability of flows up to 189 $m^3 s^{-1}$ to remove substantial numbers of seedlings illustrates an impact of Alamo Dam, as unregulated flows would have been much larger and more destructive to seedlings.

For seedlings that became established in 1995, the absence of high flows since 1995 has resulted in the continued survival of even those seedlings that became established at floodplain elevations generally considered too low to allow long-term survival. Some of these plants are now quite large (5–15 cm diameter at base), and on sites where bare bars or overflow channels occur near the low flow channel, the resistance to flow of the 1995 saplings could result in movement of the primary channel during a relatively high flow event and, consequently, protect these seedlings from potentially damaging effects of high flows. Saplings in these low elevation locations will continue to grow rapidly, as they have ready access to moisture and a very long growing season. If the absence of high flows continues, their large size alone could enable them to survive future high flows, although these saplings are extremely shallow-rooted.

High stand basal area can inhibit seedling establishment through various integrated mechanisms, including poor germination on accumulated leaf litter (Johnson et al. 1976), reduced soil moisture, and low light (c.f. Table 4). The tendency for seedlings to establish where basal area was low has been observed on other western rivers (Auble et al. 1997).

Trends in the raw data suggest that plots with seedlings contained greater herbaceous cover than those without, a pattern that appears to differ from previous work (Stromberg et al. 1991). Our results may simply indicate that sites favorable for seedling establishment are also favorable for herbaceous vegetation growth and that, in most cases, the amount of herbaceous cover we observed was not large enough to completely exclude seedlings. Another possible explanation is that the herbaceous cover developed after the seedlings had established.

Photosynthetically active radiation was significantly greater in plots with seedlings for only one species-year, but the light levels we measured were generally high, with average values ranging from 46.0 to 88.8% of full sunlight. Many authors have observed that *Populus* seedling establishment tends to occur in high light conditions (Cooper and Van Haverbeke 1990, Braatne et al. 1996), although some studies have revealed relatively high early survival of seedlings growing in shady conditions (Shafroth et al. 1995a). Even where early survival occurs in shade, longer term survival may be reduced because low light conditions can inhibit woody riparian seedling growth (Sacchi and Price 1992, Shafroth et al. 1995a).

Electrical conductivity of surface soil was generally low in our study quadrats, and this variable appeared to be a weak determinant of seedling establishment success. High soil salinities can limit riparian seedling establishment and growth (Jackson et al. 1990, Shafroth et al. 1995b), and the reduced flushing of floodplain soils along regulated rivers can lead to elevated salinities (Ohmart et al. 1988). Soil salinity is generally higher in soils composed of large proportions of silt and clay (Table 4), whereas soils in our plots were generally coarse-textured. Soils relatively high in silt and clay tend to have relatively high water holding capacity, which was implicated in lower seedling mortality at sites along the Green and Yampa Rivers (D. J. Cooper pers. comm.). Trends in our data suggest that seedlings generally established on sites with less silt and clay, implying that these seedlings are likely relying largely on water at or near the capillary fringe. *Tamarix* has previously been observed to establish preferentially on sites with high proportions of silt and clay (Everitt 1980), which we did not observe.

Species Variation

The timing of seed dispersal, relative to the pattern of annual flow, is a critical component of *Populus* establishment models because of the short seed-viability period and the need for seed to germinate on a moist site. The long dispersal window of *Tamarix* has been implicated in its successful invasion of western riparian ecosystems (Horton et al. 1977, Everitt 1980). However, the later onset of *Tamarix* seed dispersal has also been observed to inhibit its establishment, as potential germination sites may be occupied by earlier germinating woody and herbaceous plants (Stromberg et al. 1993, Stromberg 1997).

Our results did not show clear species differences in the variables that may influence seedling establishment (Tables 2, 3). However, these species are known to differ in their responses to some variables; therefore, differences may have been detected under other conditions. For example, *Tamarix* seed and seedlings have been shown to be more salt-tolerant than *Populus* and *Salix* (Jackson et al. 1990, Shafroth et al. 1995b). Also, adults of *Tamarix, Populus,* and *Salix* differ in their ability to withstand water stress (Busch and Smith 1995), with *Tamarix* being the most drought-tolerant. Along the Bill Williams River, we have observed apparent drought-induced mortality of *Salix* and *Populus* at sites where *Tamarix* and *Baccharis* individuals have survived.

Our results suggest that *Baccharis* may differ in its establishment requirements. For example, our data indicate that *Baccharis* can establish on sites with deeper first (1995; Table 3) and second (1994; Table 2) year water tables and in plots with greater basal area (Table 2). We speculate that *Baccharis* may have different seed-germination requirements as well as lower water requirements than the other species. At least one previous study provides some support for these speculations (Horton et al. 1960), although a thorough understanding of the autecology of *Baccharis* is lacking.

Flow Management Implications

Our results have important implications for prescribing reservoir releases to promote riparian tree establishment and for determining reasonable expectations for the outcomes of the flow prescriptions. The timing of peak and recession flows relative to differences in seed-dispersal phenologies can result in spatial separation of species when new substrate is exposed during flow recessions (Stromberg et al. 1993, Zentner and Talley 1993). Our phenology observations suggest that, on the Bill Williams River, a flow recession beginning in early March could result in seedling zones with only *Populus*. As flows continue to decline through the spring and summer, however, more bare sediment would be exposed, which can be colonized by later dispersing species such as *Salix, Tamarix,* and *Baccharis*. If a zone of undesirable vegetation (e.g., *Tamarix*) became established below the *Populus* zone, then raising flows late in the growing season to inundate these seedlings could be an effective control measure (Gladwin and Rolle 1998).

Our results suggest that the effectiveness of prescribed flows is likely to be enhanced by a knowledge of reach variation in stage-discharge relations, wetted perimeter, water-table depths, and basal area. Understanding this spatial variation can lead to flow prescriptions that provide conditions favorable for seedling establishment along reaches where recruitment of new woody plant cohorts is a management priority. Conversely, use of a single cross-section or site to determine flow prescriptions may provide an unrealistic representation of the range of conditions present, thereby limiting the effectiveness of managed flows for the river as a whole.

Along a regulated river, even carefully managed flows are unlikely to supply the full degree of natural functions provided by unregulated flows (Ellis et al. 1996, Schmidt et al. 1998). These limitations may simply need to be recognized and accepted, or there may be other actions that can be taken to mimic the missing function. For example, in densely vegetated reaches, even the maximum possible, post-dam discharge of the Bill Williams River is not large enough to result in geomorphologic change that would produce extensive new bare areas ideal for seedling establishment. Removal of overstory vegetation from densely vegetated areas, in conjunction with prescribed flows to provide favorable hydrologic conditions, could be used to enhance seedling establishment (Friedman et al. 1995).

Development of a single flow regime to promote recruitment of woody riparian vegetation will likely be most effective for particular species within certain reaches. Maintenance of healthy populations of various species throughout a dam-regulated river system would likely require implementation of a greater variety of flow prescriptions over a multi-decadal time scale (Poff et al. 1997, Toth et al. 1998). Managing for variability of key processes over large space and time scales is at the heart of ecosystem management (Christensen et al. 1996) and should help avoid potential pitfalls and criticisms of single-species management.

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