SRP14311

RIVER RESEARCH AND APPLICATIONS

River Res. Applic. **21**: 925–938 (2005)

Published online 1 June 2005 in Wiley InterScience
(www.interscience.wiley.com). DOI: 10.1002/rra.858

EFFECTS OF STREAM FLOW INTERMITTENCY ON RIPARIAN VEGETATION OF A SEMIARID REGION RIVER (SAN PEDRO RIVER, ARIZONA)

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ABSTRACT

The San Pedro River in the southwestern United States retains a natural flood regime and has several reaches with perennial stream flow and shallow ground water. However, much of the river flows intermittently. Urbanization-linked declines in regional ground-water levels have raised concerns over the future status of the riverine ecosystem in some parts of the river, while restoration-linked decreases in agricultural ground-water pumping are expected to increase stream flows in other parts. This study describes the response of the streamside herbaceous vegetation to changes in stream flow permanence. During the early summer dry season, streamside herbaceous cover and species richness declined continuously across spatial gradients of flow permanence, and composition shifted from hydric to mesic species at sites with more intermittent flow. Hydrologic threshold values were evident for one plant functional group: *Schoenoplectus acutus*, *Juncus torreyi*, and other hydric riparian plants declined sharply in cover with loss of perennial stream flow. In contrast, cover of mesic riparian perennials (including *Cynodon dactylon*, an introduced species) increased at sites with intermittent flow. Patterns of hydric and mesic riparian annuals varied by season: in the early summer dry season their cover declined continuously as flow became more intermittent, while in the late summer wet season their cover increased as the flow became more intermittent. Periodic drought at the intermittent sites may increase opportunities for establishment of these annuals during the monsoonal flood season. During the late summer flood season, stream flow was present at most sites, and fewer vegetation traits were correlated with flow permanence; cover and richness were correlated with other environmental factors including site elevation and substrate nitrate level and particle size. Although perennial-flow and intermittent-flow sites support different streamside plant communities, all of the plant functional groups are abundant at perennial-flow sites when viewing the ecosystem at broader spatial and temporal scales: mesic riparian perennials are common in the floodplain zone adjacent to the river channel and late-summer hydric and mesic annuals are periodically abundant after large floods. Copyright © 2005 John Wiley & Sons, Ltd.

KEY WORDS: *Cynodon dactylon*; ground water; herbaceous vegetation; intermittent stream; instream flow; introduced species; riparian; riverine marsh; semiarid; temporary stream

INTRODUCTION

Increasing demands on global freshwater resources placed by growing human populations are altering the water regimes of wetland and riverine ecosystems (Nilsson and Svedmark, 2002). The semiarid southwestern United States is no exception to this trend. The flow regime of many rivers in this region has been altered by stream diversion, ground-water pumping, or dams. The San Pedro River in southern Arizona has several reaches with perennial stream flow and shallow ground water and retains a natural flood regime over its length. In the Upper Basin of the river, however, there are concerns regarding the future status of the riparian and aquatic system; urban water use has caused regional ground-water levels to decline and altered ground-water flow paths to the river (Glennon, 2002; Steinitz *et al.*, 2003). In the Lower and Upper Basins, many perennial reaches have become intermittent due to pumping of ground water from the floodplain aquifer, but retirement of agricultural ground-water pumping for biodiversity conservation purposes is expected to increase stream flows in some presently dry reaches (Haney, 2002).

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Received 5 May 2004
Revised 8 November 2004
Accepted 17 November 2004

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It is challenging to design and implement programmes that provide for societal water needs and water needs of aquatic and riparian biota (Naiman *et al*., 2002; Richter *et al*., 2003). Environmental flow studies can determine the degree to which the flow regime of a river can be altered for water resource development while maintaining acceptable conditions within the aquatic–riparian ecosystems (Tharme, 2003). Environmental flow assessments typically evaluate hydrologic regimes needed for in-stream biota as well as for establishment and maintenance of riparian vegetation on river floodplains and terraces (Ward and Stanford, 1987; Hughes and Rood, 2003). Quantitative models are being increasingly used throughout the world to assess change in riverine vegetation caused by changes in water availability (Van Diggelen *et al*., 1991; King and Louw, 1998). The San Pedro River is notable for sustaining high regional biodiversity, and the riparian corridor is valued for its role as a migratory bird corridor (Arias, 2000), thus efforts are underway to determine the flow needs of its aquatic and riparian biota.

Riparian vegetation is influenced by surface and subsurface water flows, and by low-flow and high-flow aspects of the flow regime (Poff *et al*., 1997). Biohydrology studies have examined relationships of riparian vegetation with many hydrologic parameters including seasonal or annual stream flow rate, magnitude and variability of base flows, depth to ground water or saturated soil, and frequency, timing and magnitude of flood pulses (Nestler and Long, 1997; Friedman and Auble, 1999; Johnson, 2000; Pettit *et al.*, 2001; Elmore *et al.*, 2003). Vegetation can be characterized in many ways, and studies have examined effects of surface- and ground-water flow regimes on vegetation abundance, plant species diversity, species composition, establishment and survival of tree species, and plant growth and vigour (Stromberg and Patten, 1990, 1995; Smith *et al.*, 1991; Shafroth *et al.*, 1998, 2000, 2002; Johnson *et al.*, 1999; Scott *et al.* 1999; Munoz-Reinoso, 2001; Capon, 2003; Cooper *et al.*, 2003).

On the San Pedro River, the hydrologic parameters of greatest management concern are the availability of stream flows and shallow ground water in the stream alluvium during the summer and autumn dry seasons. Vegetation elements of high management concern include the riparian forests that grow on floodplains and terraces and the riverine marshlands that line the channel. Lite and Stromberg (in press) have determined threshold values for ground-water depth, annual ground-water fluctuation, and stream flow permanence that maintain dense, multi-age forests of Fremont cottonwood–Goodding willow (*Populus fremontii–Salix gooddingii*). Other studies have determined evapotranspiration rates (thus, water needs) of cottonwood–willow forests, mesquite (*Prosopis velutina*) forests and other vegetation types along the river, and partitioned water usage between ground water and other sources (Schaeffer *et al.*, 2000; Scott *et al.*, 2000, 2003, 2004).

Along the low-flow channel of the San Pedro River, a diverse group of herbaceous wetland plants form a riverine marshland community. Riverine marshlands have become regionally rare but are functionally important in many ways. In addition to being visually appealing, they reduce stream bank soil erosion, enhance soil water infiltration and bank storage, create well-defined channels that provide habitat for fish and other aquatic biota, and provide habitat for many terrestrial animals (Crandall *et al.*, 1992; Beeson and Doyle, 1995; Andersen and Nelson, 1999). Like the phreatophytic trees that populate the San Pedro River floodplain, these riverine marsh species also may rely on inflowing ground water to maintain saturated soils during dry seasons. Relationships with standing water or depth to saturated soil have been described for a few regional wetland plant species (Yatskievych and Jenkins, 1981; Grace, 1989; Stromberg *et al.*, 1996), but a comprehensive study of the relationships of channel vegetation to stream flow regimes has not been undertaken.

As the San Pedro River becomes dewatered or rewatered, the relative abundance of perennially flowing versus intermittent segments will change, as will the percentage of time surface water is present in the channel within the intermittent segments. The goal of this study was to determine how cover, species richness, and composition of herbaceous vegetation in the San Pedro River low-flow channel vary across a spatial gradient of stream flow permanence; this information can be used by managers for predicting vegetation change following river dewatering or rewatering and for setting hydrologic thresholds for maintaining desired vegetation. We hypothesized that streamside vegetation during the summer dry season would be highly sensitive to differences in flow permanence, with cover and richness declining and composition shifting towards mesic and xeric species at sites with intermittent flow. We expected that plants classified as hydric riparian would decline most sharply across the intermittency gradient, with other groups showing neutral relationships. We further hypothesized that channel vegetation, following the summer flood season, would be insensitive to differences in annual flow permanence and would be more strongly correlated with other environmental factors.

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STUDY SITES AND METHODS

The San Pedro River is an interrupted perennial river, meaning that it has alternating perennial and intermittent segments. In 2000, we established 18 sites that spanned the gradient in the flow regime (Figure 1). Sites were distributed in the Lower and Upper Basins of the river (Cochise and Pinal counties, Arizona) across an elevation range from 1295 to 600 m a.s.l. Intermittent segments are more extensive in the Lower Basin than the Upper Basin. Six of the sites were in the Upper Basin, all in the San Pedro Riparian National Conservation Area (SPRNCA); most of the 12 Lower Basin sites also were in riparian preserves although a few were on private or state-leased grazing lands. Ten additional study sites were established in the Upper Basin in 2001 as part of a study focusing on water needs of the SPRNCA riparian vegetation. Upland vegetation grades from Chihuahuan desert scrub in the Upper Basin to Sonoran desert scrub in the Lower Basin. Riparian forest vegetation in the San Pedro River floodplain is primarily sonoran riparian deciduous forest, cottonwood–willow series (Brown, 1994).

Vegetation data were collected in the early summer dry season (May–June), when stream flows are typically lowest, and during the late summer monsoonal wet season (August). Data were collected in multiple years (2000, 2001, 2002, 2003) that differed in flow conditions. Average stream flow rate at the US Geological Survey (USGS) San Pedro River gauge at Charleston (no. 9471000) is 1.53 $m^3 s^{-1}$ for a 90-year period of record. The 2000 (1.04 $m^3 s^{-1}$), 2002 (0.29 $m^3 s^{-1}$) and 2003 (0.28 $m^3 s^{-1}$) water years had below-average stream flow rate. Stream flow during the 2001 water year was above average (2.53 $m^3 s^{-1}$), partly due to runoff and subsequent release of recharge associated with a large flood in October 2000. The flood had instantaneous peak flows of 450 $m^3 s^{-1}$ at the San Pedro River gauge at Palominas (no. 9470500; 23 October) and 494 $m^3 s^{-1}$ at the Charleston gauge (23 October), with values in the range of a 10-year to 25-year recurrence interval event. Monsoon-season floods during the study

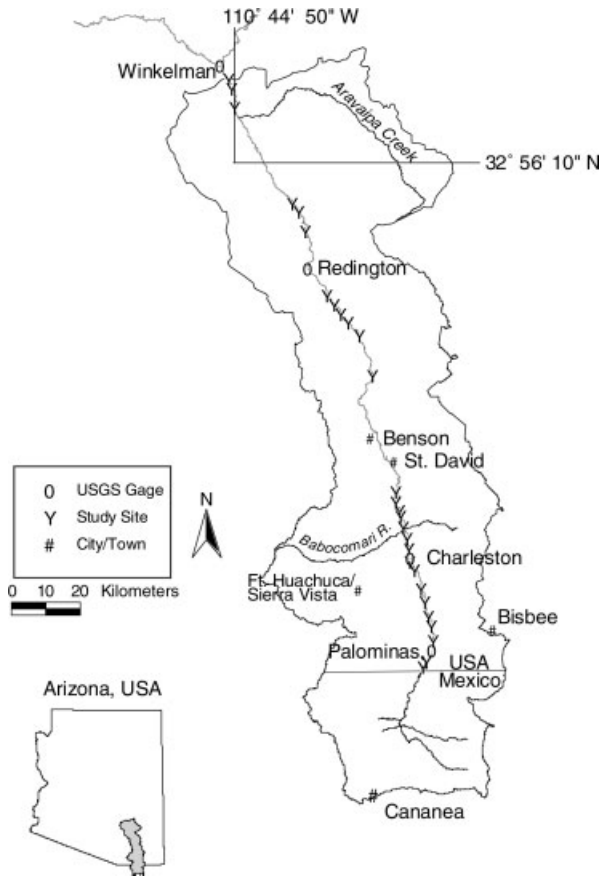

Figure 1. Map of San Pedro River Basin showing 28 study sites. Also shown are locations of USGS stream gauges

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period had peak instantaneous discharges of 233 $m^3 s^{-1}$ (7 August 2000), 117 $m^3 s^{-1}$ (14 August 2001), 19 $m^3 s^{-1}$ (26 July 2002) and 83 $m^3 s^{-1}$ (25 July 2003) (Charleston gauge), with recurrence intervals ranging from one to three years.

We collected data within the streamside zone, which comprises active channel bars and stream banks. Cover of herbaceous vegetation, by species, was estimated in five to 25, 1-m^2 quadrats per site, using cover classes. The number of sites sampled varied between sampling times, ranging from five (dry season of 2003) to 23 (both seasons of 2001). Plants were identified to species using Kearney and Peebles (1960) and recent taxonomic treatments in the *Journal of the Arizona-Nevada Academy of Science.* Aggregate herbaceous cover, species richness, and wetland indicator scores were averaged across quadrats to produce site means. The weighted average wetland indicator score is an indicator of species composition and was calculated by multiplying the relative abundance of plants within each of five wetland indicator classes by class weights from 1 (obligate wetland) to 5 (obligate upland). Wetland indicator scores were obtained for Southwest Region 7 as listed in the USDA PLANTS national database (USDA-NRCS, 2002).

Mean cover was also calculated for plants classified into six functional groups that characterized plant response to water resource availability and disturbance. We used annual or biennial life span (versus perennial life span) as an indicator of ruderal tendency and also placed plants into one of three water relationship categories (hydric, mesic, xeric) on the basis of published values for wetland indicator scores. These scores indicate the probability of species occurrence in wetland habitats and thus sort species along a water-availability gradient. Obligate wetland and facultative wetland species were classed as hydric riparian, facultative and facultative upland species as mesic riparian, and non-wetland (upland) species as xeric.

We use the term flow permanence in this study to refer to the percentage of time surface water is present in the stream channel. Annual flow permanence during the water year (1 October to 30 September) for the 18 original sites was calculated for 2000 and 2001 on the basis of surface flow presence/absence data collected during monthly site visits. Flow was considered to be present even if water was ponded but not flowing. Monthly and annual (water year) flow permanence were calculated in 2002 and 2003 for six of the original 18 sites and the ten additional Upper Basin sites using data from USGS continuous stream stage recorders and in-stream temperature sensors. During 2002, data were collected at a subset of sites by both methods; paired comparisons indicated that the methods yielded similar values for annual flow permanence.

At the 18 original sites, we also collected data within the streamside zone on other abiotic variables that might influence vegetation. These were site elevation (m a.s.l.), stream gradient, tree canopy cover, and electrical conductivity, nitrate content, available phosphorus, and texture of the substrate. Site elevation and stream gradient were derived from USGS topographic maps. Canopy cover was measured at five points per site within a 5×20 m area using a spherical densiometer. Three substrate subsamples were collected from the upper 15 cm in the streamside zone of each site during May/June 2000 and August 2000. Samples were analysed for sand, silt and clay percentages, nitrate nitrogen, available phosphorus, and electrical conductivity by a local analytical laboratory (Laboratory Consultants Ltd, Lordsburg, NM); values were averaged for the two seasons. Because of the occurrence of the large October 2000 flood, we also calculated total flood stream power at 18 study sites using model outputs from WinXSpro (see Bagstad *et al.*, 2005 for detailed methodology). Stream power for each site was calculated as the product of the unit weight of water (i.e. a force per unit volume; 9799 N m^{-3}), the hydraulic radius of the wetted area (m), the width of the water surface (m), the slope of the channel, and the flow velocity (m s^{-1}). Stream power is expressed in units of N s^{-1} and provides a measure of the rate of energy available to rework channel and floodplain materials (Gordon *et al.*, 1992).

We used Pearson product-moment correlation analysis to analyse vegetation variables (cover, richness, wetland indicator score, cover by functional group) in relation to annual and seasonal flow permanence. Patterns were not analysed for the two xeric functional groups, as they had very low cover. Correlations were conducted separately for dry and wet seasons and for individual year and multi-year data sets. To determine whether environmental factors other than stream flow permanence influenced the channel vegetation, we conducted forward-stepping multiple regression on the 2000 dry and wet season data sets for cover, richness, and wetland indicator score; independent variables were stream flow permanence, site elevation, stream gradient, canopy cover, and percentage sand content, electrical conductivity, nitrate content, and phosphorus content of the substrate. Prior to analysis, percentage values (e.g. plant cover, stream flow permanence) were square-root transformed to approximate normal

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distributions. Within-test analyses were considered statistically significant at $p < 0.05$. Analyses were conducted with Systat version 9.0 (SPSS, 1998).

RESULTS

Cover, richness and composition of the dry-season streamside herbaceous plant community varied among sites along a gradient of flow permanence. Dry-season herbaceous cover increased significantly among sites with annual flow permanence for the multi-year data set (Table I) and in two of the four years (Table II). Cover declined to nearly zero at the driest sites (Figure 2). Dry-season species richness increased significantly with annual flow permanence in two of four years (2000 and 2003) and with annual and seasonal (May–June) flow permanence for the multi-year data sets. Species richness was secondarily influenced by stream gradient in multiple regression analysis, with slightly greater richness at flatter sites (0.002 m/m) than steeper sites (0.005 m/m) (Table III). In the dry season of 2001, herbaceous species richness did not vary with flow permanence; rather, richness showed a peaked

Table I. Correlation coefficients (r-values) between flow permanence (seasonal and annual) and seasonal site means for streamside-zone herbaceous cover, species richness, and wetland indicator score. Dry-season vegetation data were collected in May–June, wet season data in August. Seasonal flow permanence was based, respectively, on May–June and July–August periods. Correlations are based on data pooled among years (sample size in parentheses)

	Correlation with seasonal flow permanence		Correlation with annual flow permanence	
	Dry season ($n = 21$)	Wet season ($n = 19$)	Dry season ($n = 62$)	Wet season ($n = 62$)
Cover	0.30	−0.18	0.67*	−0.18
Species richness	0.55*	−0.21	0.72*	−0.06
Wetland indicator score[a]	−0.77*	−0.66*	−0.57*	−0.11
Cover by group				
Hydric perennials	0.73*	0.72*	0.49*	0.29*
Hydric ruderals	0.77*	−0.41	0.60*	−0.30*
Mesic perennials	−0.48*	−0.61*	0.04	−0.20
Mesic ruderals	0.49*	−0.27	0.32*	−0.10

[a] Negative correlation indicates increased abundance of wetland species with increasing flow permanence.
* $p < 0.05$.

Table II. Correlation coefficients (r-values) between water-year flow permanence of San Pedro River sites and seasonal site means for streamside-zone herbaceous species richness, wetland indicator score, and herbaceous cover (total and by functional group). Dry-season vegetation data were collected in May–June, wet season data in August (site sample size in parentheses)

	Dry season				Wet season			
	2000 ($n = 18$)	2001 ($n = 23$)	2002 ($n = 13$)	2003 ($n = 8$)	2000 ($n = 18$)	2001 ($n = 23$)	2002 ($n = 14$)	2003 ($n = 5$)
Cover	0.76*	0.45*	−0.07	0.56	−0.13	−0.26	−0.49	0.77
Species richness	0.84*	0.05	0.38	0.82*	−0.17	−0.11	−0.14	−0.54
Wetland ind. score[a]	−0.63*	−0.23	−0.79*	−0.65	0.01	−0.16	−0.67*	−0.67
Cover by group								
Hydric perennials	0.55*	0.52*	0.73*	0.66	0.29	0.40	0.74*	0.83
Hydric ruderals	0.62*	0.25	0.71*	0.97*	−0.58*	−0.41*	−0.18	−0.78
Mesic perennials	0.23	−0.19	−0.76*	0.06	−0.15	−0.15	−0.64*	−0.68
Mesic ruderals	0.20	0.33	0.51	0.50	−0.46*	−0.21	−0.23	−0.70

[a] Negative correlation indicates increased abundance of wetland species with increasing flow permanence.
* $p < 0.05$.

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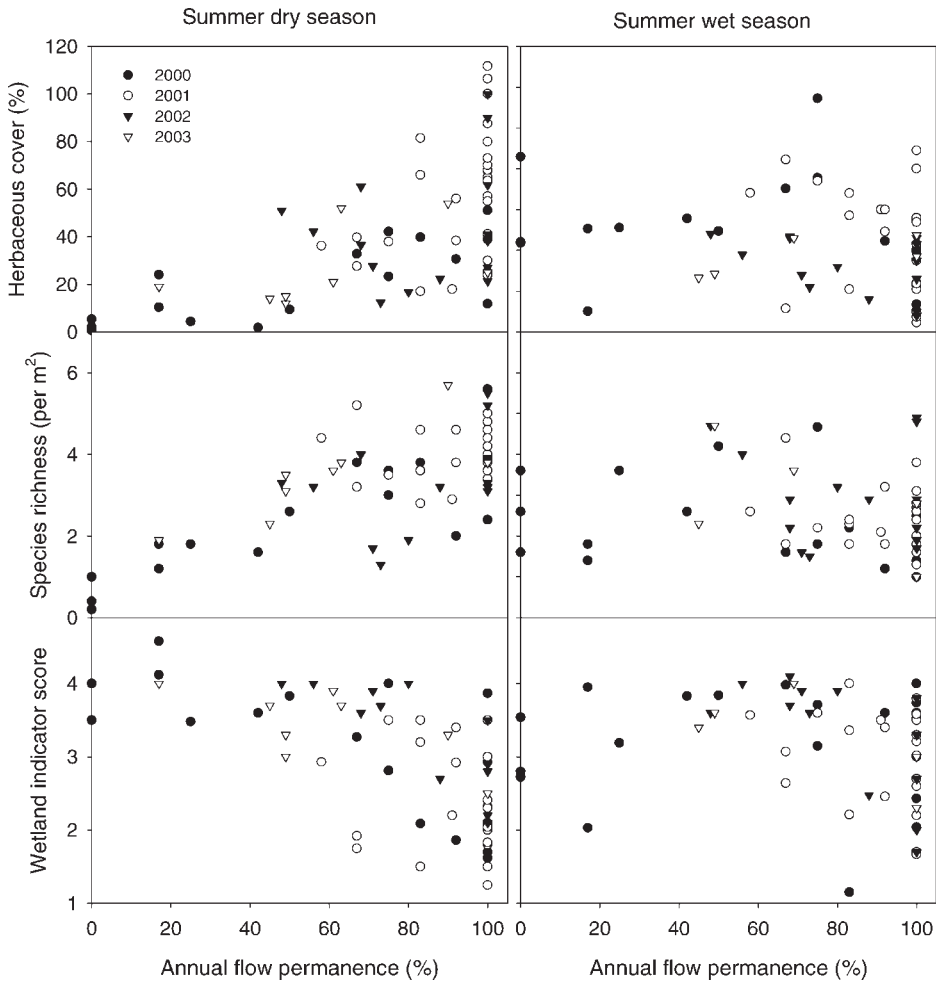

Figure 2. Streamside-zone herbaceous cover, species richness, and wetland indicator score (a measure of relative abundance of plants within different wetland indicator categories) in relation to annual flow permanence at San Pedro River study sites. The left panel shows vegetation measured during the early summer dry season of four study years; the right panel shows measurements during the late summer monsoon season. Each data point represents a site

Table III. Environmental variables significantly related to San Pedro River channel herbaceous vegetation during two sampling seasons, as indicated by multiple regression analysis ($n = 18$ sites). Values shown are the significance level (p-value) of each variable in the multiple regression model, the direction of the relationship (positive or negative), and the total variance explained by the model (adjusted r^2-value)

	Annual flow permanence	Site elevation	Stream gradient	Substrate sand content	Substrate nitrate content	Model r^2
Summer dry season, 2000						
Cover	<0.01 (+)					0.56
Species richness	<0.01 (+)		0.06 (−)			0.73
Wetland indicator score	0.01 (+)					0.36
Summer wet season, 2000						
Cover				0.06 (+)	0.09 (+)	0.19
Species richness		0.01 (+)				0.30
Wetland indicator score						n.s.

n.s. = not significant.

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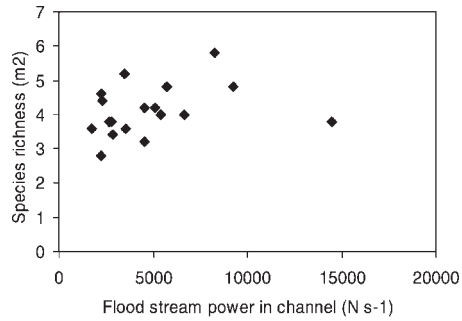

Figure 3. Herbaceous plant species richness in the San Pedro River streamside zone during June 2001 in relation to total stream power of a flood that occurred in October 2000. Each data point represents a study site

relationship with the intensity of a flood in the previous year (Figure 3). Compositionally, vegetation shifted towards more hydrophytic species across the flow permanence gradient: the wetland indicator score decreased significantly with annual flow permanence in all years except 2001, a wet year with relatively little variance in flow permanence among sites, and decreased with annual and seasonal (May–June) stream flow permanence for the multi-year data sets. Lowest (wettest) wetland scores occurred at the perennial flow sites (Figure 2). In multiple regression analyses, stream flow permanence was the only variable that contributed significantly to the models for dry-season cover and wetland indicator score (Table III).

During the summer monsoon rain and flood season, stream flows were present at most of the San Pedro River study sites for at least part of the time (Figure 4). Cover and richness during the monsoon season were not

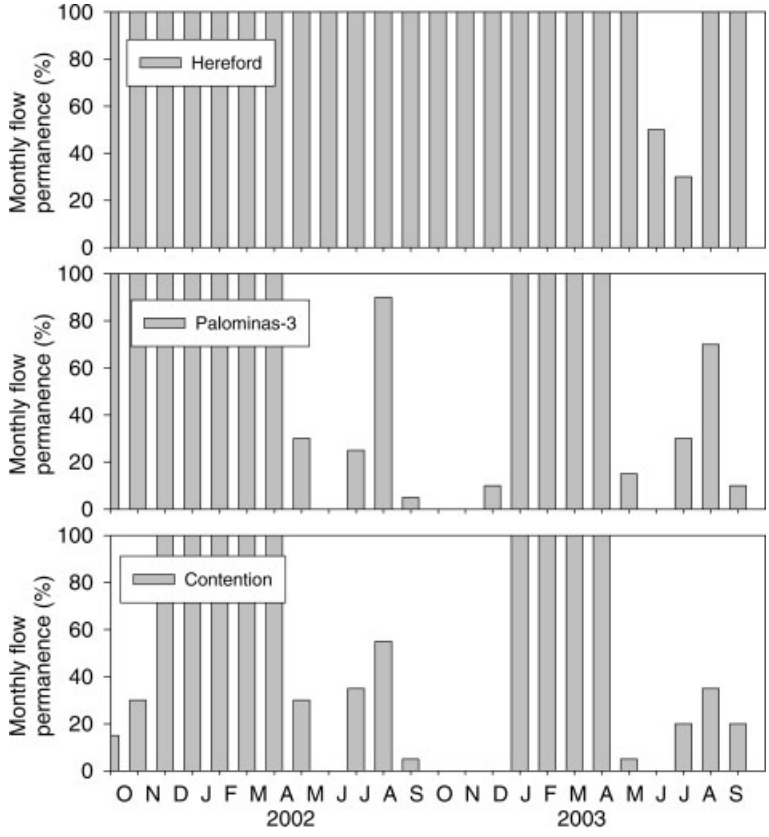

Figure 4. Monthly flow permanence during the 2002 and 2003 water years at three San Pedro River sites with varying degrees of flow intermittency

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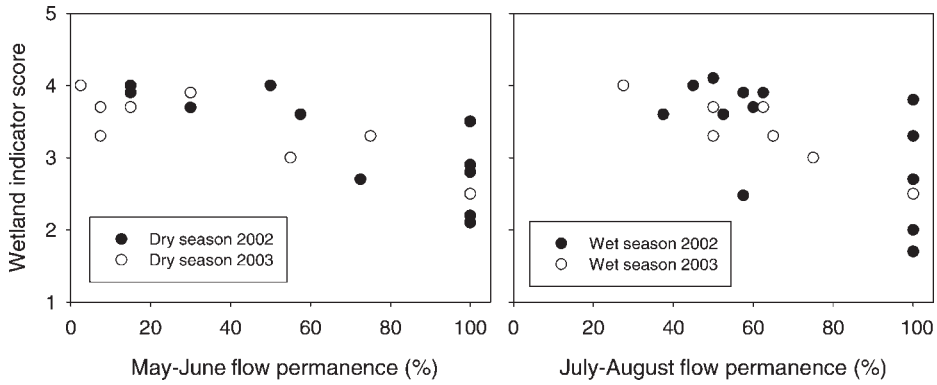

Figure 5. Wetland indicator score of herbaceous plants in the streamside zone of the San Pedro River during the summer dry season (left graph) and summer monsoon season (right graph) in relation to seasonal flow permanence. Each data point represents a study site

significantly correlated with annual or seasonal (July–August) flow permanence (Tables I, II). Cover was weakly related to substrate nitrogen content (values of which ranged among sites from 10 to 23 ppm) and sand content (range from 58 to 94%), while richness increased significantly with site elevation as indicated by multiple regression analysis (Table III). The wetland indicator score varied with July–August flow permanence (Table II; Figure 5) but was not significantly related to annual flow permanence or other abiotic variables.

Three of the four plant functional groups analysed showed positive associations with stream flow permanence, with hydric riparian perennial herbs showing the most consistent positive response across wet and dry seasons alike (Tables I, II). Hydric riparian perennials had greatest cover where flows were perennial, with values dropping sharply as flow became intermittent (Figures 6, 7). Some species in this group, including hardstem bulrush (*Schoenoplectus acutus*) and Torrey rush (*Juncus torreyi*), had measurable cover only at perennial-flow sites, while others, including smooth horsetail (*Equisetum laevigatum*), maintained sparse cover at some intermittent sites (Figure 8). Other common hydric riparian perennials at the study sites included smooth sand spikerush (*Eleocharis montevidensis)*, Baltic rush (*Juncus arcticus* var. *balticus)*, and water speedwell (*Veronica anagallis-aquatica*).

Hydric and mesic riparian annuals showed divergent patterns by season, increasing with annual and seasonal flow permanence only during the dry season (Tables I, II). The most abundant hydric annual in the streamside zone during early summer was annual rabbitsfoot grass (*Polypogon monspeliensis*), a small, shallow-rooted species. Although present at intermittent-flow sites, it had greatest cover where flow was perennial (Figure 8). The most abundant mesic annual species during the pre-monsoon season was white sweetclover (*Melilotus alba*); it declined among sites as flow permanence declined (Figure 8) but maintained greater cover than its hydric annual counterpart (rabbitsfoot grass) at intermittent sites. Thurber's sneezeweed (*Helenium thurberi*), golden crownbeard (*Verbesina encelioides)*, seep monkey-flower (*Mimulus guttatus*), barnyard grass (*Echinochloa crus-galli*), curlytop knotweed (*Polygonum lapathifolium*), and Pennsylvania knotweed (*Polygonum pensylvanicum*) were among the other hydric and mesic annuals present in the streamside zone during early summer. Many in this group, including *Echinochloa crus-galli*, persisted through late summer.

Wet-season cover of hydric annuals was negatively correlated with flow permanence as measured for each water year and for the summer wet season (Tables I, II). Wet-season cover of mesic annuals was negatively correlated with annual flow permanence in one year but otherwise showed neutral relationships with stream flow. The most abundant mesic annual during the summer wet season was rough cocklebur (*Xanthium strumarium*). Other annuals present in late summer included San Pedro matchweed (*Xanthocephalum gymnospermoides*), tapertip cupgrass (*Eriochloa acuminata*), jungle rice (*Echinochloa colona*), and curlytop knotweed (*Polygonum lapathifolium*).

Mesic riparian perennials declined in cover as seasonal flow permanence increased, during dry and wet seasons (Table I). Cover of this group declined with annual flow permanence in 2002 (Table II) but did not vary with annual flow permanence for the multi-year data set (Table I). The most common mesic riparian perennial was Bermuda grass (*Cynodon dactylon*), a relatively drought- and flood-scour-tolerant rhizomatous grass; others included deer grass (*Muhlenbergia rigens*) and Johnson grass (*Sorghum halepense*). Cover of Bermuda grass increased as stream flow became intermittent (Figures 8, 9).

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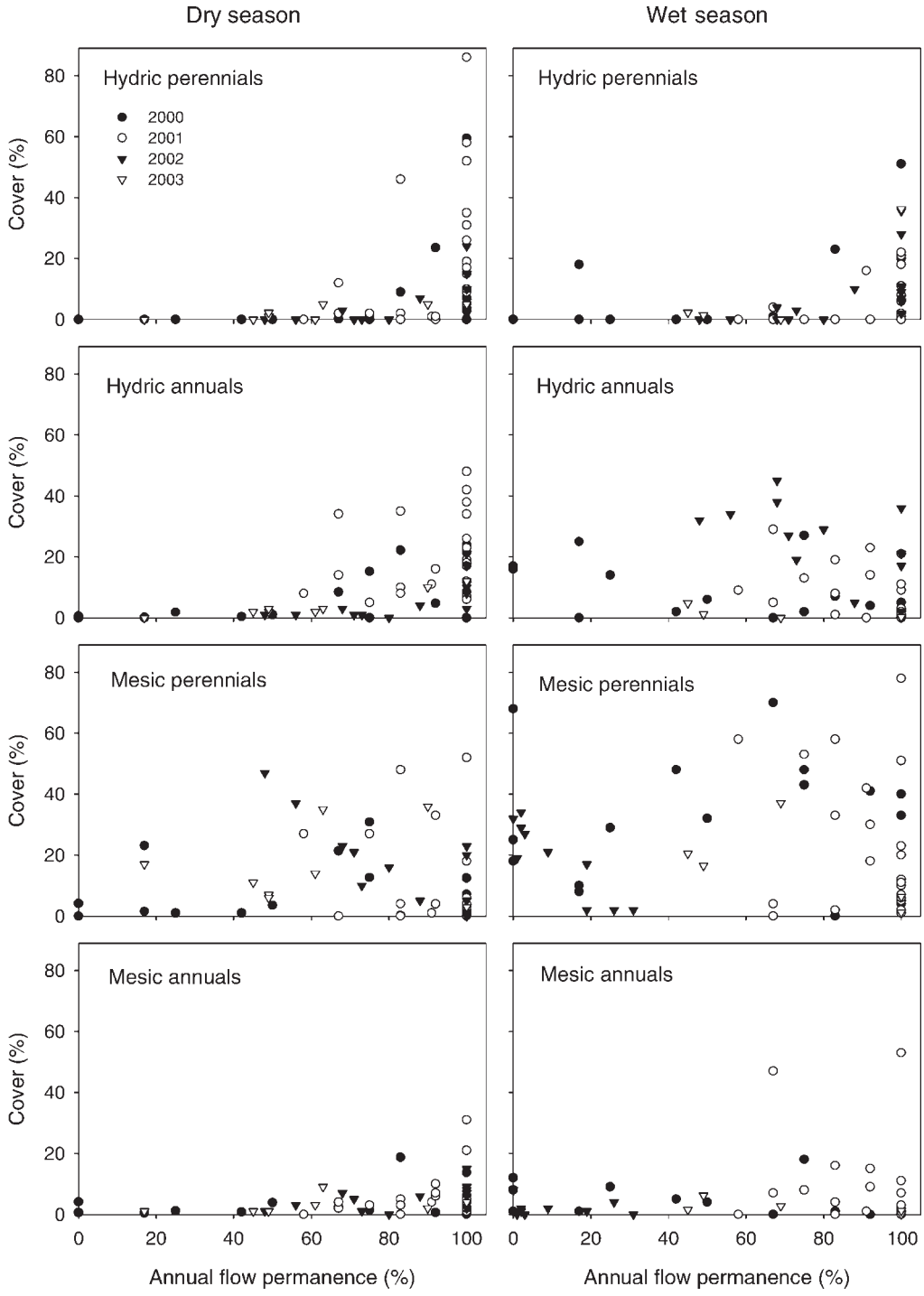

Figure 6. Mean cover of herbaceous plant species, by functional group, in relation to water-year flow permanence. Measurements are for data collected in the early summer dry season and the end of the summer monsoon season, during four study years. Each data point represents a study site

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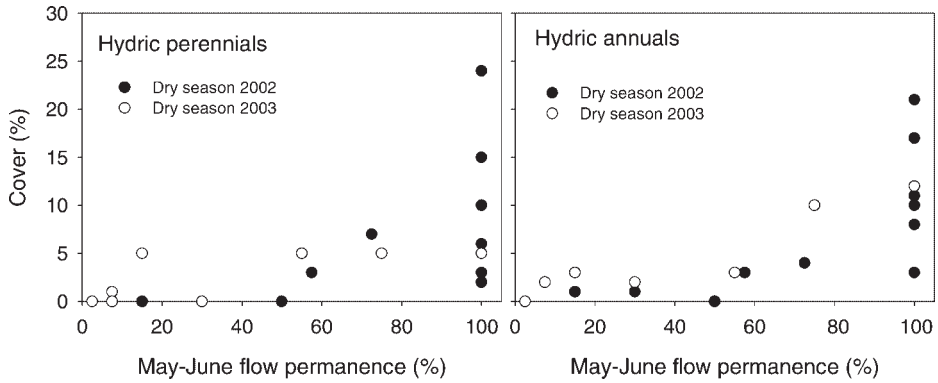

Figure 7. Cover of hydric herbaceous plants (perennials and annuals) in the streamside zone of the San Pedro River during the summer dry season of 2002 and 2003, in relation to seasonal flow permanence. Each data point represents a study site

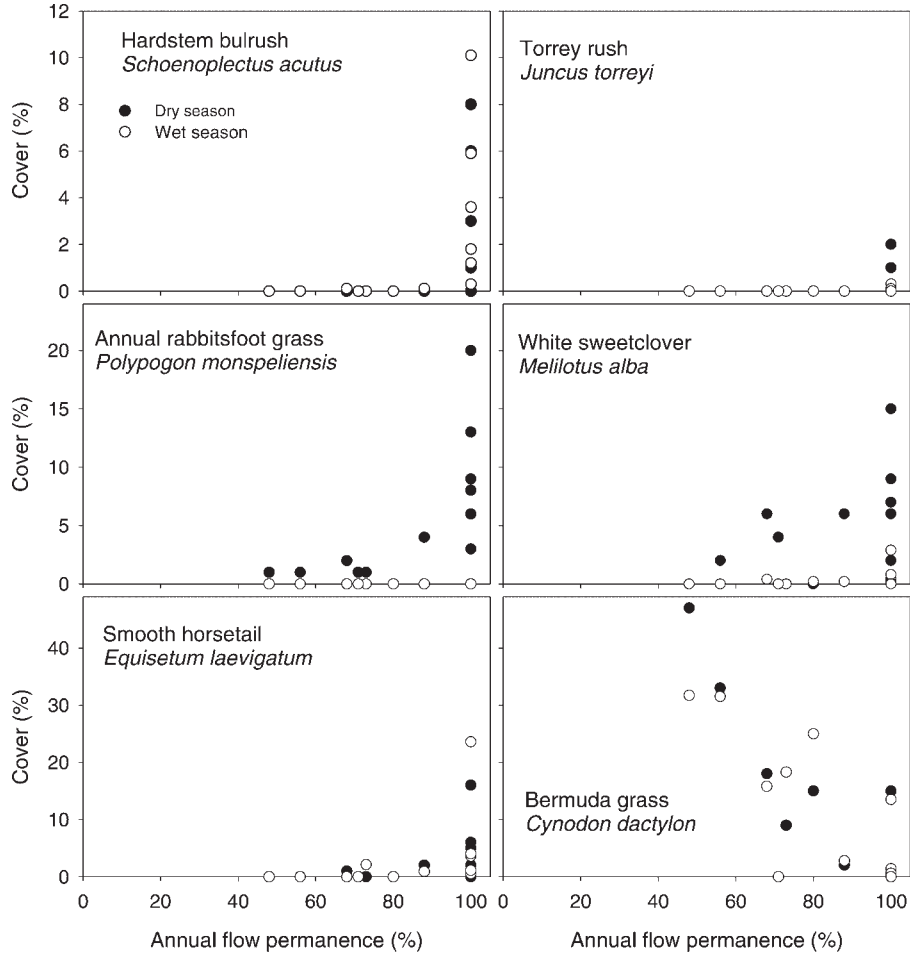

Figure 8. Mean cover values for several common herbaceous species in the San Pedro River streamside zone, during pre-monsoon and monsoon periods of 2002, in relation to annual flow permanence. Each data point represents a study site

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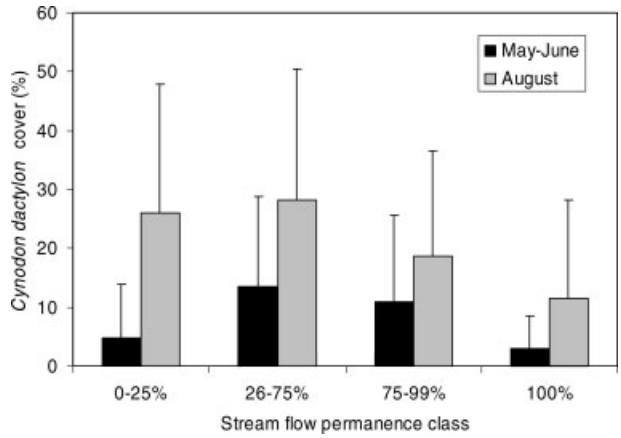

Figure 9. Mean streamside-zone cover of Bermuda grass (*Cynodon dactylon*) within four stream-flow permanence classes. Cover values are shown for the summer dry season (May–June) and summer wet season (August); values are means plus standard deviation of data pooled across sites and years

DISCUSSION

This study contributes to the growing body of reports quantifying relationships between San Pedro River hydrology and riparian vegetation (Stromberg *et al*., 1996; Stromberg, 1998; Schaeffer *et al.*, 2000; Scott *et al*., 2000, 2003, 2004; Lite and Stromberg, in press; Bagstad *et al*., in press) and thus to the ability of managers to predict vegetation change and specify the hydrologic conditions needed to maintain desired vegetation. Threshold values for hydrologic conditions are particularly useful for developing management guidelines (Ferrington, 1993; Rogers and Biggs, 1999; Richter and Richter, 2000; Eiswerth and Haney, 2001). The sharp decline in abundance of the hydric riparian perennial herbs (such as bulrush) with the shift from perennial to intermittent flows qualifies as a critical threshold, defined as small changes in physical conditions that produce abrupt biological responses (With and Crist, 1995). The species in this functional group are intolerant of drought and typically grow on low fluvial surfaces where soils are saturated by stream flow or inflowing ground water. Perennial flow thus appears essential for sustaining the wetland plants that comprise the riverine marshland association. Perennial flows also provided for consistently highest herbaceous cover and species richness. Researchers in other semiarid regions also have observed perennial stream flows and high soil moisture to be positively associated with plant species richness in riparian zones and to be important for maintaining particular groups of species (Tabacchi *et al.*, 1996; Fossati *et al.*, 1999; Ali *et al.*, 2000). Loss of perennial flows can also affect riparian vegetation across the floodplain. Ground-water levels in the stream alluvium of the San Pedro River deepen and have more interannual variance at sites with intermittent (versus perennial) flow, with the drier conditions driving shifts from *Populus–Salix* forests to *Tamarix* shrublands (Lite and Stromberg, 2005).

Once flow becomes intermittent, there is a continuum of response. Cover, richness, and wetland indicator score of the streamside herbaceous vegetation changed continuously as flow permanence declined. Prior studies along the San Pedro River described a continuum of response for floodplain vegetation across a hydrogradient of declining ground-water level in the stream alluvium and declining inundation frequency (Stromberg *et al.*, 1996). However, as expected for dynamic river systems, there was considerable variability in the relationships between flow permanence and plant community characteristics. Some of this variation was due to annual differences in flood disturbance, as evidenced by the effects related to the large October 2000 flood; some may also be due to legacy effects of antecedent stream flow conditions.

Typically, when environmental conditions change, some species increase in population size while others decrease. Whereas cover of hydric riparian perennials decreased as flows became less permanent, cover of mesic riparian perennial herbs (including Bermuda grass, an introduced species) in the streamside zone increased. This pattern has a parallel within the San Pedro floodplain forest, wherein the hydric pioneer trees (Fremont cottonwood–Goodding willow) increased while mesic pioneer trees/shrubs (tamarisk, an introduced species) declined

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in abundance across site moisture gradients of decreasing depth to ground water and increasing stream flow permanence. Particular flow regimes, including continuous low-level flows, may favour some regional, native species over introduced species in other regions as well (Howell and Benson, 2000).

Seasonal flood pulses increase productivity of wetland plant groups along river channels (Robertson *et al.*, 2001). During the late summer convective rainy season, the San Pedro River typically experiences small flood spikes and elevated stream discharge. Flow was more permanent during this season, and water less of a limiting factor to the streamside vegetation. Nutrients may limit herbaceous productivity in this season, given the weak positive correlation between herbaceous cover and nitrate nitrogen. Species composition remained responsive to seasonal flow permanence, however, with wetland indicator values lowest (wettest) at sites with the most permanent flows.

Due to seasonal flooding, perennial and intermittent river reaches alike had a species-rich summer streamside herbaceous community. Hydric and mesic riparian annuals that complete their life cycle prior to monsoon rains and floods depend on inflowing ground water or surface flows to moisten disturbed fluvial surfaces such as channel bars. Many warm-season annuals, however, can complete their life cycle during the late summer rain and flood season and thrive along primary or secondary channels at intermittent-flow sites. The 'disturbance' provided by periodic drought at the intermittent-flow sites (Lake, 2003) may have increased opportunities for establishment of the annuals during the monsoonal flood season, producing the pattern of increased late-summer cover of hydric and mesic annuals at sites with less permanent flows. These findings have management implications for the many dammed rivers in the southwest, given that summer flood pulses typically are captured in reservoirs either for delivery to irrigation canals or to maintain high water levels in the reservoir for recreation.

Spatial habitat heterogeneity and temporal variability in flow regimes are associated with high species diversity in riverine ecosystems (Ward and Tockner, 2001). Our findings suggest that a riverine landscape comprising perennial and intermittent reaches may provide for highest regional plant species richness. However, when considered over larger temporal and spatial scales than analysed for this study, all of the streamside plant functional groups we examined, including those that were most abundant in the intermittent reaches, are common in perennial reaches. Opportunities for warm-season hydric riparian annuals to establish at perennial-flow sites are provided periodically by large scouring floods (Bagstad *et al*., 2005). In between flood events, the annuals are probably retained in soil seed banks (JA Boudell and JC Stromberg, unpublished data). With respect to mesic perennials, they too are abundant at perennial-flow sites, but have their zone of abundance shifted laterally to the aggraded floodplain surfaces adjacent to the active channel. Shifts from intermittent to perennial flow appear to increase the number of wetland plant species and functional groups, with no net loss of more xerophytic groups.

Clearly, many biotic elements of the San Pedro River riparian ecosystem depend on perennial stream flows. This begs the question of what hydrologic processes sustain flows throughout the dry seasons. San Pedro river flows are maintained by a combination of influent regional ground water and the release of flood-induced recharge, although the relative contribution of each source varies spatially and temporally (Pool and Coes, 1999). Flood recharge can contribute greatly to dry season flows but is an episodic phenomenon. Influent regional ground water has a much longer residence time in the system and buffers short-term climatic vagaries; it is essential for maintaining year-round stream flow in the channel during years without large floods. Much of the water that flows from the stream-alluvium aquifer to the channel is sustained by water flowing from the larger regional aquifer, thus connecting water use patterns of the surrounding urban areas to biodiversity levels in the river. As hydraulic gradients and ground-water flow patterns are changed in the regional aquifer, stream base-flow patterns will change accordingly. A shift from perennial to intermittent stream flow, in turn, will result in decline of the densely rooted and productive wetland perennials in the stream channel and may alter a range of ecosystem functions including provision of animal habitat, stream bank erosion control, bank storage of water, and creation of aesthetically pleasing sites for recreation. Conversely, increased flow rates stemming from declines in ground-water pumping should allow for rapid redevelopment of a variety of wetland plant species.

ACKNOWLEDGEMENTS

Funding for this project was provided by the US Environmental Protection Agency's Water and Watershed Research Program (no. R82-7150), the National Science Foundation's Center for Sustainability of semi-Arid

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Hydrology and Riparian Areas (no. PO Y542149), and the Upper San Pedro Partnership/Bureau of Land Management (San Pedro Water Needs Study no. AAA010019). We are grateful to these groups and to the many landowners who provided permission to access sites: Arizona Nature Conservancy, Arizona State Lands Department, Barbara Clark, Carole and Mack Skeen, Bureau of Land Management, and Bureau of Reclamation. Greg Auble, US Geological Survey, and anonymous reviewers provided valuable comments.

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