

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 m³/s vs. 148 m³/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 m²/ha vs. 10.7 m²/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 1998a, Shafroth et al. 2000), both of which tend to retard vegetation development (Zimmerman 1969, Stromberg 1998a). 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

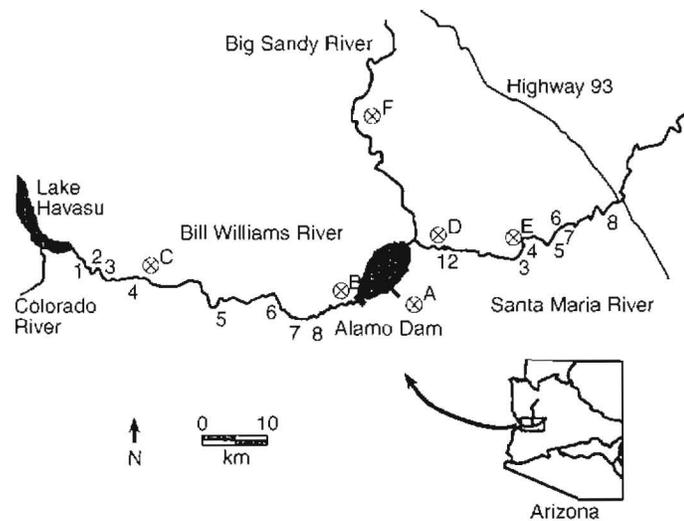
riparian forests (Ohmart and Anderson 1982, Saab 1999).

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 1998a, 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 1998a, 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 1998a). 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; ⊗ symbols 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) #09-26500, 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 km² 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 km², and the Big Sandy River drains ~7278 km² (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 × 10⁶ m³. 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 m³/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 m³/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 ($\sim 19 \times 19$ 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 ARC/INFO) 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 <i>Populus</i> and/or <i>Salix</i> dominant and other woody species subdominant. 3) Woody vegetation on floodplain surface. Total cover 2–50%, with <i>Tamarix</i> dominant and other woody species subdominant.
Dense floodplain vegetation	1) Woody vegetation on floodplain surface. Total cover >50%, with <i>Populus</i> and/or <i>Salix</i> dominant and other woody species subdominant. 2) Woody vegetation on floodplain surface. Total cover >50%, with <i>Tamarix</i> dominant and other woody subdominant.
Sparse terrace vegetation	1) Woody vegetation on high floodplain or terrace. Total cover 2–50% with <i>Prosopis</i> dominant. 2) Woody vegetation on high floodplain or terrace. Total cover 2–50% with xeric riparian shrub species (e.g., <i>Hymenoclea monogyra</i> , <i>Tessaria sericea</i> , <i>Atriplex</i> sp., <i>Lycium</i> sp.) dominant.
Dense terrace vegetation	1) Woody vegetation on high floodplain or terrace. Total cover >50% with <i>Prosopis</i> dominant. 2) Woody vegetation on high floodplain or terrace. Total cover >50% with xeric riparian shrub species (e.g., <i>Hymenoclea monogyra</i> , <i>Tessaria sericea</i> , <i>Atriplex</i> sp., <i>Lycium</i> 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 ARC/INFO 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 fre-

quency 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) = $-2.136 + 0.86 \times$ (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*, *Hy-menoclea*, *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* in-

dividuals, 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 greggii*) 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

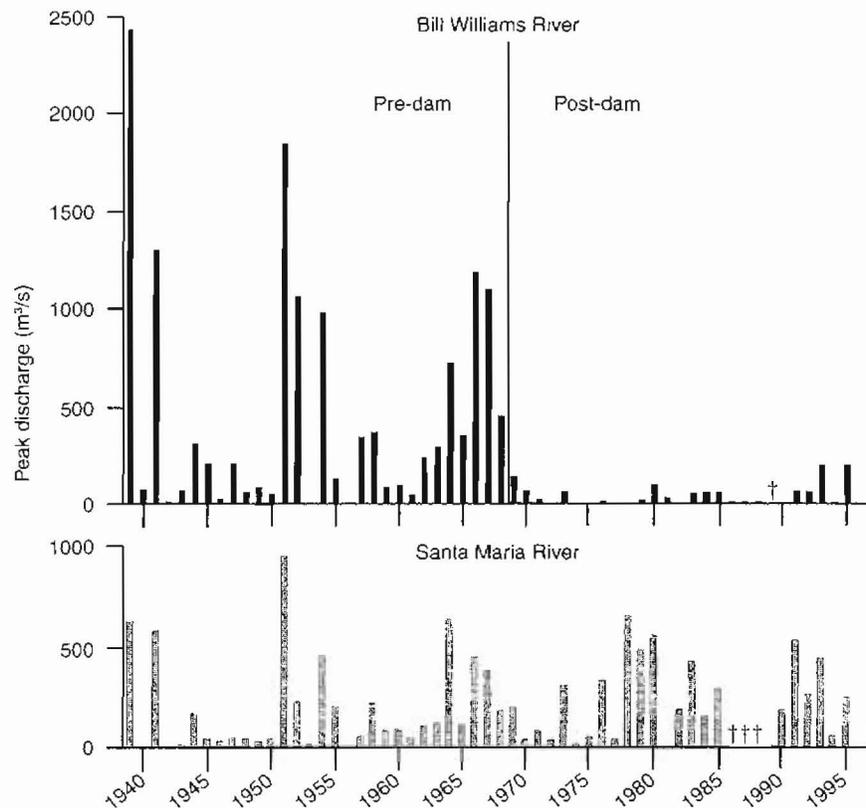


FIG. 2. Annual flood series, Bill Williams and Santa Maria rivers. Data are from the following USGS stream gages. #09426000, Bill Williams River near Alamo, Arizona, 1939–1968; #09426000, Bill Williams River below Alamo Dam, Arizona, 1969–1997; #09425500, Santa Maria River near Alamo, Arizona, 1939–1966; #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 \pm 1 SE).

Streamflow variable	Pre-dam difference	Post-dam difference	df	<i>t</i>	<i>P</i>
Peak instantaneous flow (m ³ /s)	238.1 \pm 81.5	-183.9 \pm 36.7	28.3	-4.65	<0.0001
Average flow, October–April (m ³ /s)	2.3 \pm 1.0	2.5 \pm 1.4	25.9	0.94	0.36
Average flow, May–September (m ³ /s)	0.5 \pm 0.1	2.3 \pm 1.0	26.6	2.43	0.02

Notes. We used *t* tests to compare 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 log₁₀-transformed data.

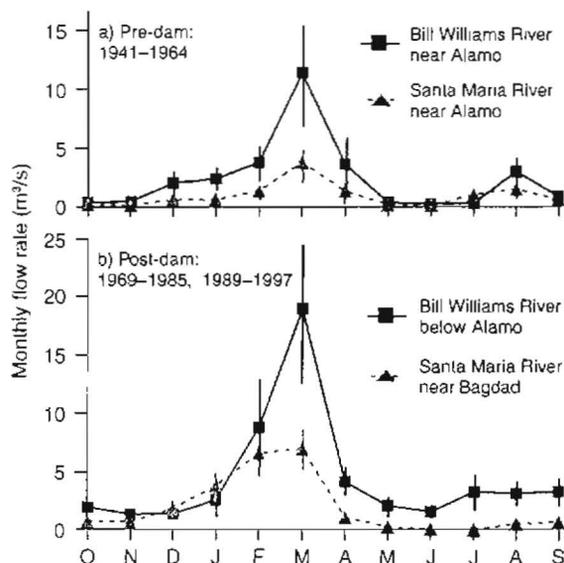


FIG. 3. Monthly flow comparisons, Bill Williams and Santa Maria rivers, Arizona (means \pm 1 SE). Keys refer to names of USGS gaging stations where data were obtained (see Fig. 1). Data from the period of dam construction (March 1965–July 1968) are excluded, as are water years 1986–1988 when data were 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 m³/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 m³/s during the 5 yr preceding the 1953, 1964, and 1976 photographs and >2.5 m³/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 Mallows' 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 m³/s), 1983 (796 m³/s), and 1993 (2389 m³/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 m²/ha (mean \pm 1 SE) on the Bill Williams

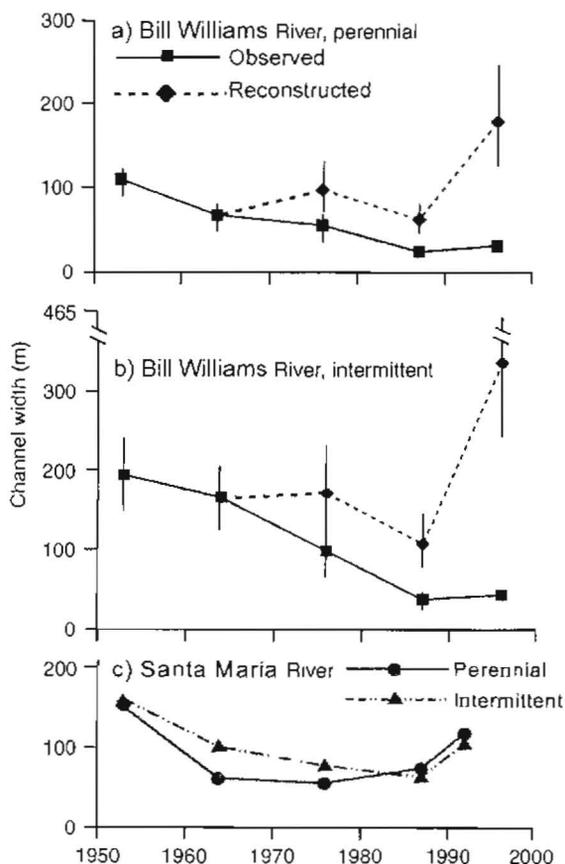


FIG. 4. Observed and reconstructed (predicted) change in channel width through time (means \pm 1 SE). For the Bill Williams River, $n = 4$ for perennial and intermittent reaches, for the Santa Maria River, $n = 1$ for perennial and intermittent reaches. Alamo Dam was constructed between March 1965 and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

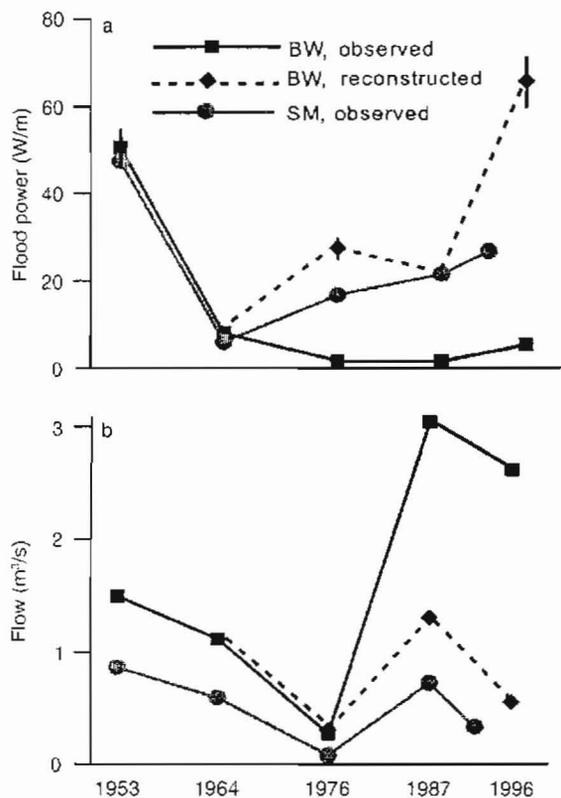


FIG. 5. Values for independent regression variables, Bill Williams (BW) and Santa Maria (SM) rivers, Arizona. (a) Maximum stream power in five years preceding aerial photograph data (means \pm 1 SE, where given). (b) Mean flow from May to September in five years preceding aerial photograph date. Alamo 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 (27737 ± 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 = 14839 ± 5118 stems/ha; Santa Maria River = 5816 ± 1971 stems/ha; $n = 8$, $t = 1.64$, $P = 0.13$; high surfaces,

Bill Williams River = 12898 ± 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 (33725 ± 8682 stems/ha) than on the Santa Maria River (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		Post-dam		<i>t</i>	<i>P</i>	Adjusted <i>P</i>
	Mean	SE	Mean	SE			
Channel	0.29	0.05	0.11	0.02	4.90	<i>0.002</i>	<i>0.01</i>
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	<i>0.05</i>	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	<i>n</i>	<i>t</i>	<i>P</i>	Adjusted <i>P</i>
Basal area (m ² /ha)	<i>Populus/Salix</i>	45.3 ± 7.1	24.1 ± 6.1	13, 28	2.08	<i>0.04</i>	0.15
	<i>Tamarix</i>	23.9 ± 3.7	7.5 ± 2.3	33, 16	3.73	<i>0.0005</i>	<i>0.002</i>
	<i>Prosopis</i>	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)	<i>Populus/Salix</i>	21.3 ± 7.4	16.1 ± 3.9	13, 28	0.70	0.49	0.93
	<i>Tamarix</i>	25.1 ± 3.9	13.7 ± 2.2	33, 16	2.56	<i>0.01</i>	<i>0.04</i>
	<i>Prosopis</i>	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)	<i>Populus/Salix</i>	6.5 ± 2.5	1.6 ± 0.8	8, 8	-1.11	0.30	0.76
	<i>Tamarix</i>	30.6 ± 9.5	7.4 ± 2.3	8, 8	2.36	<i>0.05</i>	0.19
	<i>Prosopis</i>	5.0 ± 2.3	34.2 ± 8.3	8, 8	-3.38	<i>0.009</i>	<i>0.04</i>
	Xeric shrub	33.2 ± 8.1	10.7 ± 3.4	8, 8	2.55	<i>0.03</i>	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.

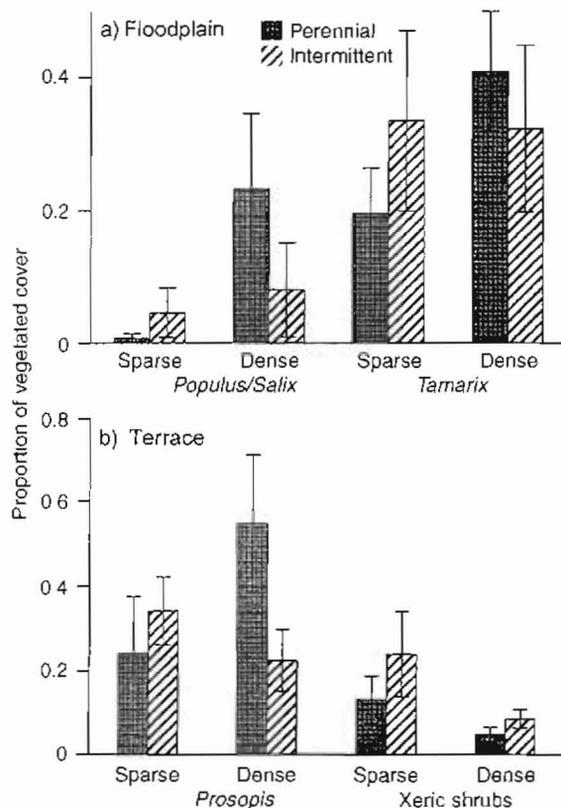


FIG. 6. Proportion of (a) floodplain and (b) terrace vegetation occupied by different cover types in 1996, Bill Williams River, Arizona (means \pm 1 st). "Sparse" cover types were characterized by 2–50% total cover, whereas "dense" cover types were characterized by >50% cover. Data are from aerial photograph 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/m² (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 m³/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 m³/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

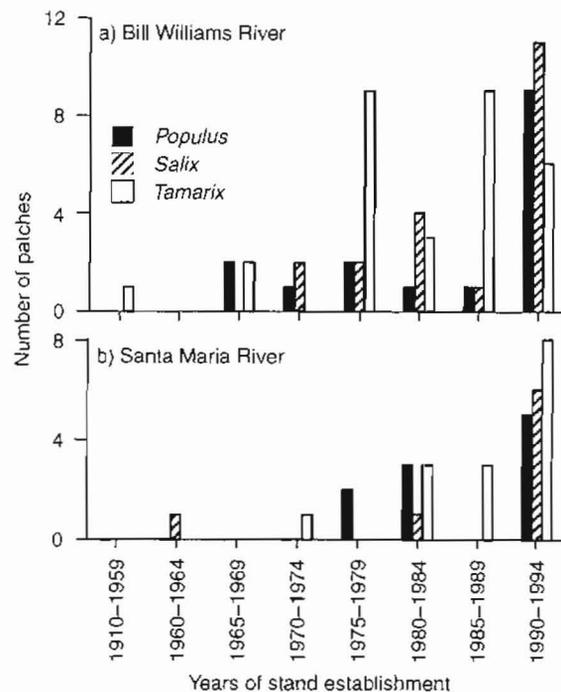


FIG. 7. Age distribution of three dominant tree species within floodplain vegetation patches at study transects along the Bill Williams and Santa Maria rivers, Arizona.

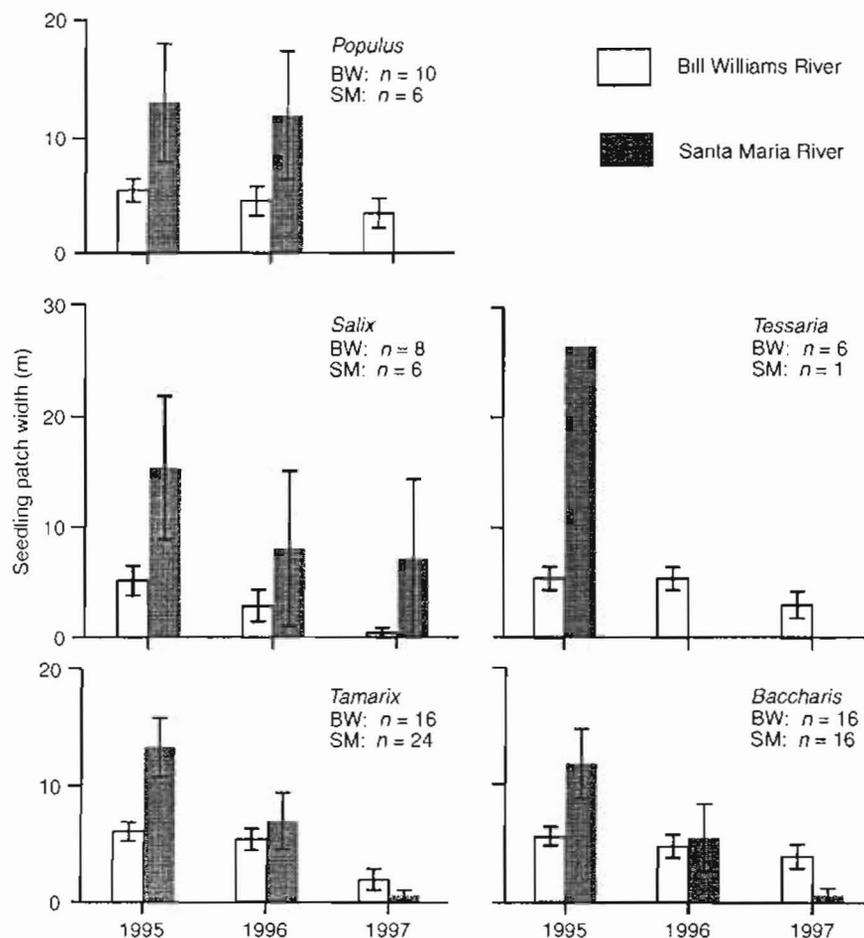


FIG. 8. Width of patches containing five woody species that germinated in 1995 along the Bill Williams (BW) and Santa Maria (SM) rivers, Arizona (means \pm 1 SE). Mean values for all years are calculated as the total patch width containing live seedlings divided by the total number of patches containing 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 1998a). 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-

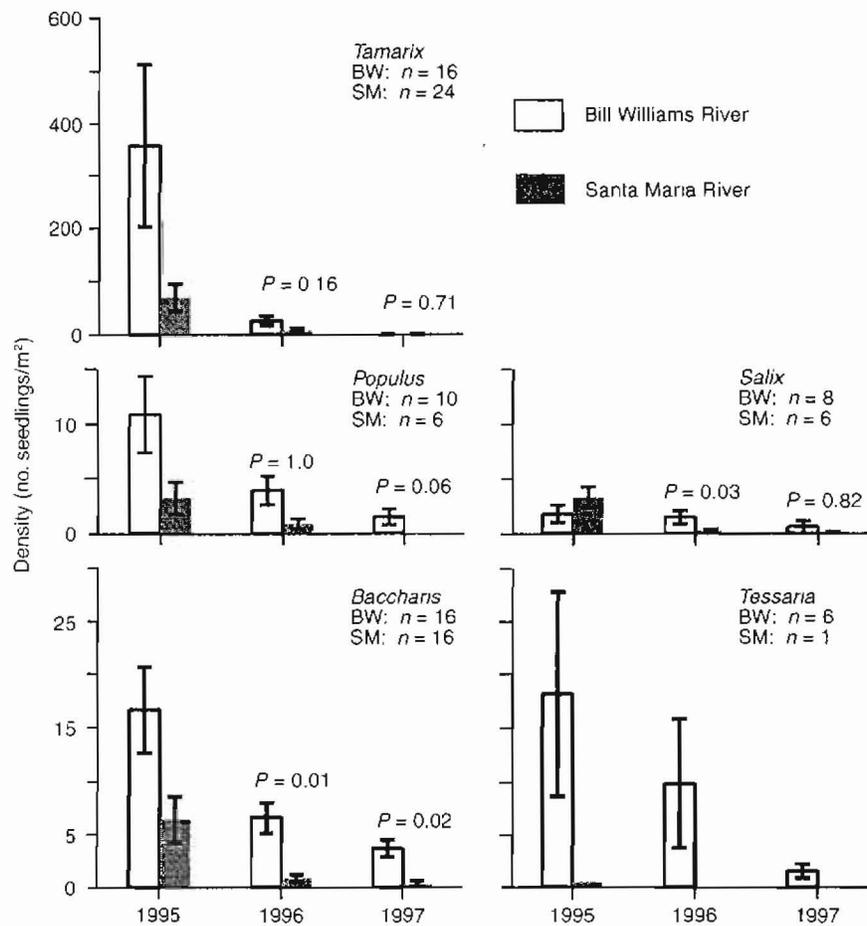


FIG. 9. Density of seedlings of five woody species that germinated in 1995 along the Bill Williams (BW) and Santa Maria (SM) rivers, Arizona (means \pm 1 SE). Note scale difference for *Tamarix*. *P* values are noted above bars from 1996 and 1997 and are based on a multi-response permutation procedure 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 1998b).

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 1998a). 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 1998b), 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 1998b). 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 (Merriam 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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