

Disturbance Regime Mediates Riparian Forest Dynamics and Physiological Performance, Arkansas River, CO

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ABSTRACT.—*Tamarix ramosissima* has caused dramatic morphological changes to riparian ecosystems and their bank structures over the last century throughout the southwestern United States. Growing as either small trees or dense stands of shoots, *Tamarix* species displace or actively outcompete native species of willow (*Salix exigua*) and cottonwood (*Populus deltoides*) on the Arkansas River in Colorado. Under normal conditions for colonization by native species, *Tamarix* seedlings are at a great competitive disadvantage due to slow above ground biomass accumulation. However, damming and the resulting altered disturbance regime may give *Tamarix* an advantage over native species. Damming on the Arkansas River, Colorado, dramatically reduces the intensity and recurrence interval of downstream flooding. Using two dams in eastern Colorado as proxies for flood control, we assessed physiological, demographic and abiotic factors in order to understand how flooding and damming might influence riparian community dynamics. Our study demonstrates that drought and salinity stress may influence native species recruitment and survival in areas with reduced flooding. Moreover, *Tamarix* water-use may be quite plastic in drought conditions, suggesting that it conserves water at below dam sites.

INTRODUCTION

Invasive species can change plant community composition by outcompeting local taxa, altering the local environment, or both; such species are ecosystem engineers because their life history and growth patterns in large part determine the type of environment they occupy (Crain and Bertness, 2006). In fact, invasive species can directly alter environmental conditions to promote their own establishment and persistence through time. *Tamarix ramosissima* (Tamaricaceae) is such a species; it has caused massive changes to riparian ecosystems and stream bank structures over the last century throughout the southwestern United States (Robinson, 1965; Stromberg, 1998; Pearce and Smith, 2002). Growing as either small trees or dense stands of shoots, *T. ramosissima* can displace or actively outcompete native species of willow (*Salix exigua*) and cottonwood (*Populus deltoides*) in the western United States (Robinson, 1965).

In concert with damming and flood discharge regime changes, the invasion of *Tamarix* has contributed to the degradation of many geomorphic and ecological aspects of bank structure (Nilsson *et al.*, 1991; Merritt and Cooper, 2000). Without flooding, many of the edaphic processes necessary for native species establishment and survival diminish (Pataki *et al.*, 2005). The high intensity erosion followed by sandbar deposition associated with flooding promotes the establishment of native species by creating open substrate with a relatively high availability of light, water and nutrients (Taylor *et al.*, 1999; Merritt and Cooper, 2000). Due to the density of its roots, *Tamarix* is able to engineer the bank structure by preventing erosion and the subsequent formation of sand bars and floodplains (Merritt and Cooper, 2000). Therefore, *Tamarix* individuals might be able to competitively exclude other taxa by physically altering the bank structure and geomorphological processes.

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Tamarix might also gain a competitive advantage by chemically inhibiting the growth of surrounding individuals. By allocating excess salt to abscising leaves, *Tamarix* can increase the salinity of the substrate in its immediate vicinity (Busch and Smith, 1995; Shafroth *et al.*, 1995). Due to a moderate tolerance to soil salinity, *Tamarix* can gain a distinct advantage over native species through this potentially allelopathic mechanism (Busch and Smith, 1993; Shafroth *et al.*, 1995). This process is exacerbated below dams by a lack of soluble ion leeching because of reduced flooding and consequently lower water tables. Moreover, *Tamarix* can further increase salinity levels by directly reducing soil moisture levels (Blackburn *et al.*, 1982). Thus, *Tamarix* has the potential to engineer a stressful riparian environment that can promote the persistence and expansion of conspecific populations, especially in areas below dams (Glenn and Nagler, 2005).

The recruitment of woody species along the Arkansas River was historically driven by competition for light and space; uncontrolled flood regimes resulted in high water and nutrient availability (Graf, 1978). Competition may have been highest at the seedling stage when space for rooting and sunlight are limited due to the high numbers of individuals; Sher and Marshall (2003) demonstrated that competition among *Populus*, *Salix*, and *Tamarix* for available resources can be magnified at high plant densities. These competitive forces may have been intensified by the fact that woody riparian species native to the Arkansas River, like *Populus* and *Salix*, are relatively shade intolerant (Hewitt, 1998). Therefore, growth rate and light acquisition ability should have been targets of natural selection. As a result, intense competition for light and constantly available water have selected for rapid stem growth rates by these native species (Brotherson *et al.*, 1983) with relatively little root development (Horton and Clark, 2001). As a result, they are very competitive for light (Sher *et al.*, 2000). Essentially, the cottonwood and willow species in this riparian system demonstrate shade-avoidance responses; this response can increase light acquisition, but can be costly with regard to root growth and water acquisition (Schmitt *et al.*, 2003).

The non-native species, *Tamarix ramosissima* (Ledebour), has a much different growth strategy. Historically inhabiting somewhat arid riparian zones in central Asia, *Tamarix* is drought tolerant (Cleverly *et al.*, 1997) and invests relatively more energy in root development than other species in this system (Horton and Clark, 2001). Consequentially *Tamarix* taproots can extend much deeper than native root systems (Gary, 1963; Horton and Clark, 2001; Sher and Marshall, 2003). Like native Colorado species, *Tamarix* is shade intolerant with regard to seedling growth and establishment (Howe and Knopf, 1991). However unlike the native species, its above ground growth rate is relatively slow (Cleverly *et al.*, 1997; Sher *et al.*, 2001). That is, *Tamarix* does not shade-avoid in response to neighbors. Therefore, due to competition for light, *Tamarix* has been unable to invade many naturally flowing river systems (Sher *et al.*, 2001). However, damming and the resulting altered flooding regimes has decreased soil moisture availability and given *Tamarix* an advantage over native species (Glenn and Nagler, 2005). Due to a dynamic water table, above dam sites may have high soil moisture and consequently reduced salinity levels, whereas below dam sites may experience an increase in drought stress and salinity (Stromberg, 1997; Stromberg, 1998). Decreased disturbance and increased stress may make cottonwood and willow recruitment more difficult below dams (Horton and Clark, 2001). *Tamarix* may also compete with native species at these sites by stealing and wasting any available water (Sala and Smith, 1996; Cleverly *et al.*, 2002).

Competition for resources is especially intense for these woody riparian species because they do not rely on a seed bank (Stevens *et al.*, 2001). *Tamarix* and *Salix* saplings and *Populus*

adults must assimilate an excess of carbon throughout the growing season in order to flower and produce seeds at the beginning of the next season. Moreover, transitioning between life history stages might be paramount for species that cannot rely on seed bank structure to perpetuate community structure. The potential amount of fixed carbon can be maximized by high quantities of leaf chlorophyll and increased stomatal conductance of water vapor (Heschel *et al.*, 2004); these two physiological factors should therefore be determinants of potential fitness (Caruso *et al.*, 2006). Moreover, a reduction in either factor may be indicative of drought stress (Caruso *et al.*, 2006). Chlorophyll content levels can reveal a given plant's relative exposure to stressful conditions because drought stress can result in decreased chlorophyll production (Larcher, 2003). Seedlings and saplings will typically reduce water loss by decreasing stomatal conductance in stressful conditions (Heschel and Riginos, 2005). In contrast, plants inhabiting mesic sites will often have greater water-use and thus higher rates of stomatal conductance (Cleverly *et al.*, 1997). Decreasing gas exchange can be costly because increased stomatal conductance can increase carbon assimilation per unit time and potentially increase seed production (Heschel *et al.*, 2002, 2004; Heschel and Riginos, 2005). Nonetheless, in drought conditions, decreased stomatal conductance and higher water-use efficiency can afford fitness gains due to increased survivorship (Heschel and Hausmann, 2001; Heschel *et al.*, 2002). Therefore, individuals will typically close their stomata only when water is not available, or when other stressful conditions prohibit carbon sequestration.

Through morphological, physiological and life-history mechanisms, *Tamarix* has been able to dominate many riparian floral communities. By reproducing asexually (Everitt, 1980) and accumulating salt from leaf litter (Shafroth *et al.*, 1995), *Tamarix* stands become so dense that colonization by other species is impossible (Busch and Smith, 1995). These monospecific stands effectively engineer the surrounding landscape and can prevent the recruitment of native species. However, several studies have demonstrated that restoring historical flooding regimes and clearing stands of *Tamarix* can result in re-colonization by native species (Sher *et al.*, 2000; Sprenger *et al.*, 2001; Stevens *et al.*, 2001; Tallen-Halsell and Walker, 2002; Rood *et al.*, 2003).

In this study we utilized the dramatic reduction in historic flooding intensity observed below two dams on the Arkansas River in southeastern Colorado to gauge the relative role of flooding on riparian community structure. Through demography, monitoring of plant-water relations, and an assessment of abiotic factors, we designed our study to answer the following questions: (1) How has damming and the resulting decrease in flood frequency and intensity affected populations of *Tamarix*, *Salix* and *Populus* below dammed sites on the Arkansas River? and (2) How does damming on the Arkansas River affect competitive interactions between *Tamarix*, *Salix* and *Populus*?

MATERIALS AND METHODS

Study system (tamarix, salix and populus).—Historically, riparian systems in southeastern Colorado have a diverse assemblage of forbs and graminoids, with only two main woody species. The plains cottonwood, *Populus deltoides* (H. Marshal), is a tall, broad-leaved tree that forms the overstory in older forests. The sandbar willow, *Salix exigua* (Nuttall), grows in dense stands of single shoots and dominates low banks and young floodplains. Both species produce small, buoyant seeds and require a natural flood regime in order to recruit seedlings (Sher *et al.*, 2001; McBride and Strahan, 2006). *Salix* and *Populus* seed production usually occurs during the early spring and ends by early summer, when flood heights are at their peak (Busch and Smith, 1995; Mahoney and Rood, 1998). Seeds fall into the receding

floods and are deposited on the fertile moist sandbars as the floods subside. Due to high seed production, these floodplains are covered with many seedlings after a few weeks.

Like *Populus* and *Salix*, *Tamarix* seeds are comose and well-suited for Colorado riparian systems, often being distributed by the surface waters of rivers (Pearce and Smith, 2002). However, *Tamarix* seeds are as much as five times smaller than native species and can be wind dispersed over potentially longer distances than native species (Merkel and Hopkins, 1957; Sher *et al.*, 2000). Furthermore, *Tamarix* seed production is not limited to spring; instead individuals produce seeds throughout the growing season in large numbers (Horton *et al.*, 1960). In fact, adults can produce several thousand seeds per growing season (Warren and Turner, 1975).

Native species of *Salix* and *Populus* will recruit on the bare floodplains after flooding in the spring and will quickly shade *Tamarix* seedlings (Moss, 1937; Karrenberg *et al.*, 2002). However, if flooding does not occur, the lack of open, fertile substrate will dramatically reduce native species potential for establishment (Moss, 1937). Furthermore, if flooding is timed later in the season, native species will have little competitive advantage due to low, or no seed production in the late spring or early summer (Taylor *et al.*, 1999). Historically, gaps formed by stochastic, late-summer disturbance events were left uncolonized until the following spring's seed dispersal events. However, *Tamarix* recruits aggressively throughout the summer (Horton *et al.*, 1960; Young *et al.*, 1995), leaving little open space for native species' spring colonization in the following year. These late season flooding events may allow for increased establishment by *Tamarix* at regularly flooded sites (Young *et al.*, 1995).

Study sites.—The flow of the Arkansas River in the eastern plains of Colorado (CO), USA, is highly controlled by two containment reservoirs. The Pueblo Dam located just west of the city limits of Pueblo, CO, functions mainly as a storage facility. About 160 km east of Pueblo, the John Martin Dam and Reservoir control floods and water distribution for Kansas, Oklahoma, Arkansas and eastern Colorado. In 2006 we selected multiple sites along the Arkansas River, both upstream and downstream from both dams, with sites representing both banks of the river. Sites were neither directly adjacent to a given dam nor close enough to the reservoir to be affected by its surface level fluctuations. All sites were located on highly disturbed, low bank floodplains that were created by loose material deposition. Old stands of any species were never present due to the recent formation of these sandbars.

Flood intensity and force were determined using two variables: flow height and flow rate. Flow height measures the increase of the surface water elevation above normal levels, while flow rate demonstrates increases in the volume of water passing through a given area. To compare the river flood intensity above and below the dams, we referenced stream hydrograph data for each site from USGS water data (available online at <http://waterdata.usgs.gov/co>). Using flooding data from 1975 to 2005, we calculated the height and flow rate of 1 y (100%) flood events.

In order to assess the role of flood intensity and occurrence, sites were chosen within 20 km of each dam and all sites were placed nearby United States Geological Survey (USGS) surface water stations such that no tributaries or stream flow control existed between the site and station. Four sites (within about 6 km of each other) were chosen both above and below each of the two dams resulting in a total of 16 sites along the Arkansas River from Portland, CO to Lamar, CO.

Experimental design.—In order to determine the size and age distribution of *Tamarix*, *Salix* and *Populus* populations, we created two, 10 m by 15 m plots parallel to the stream bank at each site. Each plot was 3–5 m from the stream bank. We collected demographic information (age distribution and density) for populations of each species along two

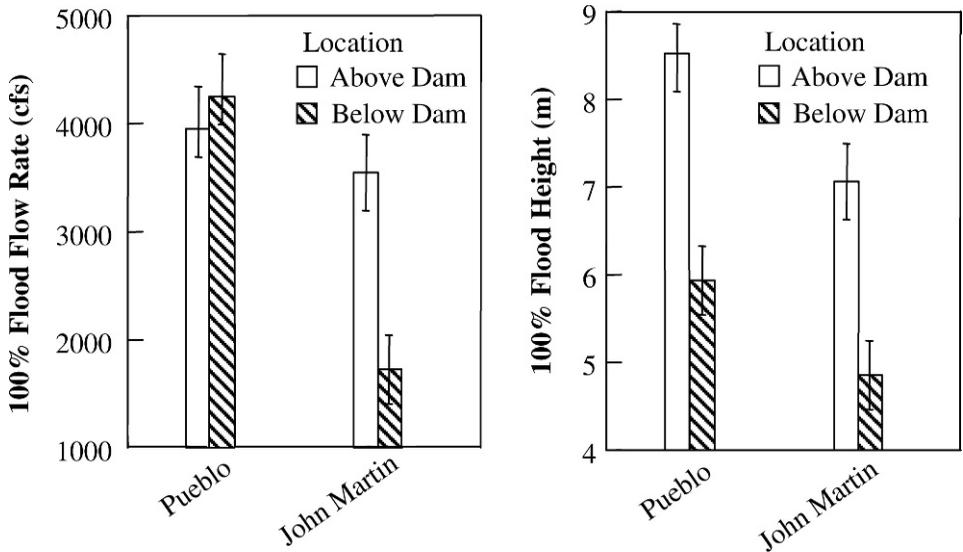
randomly placed, 15 m longitudinal transects inside these plots. Because our sites were all located on low-bank floodplains, age distribution and density data correspond to saplings and small trees rather than older trees. In each plot we collected basal diameter (mm) where the stem reached ground level for *Tamarix*, *Salix* and *Populus* plants with Fisher Scientific electronic digital calipers. Stem diameter is significantly correlated with plant age in these riparian species (Brotherson *et al.*, 1983, 1984; Lesica and Miles, 2001), so diameter was used as a proxy for plant age. Every 1.5 m along each 15 m transect we selected the nearest neighbor as a representative of each species. At each transect point stem diameter as well as stomatal conductance (leaf porometer) were measured for a total of sixty plants per plot, representing twenty *Tamarix*, *Salix* and *Populus* saplings. For half of the plants measured in each plot, leaf samples were collected to determine chlorophyll concentration for each species; 100 mg of leaf material was pulverized in 90% acetone with a tissue grinder and chlorophyll (a and b) content (mg) was determined with a spectrophotometer (ThermoSpectronic Genesis 20). Most recent fully expanded leaves were collected for chlorophyll content analysis.

Instantaneous stomatal conductance readings ($\text{mmol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were taken on abaxial leaf surfaces with a steady-state diffusion porometer (Decagon Devices Model SC-1). Conductance measurements were taken between 1000 and 1400 h in full light conditions (at least $1000 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) on most recent fully expanded leaves. Ambient temperature conditions were between 30 and 37 C. Lower temperatures result in more consistent gas exchange rates; however, eastern Colorado is rarely cooler than 30 C in full sun, mid-summer conditions. Therefore, only measurements taken at temperatures over 37 C were excluded from analyses.

Using the same marked individuals, we also determined the average understory light conditions with a one-meter line quantum sensor (LI-COR Biosciences LI-191SA). Measurements ($\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were taken as an average of one min of reading at 5 cm above the ground at randomly selected sites and individuals. We then created a regression line to correlate the stem diameter of each species with light penetration. Light measurements were taken underneath 20 individuals from each species at two sites above and two sites below both the John Martin and Pueblo Dams.

Moisture data (% volumetric water content or VWC) were collected at the same random sites that understory light penetration was measured, at a depth of 12 cm with a TDR moisture meter (Campbell Scientific Hydrosense). Twenty moisture readings were taken at each of two sites above and below each dam. Soil was also collected at these sites around *Tamarix* individuals and soil salinity (parts per million or ppm) was measured with a conductivity based salinity meter (Kelway SST).

Statistical analyses.—All statistical analyses were performed with JMP (version 4.0.4, SAS Institute, 2001). For all statistical models, the distributions of residuals were examined and the data were log-transformed where necessary. ANOVAs were used to test for light level differences between sites. Light level data were pooled across dam sites to increase statistical power for examining differences in location above and below each dam. Multiple comparisons of light levels under species canopies at different sites were performed with Tukey HSD tests. Differences in population size, stem diameter (as a proxy for population structure), stomatal conductance and chlorophyll content were compared among all three taxa at sites above and below the dams with two-way ANOVAs. Three-way ANOVAs were initially conducted on all these traits but two-way ANOVAs are reported because higher-order interactions were significant for all the analyzed traits (Tables 2, 3). Contrasts were performed to compare trait values among all three taxa above and below the dams. To



Arkansas River Reservoirs

FIG. 1.—Mean flow rate (cfs = cubic ft·s⁻¹) and flow height (m) ± 1 SE of 1 y floods at four USGS sites. The Pueblo Reservoir is upstream of the John Martin. Data were collected at USGS river gauge stations above and below each dam along the Arkansas River, CO

examine the effects of native species' densities on *Tamarix* stomatal conductance, linear regressions of conductance on density were conducted for sites above and below the dams. The slope terms were not significantly different from zero for the analyses of above dam sites, so only the below dam analyses are reported.

RESULTS

Environmental profile.—USGS data demonstrated drastic differences in the height and flow (intensity) of 1 y floods between above and below dam sites (Fig. 1). Flow rate (cubic ft·s⁻¹ or cfs) was similar above and below the Pueblo Dam sites (Fig. 1). However, due to the narrow channel and steep bank morphology of upstream sites, flooding had an increased height, indicating that small flooding events were relatively more severe at sites above the Pueblo Dam (Fig. 1). Flooding was greater in both flow rate (cfs) and flood height (m) above the John Martin Dam than below it (Fig. 1). Light penetration due to canopy density decreased significantly below both dams (Fig. 2; Table 1). Light levels were also relatively lower under *Tamarix* and *Salix* canopies than under *Populus* canopies regardless of site (Fig. 2a). Light availability generally increased below smaller, and potentially younger, *Tamarix* plants (J. Lovell and M.S. Heschel, pers. obs.). Surface soil moisture (at 12 cm depth) was not appreciably different between sites, and conditions were between 8% and 20% VWC for all sites. However, salinity levels were dramatically higher below dams than above dams (Fig. 2b).

Species distribution.—All sites contained assemblages with *Tamarix*, *Salix* and *Populus* in various proportions except those below the John Martin Dam where a *Tamarix* monoculture persists. Here, study plots contained mostly *Tamarix* seedlings, saplings and adults, and very few *Salix* or *Populus* individuals (Fig. 3). Across all sites, damming significantly predicted

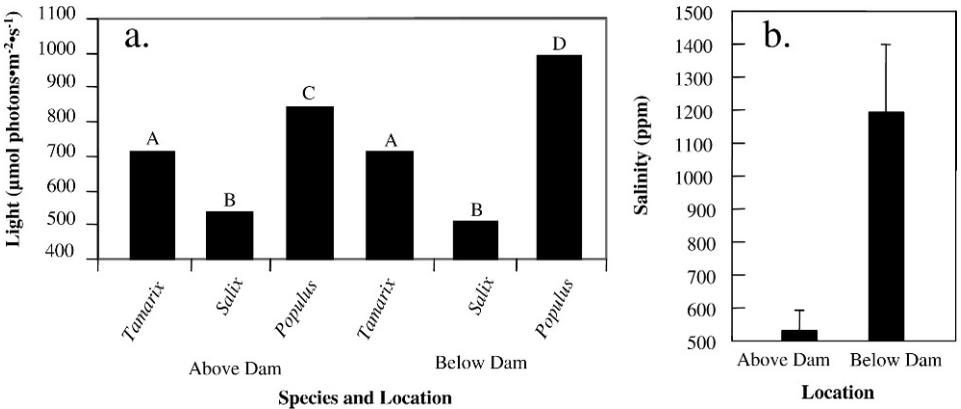


FIG. 2a.—Mean transformed light at ground level below each species for above and below dam sites. Light levels not connected by the same letter are significantly different at P = 0.05 with Tukey HSD. Fig. 2b. Mean salinity levels in parts per million (ppm) ± 1 SE in soil samples from sites below and above both dams

species density patterns. *Salix* population sizes were marginally larger while *Populus* population sizes were significantly larger at above dam sites (Fig. 3; Table 2). In contrast, *Tamarix* populations were significantly larger below dams than above dams (Fig. 3; Table 2).

Location (above/below dams) significantly predicted the age distribution of all three woody riparian species (Fig. 4; Table 2). Sites above the Pueblo Reservoir contained older *Populus* individuals, while *Tamarix* and *Salix* populations consisted of older individuals (larger stem diameter) below the Pueblo Reservoir (Fig. 4). *Tamarix* populations were younger at sites near the Pueblo Reservoir than at sites near the John Martin Reservoir (Fig. 4). Due to the lack of native trees below the John Martin Reservoir, age distribution could not be statistically compared for native species at sites downstream of the John Martin Dam.

Stomatal conductance.—Location (above/below dams) and site (Pueblo/ John Martin Dam) significantly predicted *Tamarix*, *Salix* and *Populus* stomatal conductance values (Fig. 5, Table 3). *Tamarix* individuals had higher stomatal conductance (greater water-use) at above dam sites than at below dam sites. In contrast, both *Salix* and *Populus* plants had higher stomatal conductance values at below dam sites than at above dam sites. *Tamarix* stomatal conductance was the lowest among all three taxa at below dam sites (planned contrast, *Tamarix* conductance versus *Populus* and *Salix* conductance: F = 90.967, df = 1, P = 0.002); this trend indicated that *Tamarix* was not wasting water below dams, rather it was conserving water. In contrast, *Salix* appeared to waste water and had significantly higher stomatal

TABLE 1.—Two-way ANOVA for light quantity at ground level below each species by location. (Location: Above/Below Dams)

Source	Sum of Squares	df	F	P
Location	199497	1	9.2051	0.0025
Species	12093703	2	279.0129	<.0001
Species x Location	724116	2	16.7060	<.0001

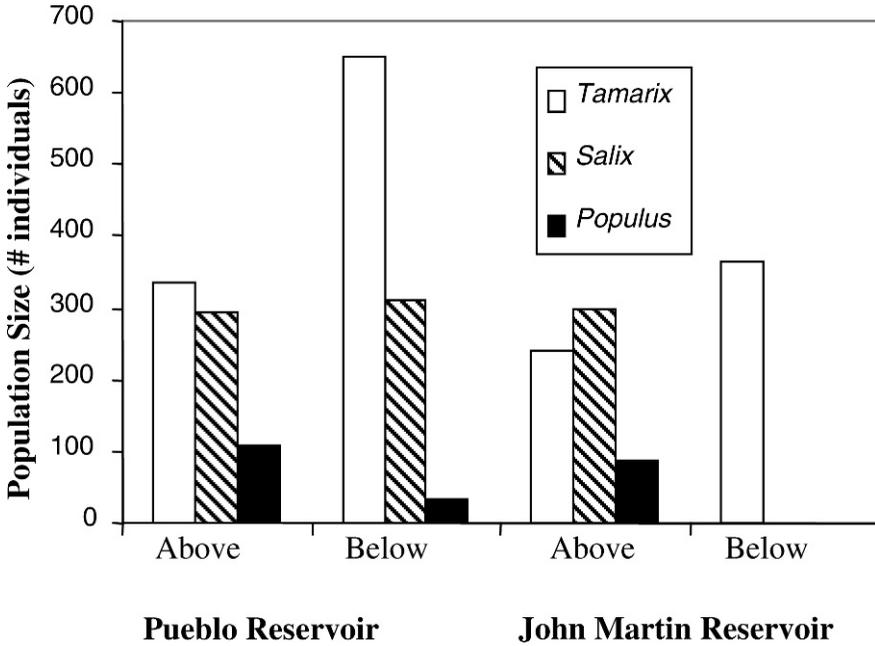


FIG. 3.—Population sizes summed across the four plots above and below each dam for each species

conductance values than *Tamarix* or *Populus* at below dam sites (planned contrast, *Salix* conductance versus *Tamarix* and *Populus* conductance: $F = 25.337$, $df = 1$, $P < 0.0001$). It was at above dam sites that *Tamarix* individuals used relatively more water than *Salix* or *Populus* (planned contrast, *Tamarix* conductance versus *Populus* and *Salix* conductance, $F = 5.054$, $df = 1$, $P = 0.025$). Moreover, native species density was positively correlated with *Tamarix* conductance at below dam sites; *Salix* density was a more significant predictor of *Tamarix* conductance than was *Populus* density (linear regressions of *Tamarix* conductance

TABLE 2.—Two-way ANOVA for population densities and age distributions of each species by location and dam site. F-statistics and P-values are presented. In the full models (three-way ANOVA), location by dam and location by species interactions were significant for population size and a dam by location by species interaction was significant for stem diameter ($P < 0.05$). (Location: Above/Below Dams) (Dams: Pueblo/John Martin Dam)

	Population Size			Stem Diameter		
	Location	Dam	Location x Dam	Location	Dam	Location x Dam
<i>Tamarix</i>	8.5655*	6.9704*	1.5586	14.8909***	47.5102***	1.5096
<i>Salix</i>	3.3752+	3.9720+	4.0762+	10.3731**	N/A	N/A
<i>Populus</i>	20.449***	1.9481	0.1995	7.1334**	N/A	N/A

*** $P < .001$; ** $P < .01$; * $P < .05$; + $P < .10$

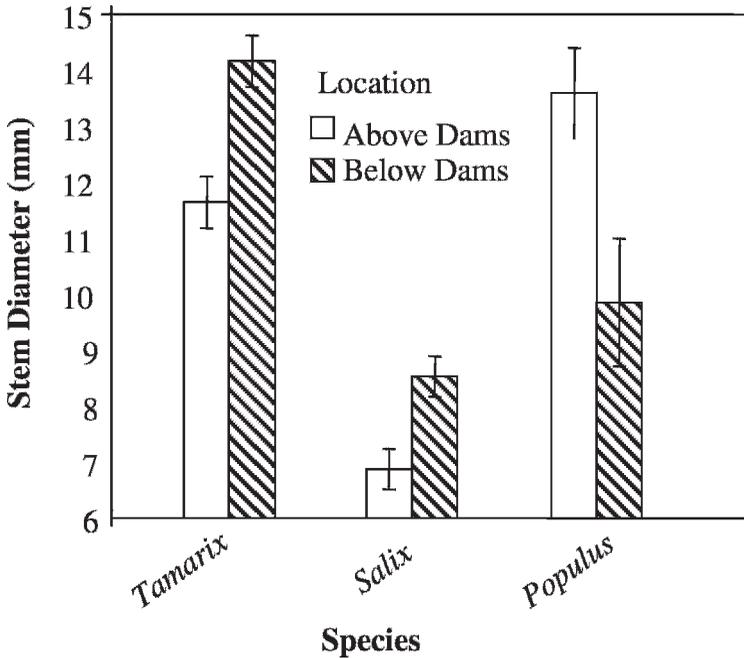


FIG. 4.—Mean stem diameter \pm 1 SE of stands above and below both dams (pooled data) for each species

on density: *Salix* density, $R^2 = 0.55$, $\beta = 0.54$, $t = 2.70$, $P = 0.03$; *Populus* density, $R^2 = 0.46$, $\beta = 4.82$, $t = 2.30$, $P = 0.06$).

Chlorophyll content.—Location (above/below dams) and site (Pueblo/ John Martin Dam) significantly predicted *Tamarix* and *Populus* chlorophyll (a/b) content (Fig. 6, Table 3). Both *Tamarix* and *Populus* individuals had lower leaf chlorophyll content at below dam sites than at above dam sites (Fig. 6, Table 3). In contrast, *Salix* plants had statistically equivalent amounts of chlorophyll (a/b) above and below the dams (Fig. 6, Table 3). This suggested that only *Tamarix* and *Populus* were effectively stressed at below dam sites.

DISCUSSION

Environmental factors, such as disturbance due to flooding can affect species distribution patterns. By altering competitive interactions, changes in disturbance regime patterns can give a poor competitor an advantage and allow it to establish in areas that would be impossible under unaltered conditions (Ewanchuk and Bertness, 2004). Previous studies have shown that under natural flooding regimes, *Tamarix* seedlings grow more slowly and are consequentially out-shaded and eventually killed by the faster growing species of *Populus* and *Salix* (Hewitt, 1998; Sher and Marshall, 2003). However, all 16 of our sites contained a varying degree of *Tamarix* colonization. Some sites had only seedlings, while others contained adult monocultures with nearly no native recruitment. Furthermore, native species experienced active recruitment at all sites except those below the John Martin Dam where a *Tamarix* monoculture persists. Here we demonstrate that *Tamarix* population sizes

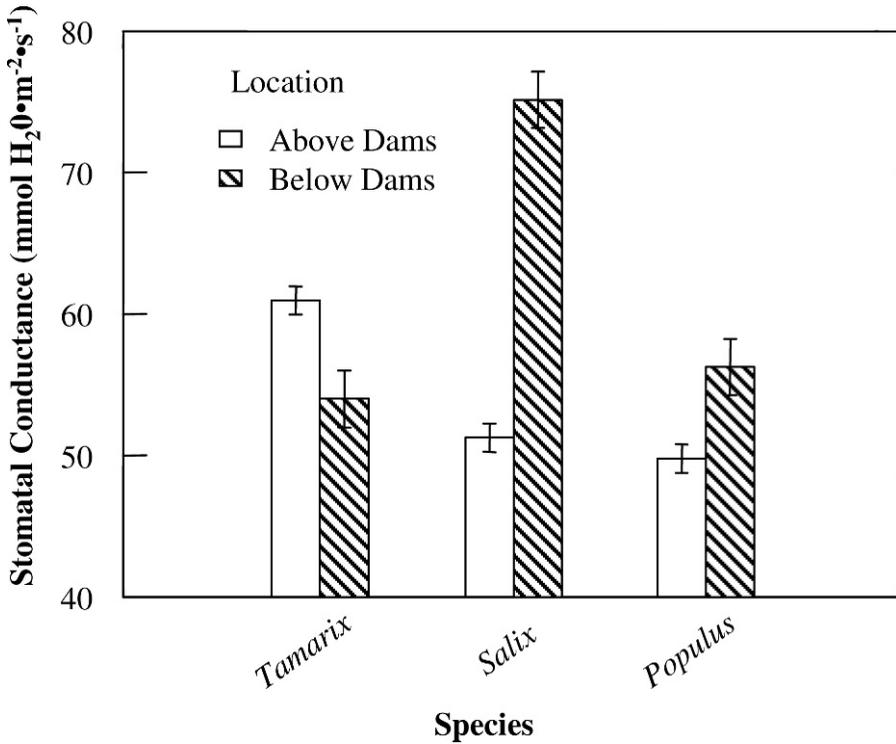


FIG. 5.—Mean stomatal conductance \pm 1 SE for each species at sites above and below both dams (pooled data)

TABLE 3.—Two-way ANOVA for stomatal conductance and chlorophyll content of each species by location and dam site. F-statistics and P-values presented. In the full models (three-way ANOVA), a dam by location by species interaction was significant for stomatal conductance and a location by species interaction was significant for chlorophyll content ($P < 0.05$). (Location: Above/Below Dam) (Dams: Pueblo/John Martin Dam)

	Stomatal Conductance			Chlorophyll Content		
	Dam	Location	Location x Dam	Dam	Location	Location x Dam
<i>Populus</i>	0.4978	0.7384	28.5605***	7.1272**	58.0849***	0.7896
<i>Tamarix</i>	56.7723***	6.0384*	75.6933***	0.7502	14.0559**	2.0989
<i>Salix</i>	2.9261+	16.7437***	69.4757***	0.0475	0.1121	0.2318

*** $P < .001$; ** $P < .01$; * $P < .05$; + $P < .10$

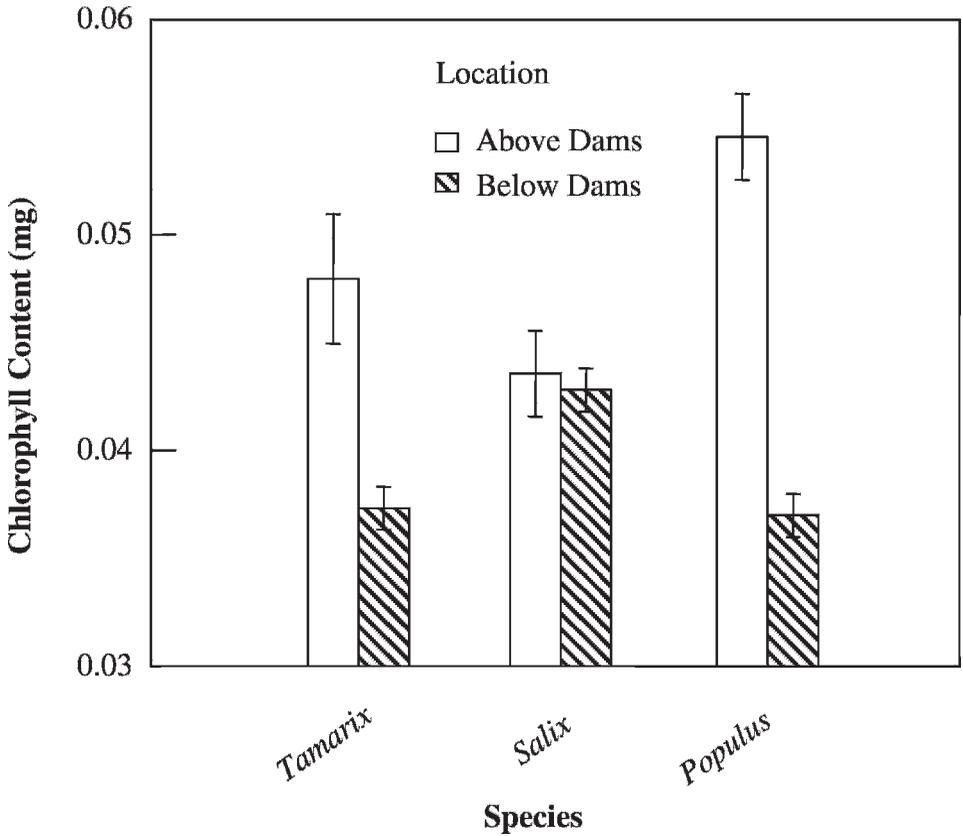


FIG. 6.—Mean chlorophyll content \pm 1 SE for each species at sites above and below both dams (pooled data)

are correlated with location above and below dams and that species distribution might be affected by an interplay between shade tolerance and water-use plasticity.

Disturbance regime, species distributions, and population dynamics.—*Tamarix* population sizes were larger below both the John Martin and Pueblo dams than above the dams. For example, above the John Martin Dam, in a relatively unregulated flow regime, the high bank (>5 m above normal flow height) had a sparse population of large *Populus*, with a few mature *Tamarix* bushes. Below the dam, *Tamarix* existed in a relative monoculture where dense bushes were separated by a few meters of barren substrate; the soil substrate below both dams was significantly more saline than it was above the dams. Due to disturbance differences, above dam sites may have higher soil moisture availability (at a depth greater than 12 cm) and consequently lower salinity levels than below dam sites. At below dam sites, increased drought and salinity stress may contribute to *Tamarix* dominance by reducing cottonwood and willow establishment. Without fresh substrate on which to establish, seeds of native species float in the spring floodwaters downstream eventually becoming sterile (Moss, 1937). Furthermore, light availability decreased from above to below dams and from upstream to downstream sites, mostly due to increases in the relative abundance of *Tamarix* below dams. Light availability was generally higher under *Populus* canopies than under

Tamarix or *Salix* canopies, which indicates that increased *Populus* density might promote the establishment of other species. Because all three taxa are somewhat shade intolerant, upstream and above dam sites may support a greater diversity of taxa at least in part because of increased light availability as well as suitable substrate.

Areas above the dams presumably lack a dense formation of *Tamarix* due to relatively frequent, large disturbances that remove adults and allow recruitment of native species; as a result, *Tamarix* populations were older below dams. *Salix* age distribution was younger above dams than below dams, suggesting that more *Salix* seedlings establish at above dam sites. Age distributions of *Populus* became older at upstream sites, which indicated a lack of young recruits above dams. However, *Populus* population counts below dams were one-quarter of those above dams. Also, significantly fewer adults were present at sites downstream of dams. This population structure indicates that saplings are not able to transition into adult age classes at below dam sites. Thus, *Populus* populations appeared healthier above dams than below dams even though populations were slightly older above dams.

Community structure and competitive interactions.—Consistently throughout our results, *Tamarix* and *Salix* population structure and number were related. Both species had younger and larger populations near the Pueblo Dam, and *Salix* population densities more strongly predicted *Tamarix* stomatal conductance than *Populus* densities. Growth similarities, in terms of morphology and size, may contribute to greater competitive interactions between *Salix* and *Tamarix* on the low floodplains where we conducted our study. *Populus* individuals seemed to be less affected by this competitive interaction (*cf.*, Sher *et al.*, 2000; Sher and Marshall, 2003); *Populus* seedlings were present in both *Salix* and *Tamarix* understories (Lovell and Heschel, pers. obs.). *Populus* is thought to be shade intolerant (*see* Henderson and Jose, 2005); however, large leaves and relatively rapid biomass accumulation in low light conditions may allow *Populus* to survive in areas already colonized by other species. In fact, *Populus* leaf morphology may make cottonwood functionally shade tolerant relative to *Tamarix* and *Salix*; both *Tamarix* and *Salix* have small, narrow leaves typical of sun-acclimated species (Heschel *et al.*, 2004). As a result, even in dense patches of *Salix* where understory light levels are relatively low (Fig. 2a), we noticed several species of forbes as well as seedlings of *Populus* present under the canopy.

Competition seemed to affect survival rates of all three taxa and these competitive interactions may be mediated by physiological responses to environmental conditions (Glenn and Nagler, 2005). Changes in water-use can directly affect the competitive ability and reproductive fitness of plants (Hacker and Bertness, 1995; Heschel *et al.*, 2002). *Tamarix* populations containing individuals with high stomatal conductance and likely low water-use efficiency were found at sites with larger populations of native species. At above dam sites, where nutrients and water were less limiting, *Tamarix* kept their stomata open, producing higher gas exchange rates which may allow *Tamarix* to initially compete with *Salix* and *Populus*. Moreover, above dams *Tamarix* stomatal conductance was relatively higher than *Salix* or *Populus* stomatal conductance. Thus, *Tamarix* may have been able to assimilate more carbon per unit time than either of the native species at above dam sites. However, *Populus* stands were older above dams, indicating that while high gas exchange rates above dams may have allowed for establishment of *Tamarix* seedlings, these seedlings may not transition into later life history stages. Once *Populus* trees become the dominant community member, light availability becomes more restricted, limiting *Tamarix* transition into later life history stages (*cf.*, Lesica and Miles, 2001).

Tamarix, *Salix* and *Populus* distribution patterns shifted dramatically below dams where presumably less nutrients and water were consistently available. Here, more stressful sites tend to be dominated by *Tamarix*. Below dam sites are generally more stressful and both

Populus and *Tamarix* individuals made less chlorophyll in these drought stressed conditions. In response to drought stress *Tamarix* individuals also decreased their water-use per unit leaf area by decreasing stomatal conductance below dams; this stomatal response is further evidence that *Tamarix* is drought tolerant (Sala *et al.*, 1996; Cleverly *et al.*, 1997). In contrast, *Populus* and *Salix* increased their water-use in these drought stress conditions. This increased gas exchange below dams may be a stress avoidance response, whereby the native species might be growing faster toward earlier reproduction to escape drought (*cf.*, McKay *et al.*, 2003; Heschel and Riginos, 2005). Alternatively, the increased gas exchange may be a shade avoidance response to the presence of neighboring plants (*cf.*, Schmitt *et al.*, 2003). Regardless of the physiological response, the increased gas exchange likely decreased soil moisture availability at these sites. Low soil water potential might result in decreased plant water potential for *Salix* and *Populus* plants, particularly due to their relatively higher gas exchange rates than *Tamarix*. This greater water-use plasticity of *Tamarix* may increase its competitive ability (at least at the sapling stage) both above and below dams (*cf.*, Cleverly *et al.*, 1997; Horton *et al.*, 2001; Sexton *et al.*, 2002). Moreover, coupled with the salt input to soils from *Tamarix* leaves, decreases in soil water potential would make the establishment of native species even less likely. Overall, whether *Tamarix* “wastes” water may depend on disturbance regime.

Conservation implications and conclusions.—Our results indicated that *Tamarix* growth potential (*viz.* increased stomatal conductance and chlorophyll content) was greatest at flood-inundated sites; however, native population sizes were larger at these sites. *Tamarix* colonization at actively flooded sites was as prevalent as sites below dams; however, physiological adaptations to low water availability at flood-controlled sites (below dams) may have allowed *Tamarix* to survive where native species could not effectively establish. In order to restore native species colonization below dams, flood management should be augmented by the removal of adult *Tamarix*. Without adult *Tamarix* removal, the larger *Tamarix* would shade native species, salinity levels would increase, and native seedlings may not be able to establish on sites already containing *Tamarix* monocultures.

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