

EFFECTS OF STREAM FLOW PATTERNS ON RIPARIAN VEGETATION OF A SEMIARID RIVER: IMPLICATIONS FOR A CHANGING CLIMATE

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ABSTRACT

As global climate change affects recharge and runoff processes, stream flow regimes are being altered. In the American Southwest, increasing aridity is predicted to cause declines in stream base flows and water tables. Another potential outcome of climate change is increased flood intensity. Changes in these stream flow conditions may independently affect vegetation or may have synergistic effects. Our goal was to extrapolate vegetation response to climate-linked stream flow changes, by taking advantage of the spatial variation in flow conditions over a 200 km length of the San Pedro River (Arizona). Riparian vegetation traits were contrasted between sites differing in low-flow hydrology (degree of stream intermittency) and flood intensity (stream power of the 10-year recurrence flood). Field data indicate that increased stream intermittency would cause the floodplain plant community to shift from hydric pioneer trees and shrubs (*Populus*, *Salix*, *Baccharis*) towards mesic species (*Tamarix*). This shift in functional type would produce changes in vegetation structure, with reduced canopy cover and shorter canopies at drier sites. Among herbaceous species, annuals would increase while perennials would decrease. If flood intensities increased, there would be shifts towards younger tree age, expansion of xeric pioneer shrubs (in response to flood-linked edaphic changes), and replacement of herbaceous perennials by annuals. Woody stem density would increase and basal area would decrease, reflecting shifts towards younger forests. Some effects would be compounded: Annuals were most prevalent, and tree canopies shortest, at sites that were dry and intensely flooded. Vegetational changes would feedback onto hydrologic and geomorphic processes, of importance for modeling. Increased flood intensity would have positive feedback on disturbance processes, by shifting plant communities towards species with less ability to stabilize sediments. Feedbacks between riparian vegetation and stream low-flow changes would be homeostatic, with reduced evapotranspiration rates ameliorating declines in base flows arising from increased aridity. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS: climate change; riparian vegetation; semiarid; flood disturbance; stream intermittency; *Populus*; *Tamarix*

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INTRODUCTION

Rising levels of greenhouse gases are bringing about changes in climate that are modifying streamflow regimes (Arnell, 2003). These effects vary by region and by stream type (Palmer *et al.*, 2008). On snowmelt-dominated rivers in western USA, regional warming is shifting snowfall to rain, thereby producing increased winter flows, earlier flood peaks and reduced summer flows (Barnett *et al.*, 2008; Rood *et al.*, 2008). On southwestern desert rivers sustained by rainfall runoff and regional groundwater inflow, regional warming is increasing evaporation rates and reducing rates of stream recharge, thereby causing declines in stream base flows and water tables (Seager *et al.*, 2007; Serrat-Capdevila *et al.*, 2007).

River flows are affected by changes in precipitation as well as by changes in temperature. In arid and semiarid regions, small changes in precipitation can bring about large changes in surface runoff (Dahm and Molles, 1992). Although there is agreement among climate models that the U.S. Southwest will become warmer, there remains much uncertainty regarding precipitation changes. Some Global Circulation Model scenarios project wetter winters while others predict drier winters, and changes in summer rainfall are highly uncertain (Dixon *et al.*, 2009). Such differences in seasonal distribution and/or amount of precipitation have important implications for hydrologic, geomorphic and biological responses. For example, large increases in precipitation may offset effects of a warming

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climate, as precipitation-caused gains to the stream aquifer compensate for warming-related evapotranspiration increase (Serrat-Capdevila *et al.*, 2007).

Increased occurrence of extreme weather events is another potential outcome of changing climates (Palmer *et al.*, 2008). Inland incursions of tropical hurricanes are one of three seasonal climatic drivers of floods in the Southwest region (Hirschboeck, 2009), and increased frequency or size of tropical cyclones associated with warming sea level (Diffenbaugh *et al.*, 2005; Webster *et al.*, 2005) may lead to larger floods. Effects of changing climates on another major driver, the North American monsoon (Sheppard *et al.*, 2002), are poorly understood and poorly represented in climate models. Pacific winter frontal systems, the third driver, often are associated with El Niño conditions, but multi-year atmospheric–oceanic teleconnections such as ENSO (El Niño Southern Oscillation) and PDO (Pacific Decadal Oscillation) also are poorly represented in climate models. Some evidence, however, suggests that El Niño conditions could become more frequent under a warmer climate (Timmermann *et al.*, 1999; Garfin and Lenart, 2007), potentially bringing greater winter precipitation to the Southwest. If winter precipitation does increase, this may cause an increase in the size or frequency of winter/spring floods (Dixon *et al.*, 2009) as has been observed in regions elsewhere (Pfister *et al.*, 2004).

Poff *et al.* in 1992 stated that ‘...ecologists would be hard pressed to answer the seemingly simple question: What specific biological changes would occur in a particular stream if average streamflow were to decline by 10%, or if flood frequencies were to increase by a factor of two?’ Over the past decades, knowledge of dryland riparian vegetation response to changing low-flow conditions has increased substantially. Linear and nonlinear responses to declining stream base flows have been quantified for various plant species and functional types, and threshold values have been identified for water table levels that cause mortality of various plant species and drive shifts between functional types (Stromberg *et al.*, 1996, 2005; Scott *et al.*, 1999; Castelli *et al.*, 2000; Horton and Clark, 2001; Horton *et al.*, 2001; Elmore *et al.*, 2003; Rood *et al.*, 2003; Lite and Stromberg, 2005). Although data gaps remain the increasing knowledge of the drought tolerance and rooting depth of dryland riparian plants is allowing for better prediction of how changes in stream intermittency or water table depth will alter plant community composition.

High-flow events (floods) also are an important force structuring dryland riparian ecosystems (Scott *et al.*, 1996; Rood *et al.*, 2007; Stromberg *et al.*, 2007). Floods can be described in terms of timing, intensity, frequency and variability, and our ability to predict vegetation response to changes in these factors is increasing. Riparian plant species differ in their ability to withstand or rapidly regenerate following flood disturbance (Bendix, 1994), thus changes in flood magnitude or frequency can produce changes in composition. Studies along longitudinal (upstream–downstream) and transverse spatial gradients reveal how mortality of tree species and distribution of community types vary among and within sites that differ in stream power, inundation frequency, sheer stress and sediment mobilization (Bendix, 1999; Friedman and Auble, 1999; Auble *et al.*, 2005; Friedman *et al.*, 2006). Recruitment phenologies of woody species have been quantified, increasing our ability to assess vegetation response to changes in flood timing and seasonality (Shafroth *et al.*, 1998; Dixon, 2003; Stella *et al.*, 2006). Models show how population structure of *Populus*, a dominant pioneer tree of southwestern rivers, varies in response to changes in flood hydrographs (Johnson, 1992; Mahoney and Rood, 1998; Lytle and Merritt, 2004). Much of the ecohydrology research in the riparian Southwest, however, has focused on a few woody species, leaving many questions about overall community structure. As population and community structure are altered, so too are an array of ecosystem functions, particularly following major shifts in plant functional types (Chapin *et al.*, 1997).

To anticipate effects of climate change on stream hydrology, and of stream hydrology on riparian vegetation, multiple approaches should be used. Modelling efforts (Baker *et al.*, 1991; Primack, 2000; Baird *et al.*, 2005) are critical but model outcomes are tempered by limitations including poor understanding of synergistic interactions among ecosystem components. Controlled experiments (Johansson and Nilsson, 2002; Cooper *et al.*, 2003) can improve mechanistic understanding but may not yield results in relevant temporal and spatial scales. Extrapolation of temporal dynamics from spatial variation is a third approach (Fukami and Wardle, 2005). Many environmental variables vary independently over the length of dryland rivers (Baker, 1989; Tabacchi *et al.*, 1996; Dixon and Johnson, 1999; Salinas and Casas, 2007) providing opportunities to empirically document spatial patterns and extrapolate changes through space-for-time substitutions. Flood magnitude, velocity and stream power are highly variable spatially along dryland rivers as a result of longitudinal changes in channel and valley geometry, stream gradient, watershed size, drainage density and transmission losses into aquifers (Nanson *et al.*, 2002). Stream

intermittency and water level depth in the stream aquifer also vary, in response to distance from humid recharge zones, proximity to tributaries and sites of groundwater pumpage or stream diversion, and differences in local geology as they influence depth to bedrock, groundwater flow paths and aquifer size. Often, there exist discrete eco-physical reaches within a river, reflecting discontinuities in hydrogeomorphology coupled with nonlinear, threshold-type relationships between biota and the physical environment (Thorpe *et al.*, 2006).

Our goal was to determine how riparian vegetation of a semiarid river varies among sites that differ in low- and high-flow conditions, as a basis for increasing our ability to predict effects on vegetation of climate-linked changes in stream hydrology. Taking advantage of the longitudinal variability in stream hydrology along one dryland river (the San Pedro, southern Arizona), we examined how low- and high-flow stream attributes interact to shape riparian vegetation at the population level and community level, inclusive of composition and structure. Specifically, we asked which biotic variables were influenced to the greater extent by low-flow conditions, which by high-flow conditions, which by both and which by some interaction thereof. Given that identification of feedbacks among ecosystem components is important for predicting effects of climate change (Bloschl *et al.*, 2007), another goal was to speculate as to how the ensuing vegetation changes might affect hydrologic and geomorphologic processes.

MATERIALS AND METHODS

Study area and study sites

The San Pedro River arises in Sonora, Mexico and flows north through the Chihuahuan and Sonoran Deserts to its confluence with the Gila River in Arizona, USA (Figure 1). The climate is semiarid. The river has been divided into two basins at the geological constriction known as the Benson Narrows. Climate along the river varies along a north to south gradient, with a Sonoran climate (50% summer, 50% winter precipitation) in the lower (northern) basin and a Chihuahuan climate (65% summer, 35% winter precipitation) in the upper (southern) basin. Total annual precipitation is similar in the two basins (average of 35 cm at Tombstone, #028619, 1893–2007; 35 cm at Winkleman 6S, #029420, 1942–1980; <http://www.wrcc.dri.edu>). Average maximum daily temperatures are 25°C in the upper basin (Tombstone station; 1893–2007) and 26°C in the lower basin (San Manuel station, #027530; 1954–2007).

Low flows in the San Pedro River derive from a combination of storm runoff and groundwater inflow from the regional aquifer (Baillie *et al.*, 2007), while floods derive from three types of storm systems (Sheppard *et al.*, 2002; Hirschboeck, 2009). Pacific frontal systems episodically produce long-duration gentle rains that trigger winter flood events of high magnitude and relatively long duration. Moisture flows from the gulfs of California and Mexico produce summer convective thunderstorms and floods with a 'flashy' hydrograph (rapid rise and fall of flood discharge); these monsoon floods presently are the most frequent type on the San Pedro. Finally, incursions of tropical storms occasionally produce large floods in late summer or fall. Tropical storm floods, although rare, historically have been associated with some of the largest events on the river (e.g. 2775 m³ s⁻¹ on 28 September 1926; 3823 m³ s⁻¹ on 1 October 1983) (Hirschboeck, 2009). The relative frequency of these three flood types has varied on a decadal to multi-decadal scale in the past for reasons that are not fully understood but that likely relate to global changes in oceanic–atmospheric teleconnections (Webb and Betancourt, 1992).

We established 18 sites along the river at elevations ranging from 600 to 1285; 6 sites were in the upper basin and 12 were in the lower basin (Figure 1). Sites were selected to capture the range of hydrologic conditions that occur over the length of the river. The 18 sites were classified dichotomously into 'wet hydrology' or 'dry hydrology' and 'low flood intensity' or 'high flood intensity' (Table I). Our metric for wet versus dry hydrology was stream flow permanence. This measure of stream intermittency was calculated as the percentage of months in which surface flow was present during a 2-year (2001 and 2002) period of monthly monitoring (Lite and Stromberg, 2005). The monthly values correlate strongly with data collected on a daily basis (Leenhouts *et al.*, 2006). Stream flow permanence at the dry sites ranged from 29% to 71% and averaged about 50% lower than at the wet sites where values ranged from 79% to 100%. The wet and dry sites were distributed equitably among the upper and lower basins. We used stream flow permanence rather than depth to groundwater in the stream aquifer as the indicator of low-flow hydrology because our prior research (Lite and Stromberg, 2005) suggests that it is a useful indicator of long-term fluctuations in depth to groundwater (with the more intermittent sites having greater seasonal drawdowns

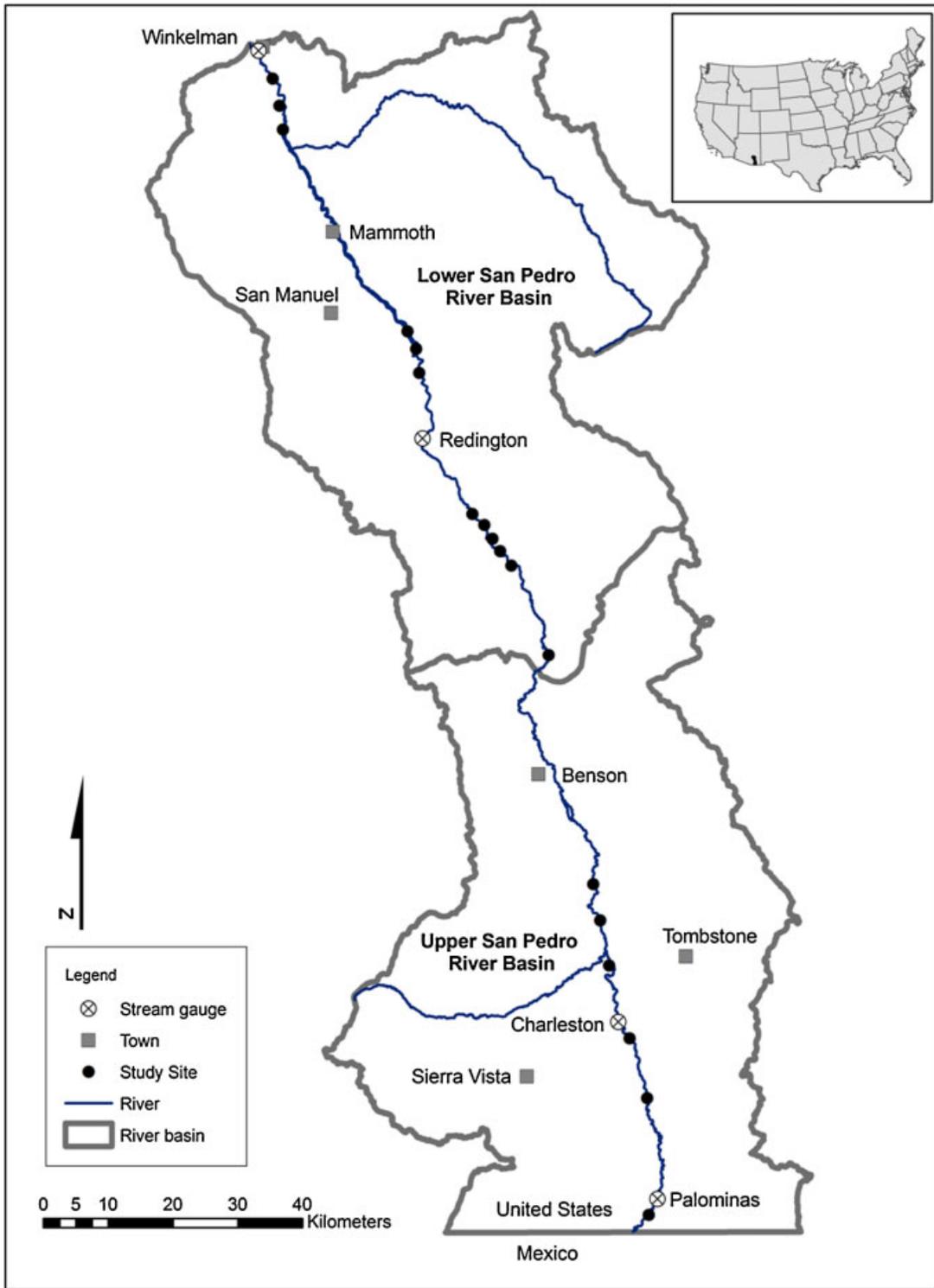


Figure 1. Map of San Pedro River basin, showing locations of study sites and USGS stream gauges

Table I. Descriptions of hydrologic site types

Site types		Range of values	Mean value	Number of sites (<i>n</i>)
Dry sites	<75% surface flow permanence	29–71%	52%	9
Wet sites	>75% surface flow permanence	79–100%	95%	9
Low flood intensity sites	<15 000 N s ⁻¹ total stream power of 10-year recurrence flood	6700–13 300 N s ⁻¹	10 083 N s ⁻¹	10
High flood intensity sites	>15 000 N s ⁻¹ total stream power of 10-year recurrence flood	15 000–28 500 N s ⁻¹	20 116 N s ⁻¹	8

and greater average depths to water). Mean depth to the water table, as averaged across the floodplain, ranged among sites from about 5 to 1 m.

For the flood intensity classification, our metric was total stream power of the 10-year recurrence flood (Lite *et al.*, 2005). Total stream power of the 10-year recurrence flood ranged among sites from 6700 to 28 500 N s⁻¹, with values peaking at mid-elevation sites along the river in an area with high drainage density and moderate stream gradient. Our threshold between low and high flood intensity sites was set at 15 000 N s⁻¹ (Table I), producing eight low flood intensity sites (in the lower basin) and 10 high flood intensity sites (four in lower basin and six in upper basin). Flood stream power at the low flood intensity sites averaged about half that at the high flood intensity sites.

Vegetation sampling and analysis

At each study site, two cross-floodplain transects were established that were perpendicular to the main axis of the river. The transects extended on both sides from the thalweg (channel low point) to closed *Prosopis velutina* (velvet mesquite) forest or *Sporobolus wrightii* (big sacaton) grassland, typically located on a terrace two or more meters above the channel bed. We refer to this zone below the terraces as the floodplain, as it is built of sediments deposited in the present regime of the river, after the channel incision of the late 19th and early 20th centuries (Hereford and Betancourt, 2009). Along one of the transect lines per site, 100 m² quadrats (5 × 20 m², long axis parallel to the river) were placed in stratified random fashion within discrete vegetation zones (patch types). A patch type consisted of a homogenous vegetation zone with respect to canopy, mid-stratum and ground cover of the dominant species. Each plot represented conditions in the patch. The number of quadrats sampled varied among sites depending on the floodplain width and number of patch types. Within each quadrat, data were collected in 2000 or 2001 on tree stem density and basal area, by species. Shrub cover, by species, was measured using the horizontal line intercept method (two, 10-m lines per quadrat). Vegetation volume was measured using the vertical line intercept method (three points per quadrat) and canopy cover was measured using a spherical densiometer (five readings per quadrat). Maximum canopy height along each transect was measured with a telescoping pole or a relascope. For analyses, plot-level data were scaled to the site level by weighting plot-level values by the per cent of the floodplain occupied by a plot's representative patch.

Herbaceous plant cover, by species, was sampled in 1-m² quadrats using Domin–Krajina cover classes. These small quadrats were randomly placed within discrete patches located along one cross-floodplain transect per site. For herbaceous sampling, if patches along a transect were wider than 25 m, another quadrat was added for each additional 25 m of that patch type (i.e. two quadrats for patches 26–50 m wide). Herbaceous quadrat number ranged among sites from 9 to 27. Data were collected during the early summer dry season (late May–early June) and late summer monsoonal wet season (late August–early September) in 2000 and 2001. Cover values were averaged across the four sampling times, and these plot-level data were scaled up to the site level by weighting values by the per cent of the floodplain occupied by a plot's representative patch.

Plant species were identified using Kearney and Peebles (1960) and recent treatises in the Journal of the Arizona-Nevada Academy of Sciences. Woody species were placed into five broad functional types according to a disturbance–stress matrix. Classifications were based on information on drought tolerance as inferred in part from wetland indicator scores and on life history characteristics such as reproductive output, seed size and shade

tolerance obtained from various databases (<http://plants.usda.gov/>; <http://www.fs.fed.us/database>). Of the 35 woody species recorded, 7 were in the hydric pioneer functional type, 3 in mesic pioneer, 4 in xeric pioneer, 9 in mesic competitor and 12 in stress tolerator (Table II). Herbaceous species were classified into two broad categories—annual (or biennial) vs. perennial—using information from the USDA PLANTS database (<http://plants.usda.gov/>).

As an estimate of population age structure, the median stem diameter at a site was determined for each common tree species. As a measure of population size class diversity (a rough surrogate of age class diversity for these episodically establishing species), counts were made of the total number of stem diameter size classes present at a site, using size increments of 10 cm. For one analysis, the three common pioneer tree species were divided into three age classes using age/stem diameter relationships (Stromberg, 1998). *Populus fremontii* and *S. gooddingii* have similar radial diameter growth rates, and grow faster than *Tamarix* sp. The following size thresholds produce roughly similar age classes for the three species along the study river: *P. fremontii* and *S. gooddingii* young (<20 cm), mature (21–90 cm), old (>90 cm); *Tamarix* sp. young (<5 cm), mature (5–20 cm), old (>20 cm).

Two-way analysis of variance (with factors of wet vs. dry and low vs. high flood intensity) was used to determine whether the suite of measured vegetation variables were influenced by one or both factors or by interactions thereof.

Table II. Frequency of occurrence for woody species recorded within San Pedro River flood-plain plots (total $n = 343$)

Scientific name	Common name	Functional type	Plots (n)	Frequency (%)
<i>P. fremontii</i>	Fremont cottonwood	Hydric pioneer	205	60
<i>Tamarix</i> sp.*	Salt cedar	Mesic pioneer	181	53
<i>B. salicifolia</i>	Seep willow	Hydric pioneer	165	48
<i>P. velutina</i>	Velvet mesquite	Mesic competitor	132	38
<i>S. gooddingii</i>	Goodding willow	Hydric pioneer	102	30
<i>H. monogyra</i>	Burrobush	Xeric pioneer	49	14
<i>Celtis laevigata</i> var. <i>reticulata</i>	Netleaf hackberry	Mesic competitor	28	8
<i>Baccharis sarothroides</i>	Desert broom	Mesic pioneer	19	6
<i>Ericameria nauseosa</i>	Rabbit brush	Xeric pioneer	19	6
<i>Fraxinus velutina</i>	Velvet ash	Mesic competitor	18	5
<i>Clematis drummondii</i>	Drummond's clematis	Stress tolerator	17	5
<i>Juglans major</i>	Arizona walnut	Mesic competitor	13	4
<i>Baccharis emoryi</i>	Emory's false willow	Hydric pioneer	11	3
<i>Chloracantha spinosa</i>	Spiny aster	Mesic pioneer	11	3
<i>Salix exigua</i>	Coyote willow	Hydric pioneer	10	3
<i>Rhus microphylla</i>	Littleleaf sumac	Stress tolerator	8	2
<i>Acacia greggii</i>	Catclaw acacia	Stress tolerator	7	2
<i>Sambucus nigra</i> spp. <i>canadensis</i>	American elderberry	Mesic competitor	6	2
<i>Atriplex canescens</i>	Four wing saltbush	Stress tolerator	6	2
<i>Cylindropuntia spinosior</i>	Cane cholla	Stress tolerator	6	2
<i>Lycium pallidum</i>	Pale desert-thorn	Stress tolerator	6	2
<i>Platanus wrightii</i>	Arizona sycamore	Hydric pioneer	5	1
<i>Isocoma tenuisecta</i>	Burrowweed	Xeric pioneer	5	1
<i>Ziziphus obtusifolia</i>	Greythorn	Stress tolerator	5	1
<i>Acacia constricta</i>	Whitethorn acacia	Stress tolerator	4	1
<i>Juniperus deppeana</i>	Alligator juniper	Stress tolerator	4	1
<i>Mimosa biuncifera</i>	Catclaw mimosa	Stress tolerator	4	1
<i>Ephedra trifurca</i>	Longleaf jointfir	Stress tolerator	3	1
<i>Sapindus saponaria</i>	Wingleaf soapberry	Mesic competitor	2	<1
<i>Pluchea sericea</i>	Arrowweed	Hydric pioneer	1	<1
<i>Gutierrezia microcephala</i>	Threadleaf snakeweed	Xeric pioneer	1	<1
<i>Acer negundo</i>	Box elder	Mesic competitor	1	<1
<i>Morus microphylla</i>	Texas mulberry	Mesic competitor	1	<1
<i>Vitis arizonica</i>	Arizona grape	Mesic competitor	1	<1
<i>Celtis ehrenbergiana</i>	Spiny hackberry	Stress tolerator	1	<1

**T. ramosissima*, *T. chinensis* or hybrids

Of the 35 woody species, only 6 (4 trees, 2 shrubs) had sufficient abundance to allow statistical analysis. For the four tree species, basal area and stem density were used as measures of abundance; for the two shrub species, per cent ground cover was used. Variables used in analysis were transformed as necessary to meet assumptions for normality and constant variance. Statistical analyses were conducted using SYSTAT 12.

RESULTS

Tree and shrub species abundance

The six common woody species responded individually to the water availability and flood intensity factors, with some commonalities by functional type (Figure 2, Table III). Abundances of the two hydric pioneer tree species (*P. fremontii* and *S. gooddingii*) were strongly ($p \leq 0.01$) related to site water availability, with greater basal area and stem density at wet sites. *P. fremontii* showed some interaction ($p = 0.08$) between variables, with strong differences in basal area between low and high flood intensity conditions for wet sites and uniformly low basal area at dry sites regardless of flood intensity. Abundance of *Baccharis salicifolia* (hydric pioneer shrub) was weakly ($p = 0.08$) related to site water availability, with cover greater at wet sites. *Tamarix* (mesic pioneer tree/shrub)

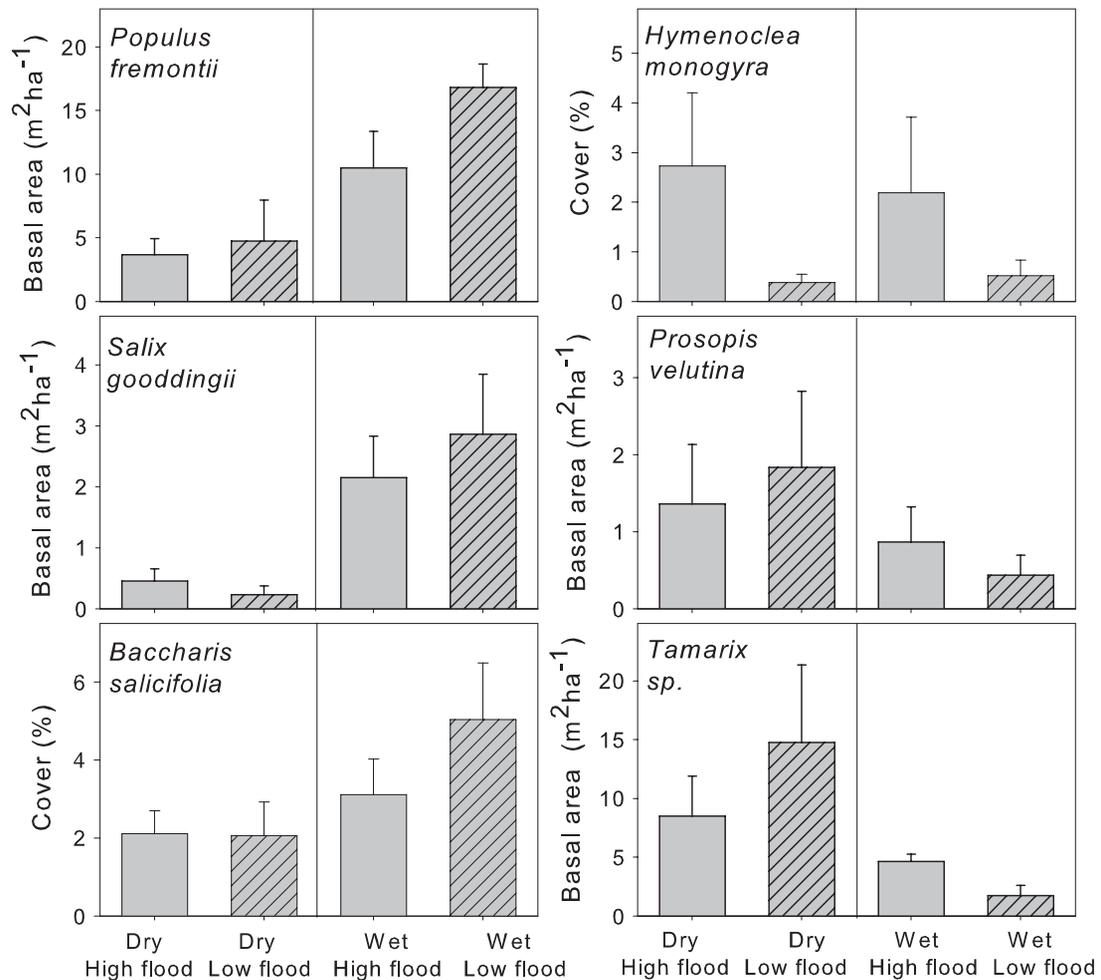


Figure 2. Basal area (trees) or cover (shrubs) of the six most abundant woody species along the San Pedro River, by site hydrology class. Values shown are means (± 1 SE). Note differences in y-axis scales

Table III. Significance of water availability (infrequent vs. frequent stream base flow) and flood intensity (high vs. low) on several attributes of riparian vegetation, as measured within the San Pedro River floodplain, and based on ANOVA ($n = 18$ sites; 17 df)

	Factor 1: water availability		Factor 2: flood intensity		Interaction	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Tree abundance, by species						
<i>P. fremontii</i> basal area	14.35	<0.01	2.12	0.16	1.13	0.31
<i>P. fremontii</i> density	9.42	0.01	0.91	0.36	3.48	0.08
<i>S. gooddingii</i> basal area	11.57	<0.01	0.15	0.71	0.54	0.48
<i>S. gooddingii</i> density	8.42	0.01	0.80	0.39	0.61	0.55
<i>Tamarix</i> basal area	4.42	0.05	0.18	0.68	1.30	0.27
<i>Tamarix</i> density	1.47	0.25	4.87	0.05	0.75	0.41
<i>P. velutina</i> basal area	1.88	0.19	0.43	0.52	0.43	0.52
<i>P. velutina</i> density	0.21	0.65	0.17	0.69	0.78	0.39
Tree population structure						
<i>P. fremontii</i> median size	2.73	0.13	5.10	0.05	2.88	0.12
<i>S. gooddingii</i> median size	1.11	0.32	5.49	0.04	2.38	0.15
<i>Tamarix</i> median size	1.81	0.21	3.32	0.09	1.81	0.21
<i>P. fremontii</i> size class #	11.18	<0.01	0.35	0.57	0.52	0.48
<i>S. gooddingii</i> size class #	9.0	0.01	2.37	0.15	0.02	0.90
<i>Tamarix</i> size class #	1.12	0.31	0.09	0.77	6.61	0.02
Shrub abundance, by species						
<i>H. monogyra</i> cover	0.04	0.85	4.87	0.05	0.10	0.76
<i>B. salicifolia</i> cover	3.58	0.08	0.09	0.77	0.77	0.39
Woody vegetation structure						
Vegetation height	6.82	0.02	4.57	0.05	1.59	0.23
Canopy cover	2.45	0.14	0.97	0.34	0.12	0.74
Stem density	0.03	0.86	2.99	0.11	0.05	0.83
Basal area	0.32	0.58	2.34	0.15	0.27	0.61
Vegetation volume	1.54	0.23	1.09	0.31	2.02	0.18
Herbaceous vegetation						
Relative cover of annuals	4.75	0.05	11.3	<0.01	1.13	0.31
Annuals (% cover)	3.56	0.08	6.36	0.02	0.38	0.55
Perennials (% cover)	2.17	0.16	4.85	0.05	0.10	0.76
Cover (%)	0.29	0.60	0.09	0.72	0.04	0.82

abundance was related to both water availability (with significantly greater basal area at dry sites) and flood intensity (with greater stem density at the high flood intensity sites). Abundance of *Hymenoclea monogyra* (xeric pioneer shrub) was related to flood intensity, with greater cover at sites with high flood intensity. *P. velutina* (mesic competitor tree) showed little difference in basal area or density among hydrologic site types.

Pioneer tree population structure

For *P. fremontii* and *S. gooddingii*, there were significantly more stem size classes at wet sites (Table III). *Tamarix* showed an interaction effect: Within the low flood intensity sites, it had more size classes at dry (vs. wet) sites, but within the high flood intensity sites it had more size classes at wet (vs. dry) sites. Number of 10-cm diameter stem size classes at wet versus dry sites were 9.1 ± 0.9 versus 3.9 ± 1.2 (*P. fremontii*), 5.0 ± 0.7 versus

2.1 ± 0.6 (*S. gooddingii*) and 3.4 ± 0.6 versus 4.3 ± 0.5 (*Tamarix*) (values are means \pm 1 SE of nine wet sites and nine dry sites).

For all three common pioneer tree species (*P. fremontii*, *S. gooddingii*, *Tamarix* sp.) the median stem diameter varied as a function of flood intensity, with stems smaller at high flood intensity sites (Table III). Median stem diameters for the species at high versus low flood intensity sites were 9 ± 1 cm versus 26 ± 9 cm (*P. fremontii*), 9 ± 2 cm versus 16 ± 3 cm (*S. gooddingii*) and 1.3 ± 0.2 cm versus 1.9 ± 0.3 cm (*Tamarix*) (values are means \pm 1 SE of 8 high intensity and 10 low intensity sites). For *P. fremontii*, older individuals were more abundant at the low flood intensity sites, and were absent from sites with the combination of dry hydrology and high flood intensity (Figure 3). Old *Tamarix*, in contrast, were absent from wet sites with low intensity floods.

Woody vegetation structure

Maximum canopy height within the floodplain varied as a function of both site water availability and flood intensity, with the tallest canopies at sites with wet hydrology and low flood intensities, and shorter canopies at sites that were either dry or had high flood intensity (Figure 4, Table III). Canopy cover was weakly related to site water availability, with values greater at wetter sites. Vegetation volume showed a similar, but even weaker, tendency. Basal area and stem density were both weakly related to flood intensity, with values for basal area greater at the low flood intensity sites (reflecting abundance of old, large *Populus* trees), and values for stem density greater at the high flood intensity sites (reflecting shifts towards younger trees and in particular towards young, high-density *Tamarix*).

Herbaceous vegetation

Seasonally averaged covers of annual plants and of perennial plants in the floodplain were related to flood intensity (strongly) and to water availability (weakly), but in opposing fashion (Figure 5, Table III). Annuals had greater cover at sites with high flood intensity and/or dry hydrology, while herbaceous perennials had greater cover at sites with low flood intensity and/or wet hydrology. Relative cover of annuals thus was greatest at sites with the combination of dry conditions and high flood intensity. Given the opposing patterns of the two plant groups, total

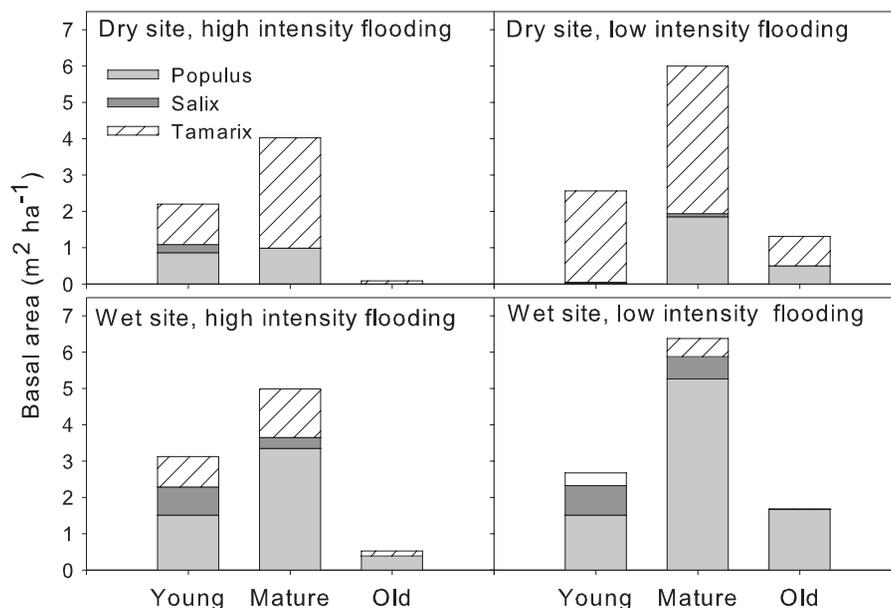


Figure 3. Basal area of the three most abundance pioneer trees within the San Pedro River floodplain, by age class and by site hydrology class. Values shown are means (\pm 1 SE)

EFFECTS OF STREAM FLOW PATTERNS

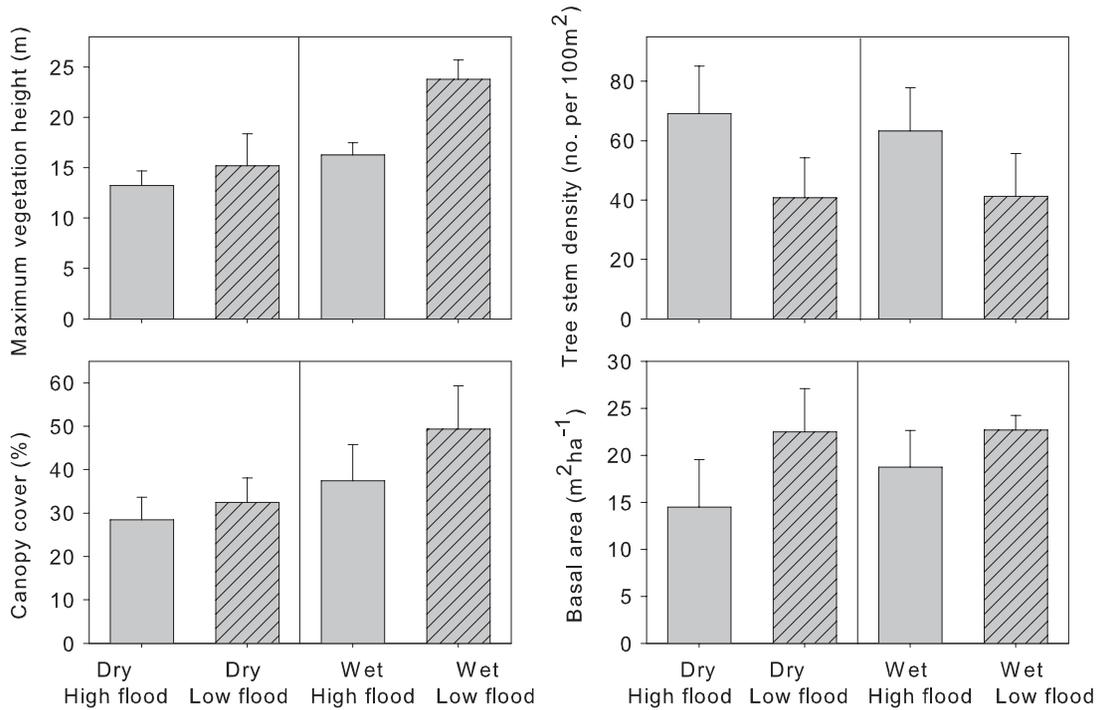


Figure 4. Stand structural traits of the woody plant community within the San Pedro River floodplain, grouped by site hydrology class. Values shown are means (± 1 SE)

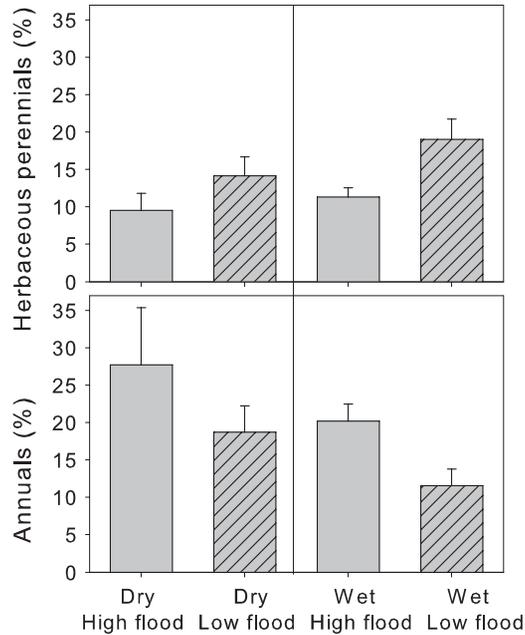


Figure 5. Seasonally averaged cover of annual species and herbaceous perennial species within the San Pedro River floodplain, grouped by site hydrology class. Values shown are means (± 1 SE)

herbaceous cover did not differ appreciably among hydrologic site types. Common annual species included *Acalypha neomexicana*, *Bidens leptcephala*, *Boerhavia coulteri*, *Bouteloua aristoides*, *Echinochloa crus-galli*, *Echinochloa colona*, *Eriochloa acuminata* and *Setaria grisebachii*. Common perennials included *Cynodon dactylon*, *Sorghum halepense*, *Sporobolus contractus* and *S. wrightii*.

DISCUSSION

This empirical study provides insight into the ways in which riparian vegetation on the semiarid San Pedro River might change in response to climate-induced changes in stream low- and high-flow conditions, recognizing that extrapolation of temporal trends from spatial gradients has caveats. The differences in site water availability and flood intensity that occur over the length of the River influenced several population- and community-level aspects of the floodplain vegetation. Some variables were related strongly to site water availability, and others to flood intensity; in some cases dry conditions and high flood intensities produced similar, and compounding, changes in the vegetation (e.g. shifts towards annual species and shorter tree canopies under both conditions). For some stand structure attributes (e.g. vegetation volume), few differences were observed among hydrologic site types because of replacement of one plant group (*Populus–Salix* with abundant volume in upper canopy layers) by another (*Tamarix*, with abundant vegetation in lower strata). Some of the statistical effects detected are not a direct result of plant response to the metrics of stream intermittency and flood intensity, but rather to affiliated variables that change in tandem including depth to water table and flood frequency and duration. In all cases, riparian vegetation responses to long-term climate shifts will overlay and integrate with responses to other ongoing environmental changes including cyclic weather phenomenon, introduced species expansions, human land and water use and past extreme events that set in motion trajectories of change.

Vegetation and floods

Woody plant communities. The San Pedro River is a high disturbance system. *P. fremontii* and *Salix gooddingii*, two of the common species, typically establish following large winter/spring flood events, or following spring runoff that occurs soon after very large tropical fall storms (Stromberg, 1998). Other common woody plants along the river (e.g. *B. salicifolia*, *Tamarix* sp.) also are pioneer species associated with sites that experience high unit stream power during floods (Bendix, 1999). Species in the competitor (e.g. *P. velutina*) and stress tolerator (e.g. *Lycium* spp.) groups are much less abundant. Thus, if flood intensities increased (and assuming no change in other variables), the currently dominant pioneer species would be expected to remain as such. There would, however, be changes in population size structure, with shifts towards younger median age as indicated by the smaller median stem size at the high flood intensity sites. The sites we classified as high flood intensity have a higher frequency of floods that are of sufficient size to cause scour and sediment flow and thus trigger stand replacement events.

Legacies. On highly dynamic rivers such as the San Pedro, vegetation often is not in equilibrium with the observed hydrologic conditions. One ongoing change on the San Pedro is immigration of *Tamarix*. This pioneer species colonized the San Pedro in the mid-1900s, and its relatively young age structure along the river suggests that it is still undergoing population expansion (Stromberg, 1998). It had greater stem density at higher flood intensity sites presumably because such sites have had a higher frequency of the stand-replacing flood events that create opportunities for establishment. Increasing flood intensity likely would hasten the process of *Tamarix* immigration and expansion to equilibrium conditions, with the rate also driven by water table changes.

Vegetation patterns on the San Pedro River also are changing in response to the flood-induced river entrenchment, and subsequent channel widening, that occurred in the late 19th and early 20th centuries on the San Pedro and other alluvial rivers in the Southwest (Hereford and Betancourt, 2009). Such extreme events can shape population structure and recruitment processes of pioneer trees for decades (Friedman *et al.*, 1996). On the San Pedro, *Populus/Salix* pioneer forests have been increasing in abundance since the early 1900s, with vegetation colonization accompanying channel narrowing and formation of an inset floodplain within the former, widened channel trench. Recruitment has been episodic, but concentrated in decades of increased winter flooding associated with atmospheric–oceanic teleconnections (Stromberg, 1998; Webb *et al.*, 2007). On some reaches of the river, the long-term, cumulative processes of vegetation colonization appears to be leading to greater stabilization of the

flood channel, and with it, reduced opportunities for recruitment of pioneer woody species during future flood events (Dixon *et al.*, 2009). Thus, in such areas, increased flood intensity arising from climate change would slow or reverse this process, while reduced flood intensity would accelerate the successional shift from pioneer species towards more competitive species.

Flood–soil interactions. Floods also can influence woody species by modifying edaphic conditions. In the Southwest, flood duration often increases in tandem with flood intensity (i.e. stream power), at least for storms produced by Pacific frontal systems. Large, long floods can deposit thick lenses of coarse soils that lie several meters above the water table. Such coarsening of soil textures, and changes in surface elevation relative to the water table, can select for xeric pioneer species over mesic ones (Stromberg *et al.*, 1997; Merigliano, 2005). Such processes likely explain the positive association of the xeric pioneer *H. monogyra* with high flood intensity sites in this study.

Woody vegetation structure. Responses for vegetation structure traits tended to be weaker than responses for individual plant species. Nevertheless, given greater flood intensities, vegetation structure would change in response to changes in woody species composition and forest age structure. Reduction in canopy height and basal area, and increased in woody stem densities, are typical responses to shifts towards young age of pioneer trees. Such patterns are the inverse of those occurring during *Populus* forest succession, wherein tree density decreases through successional time while basal area and tree height increase (Fierke and Kauffman, 2005; Stromberg and Tiller, in review).

Herbaceous vegetation. The herbaceous understory would become dominated by greater relative cover of annual species (vs. perennials) in response to both flood intensity increase and stream drying. The shift towards short-lived species at sites with high flood intensity is consistent with life-history theories regarding adaptations to disturbance (Grime, 1979; Walker *et al.*, 1986). It is also consistent with empirical studies conducted in riparian zones, wherein annuals increase following flooding and/or give way to herbaceous perennials with increased time since major flood disturbance (Friedman *et al.*, 1996; Cosgriff *et al.*, 2007).

Within the herbaceous layer, seasonally averaged values for cover on the San Pedro are not expected to vary with changes in flood intensity or stream intermittency because annuals would increase as perennials decrease. However, this pattern may not occur at all rivers in the Southwest. Tieg *et al.* (2005), on the arid Lower Colorado River, found less total ground cover (inclusive of woody and herbaceous species) on moderately disturbed plots than on low-disturbance plots. The semiarid San Pedro in contrast, receives sufficient moisture from winter and summer rains and floods to sustain large numbers of seasonal annuals (Bagstad *et al.*, 2005).

Vegetation response to stream-low-flow changes

Woody plant communities. The process of riparian plant community change in response to stream low-flow changes can occur in step-wise fashion, as hydrologic thresholds are sequentially exceeded for dominant species (Stringham *et al.*, 2001). Major shifts in vegetation composition following low-flow changes can be episodic, mediated by flood disturbance. Large, geomorphically effective floods cause turnover of patches within the floodplain mosaic by mobilizing sediment, eroding root zones and causing tree death (Friedman and Lee, 2002; Whited *et al.*, 2007). Following flood scour, post-flood recruitment surfaces are available for colonization by other types better adapted to the new environmental conditions.

Presently, a portion of the San Pedro River floodplain supports tall, hydric, broad-leaved pioneer trees (*P. fremontii* and *S. gooddingii*) that have moderately deep roots (Zimmerman, 1969; Braatne *et al.*, 1996; Williams and Cooper, 2005) but are drought intolerant (Scott *et al.*, 1999; Rood *et al.*, 2003). Population size of these obligate phreatophytes would decline as water tables dropped below root zones for extended periods (Horton *et al.*, 2001; Lite and Stromberg, 2005). Size class diversity also would decline, because of selective mortality of susceptible age classes and because of reduced recruitment success during flood events (Smith *et al.*, 1991; Shafroth *et al.*, 1998; Horton and Clark, 2001; Amlin and Rood, 2002). Hydric pioneer shrubs, including *B. salicifolia*, also likely would decline in abundance if stream flows declined (Williams *et al.*, 1998).

In response to increased stream intermittency and water table decline, dominance would shift from *Populus* and *Salix* to small woody mesic pioneer trees, represented in the San Pedro ecosystem by *Tamarix*. *Tamarix* sp. has many adaptations including great root length (approximately 7–10 m) that allow it to thrive along intermittent

streams with deep and fluctuating water tables and shallow, seasonal moisture sources (Merkel and Hopkins, 1957; Smith *et al.*, 1998; Horton *et al.*, 2001, 2003; Glenn and Nagler, 2005). Further, *Tamarix* would undergo less competitive suppression by *Populus* as hydrologic thresholds for survival of the latter were exceeded (Sher *et al.*, 2000). A third low-flow vegetation state consists of predominance by short, xeric pioneer shrubs (e.g. *H. monogyra*) sustained by seasonal flood water sources. Such species are common on ephemeral desert rivers, and would likely increase along the San Pedro if extreme dewatering caused water table conditions to exceed thresholds for survivorship of deep-rooted mesic pioneers.

Woody vegetation structure. With increasing site dryness, stand structure would change as certain woody species were replaced by others with strongly differing morphologies. The strong trend for shorter canopies and weak trend for less dense canopy cover at the drier sites reflect inherent physiological constraints on plant architecture and vegetation structure under increasing water stress (Sperry *et al.*, 2002). Both of these changes on the San Pedro River resulted from replacement of tall, broad-leaved *Populus* and *Salix* by the shorter-canopied and needle-leaved *Tamarix*. Salinas and Casas (2007), along a dryland river gradient, similarly found woody plant cover to decline with shorter hydroperiod (less permanent stream flows), suggesting a strong role of surface flow permanence in structuring woody vegetation in semiarid rivers. Williams and Cooper (2005) reported reduced stand leaf area in *Populus* stands on a flow-regulated river, which they attributed to a prior period of severe water stress associated with flow regulation.

Herbaceous vegetation. There are several reasons why annuals would become relatively more abundant at dry sites. First, given the sparser tree canopies, reduced competition for light and space allows annuals to attain high abundance in bare patches of soil following seasonal rains and floods (Stromberg *et al.*, 2009). Second, many of the perennial herbs in the floodplain presumably require a permanent water source to sustain high cover. If a shallow water table is not present, they are replaced by annuals that avoid drought through temporal escape, analogous to patterns in upland deserts (Burgess, 1995). In meadows along streams in the Great Basin (a cold desert), however, perennial graminoids were abundant across a wide range of water table depths (Castelli *et al.*, 2000). The San Pedro is comparatively more arid, and its sandy soils have less water-holding capacity. This combination of factors (together with periodic flood disturbance) may preclude development of dense graminoids at sites with deep water tables.

Temporal pattern of low-flow change. In predicting ecological outcomes, time scales of change of abiotic factors can be important (Bloschl *et al.*, 2007). With increasing aridity, stream base flow and water tables will decline. If the rate of decline is gradual, some phreatophytic trees will maintain root contact with the slowly receding capillary fringe and have greater survivorship than would occur under more abrupt water table declines (Scott *et al.*, 1999). Variability of flows in preceding years also will be influential, in part as it affects root distribution; phreatophytes acclimated to stable, shallow water tables would have greater mortality than those growing at sites subject to greater seasonal water table fluctuation (Shafroth *et al.*, 2000; Williams and Cooper, 2005).

Over the long-term, climate changes will interact with and overlay existing climate patterns driven by large-scale atmosphere–ocean connections. The desert Southwest undergoes severe drought approximately once per century, relating to patterns in the El Niño—Southern Oscillation, the Pacific Decadal Oscillation and the Atlantic Multi-decadal Oscillation (Jacobs *et al.*, 2005). Vegetation processes sensitive to stream low flows, including mortality of *Populus* trees, would be more pronounced during such drought periods (Gitlin *et al.* 2006).

Spatial patterns of low-flow change. On spatially intermittent streams such as the San Pedro, the extent of perennially flowing segments contracts and expands in response to annual and decadal wet and dry cycles (Stanley *et al.*, 1997). Long-term, sustained reductions in recharge would cause a more permanent contraction of the perennial-flow segments. The spatial pattern of change, however, would be nonuniform. Certain reaches of the river would be buffered from the change because of their hydrogeomorphical setting. Some reaches are nearer the thresholds for major changes between woody vegetation types, and small changes in hydrology in such areas would more rapidly produce shifts in vegetation composition (Leenhouts *et al.*, 2006).

Spatial patterns also will be influenced by water and land use in the riparian zone and watershed (Patten, 1998). On the San Pedro, conservation efforts to reduce pumping from the stream aquifer may increase base flows in certain parts of the river, while in other sections base flows may decline in response to ongoing pumping from the regional aquifer (Stromberg and Tellman, 2009). Watershed land cover changes also will modify hydrologic

processes, by affecting infiltration and runoff processes (Lopez-Moreno *et al.*, 2006; Li *et al.*, 2007). Recent urbanization of portions of the San Pedro watershed, together with other land cover changes, may intensify flood runoff, increase flow variability and reduce base flows (Miller *et al.*, 2002).

Interactions and feedbacks

The influences between hydrology and vegetation are bi-directional, and such feedbacks between ecosystem components can complicate predictions of effects of climate change (Bloschl *et al.*, 2007). Changes in evapotranspiration rate and relative use of groundwater versus other water sources following vegetation shifts are particularly important feedbacks on stream hydrology (Williams and Scott, 2009). Although more research is needed, data suggest that reduced recharge from increasing aridity would result in negative feedback in the San Pedro riparian zone: The ensuing water table decline would result in less ground water use by vegetation, leading, in turn, to less depletion of the aquifer. Within the herbaceous community, phreatic, perennial grasses (such as *S. wrightii*; Scott *et al.*, 2000) would be replaced by annual species that rely more heavily on soil water derived from rain or flood pulses. Within the pioneer forest, shifts from *Populus* and *Salix* to the facultative phreatophyte *Tamarix* would likely reduce or maintain total evapotranspiration rates, while also resulting in greater use of precipitation or flood water (vs. ground water) (Nagler *et al.*, 2005; Shafroth *et al.*, 2005). Seasonal declines in groundwater below root zones would reduce evapotranspiration rates within *Populus*–*Salix* stands (Gazal *et al.*, 2006), while the overall declines in canopy cover and vegetation volume (albeit small) likely would result in declines in stand-level water use (Dahm *et al.*, 2002). Greatest changes in evapotranspiration rate would occur as the deep-rooted phreatophytic trees and shrubs were replaced by xeric pioneer shrubs sustained by seasonal water pulses (Wilcox *et al.*, 2006).

Increased flood intensities also would influence evapotranspiration rates, by shifting herbaceous vegetation towards annuals, shifting pioneer tree population structure towards younger stands, and producing forest stands with greater stem density but lower basal area. Within the San Pedro riparian ecosystem, Schaeffer *et al.* (2000) found stand-level evapotranspiration to be greater in young (and near-channel) *Populus*–*Salix* forests than in older forests, but more research is needed to determine how stand-level evapotranspiration in these riparian forests will change in response to linked changes in stand age and biomass structure (Boggs and Weaver, 1994; Dawson, 1996).

There also are bidirectional interactions between stream geomorphology and riparian vegetation (Hughes, 1997; Bendix and Hupp, 2000; Corenblit *et al.*, 2007). For example, substrate type influences plant cover and composition, and these variables in turn influence substrate stability. Perennial grasses, given their dense, shallow root systems, are particularly effective at stabilizing sediments (Gyssels *et al.*, 2005). The shifts to annual plants that would occur with increased flood intensity and/or site drying would likely reduce substrate stability (Micheli and Kirchner, 2002). This would constitute a positive feedback that, by resulting in greater mobilization of substrates, would further increase the disturbance susceptibility of the site.

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