**Riparian plant functional types of intermittent rivers of the American Southwest**

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Summary

1. Plant functional types increasingly are being used to predict vegetation response to global changes. This necessitates research to identify suitable traits for region-specific delineations. For rivers of the American Southwest, the future will bring decreases in base flow and increases in flood magnitude. Riparian functional type delineation must be grounded in traits linked with both of these physical processes.

2. My goals were (1) to identify plant traits indicative of water resource availability and flood disturbance and (2) to identify woody plant functional types associated with distinct riparian habitat types of arid southwestern USA.

3. Woody vegetation structure and composition were measured in 167 plots, among 14 sites, in river floodplains, terraces and uplands of two Arizona rivers. Community-weighted values, using species Importance Values, were calculated per plot for seven plant traits. Depth to water table and a surrogate measure of flood frequency were calculated at the plot level; stream flow intermittence (percent of time flow was present) was calculated at the site level.

4. Regression and correlation analysis were used to determine strength of relationships between community-weighted plant traits and hydrological variables. K-means clustering was used to identify plant functional types.

5. Community-weighted leaf area, specific leaf area, and plant height were strongly related to depth to water table. These traits increase regionally along precipitation gradients but as shown here vary locally with stream hydrology for riparian habitats. Community-weighted root depth showed a unimodal pattern, increasing from shallow to medium-depth water table areas but then declining where water tables were below root zones of floodplain vegetation. Community-weighted seed mass and dispersal mode (regeneration-linked traits) were related most strongly to flood frequency. Spines were affiliated with the combination of dry conditions and infrequent disturbance.

6. K-clustering revealed nine plant functional types among 29 woody species. All seven traits contributed to functional type delineation. These results highlight the importance of using above-ground and below-ground traits in classifying plant functional types in dryland regions and of including traits that reflect environmental factors operating at discrete plant life stages.

7. Three dominant pioneer types (with small wind-dispersed seeds) were recognized that represent changes between ecosystem states and hydrogeomorphic settings: Broad-leaved, medium-rooted tall trees prevailed on floodplains of perennial streams with shallow water tables; small-leaved, deep-rooted, short trees were abundant on sites with water tables to about 6 m; and small-leaved, medium-rooted shrubs dominated floodplains of ephemeral streams with the deepest water tables (15 to 25 m). A prevalent type on terraces had small leaves, deep roots, medium canopy height, and large, animal dispersed seeds. This classification scheme will enable prediction of changes in the relative abundance of plant types in response to ensuing changes in stream flow regimes.

8. Perennial streams sustained the greatest number of functional types. Of interest, the functional types in floodplains of ephemeral-phreatic streams (those with infrequent surface flow but shallow water table) were more similar to those of intermittent-phreatic streams than to ephemeral-non phreatic streams. This highlights the importance of conserving this frequently overlooked stream type.

*Keywords*: Arid region, ecohydrology, ephemeral stream, floodplain, intermittent flow, plant functional type, riparian vegetation, trait

**Introduction**

Anthropogenic changes to stream hydrology have substantially altered the abundance and composition of dryland riparian plant communities (Patten, 1998; Tockner & Stanford, 2002; O’Connor, 2010; Stella *et al.*, 2012). Increasing global pressures on freshwater resources, coupled with climate change, will drive further changes in stream surface and subsurface flows (Palmer *et al*., 2009). Alterations are likely to be greatest in highly populated dryland regions (Doll *et al*., 2009).

Water, the primary limiting factor in dryland regions, is decreasing in desert rivers owing to groundwater pumping, diversion of water, and climate-linked reductions in stream recharge (Serrat-Capdevila *et al*., 2007; Jobbágy *et al*., 2011). Increasingly, perennial stream segments (already rare in arid landscape) are becoming intermittent or even ephemeral (sensu Meinzer, 1923; Steward *et al*., 2012). Depth to groundwater is increasing in the alluvial aquifers that sustain riparian phreatophytes (Castle *et al*., in press). Flood patterns also are changing. People continue to build flow-regulating dams and reservoir systems to capture flood pulses (Shafroth *et al*., 2002; Wang *et al*., 2014). Unregulated rivers, in contrast, are experiencing more intense floods as the global climate changes (Dominguez *et al*., 2010; Dallas, 2014).

Stream and riparian management is informed by knowing the hydrological ranges over which conservation targets occur (Eamus & Froend, 2006). Researchers in drylands throughout the world have identified changes in species composition and plant growth form that occur as hydrologic thresholds of depth to water table and stream flow permanence are crossed and as flood patternsdeviate from historic norms **(**Higgins *et al*., 1997; Liu *et al*., 2005; Lite & Stromberg, 2005; Stromberg *et al*., 2005; Froend & Sommer, 2010; Merritt & Poff, 2010; Gonzalez-Sanchis *et al*., 2012; Li *et al*., 2013; Liu *et al*., 2013). There remains a need, however, for a more globally transferable approach that goes beyond taxonomy, beyond simple life-form classification schemes, and certainly beyond artificial constructs such as native vs. exotic species.

Plant functional types and functional traits increasingly are being used to understand and predict vegetation response to environmental changes (Gitay & Noble, 1997; Diaz & Cabido, 1997; Dubois *et al*., 2013). Species can be classified into functional types based on shared suites of morpho-physiological traits that correspond to patterns of resource use and allocation (Reich *et al*., 2003). Searches are ongoing for a small and unifying suite of response traits that link plants with environmental conditions (Westoby, 1998; Diaz *et al*., 2004) but for conservation and management purposes it is clear that traits, and functional types, need to be tailored for the particular stressors and limiting factors of a given region (Grime, 2001; Eallonardo *et al*., 2013).

Functional plant types have yet to be comprehensively described for riparian plants of dryland regions. Some riparian studies, including my own, have utilized ‘habitat preference guilds’ such as Wetland Indicator Groups that synthesize the combination of traits that adapt plants to different levels of water availability (Stromberg *et al*., 1996; Goebel *et al*., 2006; Laidig *et al*., 2010). Others have delineated water plant functional groups, composed of species that have similar responses to the complex environmental axis of soil wetting and drying patterns (Brock & Casanova, 1997; Casanova, 2011). Such studies are critically important building blocks for understanding how non-phylogenetic groups respond to changes in environmental flows (Merritt *et al*., 2010; Campbell *et al*., 2014). But, to further enable cross-global synthesis within arid regions, we need to address the functional traits that capture the causal mechanisms underlying the habitat preferences and to identify suites of species that share combinations of traits that adapt for the multiple axes that structure riparian plant communities (Hunt *et al*., 2004; Aguiar *et al*., 2013; Verberk *et al*., 2013).

The objectives of this study were: (1) To determine how selected functional traits of riparian plants vary along two types of hydrological continua- water availability and flood pulsing; (2) To identify thresholds of change; and (3) To identify riparian plant functional types associated with distinct hydrological habitat types based on permutations of water availability and flood disturbance. The study system was the riparian zones of ephemeral, intermittent, and perennial river reaches of arid southwestern USA. The intent was to provide information useful for local river managers, and to build towards a global understanding of plant-hydrology relations for desert rivers.

**Methods**

*Experimental design and study sites*

Two interrupted perennial rivers in Arizona, USA served as study areas. Along both rivers, perennially-flowing reaches co-occur with intermittent to ephemerally-flowing reaches over scales of meters to kilometers. This variation in base flows allows for between-site comparisons of water availability effects while controlling for flood disturbance. The beds of both rivers incised approximately a century ago, creating sharp lateral discontinuities between the floodplain (post-entrenchment surfaces) and terrace (pre-entrenchment surfaces) (Webb & Leake, 2006). The terraces are several meters above the low-flow channel and support phreatophytes, and there is considerable topographical variation within the floodplain, allowing for comparison of riparian plant communities that experience different frequencies of flood pulsing.

Seven study sites were established on lower Cienega Creek within Pima County's Cienega Creek Natural Preserve, east of Tucson, Arizona. Another seven were along the lower San Pedro River near Cascabel, within a 30 km stretch of the river on land managed primarily by the Bureau of Land Management (Stromberg, 2007). The Cienega Creek sites ranged in elevation from 1100 m to 970 m; those at San Pedro ranged from 1010 m to 930 m. Sites were located to span the range of stream surface and subsurface conditions created by local differences in hydrogeology. Cienega Creek differs from the well-studied San Pedro in having greater extremes of water availability, with the driest sites having ephemeral flow and water tables at a depth of >20 m. Cienega Creek drains a 1,184 km2 watershed (USGS Pantano Wash- Vail station 09484600); the San Pedro River drains an 8,018 km2 square watershed (San Pedro-Redington gage 09472000; <http://waterdata.usgs.gov> ). Mean annual precipitation is 29 cm near Cienega Creek (Tucson WSO AP station) and 35 cm at the San Pedro (Cascabel station, Western Regional Climate Center, http://www.wrcc.dri.edu/). Mean annual temperature at Tucson is 20OC. Upland vegetation in the study area is Sonoran Desert Scrub and Chihuahuan Desert Scrub (Brown, 1994).

*Vegetation sampling, trait measurement, and stream hydrology*

At each site two cross-riparian transect lines were established, separated by a stream distance of 100 meters. One of each pair of transects was located near a monitoring well. At both rivers, the transect lines spanned the active channel, floodplain, secondary channels, and terrace. Along each transect, plots were sampled in stratified random fashion (two-stage sampling). Vegetation zones were delineated along each transect based on differences in vegetation physiognomy and composition, and a minimum of one 100-m2 plot (5m x 20 m; long axis parallel to the stream) was sampled per zone per transect. A total of 157 riparian plots were sampled (67 at Cienega Creek and 100 at San Pedro River). An additional 10 plots were sampled in the upland desert. Woody vegetation was the focus of study. In each plot, diameter of woody plant stems was measured using a dbh tape or caliper to obtain density and basal area per species. Canopy cover was measured at three locations per plot using a densiometer. Plots were sampled during the growing season (2009 or 2010 at Cienega Creek and 1995 at San Pedro River). Plants were identified to species using Kearney & Peebles (1960) and more recent taxonomic treatments. A modified Importance Value was calculated for each plot as the average of each species’ relative stem density, relative basal area, and relative canopy cover (Curtis, 1959).

A total of 38 woody species were detected in study plots, 9 of which were infrequent. Trait data was obtained or measured for the 29 common species. The traits- canopy height, leaf area, specific leaf area, rooting depth, presence of spines, seed mass, and seed dispersal morphology- were selected as potential indicators of water availability and ecosystem disturbance. For canopy height, the typical maximum value for the species was recorded using local floras and regional databases (SEINet, 2013). For rooting depth, the maximum depth reported in the literature (Stromberg, 2013) was used, with one exception. For *Prosopis velutina,* the maximum rooting depth in a riparian habitat was used instead of the anomalously large value reported by Phillips in 1963 for a desert upland. For leaf area, samples of three leaves were collected from three plants per species and measured with a LICOR leaf area meter. The leaf area of plants with very small or scale-like leaves was measured with a ruler. For plants with compound leaves, values are reported for the smallest functional leaf unit, the leaflet (Givnish, 1987). Specific leaf area (SLA) was calculated after weighing the collected leaves in a drying oven (60oC for 72 hours). For the defense trait, species were assigned a score of 1 if spineless and 2 if spines were present. For seed mass, seed samples from three individuals per species were collected and weighed or values were obtained from the KEW database (Stromberg & Boudell, 2013; Royal Botanic Gardens Kew, 2014). For morphological dispersal adaptations, two nominal classes were used- wind dispersed (as indicated by presence of wings or plumes that aid in aerial seed transport) or internally animal dispersed (fleshy fruit or large nutritious seeds).

A two-year data set on monthly values for depth to the water table and surface flow presence/absence was provided by the Pima Association of Governments for Cienega Creek study sites. For San Pedro River, these same variables were recorded monthly for two years from abandoned production wells or piezometers installed by ASU students. The monitoring wells, transect lines, and study plots were surveyed for elevation of the ground surface above the channel thalweg using a stadia rod and transit. The slope of the water table at each site was estimated using measurements from the monitoring wells in conjunction with the surface stream level. These data collectively were used to estimate mean annual depth to the water table per site, and the mean maximum depth to the water table, which typically occurred in June. The two-year surface flow dataset was used to generate a value indicating the percent of time each site had surface flow. For subsequent statistical analysis, I operationally defined three stream flow categories: perennial flow (those with flow present 100% of the time), intermittent flow (surface flow present from 20% to 95% of the time), and ephemeral flow (surface flow present <20% of the time). The ephemeral category was further subdivided into ephemeral-phreatic (shallow water table present) and ephemeral-nonphreatic (water table deeper than 8 m) (Fig. 1).

*Statistical analysis*

The first objective- to determine how traits of riparian plants vary along hydrological continua- was approached using correlation analysis and forward-stepping multiple regression analyses (Systat Version 13.0). In the regression models, the dependent variable was the community-weighted mean for each trait, calculated per plot. Community-weighted values can be based on mean values for traits or on extreme values (Dubuis *et al*., 2013); this study used mean values for all traits except root depth and canopy height. To generate the plot-based values, each species’ Importance Value was multiplied by its trait value (e.g., leaf area in cm2) and these values were then summed across species and divided by 100. The independent variables in the regression models were the annual maximum depth to water table per plot, the elevation of the plot above thalweg (as a surrogate for inundation frequency), and stream flow category (1 for ephemeral, 2 for intermittent, and 3 for perennial) for the site at which the plot was located. To detect thresholds of change, community-weighted variables were calculated for six depth to water table zones, and Analysis of Variance and post-hoc Tukey tests were used to detect differences between zones.

K-means clustering was used to identify plant functional types, using Euclidean Distance and 20 iterations per analysis. The data matrix contained 29 woody species and seven traits that vary along water availability and/or disturbance gradients. Each trait was standardized to have zero mean and unit variance. For variables with non-normal distributions, raw values were natural-log transformed before being standardized. I used an iterative process, conducting the K-clustering procedure with varying numbers of groups from 6 to 12. The final groupings were reasonable representations of reality based on field observations.

Finally, I classified plots into one of 10 riparian hydrological habitat categories based on permutations of flow type (ephemeral, ephemeral-phreatic, intermittent, and perennial) and flood disturbance (frequently flooded surfaces <2 m above thalweg, infrequently flooded surfaces 2 to 5.5 m above thalweg, and unflooded stream terraces >5.5 m above thalweg). The relative abundance of plant functional types was calculated for each hydrological habitat type. Radar plots were generated in Sigmaplot (Version 12.0) to display the trait ranges of plant communities in each habitat type.

**Results**

*Community-weighted traits*

Three community-weighted traits- leaf area, SLA, and canopy height-varied strongly with depth to water table (Table 1). Community-weighted leaf area ranged among plots from 0.3 cm2 to 46 cm2 (Fig. 2). In multiple regression models, community-weighted leaf area increased significantly as water tables became shallower, flow permanence increased, and plot surface above thalweg decreased, confirming the importance of water as a strong control on leaf size in arid region riparian zones (Table 2). Community-weighted leaf area differed significantly among depth to water table zones, with two apparent thresholds (Fig. 3). Where the water table was <1 m, leaf area averaged 26.6 ± 2.5 cm2, higher than in other zones (e.g., 17.2 ± 3.4 cm2 for the 1-2 m zone). Another threshold was evident at approximately 5 m: community-weighted leaf area in the 4-6 m zone averaged 10.5 ± 3.0 cm2 whereas values were <1 cm2 in all deeper zones. Patterns for community-weighted SLA were similar to those for leaf area, with depth to water table driving variation among study plots.

Depth to water table explained the most variance in the regression model for community-weighted canopy height, followed by stream flow permanence (Table 2). However, the model r2 was low with values ranging widely within water table zones. For example, tall (30 m) *Populus/Salix* forestsco-existed withshrublands of *Baccharis salicifolia* in areas with shallow water tables.Within deeper water table zones, low stature (2 m) xerophytic shrubs coexisted with small trees.

Community-weighted rooting depth showed a complex relationship with the abiotic variables (Tables 1, 2, Fig. 3). At the phreatic sites, community-weighted rooting depth increased steeply as water tables increased from 0.2 to 5 meters, reflecting a shift from medium-rooted phreatophytes (e.g., *Populus* and *Salix*) to more deeply rooted phreatophytes (e.g., *Prosopis* and *Tamarix).* At non-phreatic sites, community-weighted rooting depth varied widely (from 2 m to 11 m) owing to the co-occurrence of medium-rooted pioneer xerophytic shrubs and deep-rooted facultative phreatophytes.

Community-weighted seed mass and dispersal mode showed similar responses. Both varied most significantly with elevation above thalweg, with a small additional effect from water table depth, pointing to the primary role of disturbance as an influence on these regenerative traits (Tables 1 and 2, Fig. 4). Small seeds (<10 g) and anemochory were prevalent traits on frequently-flooded low floodplains. Large seeds and adaptation for animal dispersal became increasingly common on higher surfaces, with terraces supporting vegetation that produced zoochores with community-weighted seed weight of 100 g. Community-weighted values for presence of spines also was related significantly to elevation above thalweg, with spinescent plants such as *Celtis pallida, Prosopis velutina,* and *Zizyphus obtusifolia* being most abundant on surfaces above the zone of frequent flood scour.

*Plant functional types*

K-means clustering produced nine functional types among the 29 woody plant species (Table 3). Functional Type 1 (*Populus fremontii* and *Salix gooddingii*) consisted of trees with tall canopies, large leaves, high SLA, moderate root depth, and small wind-dispersed seeds, and are referred to as hydromesic pioneers. Functional Type 2a (*Fraxinus velutina* and two other trees)differed from FT1 in having shorter canopy and smaller leaves. Functional Type 2b (*Baccharis salicifolia* and others) had similar leaf size to FT2a but even shorter canopies. FT2a and FT2b are collectively referred to as mesic pioneers. Functional Type 3 (*Atriplex canescens* and *Tamarix chinensis)* were tall shrubs with small leaves and deep roots, and are classed as xeromesic pioneers. Functional Type 4 (*Ambrosia hymenoclea, Baccharis sarothroides* and others) were short, small-leaved shrubs with medium-depth roots and reproductive strategies adapted for disturbance (xeric pioneers).

The remaining groups were nonpioneers. All had medium to large, animal-dispersed seeds. Functional Type 5 (*Juglans major* and *Celtis reticulata*) were large-leaved trees with large seeds (mesic nonpioneers). *Prosopis velutina* and *Acacia greggii,* with their small leaves, spines, deep roots and potential for tall canopies, formed Functional Type 6 (xeromesic nonpioneers). Functional Type 7a (*Celtis ehrenbergiana* and others) consisted of small-leaved xeric shrubs defended by spines and producing large seeds. Functional Type 7b consisted of short, spiny xerophytes with either no leaves or small succulent leaves, and intermediate-size seeds*.* Functional Types 7a and 7b collectively are xeric nonpioneers.

Relative abundance of woody plant functional types varied among riparian habitats with differing water availability and disturbance frequency. The wettest habitats had a more diverse mix of functional types than the driest ones. Hydromesic pioneer trees (FT1) prevailed on floodplains of sites with perennial stream flow (Fig. 5, top panel) and water tables <1 m (Fig. 5, bottom panel) but co-occurred with many other types. At sites with intermittent flow and deeper water tables (1 to 6 m), mesic types and deep-rooted mesoxeric pioneers increased in abundance. Xeric pioneers shrubs (FT4) prevailed on floodplains of ephemeral streams, where water table were very deep (>8 m); they co-existed with deep-rooted taxa to produce the deepest community-weighted rooting depths of all floodplain habitat types (Fig. 6). The low floodplains of ephemeral-phreatic stream reaches were more similar in functional types and traits to the intermittent-phreatic stream type than they were to the ephemeral non-phreatic type.

Terraces supported only a few functional types. They were dominated by deep-rooted xeromesic non-pioneers (FT6) with xeric nonpioneers (FT7) also common (Fig. 5). On radar plots, the prevalence of large seeds, zoochory, deep roots, mid-height canopies but small leaves is readily apparent for the terrace zone. Xeromesic non-pioneers (FT6) also were abundant on high floodplains. On radar plots one can observe the shift towards greater root depth and larger seed mass from low floodplains (solid lines) to high floodplains (dashed lines) (Fig. 6).

**Discussion**

The objectives of this study were to quantify patterns of change of functional plant traits along gradients of water availability and flood disturbance and to identify riparian plant functional types associated with discrete hydrological habitat types. Nine plant functional types were identified within two rivers of the American Southwest, ranging from pioneer xerophytes to shade-tolerant mesophytes, each with a distinct suite of values for seven traits. Each differed in relative abundance among riparian habitat types that varied in surface flow (ephemeral to perennial), subflow (depth to water table), and flood disturbance. This provides a template that researchers from other arid regions streams can test for robustness, assuming a common basis for designating hydrological or fluvial habitat types (Angiolini *et al*., 2011; Belmar *et al.,* 2013). The nine functional types are derived from seven functional traits that vary along two axes of specialization- water availability and physical disturbance. In general there is an axis of specialization that separatesplants with fast growth, high productivity, and rapid acquisition of resources (acquisitive type) from those with slow growth and high investment in storage organs or herbivore defense (conservative type) (Grime *et al*., 1997; Dıaz *et al*., 2004). Traits associated with this productivity axis- including leaf area and SLA- vary along gradients of precipitation, aridity, and mineral nutrient availability (Givnish, 1987). This study reveals a tight coupling between leaf traits and depth to water table for the specialized habitat of riparian zones nested within the regional hot and dry environment. The declines in community-weighted leaf area, specific leaf area, and plant height with depth to water table underscore the importance of groundwater to arid region riparian plant communities.

Plant communities can show continuous change or more abrupt changes in response to variation in depth to water table (Silvertown & Dodd, 1999). Community-weighted plant traits can do the same. The variables showing the strongest threshold response were community-weighted leaf area and SLA, with a steep difference between larger and smaller leaves at approximately the 1 m depth and again at the 5 m depth. “Large” leaf size needs to be placed into contact, however, as even the largest-leaved functional type in the hot desert riparian zones (hydromesic plants, leaf area of 18-49 cm2) falls within a mid-size group of Raunkiaer’s (1934) global classification system (his mesophyll category, 16 to 164 cm2). Our mesic type are mostly microphylls (2 to 18 cm2) and our xeric and mesoxeric plants were nanophylls (0.25 to 2 cm2 or leptophylls <0.25 cm2).

Maximum canopy height also was a key factor differentiating among functional types. Woody plant canopy height in arid regions increases with precipitation (Scholes *et al*., 2002) but as shown here also varies locally with depth to water table. One caveat for these results is that some phenotypically plastic species, such as *Prosopis velutina,* vary substantially in height depending on water availability(Stromberg *et al.,* 1993), and the community-weighted trait values were based on one value per species. Canopy height also can be influenced by disturbance, with plant species shorter under very high disturbance (Westoby, 1998; Pakeman & Eastwood, 2013).

Production of spines to protect against herbivores is a trait associated with plants of arid environments (Wana & Beierkuhnlein, 2011; Frenette-Dussault *et al*., 2012). Spines in this study were present on xeric plants, but only on types affiliated with infrequently disturbed habitats. Under the combination of dry and disturbed conditions, such as floodplains of ephemeral streams, the xeric pioneers did not allocate resources to mechanical defense. Presumably, this relates to long-standing resource tradeoffs, such as high allocation to reproduction by the xeric pioneers.

Disturbance constitutes **a** major axis of separation between plant types (Lavorel *et al*. 1997). Floods in desert rivers exert their greatest influence via scours and erosion. Pioneer species in frequently flooded habitat can have many strategies but typically share a common suite of traits including short life span, small seed size, water or wind dispersal, stem flexibility, and capacity for vegetative spread and re-sprout capacity (Karrenberg *et al*., 2002; Parolin, 2003; Merritt *et al*., 2010). The two indicators of adaptations to disturbance used in this study, seed mass and dispersal mode, both responded strongly to the topographical indicator of flood disturbance (elevation above thalweg), and contributed to differentiation between pioneer and non-pioneer types. Both are reflective of processes operating at the regeneration life stage. Shifts from small to large seed size have been reported along disturbance or successional gradients in riparian as well as upland ecosystems (Kyle & Leishman, 2009; Wilfahrt *et al*., 2014) as have shifts from wind-dispersed to animal-dispersed seeds (Drezner *et al*., 2001; Lamb & Mallik 2003). Community-weighted seed mass in this study showed a small additional effect from water availability, consistent with prior research suggesting that large seeds impart selective advantage for seedlings in shaded as well as dry habitats (Stromberg & Boudell, 2013).

Root architecture and tissue composition determine a plants ability to utilize water from different depths and sources (e.g., capillary water above shallow or deep water tables, shallow soil moisture from rains) and influence capacity to survive drought and scouring events (Karrenberg *et al.*, 2003; West *et al*., 2012). Rooting depth was an important factor distinguishing among functional types in this study: As water tabled declined from <1 to >20 m, the woody pioneers shifted from medium-rooted phreatophytes to deep-rooted phreatophytes, and ultimately to medium-rooted non-phreatophytes dependent on seasonal flood run-off. Rooting depth has aided in discrimination among functional types in other riparian (Liu *et al*., 2005) as well as non-riparian habitats (Garcia-Mora *et al*. 1999; Pohl et al., 2011), although its use can be limited by the difficulty in obtaining data for deeply-rooted species (Canadell et al., 1996; Stromberg, 2013).

*Conservation and management implications*

Stream dewatering (and stream rewatering for restoration projects) are ongoing process in arid regions. This study aids in helping managers to understand impending changes and to select appropriate species (and plant types) for restoration plantings. One particular contribution is providing evidence of a third state-shift that can occur in response to progressive stream dewatering. A prior study in the American Southwest identified three different “condition classes”. Each supported distinct combinations of plant communities, with sequential loss of community types occurring as surface and subsurface water thresholds were exceeded (Stromberg *et al*., 2006). The first threshold- loss of perennial surface flow- resulted in sharp decline in obligate herbaceous wetland plants. The second entailed a shift in dominance from *Populus fremontii* and *Salix gooddingii* (hydromesic woody pioneeers) to *Tamarix chinensis* (deep-rooted xeromesic pioneers) as water tables fell below the rooting depths of the former. Given the drier site conditions included in this present study, a third state-shift was detected: medium-rooted, xerophytic shrubs (e.g., *Hymenoclea monogyra* and *Baccharis sarothroides*) became dominant as water tables fell below depths attainable by deeply-rooted phreatophytes such as *Tamarix*. Species within this latter functional type appear to be common on ephemeral streams in the American Southwest (Bloss & Brotherson, 1979; de Soyza *et al*., 2004; Shaw & Cooper, 2008).

Stream managers need to be concerned with surface flows and subsurface flows. Perennial streams have been the focus of conservation efforts, and perennial flow sites did indeed have a distinctive functional type signature compared to intermittent sites, with a greater abundance of the most productive types. This pattern is related to water table dynamics, in that the gaining reaches that sustain perennial flows have shallow and stable water tables (Lite & Stromberg, 2005). This present study confirms the importance of water table in structuring woody riparian plant functional types, to some degree independent of surface flow regime. Of note, the ephemeral-phreatic sites supported the same tall, hydromesic pioneer phreatophytes as other phreatic site types (intermittent and perennial), albeit in lower abundance. The ephemeral-phreatic stream type has received little research attention (Stromberg, 2001; Shaw & Cooper, 2008) and warrants additional conservation protection.

Also of importance for conservation of functional diversity was the simplification and loss of functional types as one progresses from the wettest to the driest stream type. All of the pioneer functional types, including the xeric one, were present at the perennial sites. (The hydromesic types were the dominant group along perennial streams but xeric pioneers established in dry microsites created by deep sediment deposits; Stromberg *et al*., 1997). Simplification of functional types has been observed in other dryland rivers undergoing decline in water resources (Liu *et al*., 2005) as well as in upland habitat experiencing drought and high disturbance (Carmona *et al*., 2012).

*Future research*

This study addressed a subset of riparian habitats in the American Southwest and a subset of the flora. To broaden the scope, functional types of the herbaceous flora need to be delineated (Willby *et al*., 2000; Zelnik & Carni, 2008). The number of herbaceous plant species in riparian zones of arid and semi-arid regions is much greater than that of woody species (Stromberg and Boudell, 2013) and they play important roles in the ecosystem. It seems productive to take a hierarchical approach to this challenge (Lavorel et al., 1997) by placing plants into functional types after first dividing them into major growth form categories such as woody vs. herbaceous.

Future studies should examine additional axes of specialization within riparian plant communities and greater extremes of water availability and flood disturbance than examined herein. For example, the many streams that are ephemeral over their entire length (versus ephemeral reaches within an interrupted perennial system) warrant study (Larned *et al*., 2010). Other habitat types in need of study with respect to adaptive traits and functional types are the swamps and marshes that develop under the combination of prolonged inundation but low disturbance (Kozlowski, 2002; Catford and Jansson, 2014). Such wetlands once were common in the Southwest but are now rare (Hendrickson and Minckley, 1984; Minckley *et al*., 2013). Yet other habitat types include stream reaches with high salinity (those flowing over saline rock formation or that have salinized owing to human activities; Eallonardo *et al*., 2013), those rich in nitrogen owing to inputs of effluent (White & Stromberg, in prep), and streams of higher elevation mountainous headwaters.

In broader-based regional assessments, additional traits will be needed to differentiate among plant functional types. Conservation science must be rooted in theory but be sufficiently practical for use. The number of traits used to proscribe functional types varies widely (Westoby, 1998; Diaz & Cabido, 1997; Aguiar *et al*., 2013), as does the number of plant functional types (Box, 1995; Garcia-Mora *et al*., 1999; Grime, 2001). To maximize efficiency, we should search for a small number of nun-redundant traits within the multiple dimensions that structure riparian plant communities (Laughlin, 2014). One such trait that may be useful in future studies is lateral root spread, given that it varies independently of rooting depth (Stromberg, 2013). Another trait of potential use for broader regional treatments or cross-global comparisons is capacity for clonal spread or respouting after disturbance. A small number of woody pioneer species (and many herbaceous plants) in the riparian Southwest are rhizomatous and this may further differentiate among habitats that vary in flood magnitudes. Another potentially useful trait is C:N ratio in leaves, which may be fruitful in, among other factors, differentiating among plants that are well- defended against ungulate grazing (e.g. *Baccharis, Tamarix*) and those that are more palatable (Pringle *et al.*, 2011) .

Ultimately, we should move towards linking stream hydrology and plant functional types with the ecosystem services that riparian areas provide (Jones *et al*., 2010; Bagstad *et al*., 2012). Traits can be classified as response or effect traits, and although this study focused on the former, the categories sometimes overlap (Suding *et al*., 2008). Canopy height and leaf area, for example, are useful effects traits linked with carbon acquisition (Lavorel & Garnier, 2002) and bird habitat (Mills *et al.,* 1991; Merritt & Bateman, 2012). One often overlooked riparian ecosystem service is habitat provision for crop-pollinators (Hannon and Sisk, 2009). To address concerns regarding pollinator declines, future assessments should include traits such as morphologial adaptations for different pollen vectors (Sacchi & Price, 1988; Lamb & Mallik, 2003; Pakeman & Eastwood, 2013).

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**References**

Aguiar F.C., Cerdeira J.O., Martins M.J. & Ferreira MT. (2013) Riparian forests of Southwest Europe: are functional trait and species composition assemblages constrained by environment? *Journal of Vegetation Science,* **24**,628-638.

Angiolini C., Nucci A.,Frignani F. & Landi M. (2011) Using multivariate analyses to assess effects of fluvial type on plant species distribution in a Mediterranean River. *Wetlands,* **31**, 167-177.

Bagstad K.J., Semmens D., Winthrop R., Jaworski D. & Larson, J. (2012) Ecosystem services valuation to support decision making on public lands—A case study of the San Pedro River watershed, Arizona. *U.S. Geological Survey Scientific Investigations Report,* **2012–5251**, 93 p.

Belmar O., Bruno D., Martinez-Capel F., Barquin J. & Velasco J. (2013)Effects of flow regime alteration on fluvial habitats and riparian quality in a semiarid Mediterranean basin. *Ecological Indicators*, **30**, 52-64.

Bloss D.A. & Brotherson J.D. (1979) Vegetation response to a moisture gradient on an ephemeral stream in central Arizona. *Great Basin Naturalist,* **39**, 161-176.

Box E.O. (1995) Factors determining distributions of tree species and plant functional types. *Vegetatio,* **121**, 101-116.

Brock M.A. & Casanova M.T. (1997) Plant life at the edges of wetlands; ecological responses to wetting and drying patterns. In: *Frontiers in Ecology; Building the Links* (Eds N. Klomp & I. Lunt), pp. 181–192. Elsevier Science, Oxford.

Brown D.E. (1994) *Biotic Communities: Southwestern United States and Northwestern Mexico*. University of Utah Press, Salt Lake City, Utah.

Canadell J., Jackson R.B., Ehleringer J.R., Mooney H.A., Sala O.E., & Schulze E.D. (1996) Maximum rooting depth of vegetation types at the global scale. *Oecologia,* **108**, 583-595.

Carmona C.P., Azcarate F.M., de Bello F., Ollero H.S., Leps J. & Peco, B. (2012) Taxonomical and functional diversity turnover in Mediterranean grasslands: interactions between grazing, habitat type and rainfall. *Journal of Applied Ecology,* **49**, 1084-1093.

Campbell C.J., Johns C.V. & Nielsen D.L. (2014) The value of plant functional groups in demonstrating and communicating vegetation responses to environmental flows. Freshwater Biology, **59**, 858–869.

Casanova M. (2011) Using water plant functional groups to investigate environmental water requirements. *Freshwater Biology*, **56**, 2637–2652.

Castle S.L., Thomas B.F., Reager J.T., Rodell M., Swenson S.C., & Famiglietti J.S. (In press)Groundwater depletion during drought threatens future water security of the Colorado River Basin. *Geophysical Research Union*.

Catford J.A. & Jansson R. ((2014) Drowned, buried and carried away: effects of plant traits on the distribution of native and alien species in riparian ecosystems*. New Phytologist,* doi: 10.1111/nph.12951.

Curtis J.T. (1959) *The Vegetation of Wisconsin: An Ordination of Plant Communities*. University of Wisconsin Press, Madison.

Dallas H.F. (2014) Ecological consequences of global climate change for freshwater ecosystems in South Africa. *South African Journal of Science,* Art. #2013-0274.

de Soyza A.G.,. Killingbeck K.T., Whitford W.G. (2004). Plant water relations and photosynthesis during and after drought in a Chihuahuan desert arroyo. *Journal of Arid Environments,* **59**, 27–39.

Díaz S. & Cabido M. (1997) Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science,* **8**, 463-474.

Díaz S., Hodgson J.G., Thompson K., Cabido M., Cornelissen J.H.C. *et al.* (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, **15**, 295-304.

Doll P., Fiedler K. & Zhang J. (2009). Global-scale analysis of river flow alterations due to water withdrawals and reservoirs. *Hydrology and Earth System Sciences,* **13**, 2413-2432.

Drezner T., Fall P. & Stromberg J.C. (2001) Plant distribution and dispersal mechanisms at the Hassayampa River Preserve, Arizona, USA. *Global Ecology and Biogeography,* **10**, 205-217.

Dominguez F., Cañon J. & Valdes J. (2010) IPCC-AR4 climate simulations for the Southwestern US: the importance of future ENSO projections. *Climatic Change,* **99**, 499–514.

Dubois A., Rossier L., Pottier J., Pellissier L., Vittoz P & Guisan A. (2013) Predicting current and future spatial community patterns of plant functional traits. *Ecography,* **36**, 1158–1168.

Eallonardo A.S., Leopold D.J., Fridley J.D. & Stella J.C. (2013) Salinity tolerance and the decoupling of resource axis plant traits. *Journal of Vegetation Science,* **24**, 365-374.

Eamus D. & Froend R. (2006) Groundwater-dependent ecosystems: the where, what and why of GDEs. *Australian Journal of Botany,* **54**, 91-96.

Frenette-Dussault C., Shipley B., Leger J.F., Meziane D. & Hingrat Y. (2012) Functional structure of an arid steppe plant community reveals similarities with Grime's C-S-R theory. *Journal of Vegetation Science,* **23**, 208-222.

Froend R. & Sommer B. (2010). Phreatophytic vegetation response to climatic and abstraction-induced groundwater drawdown: Examples of long-term spatial and temporal variability in community response. *Ecological Engineering*,[Get It! @ ASU](javascript:void) **36**, 1191-1200.

Garcia-Mora M.R., Gallego-Fernandez J.B. & Garcia-Novo F. (1999). Plant functional types in coastal foredunes in relation to environmental stress and disturbance. *Journal of Vegetation Science,* **10**, 27-34.

Gitay H. & Noble I.R. (1997) What are functional types and how should we seek them? In: Smith TM, Shugart HH, Woodward FI (eds) Plant Functional Types. Their Relevance to Ecosystem Properties and Global Change. Cambridge University Press, Cambridge, pp 3-19.

Givnish, T. J. (1987) Comparative studies of leaf form – assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytologist,* **106**, 131–160.

Goebel P. C., Pregitzer K. S. & Palik B. J. (2006) Landscape hierarchies influence riparian ground-flora communities in Wisconsin, USA. *Forest Ecology and Management,* **230**, 43-54.

Gonzalez-Sanchis M., Comin F. A., & Muller E. (2012) Hydrologic thresholds for riparian forest conservation in a regulated large Mediterranean river. *River Research and Applications,* **28**, 71-80.

Grime J. P. *et al.* (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos*, **79**, 259-281.

Grime, J.P. (2001) Plant Strategies, Vegetation Processes, and Ecosystem Properties, 2nd edition. John Wiley and Sons, West Sussex, England.

Hannon L.E. & Sisk T.D. (2009) Hedgerows in an agri-natural landscape: Potential habitat value for native bees. *Biological Conservation,* **10**, 2140-2154.

Hendrickson D.A.&. Minckley W.L. (1984) Cienegas: Vanishing climax communities of the American Southwest. *Desert Plants*, **6**, 1-175.

Higgins S.I., Rogers K.H. & Kemper J. (1997) A description of the functional vegetation pattern of a semi-arid floodplain, South Africa. *Plant Ecology,* **129**, 95–101.

Hunt R., Hodgson J.G., Thompson K., Bungener P., Dunnett N.P. & Askew A.P. (2004) A new practical tool for deriving a functional signature for herbaceous vegetation. *Applied Vegetation Science,* 7, 163-170.

Jobbágy E.G., Nosetto M.D., Villagra P.E. & Jackson R.B. (2011) Water subsidies from mountains to deserts: their role in sustaining groundwater-fed oases in a sandy landscape. *Ecological Applications,* **21**, 678-694.

Jones K.B., Slonecker E.T., Nash M.S., Neale A.C., Wade T.G. & Hamann, S.R (2010) Riparian habitat changes across the continental United States (1972-2003) and potential implications for sustaining ecosystem services. *Landscape Ecology,* **25,** 1261-1275.

Karrenberg S., Blaser S., Kollmann J., Speck T. & Edwards P.J. (2003) Root anchorage of saplings and cuttings of woody pioneer species in a riparian environment*. Functional Ecology,* **17,** 170-177.

Karrenberg S., Edwards P.J. & Kollmann J. (2002) The life history of Salicaceae living in the active zone of floodplains. *Freshwater Biology*, **47,** 733-748.

Kearney T.H. & Peebles, R.H. (1960). *Arizona Flora (with supplement)*. University of California Press, Berkeley.

Kozlowski T.T. (2002). Physiological-ecological impacts of flooding on riparian forest ecosystems.[Get It! @ ASU](javascript:void) *Wetlands*, **22**, 550-561.

Kyle G. & Leishman M.R. (2009). Plant functional trait variation in relation to riparian geomorphology. *Austral Ecology*, **34**, 793-804.

Laidig K.J., Zampella R.A., Brown A.M., & Procopio N.A. (2010) Development of vegetation models to predict the potential effect of groundwater withdrawals on forested wetlands. *Wetlands,* **30**, 489-500.

Lamb E.G. & Mallik, A.U. (2003) Plant species traits across a riparian-zone/forest ecotone. *Journal of Vegetation Science*, **14**, 853-858.

Larned S.T., Datry T., Arscott D.B. & Tockner K. (2010) Emerging concepts in temporary-river ecology. *Freshwater Biology,* **55**, 717–738.

Laughlin D.C. (2014) The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology,* **102**, 186–193.

Lavorel S. & Garnier E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology,* **16**, 545-556.

LavorelS., McIntyre S., Landsberg J. & Forbes T.D. (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution* **12**, 474-478.

Li W, Zhou H., Fu A., Chen Y.(2013) Ecological response and hydrological mechanism of desert riparian forest in inland river, northwest of China . *Ecohydrology,* **6**, 949-955.

Lite S.J. & Stromberg J.C. (2005) Surface water and ground-water thresholds for maintaining *Populus - Salix* forests, San Pedro River, Arizona. *Biological Conservation,* **125**, 153-167.

Liu J.Z., Chen Y.N., Chen Y.J., Zhang N & Li W.H. (2005) Degradation of *Populus euphratica* community in the lower reaches of the Tarim River, Xinjiang, China. *Journal of Environmental Sciences,* **17**, 740-747.

Lui W., Liu G., Liu H., Song Y. & Zhang Q. (2013) Subtropical reservoir shorelines have reduced plant species and functional richness compared with adjacent riparian wetlands. *Environmental Research Letters,* **8**, #044007.

Meinzer O. E. (1923) Outline of ground-water hydrology, with definitions. *U.S. Geological Survey Water-Supply Paper,* **494**, 71 p.

Merritt D.M. & Bateman H.L. (2012) Linking stream flow and groundwater to avian habitat in a desert riparian system. *Ecological Applications,* **22**, 1973–1988.

Merritt. D.M., Scott M.L., Poff N.L., Auble G.T. & Lytle D.A. (2010) Theory, methods and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds. *Freshwater Biology,* **55**, 206-225.

Merritt D.M. & Poff N.L. (2010) Shifting dominance of riparian *Populus* and *Tamarix* along gradients of flow alteration in western North American rivers. *Ecological Applications,* **20**, 135-152.

Mills G. S., Dunning Jr J. B. & Bates J. M. (1991). The relationship between breeding bird density and vegetation volume. *The Wilson Bulletin*, **103**, 468-479.

Minckley T.A., Turner D.S. & Weinstein S.R. (2013) The relevance of wetland conservation in arid regions: A re-examination of vanishing communities in the American Southwest. *Journal of Arid Environments,* **88**, 213-221.

O'Connor, T.G. (2010) Transformation of riparian forest to woodland in Mapungubwe National Park, South Africa, between 1990 and 2007.[Get It! @ ASU](javascript:void) *Austral Ecology*, **35**, 778-786.

Pakeman R.J. & Eastwood A. (2013)Shifts in functional traits and functional diversity between vegetation and seed bank. *Journal of Vegetation Science,* **24**, 865-876.

Palmer M.A., Lettenmaier D.P., **Poff N.L,** Postel S., Richter B. & Warner R. (2009) Climate change and river ecosystems: protection and adaptation options. ***Environmental Management,* 44**, 1053–1068.

Parolin P. (2003) Fugitive and possessive establishment strategies in Amazonian floodplain pioneers. *Flora*, **198**, 436-443.

Patten D.T. (1998) Riparian ecosystems of semi-arid North America: Diversity and human impacts. *Wetlands,* **18**, 498-512.

Phillips, W.S. (1963) Depth of roots in soil. *Ecology,* **44**, 424.

Pohl M., Stroude R., Buttler A. & Rixen, C. (2011) Functional traits and root morphology of alpine plants. *Annals of Botany,* **108**, 537-545.

Pringle E.G., Adams R. I., Broadbent E., Busby P.E., Donatti C., Kurten E.L., Renton K. & Dirzo R. (2011). Distinct leaf-trait syndromes of evergreen and deciduous trees in a seasonally dry tropical forest. *Biotropica*, **43**, 299–308.

Raunkiaer C. (1934) The Life Forms of Plants and Statistical Plant Geography. The Clarendon Press, Oxford.

Reich P.B., Wright I.J., Cavender-Bares J., Craine J.M., Oleksyn J., Westoby M., & Walters, M.B. (2003) The evolution of plant functional variation: Traits, spectra, and strategies. *International Journal of Plant Sciences*, **164**, S143-S164.

Royal Botanic Gardens Kew. (2014) *Seed Information Database (SID).* Version 7.1. Available from: http://data.kew.org/sid/ (June 2014)

Sacchi C.F & Price P.W. 1988. Pollination of the arroyo willow, *Salix lasiolepis*: role of insects and wind. *American Journal of Botany*, **75**, 1387-1393.

Scholes R.J., Dowty P.R., Caylor K., Parsons D.A.B., Frost P.G.H. & Shugart H.H. (2002) Trends in savanna structure and composition along an aridity gradient in the Kalahari. *Journal of Vegetation Science,* **13**, 419-428.

Serrat-Capdevila A., Valdes J.B., Perez J.G., Baird K., Mata L.J., & Maddock T. (2007) Modeling climate change impacts and uncertainty on the hydrology of a riparian system: The San Pedro Basin (Arizona/Sonora). *Journal of Hydrology,* **347**, 48-66.

SEINet. (2013) *Southwest Environmental Information Network.*  http//:swbiodiversity.org/seinet/index.php.

Shafroth P.B., Stromberg J.C, & Patten D.T. (2002) Riparian vegetation response to altered disturbance and stress regimes. *Ecological Applications*, **12**, 107-123.

Shaw J.R. & Cooper D.J. (2008) Linkages among watersheds, stream reaches, and riparian vegetation in dryland ephemeral stream networks. *Journal of Hydrology*, **350**, 68-82.

Silvertown J., Dodd M.E., Gowing D.J.G. & Mountford J.O. (1999).Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature,* **400**, 61-63.

Stella J.C., Rodríguez-González P., Dufour S. & Bendix J. (2012) Riparian vegetation researchin Mediterranean-climate regions: common patterns, ecological processes, and considerations for management. Hydrobiologia, 10.1007/s10750-012-1304-9.

Steward A.J., von Schiller D., Tockner K., Marshall J.C. & Bunn S.E. (2012) When the river runs dry: human and ecological values of dry riverbeds. *Frontiers in Ecology and the Environment*, **10**, 202–209.

Stromberg J.C. (2013) Root patterns and hydrogeomorphic niches of riparian plants in the American Southwest. *Journal of Arid Environments*, **94**, 1-9.

Stromberg J.C. & Boudell J.A. (2013) Floods, drought, and seed mass of riparian plant species. *Journal of Arid Environments*, **97**, 99-107.

Stromberg J.C., Lite S.J., Rychener T.J., Levick L.R., Dixon M.D. & Watts J.M. (2006) Status of the riparian ecosystem in the Upper San Pedro River, Arizona: Application of an assessment model. *Environmental Monitoring and Assessment*, **115**, 145-173.

Stromberg J.C., Bagstad K.J., Leenhouts J.M., Lite S.J. & Makings E. (2005) Effects of stream flow intermittency on riparian vegetation of a semiarid region river (San Pedro River, Arizona). *River Research and Applications,* **21**, 925-938.

Stromberg, J.C. (2001) Biotic integrity of *Platanus wrightii* riparian forests in Arizona: first approximation. *Forest Ecology and Management,* **142**, 249-264.

Stromberg, J.C., Fry J., & Patten D.T. (1997) Marsh development after large floods in an alluvial, arid-land river. *Wetlands*, **17**, 292-300.

Stromberg, J.C., Tiller R. & Richter B. (1996) Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro River, Arizona, USA. *Ecological Applications,* **6**, 113-131.

Stromberg J.C., Wilkins S.D. & Tress J.A. (1993). Vegetation-hydrology models as management tools for velvet mesquite (*Prosopis velutina*) riparian ecosystems. *Ecological Applications*, **3**, 307-314.

Suding K.N., Lavorel S., Chapin III F. S., Cornelissen J. H. C., Diaz S. *et al*. (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology,* **14**, 1125–1140.

Tockner K. & Stanford J.A. (2002) Riverine flood plains: present state and future trends. *Environmental Conservation,* **29**, 308-330.

Verberk W.C.E.P, van Noordwijk C.G.E, & Hildrew A.G. (2013) Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshwater Science,* **32**, 531-547

Wana D., Beierkuhnlein C. (2011). Responses of plant functional types to environmental gradients in the south-west Ethiopian highlands. *Journal of Tropical Ecology*, **27**, 289-304.

Wang Q., Yuan X., Willison J.H.M., Zhang Y. & Liu H. (2014) Diversity and above-ground biomass patterns of vascular flora induced by flooding in the drawdown area of China’s Three Gorges Reservoir. *PlosOne,* **9**, e100889.

Webb R.H. & Leake SA. (2006) Ground-water surface-water interactions and long-term climate change in riverine riparian vegetation in the southwestern United States. *Journal of Hydrology,* **320**, 302–323.

West A. G, Dawson T. E., February E. C., Midgley G. F., Bond W. J., Aston T. L. (2012) Diverse functional responses to drought in a Mediterranean-type shrubland in South Africa. *New Phyologist,* **195**, 396-407.

Westoby M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil,* **199**, 213–227.

Westoby M., Falster D. S., Moles A. T., Vesk P. A., & Wright I. J. (2002). Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.

Westoby M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213-227.

Wilfahrt P.A., Collins B. & White P.S. (2014)Shifts in functional traits among tree communities across succession in eastern deciduous forests. *Forest Ecology and Management*, **324**, 179-185.

Willby N.J., Abernethy V.J. & Demars B.O.L. (2000) Attribute-based classification of European hydrophytes and its relationship to habitat utilization. *Freshwater Biology,* **43**, 43-74.

Zelnik I. & Carni A.D. (2008) Distribution of plant communities, ecological strategy types and diversity along a moisture gradient. *Community Ecology,* **9**, 1-9.

Table 1. Pearson correlation values (r values) relating community-weighted riparian trait variables to indicators of surface and subsurface water availability (n=157 plots).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Community-weighted: | Elevation above thalweg (m) | | | Maximum depth to water table (m) | | Stream flow type | |
|  | r | | P | r | P | r | P |
| Leaf area | -0.45 | <0.00 | | **0.57** | <0.00 | 0.35 | <0.00 |
| Specific leaf area | -0.41 | <0.00 | | **0.62** | <0.00 | 0.35 | <0.00 |
| Canopy height | -0.11 | NS | | **0.38** | <0.00 | 0.34 | <0.00 |
| Rooting depth | 0.47 | <0.00 | | -**0.49** | <0.00 | -0.27 | 0.02 |
| Spinescence | **0.68** | <0.00 | | -0.53 | <0.00 | -0.01 | NS |
| Seed mass | **0.64** | <0.00 | | -0.52 | <0.00 | -0.18 | NS |
| Seed dispersal | **0.70** | <0.00 | | -0.53 | <0.00 | -0.13 | NS |

Table 2. Stepwise forward regression models relating community-weighted trait variables to three abiotic variables- maximum depth to water table\*, stream flow type, and elevation above thalweg (n= 157 plots).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Dependent variable | Independent variables | F  ratio | P value | Model r2 |
| Community-weighted**:** |  |  |  |  |
| Leaf area | Depth to water table (+) | 12.47 | 0.001 | 0.37 |
|  | Elevation above thalweg (-) | 10.7 | 0.001 |  |
|  | Surface flow type (+) | 4.50 | 0.04 |  |
| Specific leaf area | Depth to water table (+) | 98.9 | 0.000 | 0.39 |
|  |  |  |  |  |
| Canopy height | Depth to water table (+) | 8.3 | 0.01 | 0.16 |
|  | Surface flow type (+) | 5.6 | 0.02 |  |
| Rooting depth | Elevation above thalweg (+) | 46.6 | 0.000 | 0.31 |
|  | Depth to water table (-) | 6.5 | 0.01 |  |
|  | Surface flow type code (-) | 2.2 | 0.13 |  |
| Spinesence | Elevation above thalweg (+) | 156.4 | 0.000 | 0.51 |
|  | Surface flow type (-) | 13.6 | 0.000 |  |
| Seed mass | Elevation above thalweg (+) | 53.2 | 0.000 | 0.46 |
|  | Depth to water table (-) | 15.0 | 0.000 |  |
| Seed dispersal | Elevation above thalweg (+) | 72.6 | 0.000 | 0.51 |
|  | Depth to water table (-) | 12.3 | 0.001 |  |
|  |  |  |  |  |

\* Depth to water table data was input with a negative sign such that larger values (less negative) indicate wetter conditions

Table 3. Distribution of riparian-affiliated woody plant species among functional types, based on K-means clustering. The data are for 29 common woody plant species in the floodplains or terraces of low-elevation rivers of Arizona.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Functional type | Dispersal mode | Seed mass (g) | Leaf area (cm2) | SLA | Height (m) | Root depth (m) | Spines /thorns | Species |
| FT1 | Hydromesic pioneer; tall tree | Wind | 0.1-0.6 | 18-49 | 10-12 | 30 | 2-3 | No | Populus fremontii (Salicaceae) Salix gooddingii (Salicaceae) |
| FT2a | Mesic semipioneer; midheight tree | Wind | 0.1-36 | 8-20 | 9-12 | 13-20 | 2-4 | No | Acer negundo (Aceraceae) Fraxinus velutina (Oleaceae) Salix bonplandiana (Salicaceae) |
| FT2b | Mesic pioneer; tall shrub or small tree | Wind | 0.1-8.4 | 5-15 | 6-7 | 2.5-9 | 0.6-2 | No | Baccharis salicifolia (Asteraceae) Chilopsis linearis (Bignoniaceae) Salix exigua (Salicaceae) Pluchea sericea (Asteraceae) |
| FT3 | Xeromesic, deep-rooted pioneer; tall shrub or small tree | Wind | 0.1-8.6 | 0.5-1.5 | 5-7 | 2-8 | 8-12 | No | Atriplex canescens (Chenopodiaceae)  Tamarix chinensis (Tamaricaeae) |
| FT4 | Xeric pioneer shrub | Wind | 0.2-3.6 | 0.2-0.8 | 2.5-6 | 0.6-4 | 2-5.5 | No | Ambrosia monogyra (Asteraceae) Baccharis sarothroides (Asteraceae) Ericameria nauseosa (Asteraceae), Gutierrezia sarothrae (Asteraceae) Isocoma tenuisecta (Asteraceae) Larrea tridentata (Zygophyllaceae) |
| FT5 | Mesic, large seeded & shade-tolerant tree | Animal | 92-500 | 9 | 10-12 | 10-18 | 2-5 | No | Celtis laevigata var. reticulata (Ulmaceae) Juglans major (Juglandaceae) |
| FT6 | Xeromesic deep-rooted tree or large shrub | Animal | 117-120 | 0.2-0.3 | 4-6 | ≥10 | >6 | Yes | Acacia greggii (Fabacaeae) Prosopis velutina (Fabaceae) |
| FT7a | Xeric, large-seeded & shade tolerant shrub | Animal | 33-188 | 0.3-1.5 | 5-7 | 2-4 | 1.4-2.5 | Yes | Celtis ehrenbergiana (Oleaceae) Lycium pallidum (Solanaceae) Rhus microphylla (Anacardiaceae) Ziziphus obtusifolia (Rhamnaceae) |
| FT7b | Xeric succulent shrub | Animal | 2-16 | 0-0.2 | 0-5 | 1-3 | 0.5-2.5 | Yes | C. acanthocarpa (Cactaceae) Ferocactus wislizeni (Cactaceae) Lycium andersonii (Solanaceae) Opuntia engelmanii (Cactaceae) |



Fig. 1. Mean depth to water table in the floodplain zone versus the frequency with which surface flow is present. Each point represents a study site at Cienega Creek or the San Pedro River.

Fig. 2. Community-weighted plant traits in relation to depth to water table within the riparian zones of Cienega Creek and the San Pedro River (n=157 plots).

  
Fig. 3. Community-weighted leaf area and SLA by depth to water table zone, for the Cienega Creek and San Pedro River study areas. Zones with different lower case letters differ significantly at p<0.05, based on ANOVA and post-hoc Tukey tests (df=149).



Fig. 4. Community-weighted plant traits in relation to depth to water table within the riparian zones of Cienega Creek and the San Pedro River (n=157 plots). The dispersal score ranges from 1 (adapted for anemochory) to 2 (adaptedfor endozoochory).



Fig. 5. Importance Value of woody plant functional types among riparian hydrological habitat types. Flood disturbance increases fron left to right, and site conditions become drier from top to bottom. The moisture gradient is depicted in the the top figure by surface flow frequency and in the bottom figure by depth to water table zone. Data are from Cienega Creek and San Pedro River. See Table 3 for description of functional types. Eph.= ephemeral, Eph-ph.= ephemeral phreatic, Int.= intermittent, Per.=perennial.

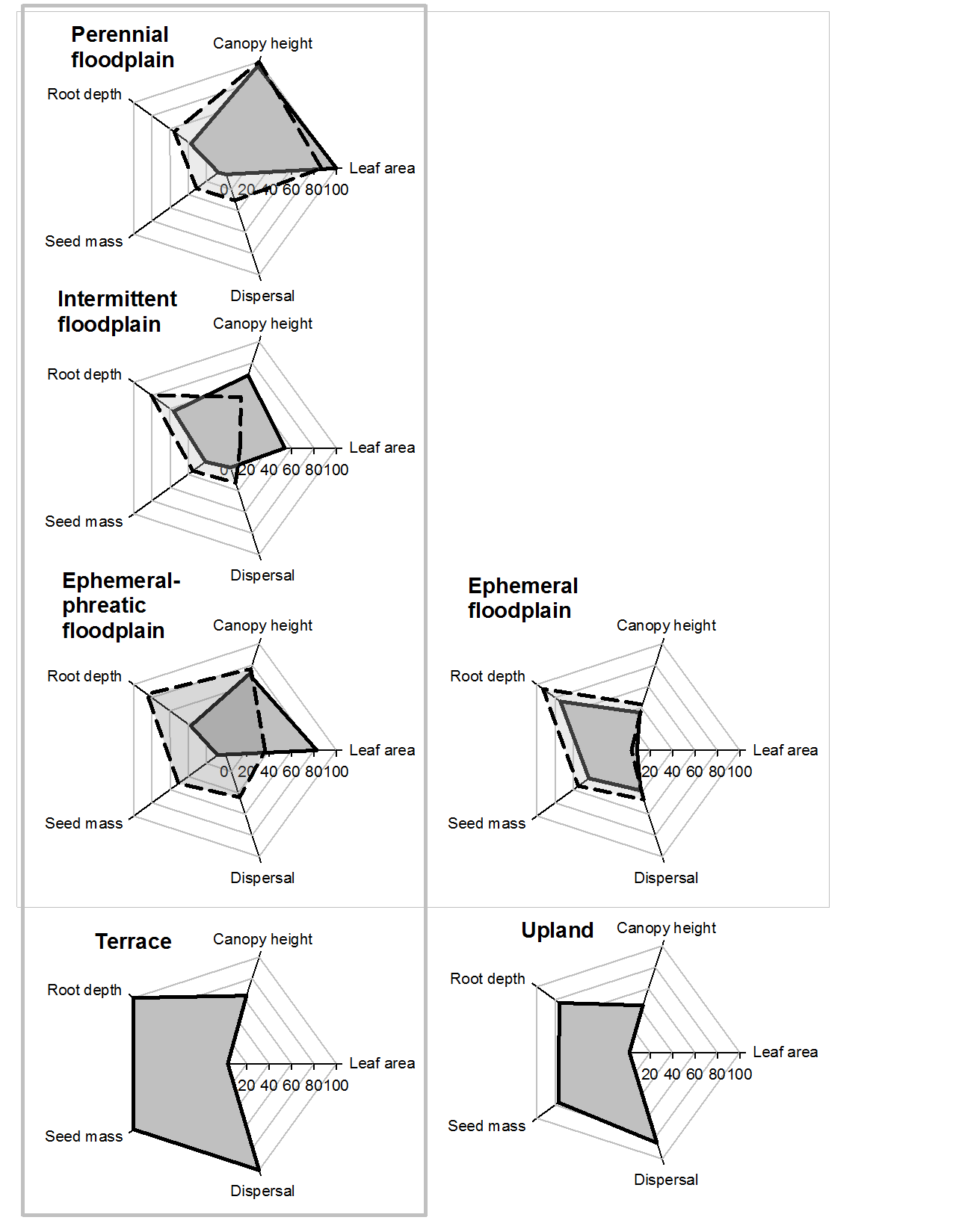


Fig. 6. “Radar” plots depicting community-weighted traits for riparian habitat types that vary in and surface and subsurface water flows and in flood disturbance. The four plots inside the thin-lined box depict floodplain sites; within each of these plots the solid lines indicate low surfaces and the dashed lines indicate infrequently flooded high surfaces. The four plots in the left panel all support vegetation that accesses the water table. Each of the five plant traits is standardized to range to a maximum of 100. For the dispersal trait, low values indicate predominance of wind dispersed seeds and high values indicate predominance of animal-dispersed seeds.