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The influence of floods and precipitation on *Tamarix* establishment in Grand Canyon, Arizona: consequences for flow regime restoration

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Abstract Decoupling of climate and hydrology combined with introduction of non-native species creates novel abiotic and biotic conditions along highly regulated rivers. *Tamarix*, a non-native shrub, dominates riparian assemblages along many waterways in the American Southwest, including the Colorado River through Grand Canyon. We conducted a tree-ring study to determine the relative influences of climate and hydrology on *Tamarix* establishment in Grand Canyon. Riparian vegetation was sparse and annually scoured by large floods until completion of Glen Canyon Dam, which allowed pioneer species, including *Tamarix*, to expand. Post-dam floods in the mid-1980s were associated with high *Tamarix* mortality but also initiated a large establishment event. Subsequent establishment has been low but continuous with some exceptions. From 1984 to 2006 establishment increased during years of high, late-summer flows followed by years of low precipitation. This combination provided moist surfaces for *Tamarix* establishment and may have caused reduced erosion of seedlings or reduced competition from native plants. Attempts to mimic pre-dam floods for ecosystem restoration through planned flood releases also have affected *Tamarix* establishment. Early (March 1996) and late (November 2004) restoration floods limited establishment, but a small restoration flood in May 2000 followed by steady summer flows permitted widespread establishment. Flood restoration is not expected to prevent *Tamarix* spread in this system because historic flood timing in May–July coincides with seed release. To decrease future *Tamarix* establishment, river managers should avoid floods during peak *Tamarix* seed release, which encompasses the historic spring and early summer flooding period. *Tamarix* dominance may be reduced by early spring floods that initiate asexual reproduction of clonal shrubs (e.g., *Salix exigua*, *Pluchea sericea*).

Keywords Tamarisk · Colorado River · River regulation · Restoration floods · Riparian · Dendroecology

Introduction

Riparian invasions and disturbance adaptations

Along regulated rivers, riverbanks and floodplains are highly susceptible to invasion by non-native plants due to changes in disturbance regimes (i.e., flood frequency, magnitude, timing, and duration) that result

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in reduced recruitment of native species and consequent resource opportunities (D'Antonio et al. 1999; Hobbs and Huenneke 1992; Shea and Chesson 2002). Disturbance adapted plants dominate riparian ecosystems, and therefore disturbances are not the impetus for invasion. Instead, the altered disturbance characteristics create opportunities for plants with different life history traits (often non-natives) to spread. The altered processes and new combination of species creates novel ecosystems (*sensu* Hobbs et al. 2006) that are especially pronounced along impounded rivers (Johnson 2002; Stevens et al. 2001).

The reproductive phenologies of disturbance-adapted riparian woody plants such as *Tamarix*, *Populus*, and *Salix* are intricately tied to flow regime characteristics, particularly the timing and magnitude of floods, because their seeds are short-lived and require open, moist areas for germination. Germination sites must be available during the short period of seed release (approximately 2–3 months for *Populus* and *Salix* and 6 months for *Tamarix*) while seeds are viable, which is often less than 4 weeks (Guilloy-Froget et al. 2002; Karrenberg et al. 2002; Shafroth et al. 1998; Stevens 1987).

Riparian woody plant establishment occurs when rare, timely flood events are of sufficient magnitude to deposit sediments at stage elevations where subsequent floods will not remove seedlings and saplings. The rate of drawdown following floods strongly influences the probability of seedling survival in semi-arid regions. Root growth must equal or exceed the rate of groundwater decline (i.e., recession rate), which is influenced by sediment texture (Mahoney and Rood 1998). Precipitation also can interact with flow regime to provide necessary moisture for seedling establishment (Baker 1990; Johnson 2000). The probability of establishment is greater for riparian phreatophytes on fine-textured substrates with a high water-holding capacity at higher elevations, or on coarser substrates (e.g., cobble bars) that are less susceptible to scouring near the river channel (Scott et al. 1997).

The *Tamarix* invasion in riparian landscapes

In the southwestern US, the composition and abundance of riparian vegetation has changed as a result of flow regime alteration and the invasion of non-native plant species, especially *Tamarix* (Johnson 2002; Turner and Karpiscak 1980; Webb and Leake 2006). *Tamarix* are arborescent shrub species native to Eurasia that have spread prolifically near springs, lakes, rivers, reservoir deltas, and other moist habitats in western North America, Mexico, and Australia (Glenn and Nagler 2005; Stromberg et al. 2007). Several *Tamarix* species and hybrids occur in the Southwest, the most common of which are hybrid *Tamarix ramosissima* Ledeb. X *Tamarix chinensis* Lour. (Gaskin and Schaal 2002). Although the ecological effects of *Tamarix* invasion have been disputed (Stromberg et al. 2009), the dominance of this shrub in many riparian habitats warrants a more thorough understanding of its autecology and interactions with local environmental factors. Research on *Tamarix* invasion may also provide insight into management of other nonnative invasions in which life history strategies are intricately tied with altered disturbance regimes.

The invasion of *Tamarix* spp. is attributed to the broad ecological amplitude (*sensu* Daubenmire 1968) of the species and to changes in disturbance regimes (e.g., construction of dams) coincident with naturalization. *Tamarix* spp. are disturbance-adapted but also have high drought and salinity tolerance (Glenn and Nagler 2005). *Tamarix* has a longer period of seed release than many native shrubs that are adapted to historical spring floods (Howe and Knopf 1991; Roelle and Gladwin 1999; Shafroth et al. 1998). Seed production throughout the growing season may confer a selective advantage to *Tamarix* along regulated rivers that no longer undergo spring floods and have midsummer peak flows when hydroelectric energy demands or agricultural needs are greater. Young *Tamarix* are inferior competitors when compared with native, riparian trees of the southwestern US (Bhattacharjee et al. 2009; DeWine and Cooper 2010; Sher and Marshall 2003; Stevens 1989), but the reproductive phenology of *Tamarix* is well-suited to altered hydrologic regimes that hinder or preclude native shrub establishment (Stromberg et al. 2007). The dominance of mature *Tamarix* in the southwestern US is generally highest along hydrologically altered rivers, whereas native *Populus* dominance is higher along rivers with minimal alteration (Merritt and Poff 2010; Mortenson and Weisberg 2010; Stromberg et al. 2007). However, *Tamarix* establishment may be limited along highly altered rivers due to lack of floods that create bare surfaces and to post-dam sediment coarsening (Merritt and Poff 2010; Stevens 1989).

Previous tree-ring investigations have identified aspects of the hydrologic regime and climate that influenced *Tamarix* establishment along the Green and Yampa Rivers (Birken and Cooper 2006; Cooper et al. 2003). On various segments of the regulated Green River, the maximum flows during, the year prior to, and the year following *Tamarix* germination explained the presence of *Tamarix* recruits. Summer precipitation during July through August also influenced *Tamarix* presence (Cooper et al. 2003). Further downstream along the Green River, high magnitude peak flows followed by low peak flows during the next year initiated *Tamarix* establishment (Birken and Cooper 2006). These conditions correspond with the requirements of *Tamarix* and other common pioneer shrubs for bare, moist sites for germination (provided by high flows) and safety from scour and burial (provided by subsequent low flows).

Grand Canyon case study

The riparian vegetation along the Colorado River in the Grand Canyon National Park serves as an excellent case study for understanding the influence of hydrologic regimes on the *Tamarix* invasion along geomorphically constrained rivers (Fig. 1). On the pre-dam Colorado River, large annual floods constrained by narrow canyons scoured vegetation in the lower riparian zone (Johnson 1991). The completion of Glen Canyon Dam in 1963 reduced flood frequency and dramatically increased riparian vegetation cover, particularly *Pluchea sericea* Nutt., *Baccharis* spp., *Salix exigua* Nutt., and *Tamarix* spp. This increase in riparian habitat differs from other regulated rivers that lost riparian vegetation cover following dam construction as a result of *Populus* population collapse (e.g., Rood et al. 2005). The Colorado River through Grand Canyon is unlike many riparian areas in the Southwest due to the scarcity of riparian trees. Pre-dam photographs of Grand Canyon reveal *Populus fremontii* S. Watson presence at tributary confluences and a few scattered sites along wide reaches of the mainstream, and *Populus* is nearly absent from the river corridor today (Turner and Karpiscak 1980). *Salix gooddingii* C.R. Ball was formerly more common, but the few remaining stands are threatened by beaver foraging, lack of springtime recruitment floods, and post-dam coarsened sand substrata (Mast and Waring 1997; Mortenson et al. 2008; Stevens 1989). Common native riparian shrubs in Grand Canyon include *Baccharis* spp., *Salix exigua*, *Pluchea sericea*, *Prosopis glandulosa* Torr., and *Celtis laevigata* Willd.

Tamarix colonized upper riparian terraces prior to 1963 (Clover and Jotter 1944), but *Tamarix* invasion and establishment on lower riparian zones along the Colorado River began after early post-dam floods in 1965 and 1973 (P. Martin and B. Hayden, written communications) which have been of significantly lower magnitude than pre-dam floods. Currently, *Tamarix* grows along 98% of the Colorado River through Grand Canyon and is the dominant riparian species, often growing in mixed patches with native shrubs (Mortenson 2009). *Tamarix* phenology along the Colorado River corridor varies according to elevation and height above river. In Grand Canyon, seed dispersal peaks in late May and early June, and plants on lower riparian surfaces continue to release seed at a low but relatively constant rate throughout the growing season (Stevens 1989; Stevens and Siemion, in review). This pattern is unlike the bi-modal seed release pattern reported along the lower Gila River by Warren and Turner (1975).

Regulation of the Colorado River dramatically decreased the magnitude of high flows, increased daily flow fluctuations, changed the season of high flows (Fig. 2), and trapped fine sediments behind Glen Canyon Dam. Fine sediments are now provided primarily by tributaries (Schmidt and Graf 1990; Topping et al. 1999). The current flow regime consists of low magnitude flows with seasonally increased magnitude depending on hydropower demands (Fig. 2d). Management of Grand Canyon is complicated by federally endangered species (*Gila cypha* Miller [humpback chub], (*Empidonax traillii extimus* Phillips [southwestern willow flycatcher] and *Oxyloma haydeni kanabensis* Pilsbry [Kanab ambersnail]) that utilize novel habitats and resources associated with the current flow regime (Stevens et al. 2001).

Flood restoration

The natural flow regime concept acknowledges the connection between components of the flow regime (magnitude, timing, frequency, rate of change, duration) and riparian ecosystem function (Poff et al. 1997). Broad acceptance of this concept, along with evident negative effects of dams on native species, has spurred interest in managing toward a natural flow

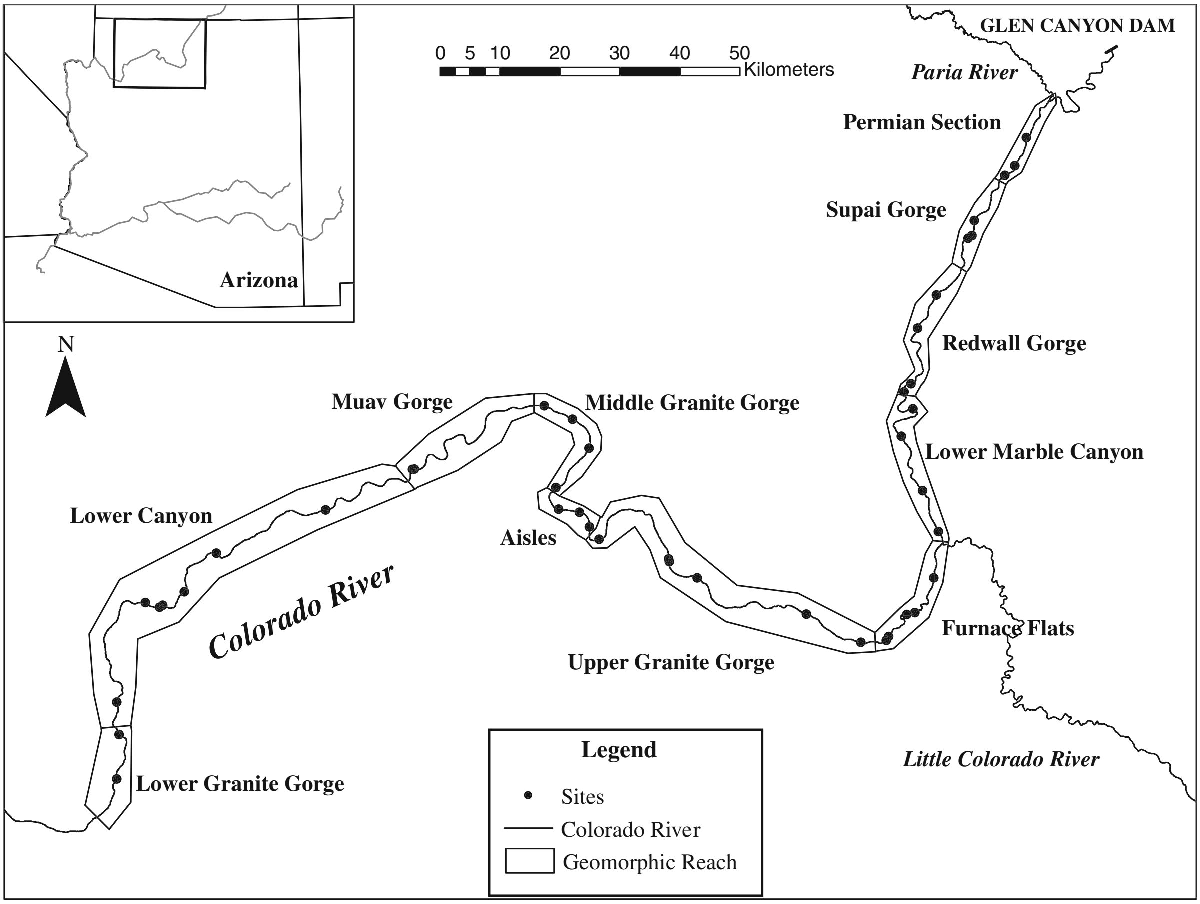

Fig. 1 Map of study area. Sites sampled for the *Tamarix* tree-ring study and geomorphic reaches as defined by Schmidt and Graf (1990) are shown

regime (Arthington et al. 2006; Hughes and Rood 2003; Richter and Thomas 2007). Because many forms of river regulation suppress floods, controlled floods are released along dammed rivers to revive ecological processes that rely on flooding (Shafroth et al. 2010; Stevens et al. 2001; Taylor et al. 2006). These restoration floods are discrete events that cannot encompass all aspects of prior flow regimes (e.g., flood frequency) and do not necessarily aim to restore historic vegetation composition and diversity.

Restoration floods in the southwestern US can be designed to reduce the dominance of invasive plants, particularly *Tamarix* (Stevens et al. 2001). For example, the Rio Grande was intentionally flooded in 1993 and 1994 during the historic pre-dam flood season. Native *Populus* establishment was facilitated by those floods (Taylor et al. 1999), and a more recent survey revealed increased abundance of *Populus* with a decrease or no change in *Tamarix* (Taylor et al. 2006). Burial and scour associated with restoration floods in 2005 and 2006 along the Bill Williams River reduced *Tamarix* seedling stem density more than native *Salix* (Shafroth et al. 2010), a finding consistent with experimental evidence that *Tamarix* seedlings are more susceptible to burial-induced mortality (Levine and Stromberg 2001). A restoration flood in 1996 along the Colorado River in Grand Canyon successfully prevented germination and establishment of *Tamarix*; however, this flood had negligible effect on adult *Tamarix* dominance (Stevens et al. 2001). Here we aimed to assess the past effects of restoration floods on *Tamarix* establishment and persistence in Grand Canyon.

In recent decades, four restoration floods have been implemented by the Bureau of Reclamation through the advisement of an adaptive management working

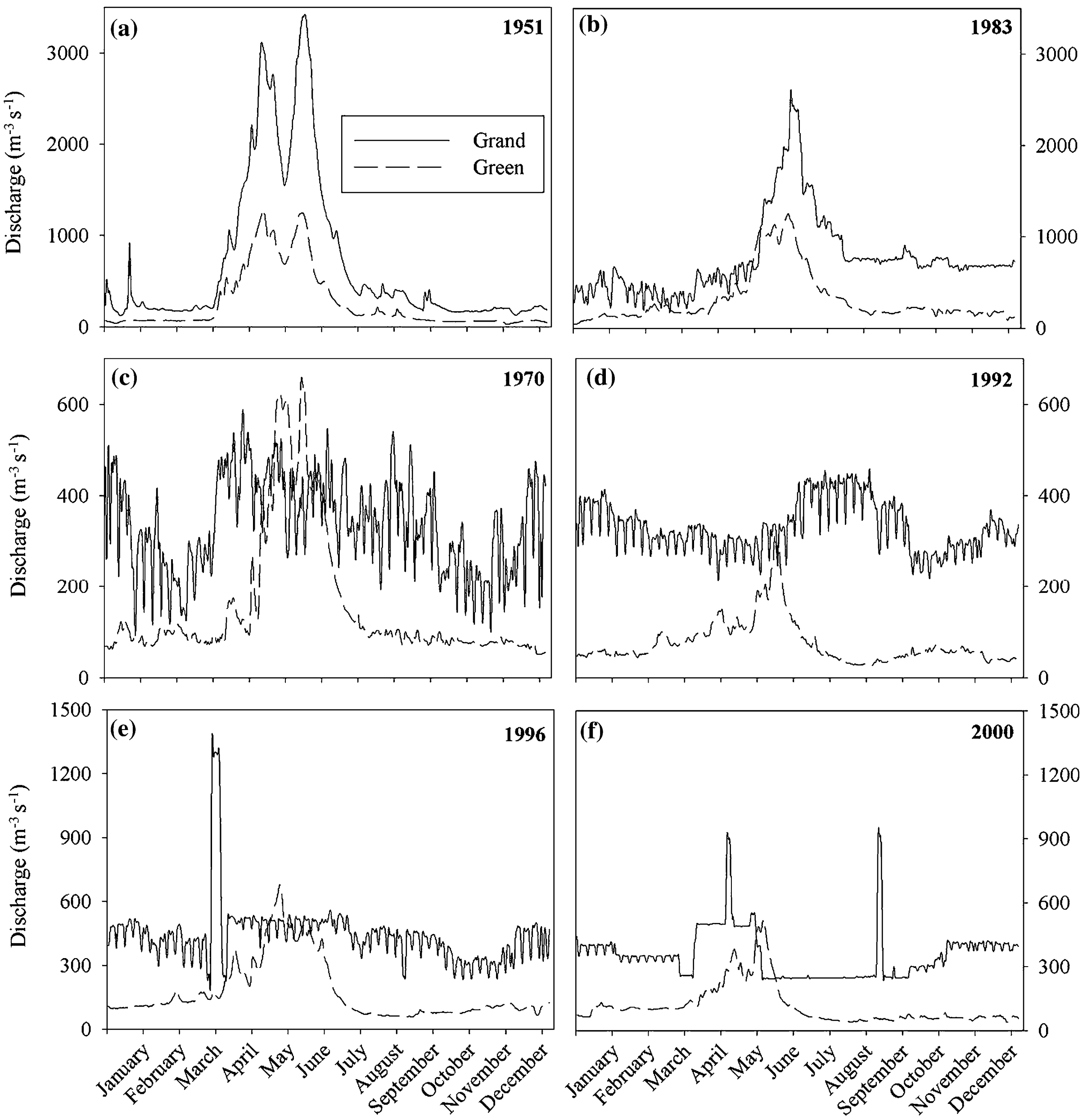

Fig. 2 Annual hydrographs of the Colorado River near Grand Canyon, AZ (USGS gage #09402500) and Green River at Green River, UT (gage #09315000). Note changes in *y*-axis scale. These hydrographs represent flow regimes characteristics of: **a** pre-dam (prior to 1963), **b** post-dam floods (1983–1986), **c** high-fluctuating flows (1965–1982; 1987–1991), **d** low-fluctuating flows (1992—present excluding restoration flood years), **e** restoration floods (1996, 2004, 2008), and **f** steady flows (2000)

group. These floods varied in timing, magnitude, and duration, and were all much smaller and shorter than the average pre-dam annual floods. High magnitude, short duration floods in March 1996 (Fig. 2e), November 2004, and March 2008 were intended to rebuild sandbars by redistributing fine sediments from the bottom of the river channel. Managers also hoped that floods would provide soil moisture to high-elevation, pre-dam vegetation (Stevens et al. 2001). A steady flow experiment was conducted in 2000, with a small, 3-day flood in May followed by low, steady flows from June to September (Fig. 2f). This flow regime was designed to enhance humpback chub recruitment through warming and reduced flow velocity in nearshore habitats (Stevens and Gold 2003). We were particularly interested in how these restoration floods affected the establishment of flood-adapted *Tamarix*.

River managers need to be able to predict the ecological effects of restoration floods (see Shafroth et al. 2010); however, restoration floods have no true experimental controls and erratic replication. Comparisons between regulated and unregulated rivers are often used in riparian ecological studies to discern potential effects of disparate flow regimes (Cooper et al. 2003; Jansson et al. 2000; Stromberg et al. 2007). Because no true controls exist for the Grand Canyon, we compared our results with that of the Green and Upper Colorado Rivers. Comparison of *Tamarix* establishment patterns along the Colorado River and regulated Green and unregulated Yampa Rivers (Birken and Cooper 2006) permitted generalizations about drivers of *Tamarix* establishment across river systems and flow regimes.

Questions

A landscape-level tree-ring analysis of *Tamarix* was used to address the following questions:

1. How have the specific flow characteristics of the regulated Colorado River, including restoration floods, influenced the probability of *Tamarix* establishment and persistence?
2. How have precipitation, temperature, geomorphology, and tributary inputs further influenced the likelihood of *Tamarix* establishment in Grand Canyon National Park?
3. How do establishment and persistence of *Tamarix* along the highly regulated Colorado River downstream of Glen Canyon Dam compare with less-regulated river segments of the Colorado River Basin?

Methods

Tree-ring study of *Tamarix* establishment

Sampling sites were randomly selected by river mile with the constraint that recreation areas and historic southwestern willow flycatcher breeding sites were avoided (Fig. 1). Four field expeditions were conducted in spring and fall of 2006 and 2007, and 43 sites and 409 *Tamarix* individuals were sampled. Sites varied in area to encompassed all geomorphic units present including terraces, sandbars, return-current channels, channel margins, debris fans, and cobble bars (Schmidt and Graf 1990). Three representative trees from all *Tamarix* size classes on each geomorphic unit were selected for tree-ring sampling and excavated with hand tools.

Precise measures of *Tamarix* age required collection of cross-sections from below the germination point (i.e., root crown) to the soil surface. Tree-ring samples were processed as in Birken and Cooper (2006). The maximum number of rings at the root crown revealed the age of the plant. We cross-dated within samples of the same individual but were unable to cross-date among most *Tamarix* individuals. Many samples were impossible to age accurately due to heart rot, insect damage, compressed rings from burial, and inability to access the root crown; these samples were not used in statistical analyses.

Statistical analyses

Because the 1980s floods resulted in high mortality of pre-1983 *Tamarix*, we analyzed the number of sites at which *Tamarix* recruited each year from 1984 to 2006 ($n = 23$ years for all analyses). Hydrologic variables were based on a calendar year, and some variables were calculated using Indicators of Hydrologic Alteration software (Smythe Scientific Software, Boulder, CO). Separate generalized linear regression models were created to define environmental conditions that allowed *Tamarix* to establish. We included annual peak flow the year prior to, during, and following germination (Table 1). Timing of maximum and minimum flows and the magnitude of maximum flow occurring during spring (April–June) and summer (July–September) incorporated the importance of flow seasonality with respect to reproductive phenology. The duration, frequency, and recession rate of flows also were included. We investigated the influence of annual peak flows of major tributaries (Paria and Little Colorado Rivers) which provide fine sediment that is limited in the

Table 1 Explanatory variables used in analyses

Climate (Phantom Ranch, AZ; station #026471)
Total precipitation from May through September
Total precipitation from May through September following year
Mean summer (June–August) maximum monthly temperature
Flow magnitude (USGS gage #09402500)
Annual peak flow magnitude Colorado River near Grand Canyon, AZ
Annual peak flow magnitude of previous year
Annual peak flow magnitude following year
Minimum flow magnitude of 30-day duration[a]
Flow timing
Magnitude of peak flow, July through September
Magnitude of peak flow, April through June
Date of peak flow: days after initiation of *Tamarix* seed dispersal (May 1)
Julian date of annual minimum flow[a]
Tributaries
Annual peak flow magnitude of Paria River (USGS gage #09382000)
Annual peak flow magnitude of Little Colorado River (USGS gage # 09402000)
Rate of change
Recession rate[a]: Median of negative daily differences (fall rate)
Flow frequency
Number of high flow pulses[a]: defined as periods where discharge 25% above median
Number of high flow pulses during 2 year period following germination[a]
Flow duration
Duration of high flow and flood pulses[a]: number of days in which high flow or flood pulses occur

[a] Indicates variables that were calculated with Indicators of Hydrologic Alteration software (Smythe Scientific Software, Boulder, CO). USGS gage and climate data obtained from http://waterdata.usgs.gov and http://www.wrcc.dri.edu

post-dam Colorado River. Climate variables that influence moisture availability (summer maximum temperature and precipitation the year of and following germination) were also included in the statistical models.

Generalized linear models were created for possible combinations of explanatory variables (Table 1), and Akaike's information criterion (AIC) scores were determined for each model using R software (R Development Core Team, Vienna, Austria). We used AICc, an index recommended for small sample sizes (Burnham and Anderson 2002), and Poisson distribution analyses, which are appropriate for right-skewed count data (Ramsey and Schafer 2002). We calculated the relative importance of explanatory variables using the sum of AICc weights for possible models, as demonstrated by Burnham and Anderson (2002). The effect sizes of explanatory variables were summarized using standardized beta coefficients. Nagelkerke pseudo-R^2 values were calculated for the most plausible models with the lowest AICc scores (Nagelkerke 1991).

Results

Influence of hydrology and climate on *Tamarix* establishment and persistence

Of 409 *Tamarix* individuals collected, 149 were accurately aged based on unambiguous evidence of root crown in the sample. An additional 89 samples lacked such evidence but were considered to be approximately aged. We were unable to accurately age many of the pre-dam *Tamarix*, and few trees were sampled that predated the 1980s floods. *Tamarix* sustained high establishment during 1983 through 1986, and 1999 through 2000 and had continuous, low levels of establishment in other years from 1987 to 2006 (Fig. 3). A positive relationship between summer peak flow and *Tamarix* establishment was primarily driven by high establishment from 1984 through 1986 and 1999 through 2000 (Fig. 4a). The association between establishment and annual peak flow was also positive, although a lower proportion of overall variation was explained (Fig. 4b).

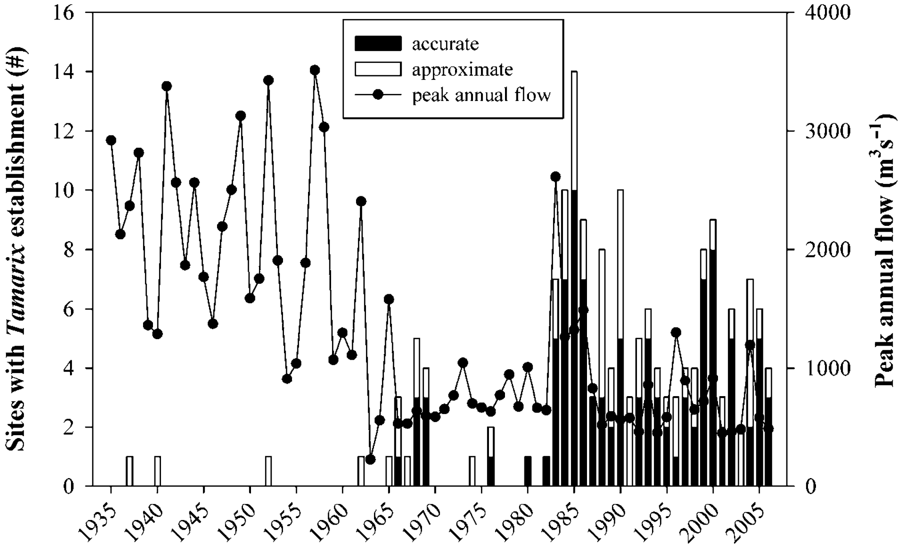

Fig. 3 Number of sites in which approximately-aged and accurately-aged *Tamarix* established by year in Grand Canyon. The peak annual flow recorded by USGS gage #09402500 is also given

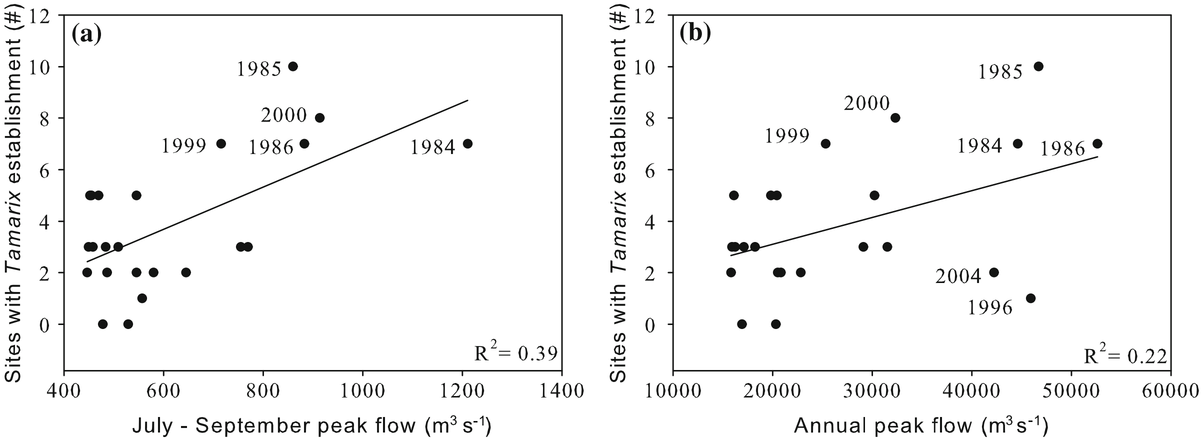

Fig. 4 The number of sites that sustained *Tamarix* establishment in each year from 1984 to 2006 according to **a** July–September peak flows and **b** annual peak flows. Note differences in *x*-axis scale. Restoration floods were conducted in 1996 and 2004

Regression analyses of post-1983 *Tamarix* establishment (1984–2006) demonstrated the overwhelming negative influence of summer precipitation in the year following germination (Table 2). Persistent *Tamarix* establishment was greater in years that had lower summer precipitation the following year. This variable was only influential in additive models that contained measures of flow magnitude (Table 3). High magnitude maximum flows were positively related to the frequency of sites with *Tamarix* establishment (Table 2).

All surviving pre-dam *Tamarix* persisted on upper riparian zone terraces. However, during the post-dam period, *Tamarix* establishment and persistence were documented on every type of geomorphic unit (Fig. 5). Individuals growing on cobble bars and rocky habitats were poorly represented in the tree-ring samples because the tree rings were often unreadable. However, a widespread cohort of *Tamarix* saplings was observed on cobble bars that established during the Year 2000 steady flow experiment (Stevens and Gold 2003). The elevation of *Tamarix* establishment above current river level was high from 1983 through 1986 and gradually decreased in recent years (Fig. 5). Recent low-elevation establishment has occurred primarily on sandbars, channel margins, cobble bars, and debris fans.

Table 2 Relative importance of each explanatory variable or sum of AIC weights (w_i) across models, standardized beta coefficients (β), and confidence intervals for coefficients (CI) for the annual frequency of *Tamarix* establishment across sites

	w_i	β	CI
Climate			
Total precipitation from May through Sept.	0.009	0.018	0.007
Total precipitation from May through Sept. following year	**0.736**	−0.112	0.043
Mean summer (June–Aug.) max. monthly temperature	0.011	−0.050	0.019
Flow magnitude			
Annual peak flow magnitude	0.212	0.110	0.042
Annual peak flow of previous year	0.022	0.089	0.034
Annual peak flow of following year	0.02	0.061	0.024
Minimum flow magnitude of 30-day duration	0.024	0.073	0.028
Flow timing			
Magnitude of peak flow, July through Sept.	**0.466**	0.130	0.050
Magnitude of peak flow, April through June	0.299	0.111	0.042
Date of peak flow	0.014	−0.087	0.033
Date of minimum flow	0.011	−0.032	0.012
Tributaries			
Annual peak flow magnitude of Paria River	0.017	0.043	0.017
Annual peak flow magnitude of Little Colorado River	0.033	0.069	0.026
Rate of change			
Recession rate	0.008	−0.008	0.003
Flow frequency			
Number of high flow pulses	0.024	−0.071	0.027
Number of high flow pulses during following 2-year period	0.009	0.001	0.001
Flow duration			
Duration of high flow and flood pulses	0.019	0.080	0.031

Bold font indicates the two most important variables

Table 3 Comparison of most plausible generalized linear models for *Tamarix* establishment

Variables	AICc	Δ AICc	AIC weight	R^2
Precip (following May–Sept) + peak flow (July–Sept)	96.096	0	0.281	0.60
Precip (following May–Sept) + peak flow (April–June)	96.228	0.132	0.263	0.59
Precip (following May–Sept) + annual peak flow	96.908	0.812	0.187	0.58
Peak flow (July–Sept)	100.910	4.814	0.025	0.29

Models with Δ AICc no greater than 5 of the best model are shown. AIC weights are relative to all possible models. Nagelkerke pseudo-R^2 values are also given

Comparison among river systems

The oldest *Tamarix* established in 1937 or earlier near Cardenas Creek; however, we were unable to determine the accurate age due to rot in the root crown section. This is consistent with the oldest *Tamarix* sampled in the Green River (1938) by Birken and Cooper (2006) and reported in Grand Canyon (Clover and Jotter 1944; Hereford, personal communication). *Tamarix* established and persisted in every year from 1983 to 2006 in Grand Canyon but in only 8 years from 1983 to 2004 along the Green River (Birken and Cooper 2006; Fig. 6).

To decipher potential hydrologic influences on establishment we compared annual hydrographs of the Green River and Colorado River through Grand

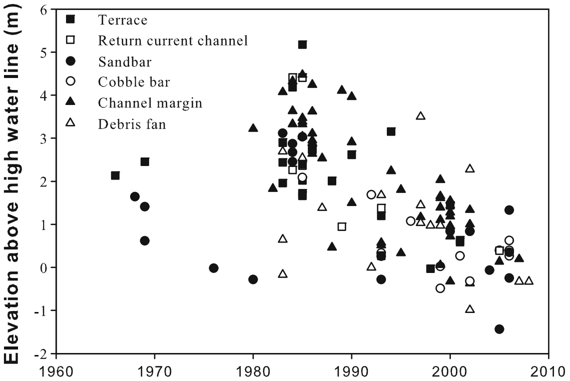

Fig. 5 Elevations of accurately-aged *Tamarix* samples above most recent high water line according to year of establishment. Geomorphic unit is indicated by symbol shape and fill. Water levels were comparable during all sampling trips (n = 131)

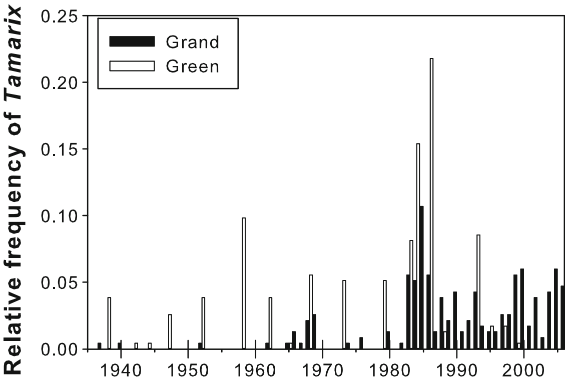

Fig. 6 Comparison of dendrochronology results of *Tamarix* establishment along the Colorado River in Grand Canyon and Green River below Flaming Gorge Dam (modified from Birken and Cooper 2006)

Canyon (Fig. 2). Both rivers were dammed in the early 1960s. Prior to dam construction, the Green and Colorado Rivers exhibited nearly identical hydrographs with distinct spring snowmelt floods in May to June (Fig. 2a). Following dam construction, the Green River continued to peak, albeit at lower magnitudes, but the Colorado River hydrographs were much more erratic (Fig. 2c, d). Due to particularly wet years associated with El Niño weather patterns, both rivers experienced floods reminiscent of pre-dam floods (similar timing, magnitude, duration) in 1983–1985 (Fig. 2b) which were associated with high levels of *Tamarix* establishment (Fig. 6).

Discussion

Along highly regulated rivers, the decoupling of climate and hydrology creates novel abiotic and biotic conditions (Johnson 2002; Stevens et al. 2001). These novel ecosystems set the stage for establishment and development of new combinations of native and non-native species. The combination of flow regimes and plant phenologies ultimately determines the composition of regulated riparian vegetation. Novel, post-dam conditions in Grand Canyon are characterized by a lack of high magnitude, long duration floods and distinctive daily and seasonal flow fluctuations. Riparian plants responded relatively quickly to post-dam hydrologic conditions in Grand Canyon and colonized low elevation surfaces that are no longer flooded annually. The relatively small post-dam floods that have occurred caused mortality and establishment of *Tamarix* but the prevailing flow regimes and geomorphic complexity of Grand Canyon are generally conducive to *Tamarix* establishment in every year. These results are relevant to other canyon-bound river systems at low elevations that have experienced reduced scouring floods due to upstream dam construction and also to places where *Tamarix* is native, along aridland waterways in southern Europe and Asia.

Flow regimes and *Tamarix* establishment and persistence

We found few *Tamarix* that had established prior to 1983 (Fig. 3), corroborating previously documented high *Tamarix* mortality caused by mid-1980s post-dam floods (Stevens and Waring 1985). However, the same floods that caused mortality also created habitat for subsequent *Tamarix* establishment. The largest extant cohort of *Tamarix* established in 1985. Floods in the mid-1980s also were associated with *Salix gooddingii* establishment in Grand Canyon (Mast and Waring 1997), *Tamarix* and *Acer negundo* establishment along the Green and Yampa Rivers (Birken and Cooper 2006; Cooper et al. 2003; DeWine and Cooper 2007), and *Tamarix* establishment throughout riparian corridors in the arid and semi-arid southwestern US (Merritt and Poff 2010). Floods are necessary for establishment pulses of disturbance-adapted riparian species and often initiate consecutive years of establishment (Cooper et al. 2003; Edwards et al. 1999; Polzin and Rood 2006; Scott et al. 1997).

The particular characteristics of floods (magnitude, timing, duration, recession rate) and their relationships to plant life history traits ultimately determine the probability of establishment (Shafroth et al. 1998; Stella et al. 2006). Restoration floods in Grand Canyon during March 1996 and November 2004 were timed to prevent high levels of *Tamarix* establishment. The timing of these floods prevented large pulses of establishment despite having similar peak flow magnitudes to the 1984 through 1986 flows (Fig. 4b). The March 1996 and November 2004 floods occurred outside of the period of seed release, and bare sediments were likely too dry for germination once seeds were available (Stevens et al. 2001). The restoration flows in 2000, which included increased flow in May (Fig. 2f), allowed elevated levels of establishment (Stevens and Gold 2003) because the short-duration, high flow in May corresponded with maximum *Tamarix* seed release. The results of these restoration floods exhibit the importance of the interaction between timing of peak flows and *Tamarix* reproductive phenology.

Even though *Tamarix* has a long period of seed release, the seasonal characteristics of flows interact with fluctuations in seed release magnitude and viability to determine the likelihood of establishment. In Grand Canyon, high flows during July through September were a better indicator of the probability of *Tamarix* establishment than annual peak flow magnitude (Table 2; Fig. 4). *Tamarix* exhibits a continuous, low level seed release peak in summer (Stevens 1987), and high flows during summer allow *Tamarix* to colonize surfaces unavailable to early-dispersing native riparian shrubs. Seed viability of *Tamarix* may be highest (Merkel and Hopkins 1957) but longevity is shortest (less than 30 days) during this time (Stevens 1987). High flows during late summer maintain high water tables and increase water availability for seedlings. In regional surveys of woody vegetation in the southwestern US, Merritt and Poff (2010) and Mortenson and Weisberg (2010) also observed greater dominance of *Tamarix* along rivers with high magnitude flows in late summer.

Climate, geomorphology, and *Tamarix*

Many factors, including erosion, drought, herbivory, and inundation cause seedling mortality. This study revealed the negative influence of summer precipitation the year following germination on *Tamarix* establishment in Grand Canyon (Table 2). We predicted that precipitation and low temperatures during the initial growing seasons would favor *Tamarix* establishment through increased water availability. However, our results may indicate that heavy summer precipitation results in erosion and collapse of banks, scouring or burying the prior year's seedlings. Middle and late summer precipitation along the Upper Green and Yampa Rivers also limited *Tamarix* establishment in some reaches (Cooper et al. 2003). *Tamarix* may be vulnerable to erosion during the second growing season because seedlings that established late in the summer have abbreviated root growth the first year and are more susceptible to scouring erosion. This process is likely responsible for the observed persistence of *Tamarix* seedlings and saplings on cobble bars as opposed to sand bars. Competition interactions may also influence *Tamarix* recruitment. For example, Sher and Marshall (2003) and Stevens (1989) demonstrated the suppression of *Tamarix* by *Populus* and *Salix* (respectively) under high water table conditions. Although our data demonstrate reduced *Tamarix* recruitment in wet summers (conditions that should favor competitive suppression), *Tamarix* seedlings usually occur in monospecific stands, and very few *Populus* or *Salix* seedlings exist in Grand Canyon. Therefore, sandbar erosion during summer monsoonal rainstorms appears to be a more plausible explanation of *Tamarix* recruitment failure.

Tributary flooding of the Paria and Little Colorado Rivers was not related to *Tamarix* establishment (Table 2). Stevens (1989) experimentally demonstrated that post-dam grainsize coarsening reduced *Tamarix* seedling establishment, and we hypothesized that tributary flooding could reduce grainsize and allow increased recruitment. However, silt- and clay-sized sediments from tributaries remain in suspension and daily fluctuating flows and occasional planned high flows quickly wash and transport those grainsizes out of Grand Canyon (Topping et al. 1999). Consequently, tributary floods may not decrease average grainsize on sandbars.

We observed *Tamarix* establishment on progressively lower-elevation surfaces, similar to observations of *Populus deltoides* establishment along the Missouri River (Fig. 5; Scott et al. 1997). Scott et al. (1997) suspected that recent establishment on lower surfaces was temporary and that seedlings and saplings would be removed during future floods in that minimally-regulated river segment. *Populus* establishment along the regulated Green River below Flaming Gorge Dam was limited to low-elevation islands and cutbanks where mortality reached 100% (Cooper et al. 1999). In Grand Canyon, recent *Tamarix* establishment on low-elevation sand and cobble bars combined with reduced flooding may result in geomorphic narrowing of the river channel in less-constrained reaches. We observed many *Tamarix* saplings on cobble bars that established during the 2000 steady flows. These seedlings grew to sufficient size to persist through the 2004 and 2008 test floods and currently stabilize cobble bars. A large flood of similar magnitude to the mid-1980s floods would most likely be needed to remove these saplings; however, such floods are not presently planned.

Flow regimes and *Tamarix* establishment among river systems

The recent, relatively continuous establishment of *Tamarix* in Grand Canyon is contrary to results of Birken and Cooper (2006) who documented years of widespread establishment dictated by inter-annual hydrologic patterns and lack of establishment in other years (Fig. 6). The pre-dam flow regime in Grand Canyon, the period of flooding in the mid-1980s, and the current flow regime of the Green River at Green River, Utah are characterized by floods extending from May to July. These hydrologic conditions are ideal for *Tamarix* establishment. However, large annual floods also scour the previous year's seedlings. For example, an entire *Populus* cohort established in 1993 was killed during restoration floods in 1994 along the Rio Grande River (Taylor et al. 1999). The current flow regime of Grand Canyon does not consist of annual floods. Instead, low magnitude, daily fluctuating flows with seasons of increased magnitude dependent on hydropower needs are the *status quo* (Fig. 2d). Consecutive years of *Tamarix* establishment in Grand Canyon are more likely than along the Green River due to lack of annual spring floods in Grand Canyon.

Hydrology alone does not explain *Tamarix* establishment patterns. *Tamarix* establishment along the Yampa and Green Rivers has been attributed to geomorphic diversity (Cooper et al. 2003). Geomorphic variability, such as occurs at debris fan complexes, increases the possibility that safe microsites for establishment are available. *Tamarix* establishment patterns are influenced by interactions among mainstem hydrology, geomorphology, and weather, which modulate the localized effects of individual hydrologic events.

Management implications

In the highly regulated Colorado River through Grand Canyon, knowledge of the hydrologic conditions that facilitated recruitment of *Tamarix* in the past may be applied to minimize establishment of *Tamarix* and other non-native phreatophytes in the future through flow manipulation. Similarly, knowledge of native species biology may allow better prediction of species-specific responses to flow. *Tamarix* germination occurs each year, but large cohorts of *Tamarix* establish in years with high flows during the period of seed release (e.g., year 2000 cohort). To prevent large cohorts of *Tamarix* from establishing in the future, floods during the time of *Tamarix* seed release (mid-late April through September) should be avoided in this system. However, lack of floods during this time may also prohibit establishment of some native pioneers (e.g., *Populus*, *Salix*).

Early spring floods were limited historically along the Colorado River, but global climate change has caused earlier snowpack melting in the Southwest (Nijssen et al. 2001; Stewart et al. 2005). Temporal shifts in flood timing are expected to reduce seedling recruitment of *Populus* and *Salix* (Rood et al. 2008), but could promote dominance of clonal plants (Barsoum 2002; Karrenberg et al. 2002). Thus, in Grand Canyon, we recommend that planned floods be conducted at the beginning of the growing season (March and early April) to limit *Tamarix* and perhaps other non-native plant germination. Such floods are expected to increase clonal expansion of native phreatophyte shrubs (e.g., *Salix exigua*, *Pluchea sericea*). *Tamarix* dominance may be reduced along less regulated rivers if native shrubs benefit from early spring floods associated with climate change.

The mid-1980 high flows were most similar to the pre-dam hydrograph, and those flows initiated high levels of *Tamarix* establishment. Reinstatement of historic flow regimes along southwestern rivers in the US may encourage *Tamarix* and other non-native phreatophyte establishment. Restoration floods may allow *Populus*, *Salix gooddingii*, *Acer negundo* L., but also non-native *Elaeagnus angustifolia* L. to establish (DeWine and Cooper 2007; Friedman and Lee 2002). Recent studies demonstrate the inferior competitive abilities of *Tamarix* seedlings and adults when compared with native riparian trees (Bhattacharjee et al. 2009; DeWine and Cooper 2010; Sher and Marshall 2003; Stevens 1989; Stromberg 1997). In reaches where native phreatophyte species are strongly dominant and currently recruiting, floods timed during spring and early summer may benefit native species. Because native riparian trees are now rare along many southwestern lowland rivers, hydrologic restoration may be detrimental to native riparian vegetation.

Differences in species composition (i.e., presence/absence of native riparian trees) and climate confound relationships between flow regimes and *Tamarix* establishment. Temperature and elevation influence seed availability of many riparian woody species, and, in unregulated to minimally regulated systems, these factors relate closely with natural flow regimes (Stella et al. 2006; Stevens and Siemion, in review). Predictions of flow treatment effects must take into account all of these factors and also must be site specific. The differences in our results compared to those of similar studies along the Green and Yampa Rivers attest to the complicated nature of these relationships. Annual fall releases of 25-day duration that inundate low stage elevations and cause mortality of *Tamarix* seedlings, as suggested by Roelle and Gladwin (1999) may be an effective management strategy for *Tamarix* in Grand Canyon. However, recent drought, increased water extraction, and energy needs limit the feasibility of such a strategy. Although well-planned floods may benefit *Tamarix* control efforts, frequent floods also degrade marsh and other shoreline habitats, prevent native plant establishment on sandbars, and risk local extirpation of endangered species (Stevens et al. 1995, 2001). Therefore, hydrograph restoration is not a panacea for river management but, like all stewardship actions, requires careful planning, implementation, monitoring, and feedback to adaptive ecosystem management.

The importance of following-year precipitation on *Tamarix* establishment and the occurrence of *Tamarix* establishment each year after 1983 (Fig. 3) suggest that flow regime treatments should not be the only mechanism for *Tamarix* control in Grand Canyon. Merritt and Poff (2010) also concluded that restoration floods are not likely to significantly reduce *Tamarix* establishment in the southwestern US. Along rivers where *Tamarix* dominance is a concern, monitoring of native and non-native woody seedling establishment like that conducted by Johnson (2000) is valuable. By following the fate of individual seedlings, researchers can understand hydrologic, geomorphic, and climatic conditions that allow establishment and persistence. Models that relate hydrology and geomorphology to population-specific life history requirements allow us to predict sites where mortality or recruitment can occur (Shafroth et al. 2010). In this way, land managers can focus invasive plant control efforts and limited funding on sites that foster long-term survival of *Tamarix* and other problematic species. Likewise, planting of native plant species can be targeted to suitable sites. As suggested by Richardson et al. (2007), a combination of site-scale and watershed-scale restoration efforts are necessary for effective control of non-native riparian plant species like *Tamarix*.

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