

How Will Hydrologic Change Alter Riparian Plant Communities  
of the Arid and Semi-Arid Southwest?

The Problem Approached from Two Perspectives

by

Andrea Florence Hazelton

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Graduate Supervisory Committee:

Juliet Stromberg, Chair  
Janet Franklin  
Mark Schmeckle

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## ABSTRACT

Climate change has the potential to affect vegetation via changes in temperature and precipitation. In the semi-arid southwestern United States, heightened temperatures will likely lead to accelerated groundwater pumping to meet human needs, and altered storm patterns may lead to changes in flood regimes. All of these hydrologic changes have the potential to alter riparian vegetation. This research, consisting of two papers, examines relationships between hydrology and riparian vegetation along the Verde River in central Arizona, from applied and theoretical perspectives. One paper investigates how dominance of tree and shrub species and cover of certain functional groups change along hydrologic gradients. The other paper uses the Verde River flora along with that river's flood and moisture gradients to answer the question of whether functional groups can be defined universally.

Drying of the Verde River would lead to a shift from cottonwood-willow streamside forest to more drought adapted desert willow or saltcedar, a decline in streamside marsh species, and decreased species richness. Effects drying will have on one dominant forest tree, velvet ash, is unclear. Increase in the frequency of large floods would potentially increase forest density and decrease average tree age and diameter.

Correlations between functional traits of Verde River plants and hydrologic gradients are consistent with "leaf economics," or the axis of resource capture, use, and release, as the primary strategic trade-off for plants. This corresponds to the competitor-stress tolerator gradient in Grime's life history strategy theory. Plant height was also a strong indicator of hydrologic condition, though it is not clear from the literature if plant height is independent enough of leaf characteristics on a global scale to be considered a second axis.

Though the ecohydrologic relationships are approached from different perspectives, the results of the two papers are consistent if interpreted together. The species that are currently dominant in the near-channel Verde River floodplain are tall, broad-leaf trees, and the species that are predicted to become more dominant in the

case of the river drying are shorter trees or shrubs with smaller leaves. These results have implications for river and water management, as well as theoretical ecology.

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## INTRODUCTION

### APPROACHING PLANT COMMUNITY CHANGE FROM TWO PERSPECTIVES

#### **Climate Change**

Due to increases in the levels of atmospheric carbon dioxide and other greenhouse gasses during the last 200 years, Earth's climate is changing. Increases in global temperature and changes in the size and frequency of storm events in some regions have already been documented, and these trends are projected to continue (IPCC, 2007). While some models predict that the southwestern United States will become warmer and drier, others predict an increase in precipitation, particularly from large storms (Bengtsson et al., 2007; McDonald, Bleaken, Cresswell, Pope, & Senior, 2005; Royer, Chauvin, Timbal, Araspin, & Grimal, 1998; Seager et al., 2007; SRAG, 2000; Wentz, Ricciardulli, Hilburn, & Mearns, 2007). Although the various models and scenarios have generated disparate predictions of how exactly the climate of the Southwest will change over the next century, a review of the available literature paints a picture of an overall reduction in precipitation, with proportionally more precipitation falling as part of large storm events and less falling as snow (Dixon et al., 2009; Garfin & Lenart, 2007).

Climate change will likely lead to changes in overall water availability as well as flooding regime along rivers in the American Southwest. These changes may occur via direct alteration in precipitation patterns and via increased evaporation due to elevated temperatures. Anthropogenic water use is anticipated to increase as a result of elevated temperatures (Garfin & Lenart 2007), which is likely to further impact floodplains through water development. The research presented in this thesis approaches the question of how riparian plant communities will adjust to these hydrologic changes.

#### **Factors that Affect Riparian Plant Communities**

Riparian plant communities are strongly influenced by physical factors, although biotic interactions certainly play a role in determining plant community structure. Naiman and Decamps (1997) provide a general list of factors that affect riparian plant

communities worldwide. Physical factors include the power and frequency of inundation, groundwater flows, presence of tributaries, water holding ability of the substrate, geomorphic template, rate of lateral channel migration, light, temperature, and the fire regime. Biotic factors that affect riparian plant community structure include competition, herbivory, and disease. Undoubtedly all of these variables do influence riparian plant communities in dry regions. However, two physical variables appear frequently in the literature as strongly shaping riparian plant communities in arid and semi-arid regions: water availability and flood regime (Auble, Friedman, & Scott, 1994; Bagstad, Stromberg, & Lite, 2005; Bendix & Hupp 2000; Campbell & Green, 1968; Capon & Brock, 2006; Friedman et al., 2006; Johnson, 1998; Lite, Bagstad, & Stromberg, 2005; Lite & Stromberg, 2005; Salinas & Casas, 2007; Shafroth, Stromberg, & Patten, 2002; Stromberg, Beauchamp, Dixon, Lite, & Paradzik, 2007; Tabacchi, Planty Tabacchi, Salinas, & Deschamps, 1996). Water availability has been repeatedly shown to strongly shape patterns in floodplain vegetation in arid regions, but the river's flood regime can also affect the species composition, amount of vegetation present, species diversity, and floodplain-scale patterns in species distribution.

### **Contents of this Thesis**

In addition to this introduction and a conclusion, this thesis is composed of two papers, each of which may stand alone conceptually. The theme that unites the two papers is a question of the relationship between hydrology and riparian vegetation. The chapters are also united geographically, as the data for both were collected in the floodplain of the Verde River in central Arizona. What differentiates the two chapters is the approach to understanding vegetation change. While vegetation change is approached from a functional and structural perspective in both papers, the first seeks an applied, management-friendly understanding of the changes, while the other seeks a more theory-based understanding.

The first chapter, "Verde River Riparian Vegetation: Linkages with Stream Hydrology," is part of a multi-disciplinary, inter-organizational study of eco-hydrological

relationships led by Jeanmarie Haney of The Nature Conservancy. That study included invertebrate, fish, and hydrologic components in addition to the vegetation portion presented here. The overall goal of the study was to determine the environmental flow requirements—including stream flow, groundwater, and flooding requirements—of Verde River aquatic and riparian biota, in a manner that would be useful and accessible to land managers. Chapter from that study presented here was co-authored by my committee chair, Julie Stromberg, and myself. The discussion includes an analysis of potential vegetation change in response to alteration of the stream flow regime. Vegetation changes are presented in terms of changes in dominant species, especially trees and shrubs, and in terms changing dominance of certain plant functional groups. In this paper, however, functional groups are treated in a relatively unsophisticated manner.

The second paper, "Can you Measure a CSR Strategy: A Test of Two Methods for Quantifying Plant Life History Strategy," deals with plant functional groups in much greater depth. This paper asks the question of whether a "universal" functional group classification method can exist, and approaches that question by using the Verde River riparian plant community to test methods that were developed elsewhere. The motivation for the research presented in this chapter was a desire frame vegetation changes predicted in the previous chapter in a manner compatible with other, similar ecosystems worldwide. While plant life history strategy theory forms the focus of this chapter, the results also shed light on the drivers of functional and morphologic variation in the geographic region where the data were collected.

Plant communities undergo constant change. That change is often driven by, among other factors, climate change and anthropogenic land use change. This thesis presents applied and theoretical views of what change may occur in the floodplain vegetation of the Verde River, given the hydrologic changes that will result from certain anthropogenic and climate drivers.

## 2. VERDE RIVER RIPARIAN VEGETATION:

### LINKAGES WITH STREAM HYDROLOGY

#### **Introduction**

Sustaining riparian ecosystems and their environmental benefits hinges on maintaining appropriate and sufficient environmental flows (Arthington, Bunn, Poff, & Naiman, 2006). Environmental flows include water flowing in the surface stream and in the stream aquifer. Both of these water sources, including low-flow and high-flow aspects of a stream's flow regime, strongly influence the structure of riparian ecosystems in the arid and semiarid Southwest (Hupp & Osterkamp, 1996; Stromberg, Beauchamp, Dixon, Lite, & Paradzik, 2007). Stream base flow is a key determinant of the abundance and types of plants that can survive along the low-flow channel during the hot dry seasons. Depth to the water table under the river's floodplain and terraces shapes vegetation structure by providing a water source accessible to deep-rooted phreatophytes. Flood flows raise groundwater levels, provide a periodic source of surface water and nutrients to riparian plants, and influence vegetation through scour, sedimentation and other fluvial processes.

Many rivers in dryland regions are undergoing changes to their flow regime. These changes occur in response to increasing demands on limited water supplies from expanding human populations and to changing land use patterns (e.g. shifts from agricultural to urban use). Stream flows also are shifting in response to global climate change as it affects local temperature and rainfall, and thus stream hydrology (Milly et al., 2008). On the Verde River in central Arizona, base flow has been altered in specific reaches by irrigation diversions (Alam, 1997), and stakeholders have expressed concern that base flows in the river will further decline as urbanization and associated groundwater pumping expands. These concerns are supported in general by hydrologic studies showing connectivity between groundwater and surface water systems (Blasch et

al. 2006). Data indicate that the Big Chino aquifer (near Prescott, Arizona) is the source of about 80 percent of the base flow in the upper Verde River (Blasch, Hoffman, Graser, Bryson, & Flint, 2006) and that aquifers to the north and underlying the Verde Valley provide base flow to the middle Verde River (Zlatos 2008).

The ultimate goals of the Verde eco-flows project are to determine the environmental flow requirements of Verde River riparian and aquatic ecosystems, and to predict how changes in stream hydrology arising from anthropogenic water use will alter these ecosystems. The specific objectives of this portion of the pilot study were to 1) describe riparian vegetation structure at three sites along the Verde River, 2) quantify relationships between stream hydrology and riparian vegetation, and 3) determine how these flow-hydrology relationships compare with those documented on other regional rivers.

## **Methods**

### **Approach**

To assess effects of changing flow regimes on riparian vegetation, various approaches can be taken. One approach uses space-for-time substitution, wherein riparian vegetation attributes are quantified along spatial gradients of water variability with the assumption the spatial patterns are reflective of, and predictive of, temporal vegetation responses to changing flow regimes. Hydrologic gradients can be examined along the longitudinal (upstream-downstream) dimension, if sufficient site-level variation exists in metrics including mean depth to the water table, base flow rate, and degree of stream intermittency. Relationships also can be explored within a riparian site along lateral gradients of depth to water table and inundation frequency.

Presently, the upper and middle Verde River maintains perennial surface flow over its entire length. Short reaches of the river located downstream from “push-up” diversion dams exhibit extremely low to no-flow (ponded) conditions during portions of the summer irrigation season. Considerable variation in depth to water table and



inundation frequency do exist within sites along the Verde River, owing in part to the high degree of topographic complexity. Utilizing this within and between-site variability, we examined vegetation-hydrology relationships along the Verde River. To determine how regionally robust these relationships are, we provide a preliminary contrast with patterns observed at the intensively-studied San Pedro River (Lite & Stromberg, 2005; Stromberg, Bagstad, Leenhouts, Lite, & Makings, 2005). We will delve more thoroughly into regional comparisons in forthcoming publications.

### **Study Sites**

Three sites were selected along the Verde River (Campbell Ranch, Dead Horse Ranch State Park, and TNC's "Otter Water" site) (Table 1; Figure 1). The sites were selected after first delineating the river into reaches with reasonably similar valley geomorphology and geology. Each of the three sites is in a different reach, as a first step towards providing comprehensive coverage of the range of conditions present along the river. Other criteria for site selection were accessibility and permission from landowners to install piezometers for measuring depth to groundwater.

At each study site, two to four cross-sectional riparian transects (perpendicular to the valley) were established, separated by intervals of 100 m. Transects extended into the *Prosopis* woodland (if present) on the terrace above the active floodplain on each side of the river. The terraces at all three study sites had been developed for anthropogenic land use (roads, back yards, livestock enclosures, and farm fields are common uses of the Verde River terrace in the Verde Valley), so the transects extended to the edge of the anthropogenic land use; most, however, included some terrace vegetation.

### **Woody Vegetation Sampling**

Woody vegetation was sampled in June 2008 along two transect lines per site (only one transect line at Dead Horse Ranch State Park, where the floodplain was greater than 300 m wide). A stratified sampling approach was utilized, wherein one 5m X 20m (100 m<sup>2</sup>) plot was sampled within homogenous patches. The patches were

delineated based on geomorphic surface elevation and on woody species composition, density and tree size classes; the vegetation and geomorphology of a 20 m length of floodplain (10 m on either side of the transect line) was considered when delineating patches. When patches were more than 25 m wide, additional plots were established (one additional plot for each 25m of patch width). Plots were oriented so that the long (20 m) edges parallel the river. The distance of each patch from the low-flow channel was recorded, and the elevation of the patch above the stream thalweg was determined based on topographical surveys of the transect line obtained using a stadia rod and transit. Within each 100 m<sup>2</sup> plot, woody stem density, by species, was measured by counting each live tree stem emerging from the ground in each plot. Woody plant basal area was quantified by measuring the basal diameter of each stem using calipers or diameter tape. Shrubs were measured at 0.1 m height. Canopy cover was measured at three points in each plot (two corners and the center) using a spherical densiometer.

Trees and shrubs were identified to species, and then placed into one of 8 functional groups relating to degree of drought tolerance and tolerance of disturbance (Table 2). We define hydric species as those classified as obligate or facultative wetland by U.S. Department of Agriculture (2010), mesic species as those defined as facultative and facultative upland, and xeric species are those defined as non-wetland. Species were also categorized into three levels of disturbance tolerance, based on information from the U.S. Department of Agriculture Forest Service (2010) and on professional judgment. Pioneer species are those that colonize newly disturbed habitats. Secondary successional species germinate in the shady understory of other trees. Facultative pioneers can germinate either in disturbed soil or in the understory.

### **Herbaceous Floodplain Sampling**

Herbaceous cover, by species, was sampled using modified Braun-Blanquet cover classes (Braun-Blanquet, 1932; p.32). The data were collected along two transect lines per site except at Dead Horse Ranch where they were collected along four transect lines per site. Twenty to twenty-five, 1 m<sup>2</sup> plots were established along each transect

line, with ten plots clustered near the stream channel (1 m apart) and the remaining plots spaced evenly across the floodplain. Data were collected twice in each plot, in June and September 2008. Plants were identified to species using Kearney & Peebles (1960) and classified according to wetland indicator status (U.S. Department of Agriculture, 2010).

### **Herbaceous Streamside Sampling**

To focus on the active-channel zone, three subsites, separated by 100 m of stream length, were established at each site. Each subsite consisted of a 20 m length of the streamside zone, which we define as the channel bars and banks of the active stream channel. At each site, 18, 1 m<sup>2</sup> quadrats (6 per subsite) were randomly placed within the streamside zone. In each quadrat, cover was recorded, by species, using modified Braun-Blanquet cover classes (Braun-Blanquet, 1932; p.32). Data were collected in June 2008 and again in September 2008. These sampling times were selected to capture the seasonal turnover of herbaceous annuals. The Verde River experiences spring snowmelt floods and summer monsoon floods, which occur July through early September. June was selected because most of the spring annuals were reproductively mature and had not yet been scoured by monsoon floods. Herbaceous vegetation was sampled again in late September to capture the species that flowered during warm-season conditions and that responded to the monsoon rains.

### **Depth to Water Table**

To measure depth to water in the shallow stream alluvium, perforated steel drive points attached to steel pipe were hand-driven at three locations at each of the study sites. Drive points were installed by team members in early summer 2008 and were positioned to span lateral hydrologic gradients within each site, with one located on a low surface near the active channel, another within the floodplain, and a third on the (high) river terrace. These temporary water level monitoring wells were located along or close to the transect lines, to allow for correlation with vegetation attributes, and were instrumented with pressure transducers to provide continuous data on depth to water.

## **Inundation Frequency**

Inundation frequency was calculated by using topographic surveys and Manning's equation to determine stage-discharge relationships for each cross section. Stage-discharge relationships were used to determine the discharge corresponding to each plot elevation. A recurrence interval corresponding to each discharge (and hence each plot) was calculated using stream gauge data fitted to a log-Pearson Type III distribution.

## **Analysis**

Synthetic vegetation traits (e.g. total basal area, species richness) and species-level attributes (basal area, cover) of the woody and herbaceous plant communities were calculated at the site level in the following fashion. For data collected in quadrats along transect lines, quadrat-level values were weighted by the respective width of each quadrat's patch along a transect line to produce a transect level value. The transect values were then averaged to produce a site mean. For data collected in the streamside zone, averages were calculated for the 18 plots sampled per site.

To examine the distribution of individual plant species and of functional type in relation to hydrologic conditions, the depth to the water table (and intra-annual variation) and frequency of inundation was calculated for each delineated patch and herbaceous quadrat along the transect lines. The water table values were estimated by using the topographical survey information (i.e. elevation of the patch surface) in conjunction with the estimated lateral profile of the water table derived from data for the three monitoring wells per site. The dry-season water table depth was calculated as the deepest measurement over the course of the sampling period (August 2008 to November 2009).

## **Results**

### **Vegetation Description**

A total of 83 species were sampled at Campbell Ranch, 99 at Dead Horse Ranch, and 89 at Otter Water. Of the 153 species that were sampled at the 3 sites, 15

are trees and 9 are shrubs. Of these 24 woody species, many were present at low frequency (Table 3). Woody species with the greatest relative abundance overall were Fremont cottonwood, Goodding's willow, and desert willow (Table 4).

At all three study sites, the stream channel was lined with herbaceous wetland vegetation, the most abundant species being Southern cattail, watercress, floating primrose-willow, horsetails, bulrushes, and rabbitsfoot grass. Mesic species including sweet clover, cocklebur, Bermuda grass, and tall fescue, are common in these herbaceous patches as well.

Inland from the herbaceous wetland patch is a mixed broadleaf forest. At Campbell Ranch, the highest elevation site, the forest is dominated by velvet ash, Fremont cottonwood, and Goodding's willow. Other woody species found in this zone are saltcedar, Fremont barberry, desert hackberry, desert olive, oneseed juniper, and skunkbush sumac. At Dead Horse Ranch, the streamside forest is dominated by Goodding's willow and velvet ash, with appearances by Fremont cottonwood, white mulberry and Arizona alder as well. The broadleaf forest at Otter Water, the lowest elevation site, is the least diverse. It is dominated by Fremont cottonwood and Goodding's willow, with sparse seepwillow. The broadleaf deciduous forest at all three sites is characterized by a sparse herbaceous understory of marsh species close to the streamside zone to primarily mesic species farther from the stream. Common understory species include horsetails, sacred datura, Cuman ragweed, and golden corydalis.

At all sites, there is an overflow channel beyond the broadleaf deciduous forest. The overflow channel has cobbly sediments and a sparse distribution of desert willow. Understory plants are sparse and mostly xeric, including Loomis' thimblehead, chenopods, and bromes. Beyond the overflow channel a bank leads up to the higher floodplain. At Campbell Ranch, the most common woody species on the high floodplain is netleaf hackberry, interspersed with mature cottonwood. Lower in elevation at Dead Horse Ranch, the high floodplain has patches dominated by desert willow, and patches of netleaf hackberry and mature cottonwood. At the lowest elevation, Otter Water's high

floodplain is characterized by desert willow mixed with singlewhorl burrobrush, with occasional groves of mature Fremont cottonwood or Goodding's willow. High floodplain herbs are a mix of mesic species such as johnsongrass, Russian thistle, and spike dropseed, and xeric species including bromes, chenopods, and silverleaf nightshade. Where there is little canopy cover, high floodplain herb cover is quite dense. At all three sites, the terrace above the floodplain has been altered for anthropogenic land use. However, a band of terrace vegetation—velvet mesquite with an understory of xeric, annual herbs and grasses—was present at the two lower elevation sites.

Otter Water had the highest woody stem density and the lowest basal area (Table 5). The high stem count and low basal area at Otter water was driven by the cottonwood and willow saplings that are abundant on the stream banks and the burrobrush shrublands on the high floodplain (Table 6). In addition, the large, mature trees (particularly cottonwood) that are abundant at Dead Horse Ranch and Campbell Ranch are less common at Otter Water.

### **Eco-Flow Relationships**

**Vegetation linkages with stream low-flow conditions.** The riverine marshland zone adjacent to the channel supported higher species richness and herbaceous cover than other portions of the floodplain (Figure 2). At Otter Water, the site with the highest annual and summer low flow rates, species richness and cover remained elevated farther away from the channel than at the other two study sites.

Data compiled for several regional rivers (Hassayampa River, San Pedro River, Santa Cruz River, Cienega Creek) indicate that the absolute (Figure 3) and relative cover (data not shown) of hydric perennial herbaceous plants growing along the low-flow channel declines sharply as the degree of stream flow permanence declines. Values for the three Verde River sites (all with perennial surface flow) are consistent with patterns for these other rivers, with high abundance of hydric perennials at sites with 100% flow permanence. Other attributes of the low-flow channel vegetation that change with the degree of stream intermittency include mean species richness (Figure 3) and ground

cover (data not shown). For these metrics, values for the Verde River plot within and above the range measured for perennial flow sites at other regional rivers.

**Vegetation linkages with depth to the water table.** The dominant woody species (Figure 4) and functional types (Figure 5) at the Verde River study sites are distributed along gradients of depth-to-water table. The functional groups that grew at the lowest elevations in the floodplain were hydric pioneer species (Fremont cottonwood and Goodding's willow) with an average seasonal maximum depth to water table of 1.9m, and mesic facultative pioneers (tree of heaven and velvet ash) at 1.8m. The mesic pioneer (saltcedar) averaged 1.3m above the water but was mostly represented by saplings. Late successional mesic species grew at a range of elevations; desert olive and Arizona walnut averaged 3.1 and 3.2m, respectively, while deep-rooted velvet mesquite and netleaf hackberry occurred at 4.4 and 4.7m above the water table. The two common xeric pioneer species, desert willow and singlewhorl burrobrush, grew at respective average maximum seasonal depth to water table of 3.2 m and 3.3m. Data are similar to patterns on the San Pedro (Figure 4, bottom panel) except that saltcedar on the Verde grow at shallower depth-to-water, likely reflecting their juvenile life stage.

Herbaceous functional groups were also distributed along a depth-to-water table gradient (Figure 6). Hydric species were abundant and diverse in the first meter above the water table and steeply declined with increases in floodplain elevation. Overall species richness and cover also peaked at the lower floodplain elevations.

**Vegetation linkages with inundation frequency.** Flood recurrence interval is highly correlated with depth to groundwater, because both are influenced by elevation relative to the stream channel. Velvet ash and Goodding's willow were most common in frequently flooded patches averaging inundation every two years (Figure 7). Fremont cottonwood and three mesic species—saltcedar, tree of heaven and desert olive—grew in slightly less frequently flooded locations, averaging a five year recurrence interval. The remaining species—burrobrush, desert willow, Arizona walnut, velvet mesquite, and netleaf hackberry—thrived in patches that flood less frequently than once per ten years.

## **Discussion**

### **Dewatering Effects on Riparian Vegetation**

Despite their present high diversity, the species least likely to persist if the Verde is dewatered are hydric perennials; these species dominate the streamside marsh communities and broadleaf deciduous forests that line the Verde River. Should the river become intermittent, the marsh species will likely be replaced by mesic species such as Bermuda grass and white sweetclover, echoing patterns from the San Pedro River (Stromberg, Bagstad, Leenhouts, Lite, & Makings, 2005).

Hydric trees are sensitive to stream flow intermittency and associated decline in water table depth. On the San Pedro River, Fremont cottonwood remained dominant where surface flow was maintained more than about 75% of the year (Lite & Stromberg, 2005). At drier sites, cottonwood and saltcedar were codominant. This relationship may hold for the Verde River. On the other hand, velvet ash, a species more common on the Verde than the San Pedro, could become more dominant within the broadleaf deciduous forests on the Verde under conditions of reduced stream flows and water tables. One horticultural study identified velvet ash as drought tolerant (Balok & St Hilaire, 2002), but no ecological studies have contrasted its water requirements with those of cottonwood, willow and saltcedar. Desert willow, a common drought-tolerant pioneer on the Verde, also could increase in abundance. It is possible that if surface flow were to become intermittent and cottonwood and willow lose their competitive advantage, velvet ash, desert willow, and/or saltcedar may become the dominant tree within the young floodplain forests.

### **Flood Regime Change Effects on Riparian Vegetation**

Another aspect of environmental flows is flooding regime. There is no reason to believe that that management decisions made in the near future will alter the flooding regime of the Verde River. However, some climate change models do predict changes in precipitation quantity, type, and timing that would alter the flood regime. Common predictions include an overall decrease in precipitation, an increase in large storms (and



thus floods), and more rain than snow in the early spring, which would lead to earlier and larger snowmelt floods in spring (Dixon et al., 2009, Garfin & Lenart, 2007). If flood size and frequency were to decrease dramatically, then recruitment of pioneer species might decline; however, predictions of larger snowmelt floods suggest this is an unlikely scenario. On the other hand, if large spring floods occur more often, then pioneer species recruitment would likely increase, the frequently flooded portions of the floodplain would experience higher patch turnover, and forest structure would shift to a higher density of small diameter (younger) trees. Work by Stella, Battles, Orr, and McBride (2006) suggests that earlier spring floods would not decouple *Populus* and *Salix* seed release from flood timing. Instead, seed release by these pioneer species appears to be triggered by spring temperatures; if early spring temperatures are higher, *Populus* and *Salix* will release seeds earlier to accompany the earlier timing of the spring floods.

#### **Value of Water-Sensitive Plant Communities**

Streamside marshes provide valuable wildlife habitat. Bird species that make use of riverine marshes on the Verde River for primary habitat include the Virginia rail, Sora rail, and Red-winged blackbird. In addition, some species including mallards and spotted sandpipers nest in marsh habitat (Stevens, Turner, & Suplee, 2008). Some species of fish benefit from marsh vegetation as well. Cover for fish is provided by both the aquatic macrophytes directly as well as the undercut banks created by the presence of dense herbaceous vegetation on the stream bank (Lyons, Trimble, & Paine, 2000). For example, roundtail chub in the Verde watershed use aquatic macrophytes and undercut banks for cover (Girmendonk & Young, 1997). The muskrat, one of three aquatic mammals found in the Verde River, prefers marsh habitat as well, and uses cattails to line its dens (Hoffmeister, 1986).

Streamside vegetation provides various hydrogeomorphic and biogeochemical functions. Vegetation stabilizes banks and reduces the amount of sediment the stream carries. It does this through a self-reinforcing process (Heffernan, 2008). The presence of vegetation provides roughness to a stream bank, which slows water velocity, causing

sediment to drop out of the water (Corenblit, Tabacchi, Steiger, & Gurnell, 2007). Some marsh species tolerate this sediment deposition, or even respond with increased growth due to the moisture subsidy from the deposited sediment, further increasing roughness (Kearsley & Ayers, 1999). This cycle can continue until a flood large enough to scour the vegetation occurs. Besides promoting aggradation, marsh species prevent bank erosion when roots physically reinforce the soil (Corenblit et al., 2007, Lyons et al., 2000).

Erosion control ability is species specific and depends on root and shoot architecture (Cornwall 1998). For example, hydric perennial species such as mountain rush (*Juncus balticus*) and sand spikerush (*Eleocharis montevidensis*) are sod-forming and have high stem density and roots long enough to reach the base of the bank on which they grow, traits that contribute to erosion control. However, the annual rabbitsfoot grass (*Polypogon monspeliensis*) has shallower roots relative to the bank elevation on which it grows and would be less effective in preventing bank erosion (Cornwall, 1998).

Streamside marshes may, to some degree, perform the same water purification functions as depressional wetlands (Heffernan, 2008). The anoxic soils and marsh species that characterize both types of wetlands provide conditions for removing or converting nitrogen, phosphorus, and heavy metals in water that passes through the soil (Karpiscak, Whiteaker, Artiola, & Foster, 2001; Bastian & Benforado, 1988).

Riparian broadleaf deciduous forests in the southwest are highly valued for aesthetic and recreational purposes. These forests are iconic in this arid region as a source of deep shade and a marker of flowing water in the midst of desert scrub. Residents of the southwest demonstrate the value they place on these forests using their pocketbooks. For example, property that is near rivers with riparian forests is more valuable than comparable property farther away (Bark, Osgood, Colby, Katz, & Stromberg, 2009). Taxpayers and philanthropists have also funded programs dedicated to conserving and restoring streamside deciduous forests. Briggs, Roundy, and Shaw (1994) discuss 27 riparian revegetation projects that were implemented in Arizona, most

of which focused on planting cottonwood and willow trees to restore declining deciduous forests.

Broadleaf deciduous forests are valuable from an ecological perspective as well. By providing dense canopy cover in upper strata and adding to the structural diversity of riparian vegetation, they provide habitat for a variety of animals. Riparian gallery forests on the Verde River serve as habitat for many bird species, including great blue heron, belted kingfisher, summer tanager, Southwestern willow flycatcher, a federally listed endangered species, and yellow-billed cuckoo, a candidate for the Endangered Species list (Stevens et al., 2008). Beaver, an ecosystem engineer and keystone species, relies on streamside gallery forests, especially cottonwood trees, for food and building materials (Hoffmeister, 1986).

Besides directly providing habitat and food for a variety of animal species, broadleaf deciduous forests affect other species indirectly by modulating environmental conditions. The forest canopy shades the stream channel, limiting fluctuations in water temperature (Karr & Schlosser, 1978). The transpiration by the trees also raises local humidity, providing evapo-transpirative cooling. Riparian gallery forests also influence water quality. Riparian trees can take up nitrogen from storm runoff and groundwater, as well as decrease stream sediment content by trapping sediment from overland runoff and slowing water velocity during floods (Lyons et al., 2000).

### **Conclusion**

Loss of streamflow in the upper and middle Verde River would result in ecological changes in the riparian zone. Streamside marsh would shrink or vanish with the loss of surface flow. The accompanying drop in the water table would lead to a shift in species dominance in the riparian gallery forests to more drought-adapted species with less capacity to provide functions such as dense shade. Coupled with these vegetation changes would be changes in ecosystem processes and loss of suitable habitat for some wildlife species. These changes would occur due to loss of streamflow, independent of

any change in flooding frequency. Flood regime changes, as a result of climate change, are not predicted to appreciably alter species dominance in the riparian zone, since the predicted increased frequency of large floods would benefit the pioneer species that already dominate the frequently flooded zone of the floodplain.

### **Acknowledgements**

We thank the Arizona Water Institute and U.S. Environmental Protection Agency for providing grant support, and Arizona State Parks, The Nature Conservancy, and the Arizona Game and Fish Department for providing site access. We thank Sarah Hunkins and Darin Jenke for assistance with vegetation sampling and/or plant species identification. Dale Turner and Jeanmarie Haney provided helpful review comments.

Table 1. Study sites along the Verde River.

Site	Location	Ownership	Elevation (m)
Campbell Ranch	Near Paulden, AZ	Arizona Game and Fish	1285
Dead Horse Ranch	Cottonwood, AZ	Arizona State Parks	1000
Otter Water	Near Camp Verde, AZ	The Nature Conservancy	963

Table 2. Functional types of woody plant species in the Verde River riparian zone.

Moisture Requirement	Successional Status	Species	Common Name
Hydric	Pioneer	<i>Alnus oblongifolia</i>	Arizona Alder
		<i>Baccharis salicifolia</i>	Seep Willow
		<i>Populus fremontii</i>	Fremont Cottonwood
		<i>Salix exigua</i>	Coyote Willow
		<i>Salix gooddingii</i>	Goodding Willow
Hydric	Facultative pioneer	<i>Amorpha fruticosa</i>	False Indigo
Mesic	Pioneer	<i>Baccharis sarothroides</i>	Desert Broom
		<i>Tamarix ramosissima</i>	Salt Cedar
Mesic	Facultative pioneer	<i>Ailanthus altissima</i>	Tree of Heaven
		<i>Fraxinus velutina</i>	Velvet Ash
Mesic	Secondary successional	<i>Acer negundo</i>	Boxelder
		<i>Celtis laevigata</i> var. <i>reticulata</i>	Netleaf Hackberry
		<i>Juglans major</i>	Arizona Walnut
		<i>Forestiera pubescens</i> var. <i>pubescens</i>	Desert Olive
		<i>Prosopis velutina</i>	Velvet Mesquite
		<i>Morus alba</i>	White Mulberry
Xeric	Pioneer	<i>Chilopsis linearis</i>	Desert Willow Singlewhorl
		<i>Hymenoclea monogyra</i>	Burrobrush
Xeric	Secondary successional	<i>Juniperus cf. monosperma</i>	Oneseed Juniper
		<i>Mahonia fremontii</i>	Fremont Barberry
		<i>Rhus trilobata</i>	Skunkbush Sumac
		<i>Ziziphus obtusifolia</i>	Lotebush

Table 3. Basal area for all woody species sampled at Verde River riparian sites, reported as weighted mean ( $\text{m}^2 \cdot \text{ha}^{-1}$ )  $\pm$  1 standard deviation.

Species	Campbell Ranch	Dead Horse Ranch	Otter Water
<i>Acer negundo</i>	<0.01 $\pm$ 0.01	0.05	<0.01 $\pm$ <0.01
<i>Ailanthus altissima</i>	<0.01 $\pm$ <0.01	0.23	<0.01 $\pm$ <0.01
<i>Alnus oblongifolia</i>	0	0.02	0
<i>Amorpha fruticosa</i>	0	0	<0.01 $\pm$ <0.01
<i>Baccharis salicifolia</i>	<0.01 $\pm$ 0.01	0	0.08 $\pm$ 0.04
<i>Baccharis sarothroides</i>	0	0	0.03 $\pm$ <0.01
<i>Mahonia fremontii</i>	0.03 $\pm$ 0.04	0	<0.01 $\pm$ <0.01
<i>Celtis laevigata</i> var. <i>reticulata</i>	3.34 $\pm$ 0.57	0.78	0
<i>Chilopsis linearis</i>	1.48 $\pm$ 2.10	0.30	0.67 $\pm$ 0.02
<i>Forestiera pubescens</i> var. <i>pubescens</i>	0.14 $\pm$ 0.14	0	0
<i>Fraxinus velutina</i>	4.87 $\pm$ 3.52	0.29	<0.01 $\pm$ <0.01
<i>Hymenoclea monogyra</i>	0	0	0.25 $\pm$ 0.07
<i>Juglans major</i>	1.21 $\pm$ 1.71	0.14	0
<i>Juniperus</i> cf. <i>monosperma</i>	0.03 $\pm$ 0.04	0	0
<i>Morus alba</i>	0	0.03	0
<i>Populus fremontii</i>	19.65 $\pm$ 22.01	17.71	3.62 $\pm$ 2.18
<i>Prosopis velutina</i>	0	0	1.25 $\pm$ 0.57
<i>Rhus trilobata</i>	<0.01 $\pm$ 0.01	0	0
<i>Salix exigua</i>	0	0	<0.01 $\pm$ <0.01
<i>Salix gooddingii</i>	1.38 $\pm$ 1.96	4.72	1.99 $\pm$ 2.11
<i>Tamarix ramosissima</i>	0.02 $\pm$ 0.03	0	0.13 $\pm$ 0.05
<i>Ziziphus obtusifolia</i>	0	0	0.07 $\pm$ 0.01

Table 4. Canopy cover, stem density, and (modified) importance values for common species Verde River riparian study sites, reported as weighted mean  $\pm$  1 standard deviation. Importance values are calculated as the average of relative stem density and relative basal area for each species. Species are sorted by descending order of Importance (averaged across sites).

Species	Canopy Cover (% cover)			Stem Density (stems*ha <sup>-1</sup> )			Importance Value (%)		
	Campbell Ranch	Dead Horse Ranch	Otter Water	Campbell Ranch	Dead Horse Ranch	Otter Water	Campbell Ranch	Dead Horse Ranch	Otter Water
<i>Populus fremontii</i>	13 $\pm$ 5	15	15 $\pm$ 5	72 $\pm$ 64	52	820 $\pm$ 735	33	42	31
<i>Salix gooddingii</i>	3 $\pm$ 4	11	8 $\pm$ 2	88 $\pm$ 125	106	278 $\pm$ 20	5	18	19
<i>Chilopsis linearis</i>	3 $\pm$ 5	<1	3 $\pm$ <1	562 $\pm$ 795	224	912 $\pm$ 146	14	13	7
<i>Celtis laevigata</i> var. <i>reticulata</i>	8 $\pm$ 2	6	0	354 $\pm$ 93	129	0	17	6	6
<i>Hymenoclea monogyra</i>	0	0	0	0	0	5362 $\pm$ 127	0	0	22
<i>Fraxinus velutina</i>	10 $\pm$ 8	2	0	205 $\pm$ 205	33	5 $\pm$ 7	17	2	1
<i>Ailanthus altissima</i>	0	3	0	0	231	3 $\pm$ 4	<1	10	3
<i>Prosopis velutina</i>	0	0	6 $\pm$ 5	0	0	126 $\pm$ 123	0	6	6
<i>Forestiera pubescens</i> var. <i>pubescens</i>	0	0	0	480 $\pm$ 151	0	0	8	0	0
<i>Juglans major</i>	<1 $\pm$ <1	1	0	17 $\pm$ 24	23	0	2	1	1
<i>Tamarix ramosissima</i>	0	<1	<1 $\pm$ <1	31 $\pm$ 44	0	184 $\pm$ 135	1	1	2



Table 5. Site-level canopy cover, basal area, and stem density at Verde River riparian sites, reported as weighted mean  $\pm$  1 standard deviation.

Site	Canopy Cover (%)	Basal Area ( $\text{m}^2 \cdot \text{ha}^{-1}$ )	Stem Density ( $\text{stems} \cdot \text{ha}^{-1}$ )
Campbell Ranch	37 $\pm$ 12	32 $\pm$ 27	2005 $\pm$ 709
Dead Horse Ranch	38	24	815
Otter Water	33 $\pm$ 8	8 $\pm$ 1	8671 $\pm$ 774

Table 6. Stem count by size class for common species at Verde River riparian study sites, reported as weighted mean (stems\*ha<sup>-1</sup>) ± 1 standard deviation. Common species are those with mean basal area >0.1m<sup>2</sup>\*ha<sup>-1</sup> at a minimum of one site.

Species	Site	31-50			
		0-10 cm	11-30 cm	cm	>50 cm
<i>Ailanthus altissima</i>	Campbell Ranch	2 ± 2	0	0	0
	Dead Horse Ranch	231	0	0	0
	Otter Water	2 ± 2	0	0	0
<i>Celtis laevigata</i> var. <i>reticulata</i>	Campbell Ranch	239 ± 25	44 ± 6	21 ± 8	0
	Dead Horse Ranch	89	40	0	0
	Otter Water	0	0	0	0
<i>Chilopsis linearis</i>	Campbell Ranch	389 ± 275	26 ± 18	5 ± 4	0
	Dead Horse Ranch	211	13	0	0
	Otter Water	909 ± 145	3 ± 1	0	0
<i>Forestiera pubescens</i> var. <i>pubescens</i>	Campbell Ranch	432 ± 109	0	0	0
	Dead Horse Ranch	0	0	0	0
	Otter Water	0	0	0	0
<i>Fraxinus velutina</i>	Campbell Ranch	117 ± 52	37 ± 18	2 ± 2	2 ± 2
	Dead Horse Ranch	21	12	0	0
	Otter Water	5 ± 7	0	0	0
<i>Hymenoclea monogyra</i>	Campbell Ranch	0	0	0	0
	Dead Horse Ranch	0	0	0	0
	Otter Water	5182 ± 381	0	0	0
<i>Juglans major</i>	Campbell Ranch	0.0	0	0	4 ± 3
	Dead Horse Ranch	23	0	0	0
	Otter Water	0	0	0	0
<i>Populus fremontii</i>	Campbell Ranch	3 ± 2	45 ± 32	11 ± 8	10 ± 7
	Dead Horse Ranch	0	14	0	38
	Otter Water	699 ± 692	132 ± 60	5 ± 7	0
<i>Prosopis velutina</i>	Campbell Ranch	0	0	0	0
	Dead Horse Ranch	0	0	0	0
	Otter Water	98 ± 102	26 ± 23	0	2 ± 2
<i>Salix gooddingii</i>	Campbell Ranch	36 ± 26	52 ± 37	0	0
	Dead Horse Ranch	57	66	18	0
	Otter Water	236 ± 59	32 ± 28	9 ± 13	0
<i>Tamarix ramosissima</i>	Campbell Ranch	31 ± 22	0	0	0
	Dead Horse Ranch	0	0	0	0
	Otter Water	184 ± 135	0	0	0

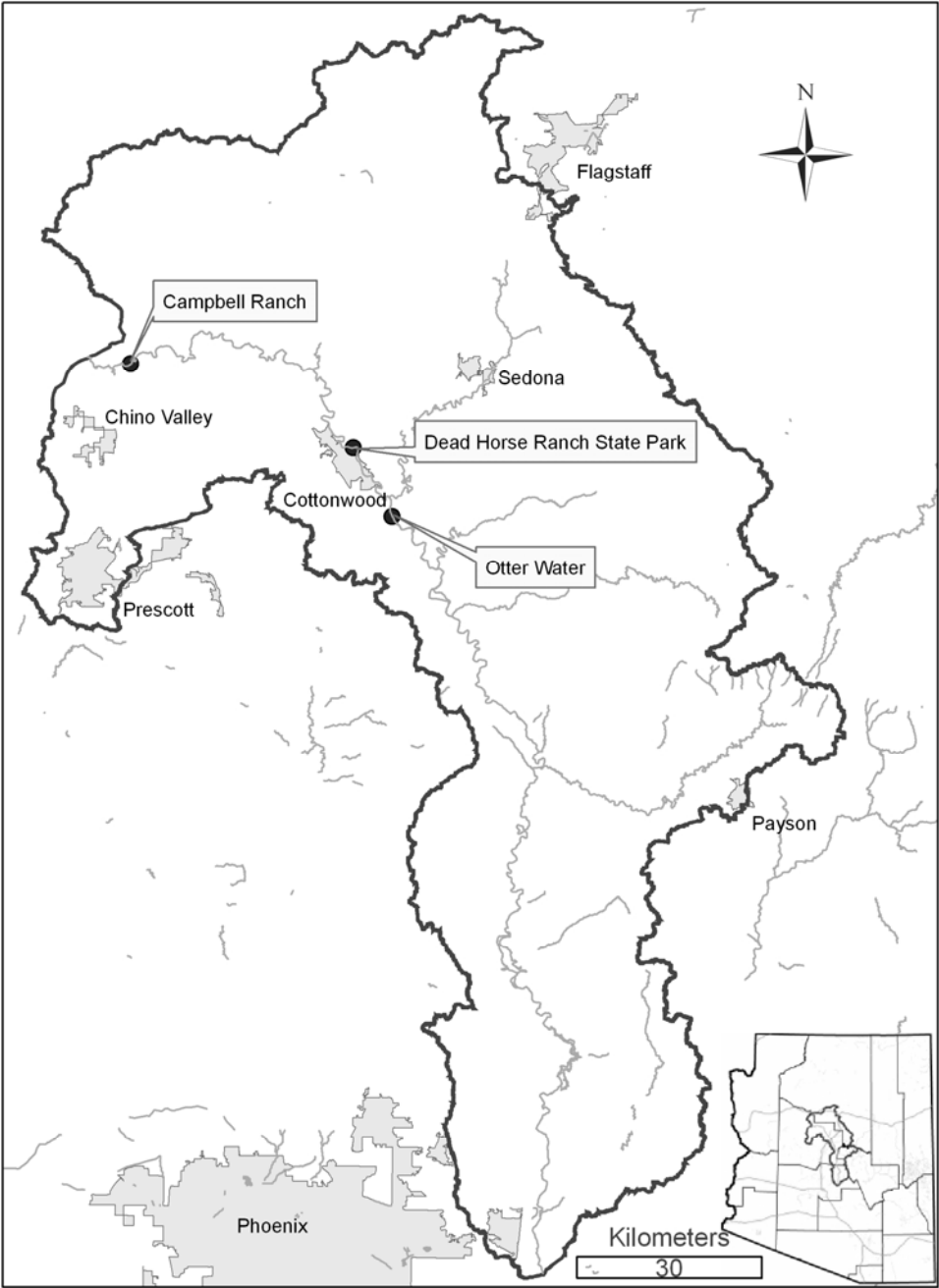


Figure 1. Project study sites in the context of the Verde River watershed.

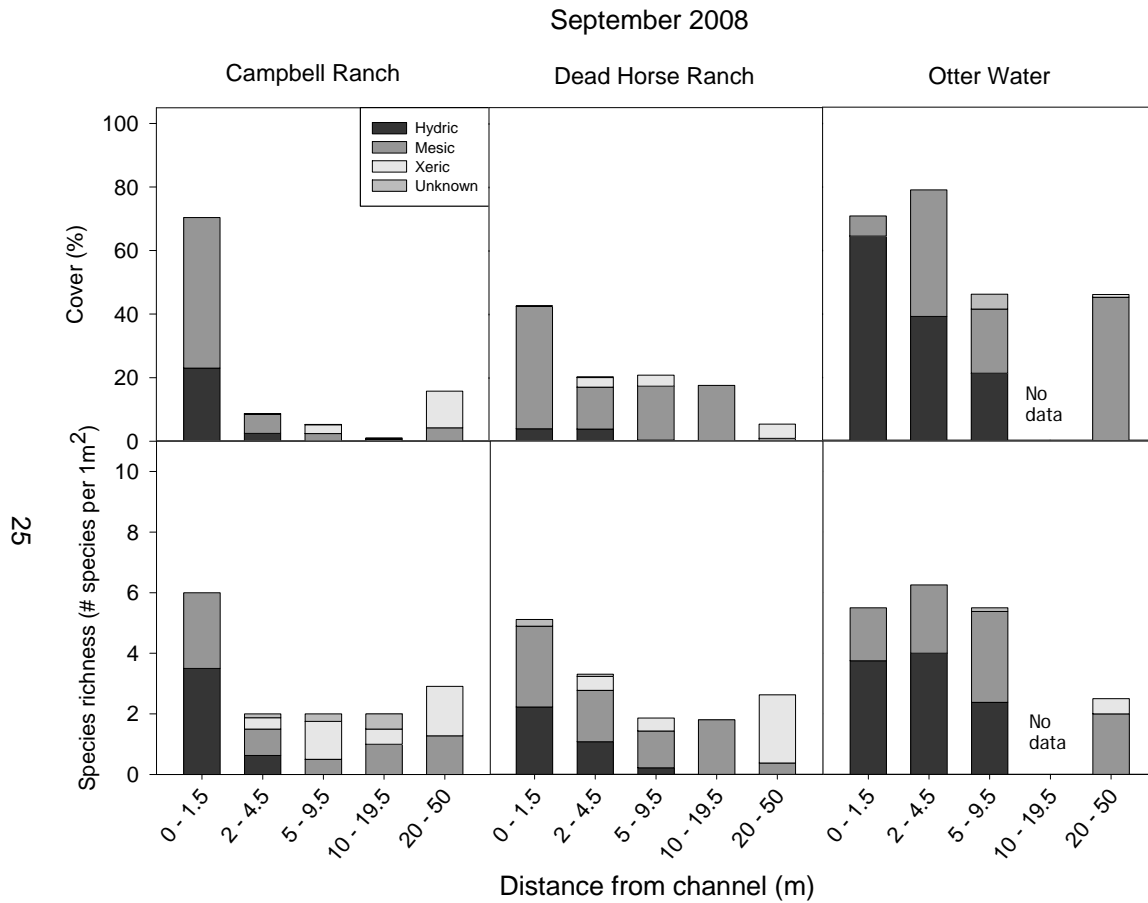


Figure 2. Changes in herbaceous cover and species richness, by functional group, as lateral distance from the Verde River low-flow channel increases. Data are shown for three sites, for September, 2008.

Low-flow channel zone, pre-monsoon season

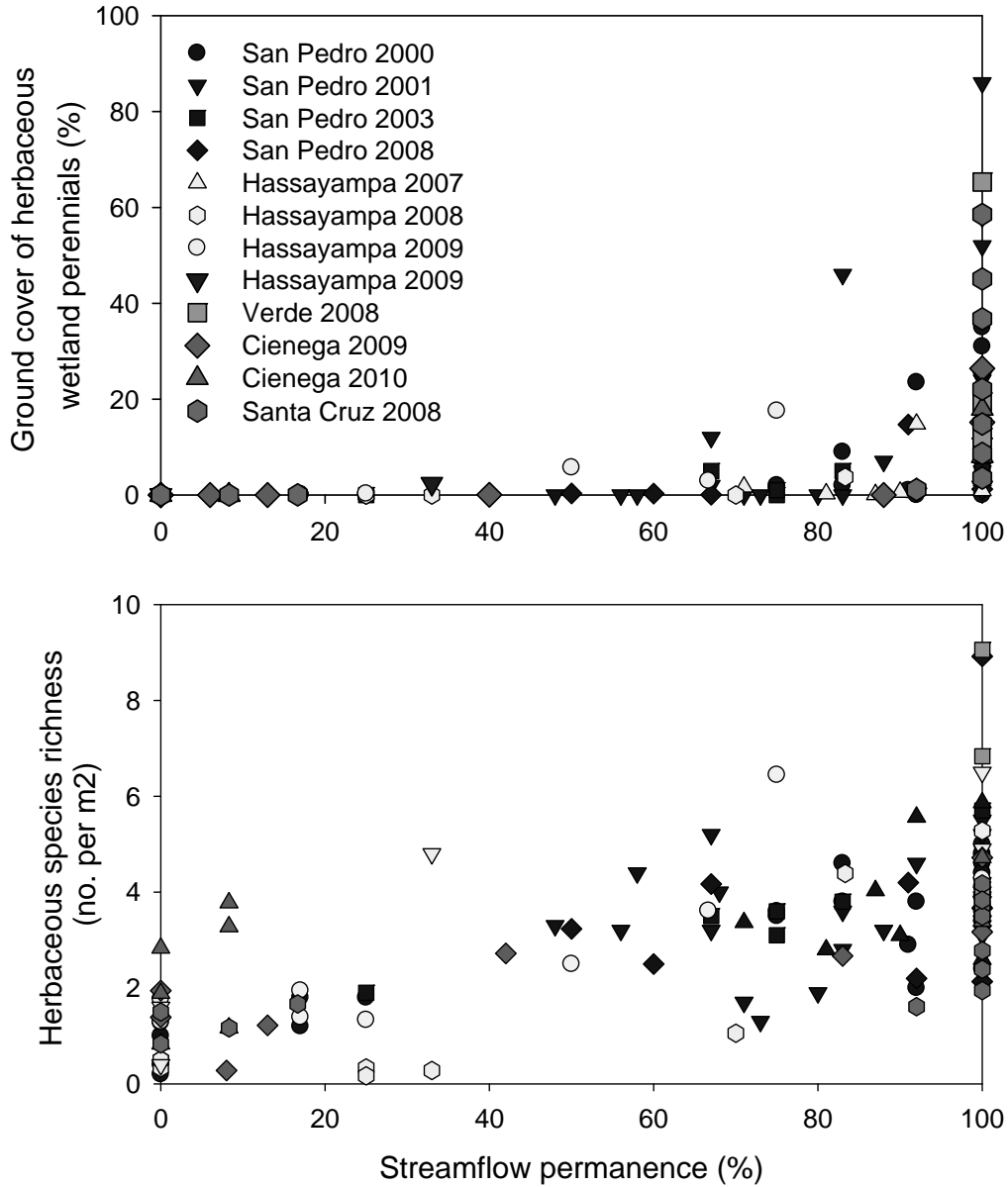


Figure 3. Cover of a drought-sensitive group of herbaceous plants (top figure) and richness of herbaceous species (bottom figure) in the low-flow channel/stream bank zone, in relation to the percentage of time surface flow is present at a site throughout the year. Data are from several rivers in central and southern Arizona, in multiple years. All data are for the pre-monsoon season. Each data point represents a study site.

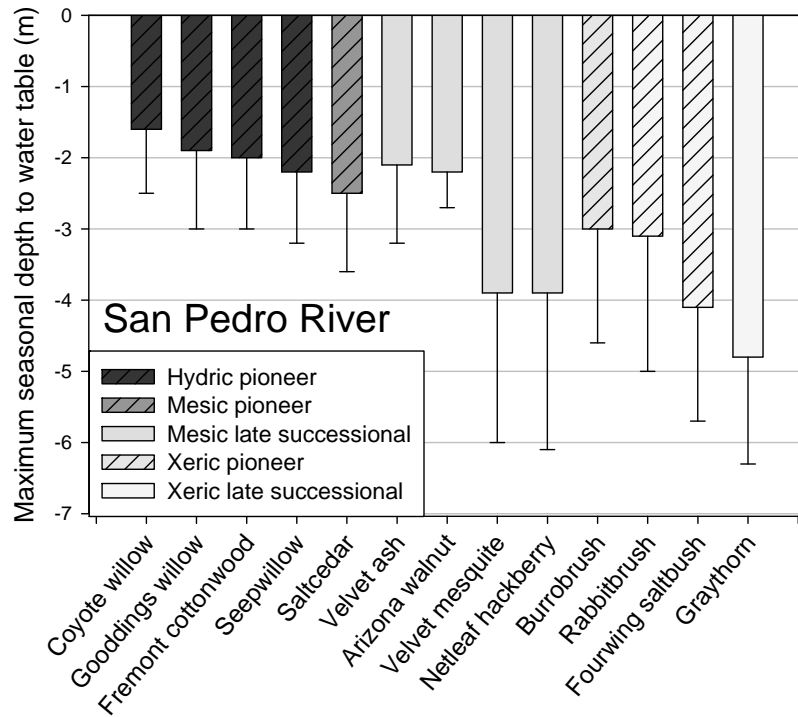
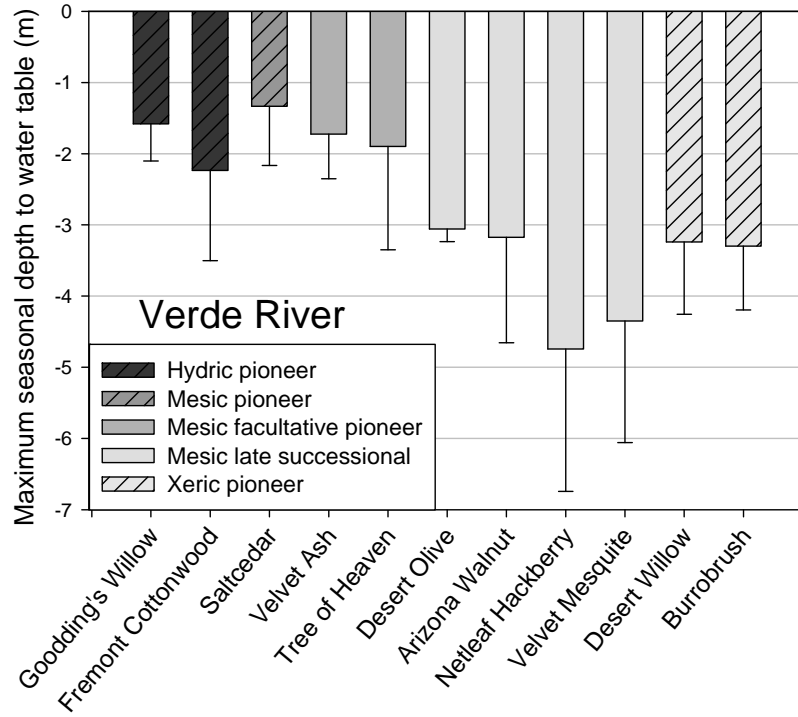


Figure 4. Average depth to water table for common floodplain trees and shrubs at the Verde River and San Pedro Rivers. Calculations for the species include a small number of plots on the river terraces. Bars represent one standard deviation.

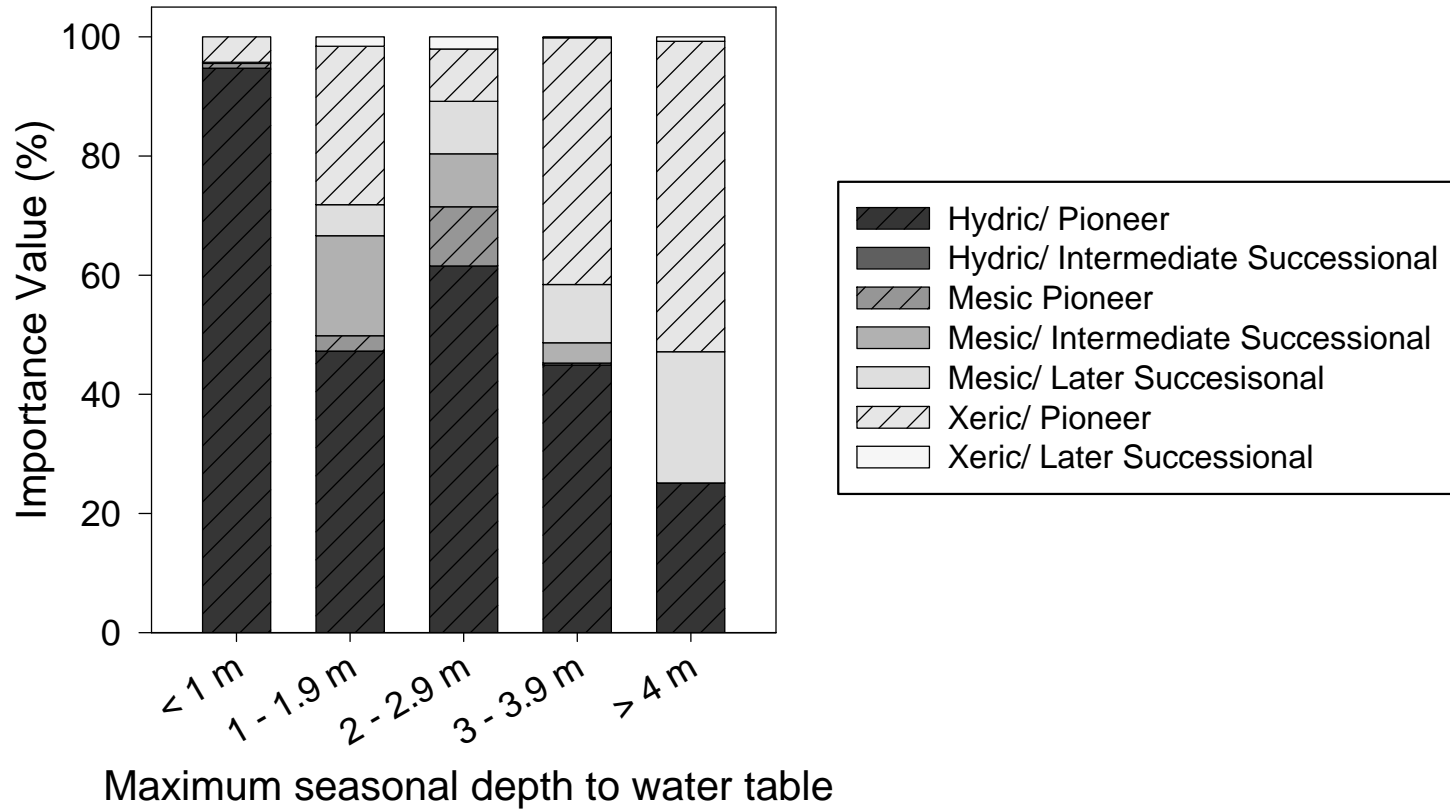


Figure 5. Relative "importance" of woody species, by functional group, in the Verde River riparian zone in relation to dry season depth to water table for the Verde River riparian zone. Importance values were calculated as an average of relative basal area, relative stem density, and relative canopy cover.

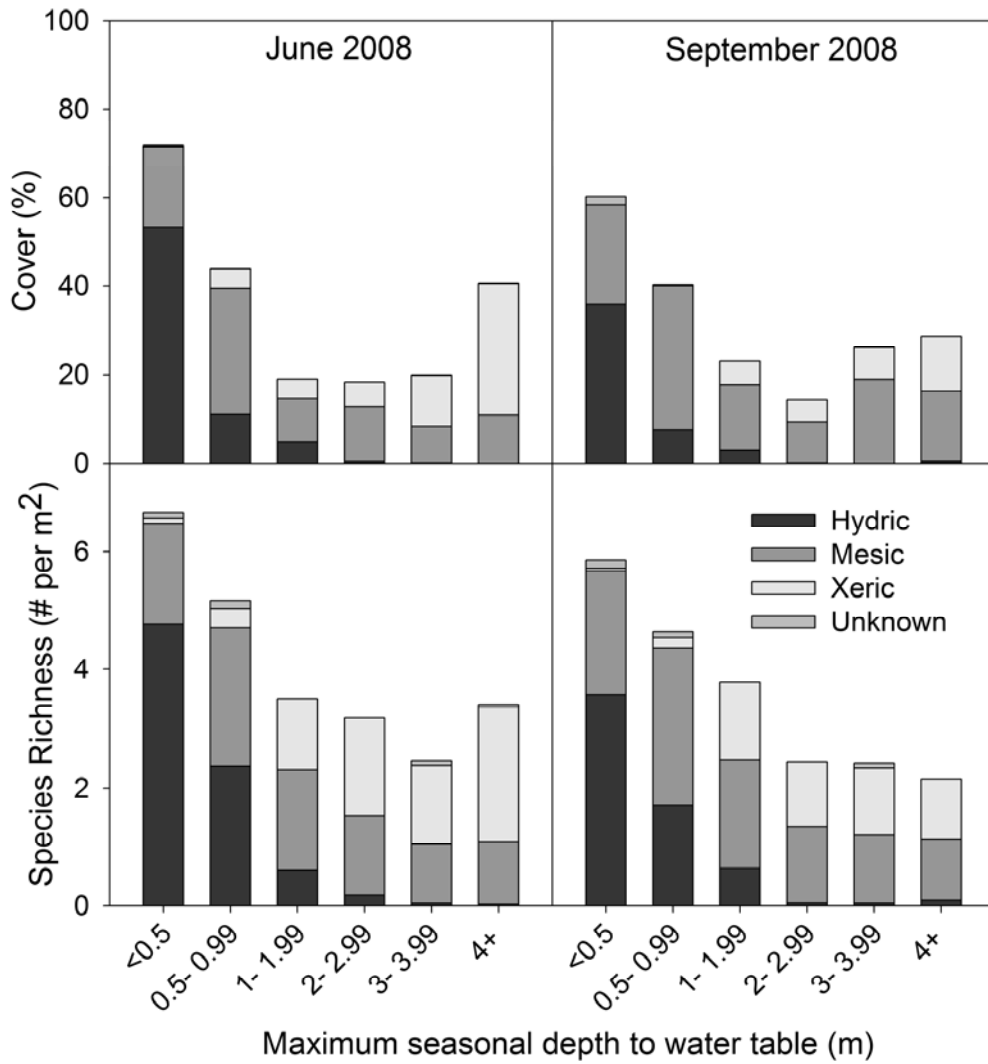


Figure 6. Changes in Verde River floodplain herbaceous cover and species richness by functional group as depth to the water table increases within the riparian zone.



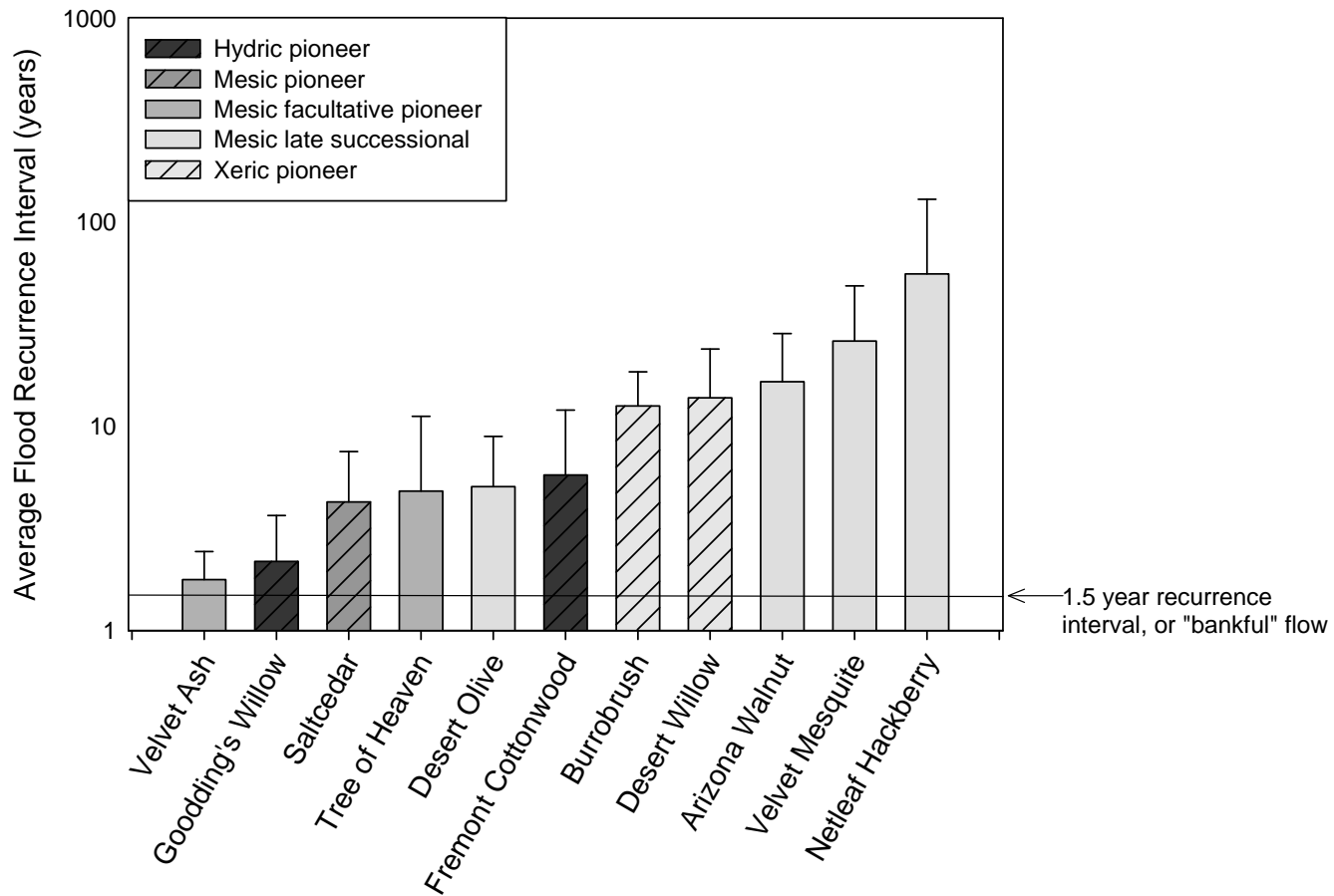


Figure 7. Average flood recurrence interval of patches containing eleven common species along the Verde River, weighted by the species' basal area in the patches. Error bars represent one standard deviation.

3. CAN YOU MEASURE A COMPETITOR- STRESS TOLERATOR- RUDERAL  
(CSR) STRATEGY? A TEST OF TWO METHODS FOR QUANTIFYING PLANT LIFE  
HISTORY STRATEGY

**Introduction**

Understanding the effects of a changing environment on plant communities has long been a goal of plant ecology (Clements, 1936; Cowles, 1899). Functional groups are an increasingly used tool for interpreting changes on a community level. There are numerous methods of classifying species into functional groups (Lavorel, McIntyre, Landsberg, & Forbes, 1997), and it is often appropriate to develop or tailor a method to a particular research question. However, in many cases it is desirable to use a standardized classification system. Standardized classification methods allow for comparison among studies and geographical areas. Also, widely used methods are more likely to be familiar to reviewers and general readers, allowing easier interpretation of study results.

One commonly cited functional group classification system, which strives for universality, is based on Grime's life history strategies (Grime, 1974, 1977). While Grime's system of classifying plant species as ruderals, competitors, or stress tolerators has not been without criticism (Austin & Gaywood, 1994; Oksanen & Ranta, 1992; Tilman, 1988), it has its merits as well. Grime's system divides environmental impacts on plants into stress and disturbance, which are respectively defined as conditions that prevent rapid growth and conditions that destroy plant biomass. The system is simple, easy to understand, and widely applicable. More than thirty years after its inception, it is still being used to understand changes in plant communities, particularly in Europe (Caccianga, Luzzaro, Pierce, Ceriani, & Cerabolini, 2006; Massant, Godefroid, & Koedam, 2009; Navas, Roumet, Bellmann, Laurent, & Garnier, 2010; Zelnik and Carni 2008).

Grime's system of classifying plant species into life history strategies—also known as CSR theory—is based on the concept of trade-offs. A plant cannot simultaneously maximize allocation to growth, reproduction, and maintenance. Species that allocate most resources to growth are competitors; species that use most of their carbon for maintenance are stress tolerators; and species that allocate most energy to reproduction are ruderals. These three strategies— competitor (C), stress tolerator (S), and ruderal (R)— form the acronym by which Grime's life history strategy theory is known. A species' life history strategy will place that species at an advantage in certain environments. CSR theory says that ruderals thrive in resource-rich, disturbed environments. Competitors thrive in resource-rich, undisturbed environments, and stress tolerators do best in resource-poor, undisturbed environments (Figure 8).

Although Grime developed this theory in the 1970s and has since published CSR scores for hundreds of species from the British flora (Grime, Hodgson, & Hunt, 2007), it was not until 1999 that he and his colleagues developed a classification procedure that was designed to be used worldwide (Hodgson, Wilson, Hunt, Grime & Thompson, 1999). Around the same time, Westoby (1999) published a simple method for describing plant strategies, also designed for worldwide use, which was also based on functional trade-offs, and loosely based on Grime's CSR regime as well. The method that Hodgson et al. (1998) developed uses seven easily measured plant traits to assign species to one of 19 categories (C, S, R, or one of 16 intermediate classes). Westoby's method uses 3 dimensional, log-scaled plots of 3 variables—specific leaf area, canopy height, and seed mass—to visualize species' strategies in relation to each other. Specific leaf area ("SLA") is intended to approximate stress tolerating ability; canopy height represents competitive ability; and seed mass approximates a ruderal score (Table 7).

Use of Hodgson et al.'s (1998) method has been surprisingly sparse, considering the ubiquity of Grime's theory in plant ecology and the fact that the method has been out for more than a decade. Only one study was explicitly designed to test the method's ability to classify plants in a non-British flora (Cerabolini et al., 2010), and this study also

took place in Europe. Westoby's (1999) method has been lightly used as well. Although the paper describing the method has been frequently cited, few studies have actually implemented the protocol and tested its ability to differentiate among species adapted to different habitat types (Golodets, Sternberg, & Kigel, 2009, Lavergne, Garnier, & Debussche, 2003).

Riparian plant communities in the North American Southwest lend themselves well to testing of Grime's CSR classification system. This is because plant community composition is strongly linked to levels of one primary resource (water) and one primary disturbance (flooding) (Bendix & Hupp, 2000; Friedman, Osterkamp, & Lewis, 1996; Lite, Bagstad, & Stromberg, 2005; Stromberg, Lite, & Dixon, 2010). Because the climate is arid to semi-arid, water is a major limiting resource. A sharp moisture gradient exists in Southwestern floodplains, with abundant soil moisture and shallow water tables adjacent to perennial streams, to extremely dry soils and deep water tables in the higher terraces and adjacent uplands. Similarly, floodplains are characterized by a gradient of flood frequency, with the lowest surfaces close to the stream channel inundated regularly and higher terraces inundated only by large floods with high recurrence intervals (i.e. long periods of time between floods).

The question driving this study is whether functional group classification systems can cross ecoregions. We approach the question by (a) testing the efficacy of two published "universal" PFG classification methods on herbaceous plants found in arid and semi-arid riparian ecosystems of the U.S. Southwest, and (b) determining which functional traits are most informative in explaining a plant's strategy in the same ecoregion and comparing the results to the claims made by the two "universal" methods of PFG classification. This research assumes that if a method was successful, or a functional trait informative, it would vary with environmental conditions at the community level, in the manner predicted by the literature.

## **Methods**

### **Study area**

The study area was the riparian zone of the Verde River in central Arizona, USA. Data were collected at three study sites in the upper and middle reaches of the Verde River (Table 8). The climate is semi-arid, with an average of 14.4 inches of precipitation per year at nearby Montezuma Castle in Camp Verde, AZ (30-year average; Western Regional Climate Center, 2010). The mean annual daily maximum temperature is 81.2° F, and the mean annual daily minimum temperature is 43.6° F (30-year average; Western Regional Climate Center, 2010).

### **Approach**

To test whether functional group classification systems can cross ecoregions, this study measured functional traits for herbaceous species in a riparian plant community and used the measurements to classify the species according to two "universal" classification systems. At the same time, data were collected on species abundance and microhabitat characteristics so that correlations could be drawn between the classification results, the functional trait measurements, and the microhabitats where the plants grow. Microhabitat characteristics (or environmental variables) were selected to represent the two axes of disturbance and resource availability that serve as the basis for Grime's life history trait scheme. Data were collected at two times within the growing season. The June data set captured the springtime plant community and environmental conditions three months after a moderately-sized snowmelt flood; the September data set captured the late summer, post-monsoon plant community, and environmental conditions two weeks after a small monsoon flood which affected 17% of quadrats.

### **Species Selection and Environmental Data Collection**

Species were selected and environmental data collected by sampling two to four cross-floodplain transects at each of three sites along the Verde River during June and September of 2008. Twenty to twenty-five systematically-located 1m<sup>2</sup> plots were sampled along each transect. Ten plots per transect were clustered near the channel,

where flood and moisture gradients are sharp, and the remaining plots were evenly distributed across the rest of the transect. Herbaceous cover by species (using modified Braun-Blanquet cover classes) was recorded for each plot (Braun-Blanquet 1932, p. 32). Unknown plants were identified using Kearney and Peebles (1960) and nomenclature updated according to the USDA PLANTS database (U.S. Department of Agriculture, 2011). All herbaceous species that appeared in these plots, minus the rare species, were used for plant classification. Rare species were defined as those that appeared in only one plot with a cover of less than 5%, or in only two plots with a cover of less than 1%. Plant traits were collected for 76% of the 119 sampled Verde River herbaceous species.

Resource availability was captured by measuring six environmental variables at each plot: soil moisture, depth to groundwater, soil nitrate and ammonium, available phosphorus content in the soil, and percent overstory cover. Soil moisture for each plot was determined by gravimetric analysis on a sample of the top 2 cm of soil. Overstory cover (a surrogate for level of light reaching the understory vegetation) was measured using a spherical densitometer. To determine groundwater depth, two to four piezometers were installed at each site and equipped with pressure transducers which were used to measure depth to groundwater every 15 minutes for one year. Each transect was surveyed using transit and survey rod to determine relative plot and well elevations. Depth to groundwater for each plot was calculated by interpolating the level of the water table among the wells and the stream thalweg.

Disturbance level was captured by determining flood inundation frequency, time since the most recent flood, and shear stress during the most recent large flood, for each plot. Inundation frequency was calculated using stage-discharge relationships in conjunction with flood recurrence intervals. A stage-discharge relationship was calculated for each transect using surveyed cross-section data and Manning's equation  $V = (1/n) R^{2/3} S^{1/2}$  modified by the relationships  $R = AP^{-1}$  and  $Q = AV$ , where  $V$  = cross-sectional average stream velocity,  $A$  = cross-sectional area of flow,  $R$  = hydraulic radius,

$S$  = water surface slope,  $P$  = wetted perimeter of the channel, and  $Q$  = stream discharge (Manning, 1891). Manning's  $n$  (roughness coefficient) values were selected for each geomorphic surface of the floodplain by referencing published values for the Verde River (Beyer, 1997), consulting experts, and back-calculating for the surveyed heights and discharges of the few floods that occurred on the Verde River during the study. Flood discharge data were obtained from the USGS National Water Information System Web Interface (U. S. Geologic Survey, 2011). Stage-discharge relationships were calculated in Microsoft Excel (Microsoft Corporation, 2001). Flood recurrence intervals were calculated using the software PKFQWin version 5.2 (U. S. Geologic Survey, 2007), which fits annual peak flow data to a log-Pearson's type III distribution. The flood record was used from the closest gauge to each site (Table 9). The discharge necessary to inundate each plot was determined using stage-discharge relationships. Each plot was then assigned a flood recurrence interval based on the output of PKFQWin.

Time since the most recent flood was determined by examining the flow record for the stream gauge nearest to each site to determine of the date of the last flow greater than the discharge corresponding to the elevation of each plot.

Boundary shear stress for the largest flood of the past winter (January 2008; 137 cubic meters per second at the Clarkdale gauge) was calculated for each plot, using  $T_b = \rho ghS$ , where  $\rho$  = density of water ( $1000 \text{ kg}\cdot\text{m}^{-3}$ ),  $g$  = acceleration due to gravity ( $9.8 \text{ m}\cdot\text{s}^{-2}$ ),  $h$  = depth of water over the study plot during the flood peak (in meters), and  $S$  is the slope of the water surface.

### **Plant Trait Data Collection**

Plant functional traits were measured on plants collected from the Verde River riparian zone and from surrounding uplands. In most cases, traits were measured on three individuals of each species (Table 10). Traits were measured on relatively large, healthy-appearing individuals. All plant traits necessary to classify species according to the Hodgson et al. (1998) and Westoby (1999) methods were measured.

## **Classifying Species**

Species were classified using spreadsheets provided by Hodgson et al. (1998). The spreadsheet accepts values for the variables for each species and uses regression equations and transformations to calculate a C-, S-, and R-score for each species. The scores are standardized to a scale that ranges from -2 to +2. Each species is assigned to a functional type (C, S, R, or one of 16 intermediate types), based on similarity of calculated scores with the pre-determined C-, S-, and R-scores for each of the functional types. A separate set of equations are used for graminoid and non-graminoid herbaceous species.

Results are reported as the number of taxa assigned to each life history strategy. Results are also reported as the number of annual vs. perennial and monocot vs. dicot taxa that were assigned to each strategy.

Westoby's (1999) leaf-height-seed ("LHS") plant strategy scheme is a primarily visual analysis in which species are compared to each other rather than assigned labels. The method calls for plotting specific leaf area, plant height, and seed mass on a three-dimensional plot with a log scale for each axis. To examine results of the LHS scheme on a community level, taxa were plotted according to instruction in Westoby (1999), then coded according to basic phylogenetic and life history groups (monocot vs. dicot, and annual vs. perennial).

## **Testing the Methods' Efficacy**

Spearman non-parametric correlation analysis was used to test whether the two classification methods detected patterns in resource availability and disturbance levels in the plants' environment. A non-parametric test was selected because many environmental variables and the results of the classification analysis did not meet assumptions of normality and homoschedasticity, and could not be transformed to meet those assumptions. Environmental variables were used in the form of species-level averages (i.e. the average environmental condition present in plots occupied by a given species). In order to ensure that the environmental conditions calculated for each



species were representative of the species' habitat requirements, this analysis was limited to species that occurred with at least 5% cover in a minimum of three plots. Analysis was done using the program R (The R Foundation for Statistical Computing, 2009).

### **Analyzing the Classification Methods: Determining which Variables Work**

To determine which functional traits contribute to the efficacy of the classification methods, Spearman analysis was used to search for correlations between functional traits and environmental variables.

## **Results**

### **Classification Results**

**Hodgson et al. (1998).** A total of 91 Verde River taxa were classified according to the two functional group classification methods (Appendix A). According to the Hodgson et al. (1998) CSR method, the suite of species selected for this study was dominated by plants with strategies intermediate between competitor and ruderal (Table 11; Figure 9). Few species were classified as ruderals, stress tolerators, or intermediate between those strategies. Monocots were more likely than herbaceous dicots to be classified as stress tolerators or intermediate between stress tolerator and competitor (Table 11). Dicots, on the other hand, were more likely to be classified in near-ruderal strategy types. Monocots had higher S-scores and lower R-scores than dicots (Figure 10). Annuals were less likely than perennials to be classified into a competitor strategy (Figure 10).

**Westoby (1999).** For the 91 taxa analyzed according to Westoby's (1999) scheme, values for specific leaf area ranged from  $5.5 \text{ mm}^2\text{mg}^{-1}$  to  $66.0 \text{ mm}^2\text{mg}^{-1}$ . Plant height ranged from 5.7 cm to 305.0 cm. Seed mass ranged from 0.01 mg to 102.4 mg. Because three-dimensional graphs viewed on a two dimensional surface are difficult to interpret, three graphs were constructed, each with two axes, in order to display the variables in all possible combinations. Visual analysis of the figures does not present any

obvious separation between annual and perennial plants for the three functional traits (Figure 11).

### **Model Efficacy**

**Hodgson et al. (1998).** Because this analysis was limited to species that occurred with at least 5% cover in a minimum of three plots, the classification results of 14 species from the June data set and 15 species in the September data set were correlated with the environmental variables. At an alpha level of 0.10, the Hodgson et al. (1998) C-score correlated with June levels of two resource-related habitat variables—soil moisture (a positive correlation) and maximum depth to groundwater (a negative correlation) (Table 12). The C-score also negatively correlated with one disturbance-related microhabitat variable in June—time since the most recent flood. In September, the C-score correlated with only one environmental variable—maximum depth to groundwater (Table 13). The Hodgson et al. S-score and R-score did not significantly correlate with any environmental variable in June or September.

Raw C-, S-, and R-scores are the results of the Hodgson et al. (1998) classification method prior to the final standardization of the scores to increments of 0.5 from -2 to 2. Because these unstandardized scores have higher resolution, they can be expected to produce more accurate results in a non-parametric analysis, where ties in data point ranks create problems. Raw C-scores from the June data set significantly correlated with two resource-related variables, soil moisture (positive) and depth to groundwater (negative) (Table 12). The raw C-score also correlated with all three disturbance-related environmental variables in June—flood recurrence interval (negative), time since the most recent flood (negative), and shear stress experienced by the species during the most recent large flood (positive). In September, the raw C-score did not correlate with any habitat variables (Table 13). In June, the raw S-score positively correlated with one disturbance-related variable, shear stress during the most recent large flood. In September, the raw S-score did not significantly correlate with any environmental variable. There were no significant correlations between the raw R-score

and any of the habitat variables in June. In September, the raw R-score correlated negatively with soil moisture and positively with depth to groundwater—both resource-related variables. The raw R-score also correlated with two disturbance-related variables in September—flood recurrence interval and time since the most recent flood. Both of those correlations were positive.

**Westoby (1999).** Like the analysis of the efficacy of the Hodgson et al. (1998) method, this analysis was limited to 14 taxa from the June data set and 15 taxa from the September data set. At an alpha level of 0.10, specific leaf area correlated positively with one resource-related variable—percent overstory cover—in both June and September (Table 14). Specific leaf area (“SLA”) did not correlate with any disturbance-related variables in either month. In June, plant height correlated negatively with two resource-related variables—percent overstory cover and depth to groundwater. Also in June, plant height correlated negatively with two disturbance-related variables—flood recurrence interval and time since flood. There were no significant correlations between plant height and any environmental variables in September. Seed mass significantly correlated with only one microhabitat variable—there was a positive correlation between seed mass and percent silt in the soil—in September only.

#### **Determining which functional traits work**

Of the functional traits used in the two life history strategy schemes, only flowering period lacked any correlation in both June and September with the microhabitat variables that were measured in this study (Tables 15, 16). Of the remaining plant functional traits, most differed between the seasons in their correlations. Correlations between the environmental variables and the three functional traits used in Westoby's (1999) scheme are summarized in the previous section. Besides specific leaf area, used in the Westoby method, two other variables reflecting leaf characteristics were measured. Leaf dry matter content, a measure of the amount of water in a healthy leaf of that species, correlated with soil clay content in June, and did not correlate with any habitat variables in September. Leaf dry mass correlated with two resource availability variables

(soil clay content and soil moisture) and two disturbance related variables (flood recurrence interval and time since flooding) in June, and did not correlate with any habitat variables in September.

Month of flowering start correlated negatively with soil silt content in September, and correlated with nothing in June (Tables 15, 16). Lateral spread also failed to correlate with any environmental variables in June. It negatively correlated with soil silt content and soil moisture in September.

## **Discussion**

### **Success of Hodgson et al. (1998)**

This study investigated whether plant functional group classification systems can cross ecoregions. The question was addressed by testing two proposed-as-universal functional group schemes on a cross-section of a dryland riparian plant community during the early and late growing season. After classifying the riparian taxa according to the functional group classification schemes, results were correlated with microhabitat characteristics in order to determine whether the strategy assigned to each taxon reflected its growing conditions.

Neither functional group classification scheme was a resounding success. Within the Hodgson et al. (1998) method, only the equation that calculates competitive ability produced the expected correlations with habitat. Species classified as having high competitive ability were more likely to be found where soil moisture is high and groundwater is shallow. This is consistent with CSR theory, which predicts that competitors thrive where resource levels are high. In arid regions, water is a primary limiting resource for plants. CSR theory also predicts that competitors will occur where disturbance levels are low; results of this study do not support that claim, as taxa assigned high C-scores occurred where flooding was more recent and intense. However, in floodplains, moisture levels are highly correlated with disturbance levels, a fact that confounds the results of this study.

The Hodgson et al. (1998) method was much less successful at predicting stress tolerating ability and ruderality than it was at predicting competitive ability. Plants classified as having high stress-tolerating ability were more likely to occur where shear stress was high during the most recent large flood. Though it is labeled as a type of stress, in this case high shear stress refers to a high level of disturbance, not stress, to the plant. This relationship is counter to CSR theory, which states that stress tolerators will grow in habitat that experiences little disturbance and low resource levels.

CSR theory states that ruderal plants will grow where disturbance and resource levels are high. However, in this study, taxa classified as ruderal were more likely to grow where moisture levels were low and disturbances infrequent. This, too, is counter to the results that would be expected by CSR theory.

### **Success of Westoby (1999)**

Specific leaf area, the leaf trait that Westoby (1999) chooses to use in his leaf-height-seed scheme, is related to potential relative growth rate (potRGR) and a species' ability to respond to periods of high resource availability with rapid growth (Poorter, Niinemets, Poorter, Wright, & Villar, 2009; Wright et al., 2004). Plants with high SLA grow larger, "cheaper" leaves that have a shorter life span than those with low SLA. Leaves with high SLA often have higher water content as well. On the other hand, taxa with low SLA produce leaves that are longer-lasting and more "expensive" to produce, often containing defensive or protective chemicals or structures (Craine 2009, Poorter et al., 2009). Strategically, high SLA is associated with a plant's ability to compete in high resource environments and low SLA is associated with a species' ability to persist in stressful environments. In the Verde River floodplain, plants with low SLA grew in full sun, and plants with higher SLA grew in the shade. If overstory cover (a surrogate for amount of light reaching a plant) is interpreted as a resource-related environmental variable, then the positive correlation it has with SLA in both June and September is counter to theories put out by Westoby (1999) and Hodgson et al. (1998) However, if full sun conditions are interpreted as stressful, then the relationship between SLA and

overstory cover is consistent with theory. This interpretation is also supported by the fact that low SLA has often been associated with open canopy environments (reviewed by Westoby, Falster, Moles, Vesk, & Wright, 2002).

While the correlation between shade and SLA is strong and persists throughout the growing season, it is also important to note that SLA did not correlate with any variable designed to capture moisture level, the system's primary limiting resource. In that respect, the LHS scheme is unsuccessful in representing a significant axis of environmental variability present in this ecoregion. However, the SLA-overstory relationship is potentially telling; perhaps shade or some unmeasured habitat characteristic related to shade is more important than soil moisture in aridland riparian ecosystems.

Westoby (1999) interprets plant height as a component of the R (ruderal) axis, in as much as it represents the stage of succession during which a species is adapted to be most successful. By his interpretation, shorter plants are adapted to early successional stages, and taller plants are adapted to later successional stages. Westoby also acknowledges Grime's interpretation of plant height as reflecting resource availability, or the CS axis. In the Verde River floodplain, tall plants grow where there is little overstory cover, shallow groundwater, and relatively recent flooding. These relationships only hold in June, however; in September, three weeks after a monsoon flood, plant height does not correlate with any environmental variables. This supports Grime's interpretation of plant height as a CS variable. If taller plant height is an adaptation for competition in favorable, stable environments, providing an advantage in situations with high resource availability (e.g. lots of light and water), it is consistent with CSR theory that the relationship would fall apart once a disturbance occurred. If Westoby's interpretation of plant height as a disturbance- or succession-related trait applied to this situation, there would have been a positive, not negative, relationship between flood recurrence interval and plant height.

The third plant functional trait in Westoby's (1999) scheme, seed mass, is proposed as representing a trade-off between the ability to survive stressful conditions as a seedling and greater opportunity for dispersal to favorable germination sites. In the Verde River floodplain, this functional trait correlated with only one environmental variable, soil silt content, in September only. This relationship is both intuitive and supported by the literature. In floodplains, soil silt may be high where low velocity flood waters have deposited sediment (as opposed to high velocity flow which would scour away sediment and vegetation). Seedlings from larger seeds have been shown to be more likely to germinate and better survive the stress of sediment deposition compared to those of small seeded species (Hodkinson et al 1998; Stromberg, Butler, Hazelton, & Boudell, in press; Xiong, Nilsson, Johansson, & Jansson, 2001).

#### **Applicability of Other Plant Functional Traits Used in Hodgson et al.'s Scheme**

In addition to specific leaf area, the Hodgson et al. (1998) CSR scheme used two other leaf-related functional traits: leaf dry matter content and leaf dry mass. At least one of these leaf traits is included in the calculation for each of the three axes (C, S, and R). Physiologically, the leaf characteristics are related to leaf longevity and plant productivity, or potRGR (Reich, Walters, & Ellsworth, 1997; Wright et al., 2004). Leaf dry matter content, in particular, is inversely related to specific leaf area and has been considered substitutable for SLA when attempting to quantify a species' position on the resource use axis (Wilson, Thompson, & Hodgson, 1999). Leaf dry mass is the denominator for specific leaf area, and is infrequently used as a functional trait. Niinemets et al. (2007) make the point that leaf mass is functionally significant because, in addition to larger leaves representing a proportionally larger resource investment, large leaves require disproportionately greater investment in support structures (e.g. stronger stems and petioles). Based on that logic, it is clear that a plant would only produce large or heavy leaves if it was adaptively advantageous. What precisely that adaptive advantage would be depends on whether the leaf mass is greater due to leaf area, thickness, or density. It is because of this variety of options that SLA (which takes into account leaf area as well

as dry mass) is considered more informative than leaf mass for predicting a plant's strategy. Interestingly, leaf dry mass correlated with more microhabitat variables than the other two leaf trait variables in this study. In the Verde River floodplain, taxa with higher leaf dry mass grow where soil moisture is high, groundwater is shallow, and floods are both frequent and recent. This relationship weakened substantially between June and September, suggesting that leaf dry mass predicts a strategy related to drought tolerating ability rather than flood tolerance.

Leaf dry matter content negatively correlated with only one variable—soil clay content—in June only. This relationship can be interpreted a moisture gradient; soil clay content and soil moisture are positively correlated in this data set (Appendix B). Verde River floodplain soils are high in sand, so soils at the high end of the clay content are loams and sandy loams. These soils are not so high in clay that the water content is unavailable to plant roots. Rather, the loams and sandy loams remain moist longer than the lower-clay sands elsewhere in the floodplain.

Unlike the leaf traits, lateral spread reflected microhabitat characteristics in September, after the monsoon flood, and not in June, before the flood. While Hodgson et al. (1998) includes lateral spread only in the equations for calculating C- and S-scores, the strengthening of this variable's negative relationship with silt and soil moisture levels after the flood suggests that in the Verde River floodplain, lateral spread is related to disturbance response. In the literature, lateral spread is associated with competitive ability as well as tolerance of disturbance, with plants of greater lateral spread, particularly those that spread clonally, being more successful in later successional, resource-rich environments (Prach and Pysek, 1994; Sammul, Kull, Niitla, & Mols, 2004). Results of this study concur, as species with greater lateral spread were more common in areas with low soil moisture and low silt content; these sites would correspond to unflooded areas.

Two variables related to flowering phenology were included in Hodgson et al.'s (1998) regression equation for calculating the R-score. Duration of flowering was



included in both the graminoid and non-graminoid equations; this phenological variable appears not to be pertinent in the Verde River floodplain, as it failed to correlate with any microhabitat characteristics. Start of flowering was only used in Hodgson et al.'s R-score equation for graminoids, not herbaceous dicots, and, interestingly, the relationship was positive, with later flowering start corresponding to more ruderal plants. On the Verde River floodplain, start of flowering negatively correlated with overstory cover in June and positively with soil silt content in September. In particular, the September relationship is consistent with Grime's predictions and intuitive to this ecoregion; if silt content is higher in areas that were flooded, late-flowering ruderals should be colonizing areas with high silt content just after a monsoon flood.

### **A Universal system**

The literature on plant functional traits largely supports the existence of an axis of resource capture, use, and release, also described as "leaf economics" (term coined by Wright et al., 2004). This gradient has been demonstrated in a variety of ecoregions as well as through global synthesis (Diaz et al., 2004; Garnier et al., 2004; Reich et al., 1997). Physiologically, this axis reflects a species' potRGR. Ecologically, the axis reflects a species' ability to thrive in stressful environments or compete in resource-rich environments. In some cases, it also reflects a species' ability to thrive in earlier or later successional environments. Morphologically, a species' position on this axis is reflected in traits related to the size, shape, density, and water content of leaves. Other plant functional traits have been reported as correlated with potRGR are maximum canopy height and onset of flowering (Golodets et al., 2009; Kyle & Leichman, 2009; Sun & Frelich, 2011). Results of this study support the existence of this axis of resource use, in that plant height and several leaf characters correlated—in the expected manner—with the microhabitat conditions in which the species grew.

Beyond the primary functional axis of resource use, there is no clear consensus as to additional "universal" gradients or axes of plant specialization. Analyses of functional trait data sets have produced varying answers as to the identity of the

secondary axis of specialization. Diaz et al. (2004) point to plant size as the secondary gradient, with plant height, leaf area, seed mass, and plant woodiness all positively correlated along Axis 2 of a principal components analysis. Laughlin, Leppert, Moore, and Steig (2010) report a second axis of seed mass and specific root length just behind the primary axis of leaf economics. In a test of Westoby's (1999) LHS functional group scheme along a gradient of grazing pressure, Golodets et al. (2009) found only one axis of variation in plant traits. High SLA was associated with high grazing pressure at one end of the axis, and at the other end of the axis, high seed mass and canopy height were associated with protection from grazing. Kyle and Leichman (2009) also found a correlation between SLA and plant size traits on the first axis, and identified a second axis that correlated with life span and vegetative spread.

Grime proposes the disturbance or ruderal gradient as the second axis of plant specialization, but the traits that define a disturbance-adapted plant are not always clear. The Hodgson et al. (1998) method measured a plant's "ruderality" based on its degree of association with vernal ephemerals, with the idea that spring annual plants exemplify the "ultimate" ruderal strategy. However, the functional traits that were included in the R-score regression equation in that same paper do not reflect the functional traits of annual lifespan or vernal phenology. Life span is not part of the R-score equation, and start of flowering is included only in the graminoid equation, with a relationship of late flowering grasses being considered more ruderal. Furthermore, this phenological definition of ruderal plants from Grime's (1974, 2007) and Hodgson et al.'s work does not apply in all ecoregions; for example, in the part of the American Southwest where this study was done, annuals germinate and complete their life cycle in response to pulses of moisture, which arrive in two distinct seasons: spring with rain and snowmelt runoff, and late summer with monsoon rains.

Craine (2009) describes Grime's ruderals as possessing the same functional traits as his competitors, except with an annual life span. However, disturbance tolerance is more complicated than is presented in Grime's CSR triangle. Multiple

strategies exist for thriving after a disturbance, including rapid regeneration, both from seed and vegetatively, and adaptations for tolerating the disturbance (Bond & Midgley, 2001, Klimesova & Klimes, 2007).

Results of this study do not support a clear second axis of plant specialization. Grime's hypothesis of disturbance adaptation as the second axis was certainly not supported; after a monsoon flood, plants with high R-scores were more likely to grow in unflooded environments, and the only plant functional traits that correlated with the disturbance level were clearly associated with the primary "leaf economics" gradient.

### **Self-Reflection**

Two major flaws in study design impair the ability of this study to answer the research question in a clear and elegant manner. First, the resource and disturbance gradients were too tightly coupled to tease out the effect of each on functional trait variability. In order to truly capture the effect of both gradients while still working in dryland riparian ecosystems, it would be necessary to extensively sample outside the floodplain, in areas of high disturbance/ low resource levels and low disturbance/ high resource levels. Second, not enough habitat data were collected for each species. This led to the unforeseen necessity of reducing the sample size of species from 91 to 14 -15 when seeking correlations with environmental variables. Rather than approaching the question from a whole community perspective and systematically sampling the study area, it would have been more efficient and informative to select a subset of locally dominant species for measuring both plant functional traits and associated habitat characteristics.

Table 7. Plant functional traits used in Westoby's (1999) LHS scheme and the strategies they are intended to represent.

Trait	Trade-off for	Grime equivalent
Specific leaf area	Growth rate vs. leaf lifespan	C-S axis
Plant height at maturity	Early successional success vs. late successional success	C-R axis
Seed mass	Colonization vs. establishing in stressful conditions	C-R axis S-R axis

Table 8. Study sites along the Verde River in central Arizona.

Site	Location	Ownership	Elevation (m)
Campbell Ranch	Near Paulden, AZ	Arizona Game and Fish	1285
Dead Horse Ranch	Cottonwood, AZ	Arizona State Parks	1000
Otter Water	Near Camp Verde, AZ	The Nature Conservancy	963

Table 9. Stream gauges used to calculate flood recurrence intervals, and distance and direction of gauge relative to each study site.

Study Site	Stream Gauge	Distance and direction of gauge from study site
Campbell Ranch	Verde River near Pauden, AZ	9 km downstream
Dead Horse Ranch	Verde River near Clarkdale, AZ	23 km upstream
Otter Water	Verde River near Clarkdale, AZ	41 km upstream

Table 10. Plant functional traits measured for this study, corresponding sample size or general methods, and the plant strategy classification method(s) (Hodgson et al., 1998; Westoby, 1999) for which each is used.

Plant Trait	Sample size or method	Hodgson et al.	Westoby
Canopy height (mm)	3 individuals	x	x
Lateral Spread (mm)	3 individuals	x	
Clonal? (yes or no)	Floras, online databases, or physical examination of the plant	x	
Leaf dry matter content (%)	3 leaves on each of 3 individuals	x	
Leaf dry mass (mg)	4 leaves on each of 3 individuals	x	
Specific leaf area (mm <sup>2</sup> /mg)	3 leaves on each of 3 individuals	x	x
Flowering duration (months)	survey of local population	x	
Flowering start (months)	survey of local population	x	
Seed mass (mg)	5 to 50 seeds from each of 3 individuals		x

Table 11. Numbers of taxa, broken down according to life span and phylogeny, that were classified into each CSR strategy according to methods described in Hodgson et al. (1998).

Plant Strategy	Total	Life Span		Phylogeny	
		Annual	Perennial	Monocot	Dicot
C	4	1	3	3	1
C/CR	18	8	10	2	16
C/CSR	4	0	4	3	1
C/SC	7	1	6	6	1
CR	22	10	12	3	19
CR/CSR	2	2	0	1	1
CSR	1	0	1	1	0
R	1	1	0	0	1
R/CR	7	4	3	3	4
R/CSR	0	0	0	0	0
R/SR	0	0	0	0	0
S	2	1	1	0	2
S/CSR	2	1	1	2	0
S/SC	4	2	2	3	1
S/SR	0	0	0	0	0
SC	9	6	3	5	4
SC/CSR	6	3	3	4	2
SR	0	0	0	0	0
SR/CSR	2	2	0	2	0



Table 12. Spearman's  $\rho$  values measuring correlation between results of Hodgson et al.'s (1998) CSR classification method for 14 Verde River taxa in June 2008 and environmental variables characterizing each species' habitat.

Environmental Variable	C-score	S-score	R-score	Raw C-score	Raw S-score	Raw R-score
<i>Resource Availability</i>						
Silt	-0.16	0.05	0.21	0.02	0.02	0.11
Clay	0.26	-0.30	0.19	0.42	0.09	-0.02
Soil moisture	0.51 †	-0.15	-0.13	0.73 *	0.25	-0.23
Max depth to groundwater	-0.50 †	0.21	-0.08	-0.77 *	-0.16	0.11
Overstory cover	-0.20	0.38	-0.08	0.17	0.35	0.02
<i>Disturbance Intensity/ Frequency</i>						
Flood recurrence interval	-0.44	0.24	-0.23	-0.87 *	-0.38	0.04
Time since most recent flood	-0.50 †	0.30	-0.10	-0.85 *	-0.36	0.15
Shear stress- 2008 flood	0.38	-0.09	0.17	0.80*	0.56 *	-0.02

\*  $p \leq 0.05$

†  $0.05 \leq p \leq 0.1$

Table 13. Spearman's *rho* values measuring correlation between results of Hodgson et al.'s (1998) CSR classification method for 15 Verde River taxa in September 2008 and environmental variables characterizing each species' habitat.

Environmental Variable	C-score	S-score	R-score	Raw C-score	Raw S-score	Raw R-score
<i>Resource Availability</i>						
Silt	-0.31	0.44	0.00	-0.39	0.12	-0.29
Clay	0.03	0.11	0.12	-0.18	0.19	-0.39
Soil moisture	0.20	0.02	-0.15	0.11	0.12	-0.66*
Max depth to groundwater	-0.56 *	0.15	0.29	-0.39	0.09	0.57*
Overstory cover	-0.14	0.25	0.28	0.19	0.33	0.10
<i>Disturbance Intensity/ Frequency</i>						
Flood recurrence interval	-0.42	0.07	0.13	-0.33	-0.15	0.48 †
Time since most recent flood	-0.41	0.06	0.08	-0.37	-0.08	0.48 †
Shear stress- 2008 flood	0.35	0.04	-0.27	0.33	0.29	-0.28

\*  $p \leq 0.05$

†  $0.05 \leq p \leq 0.1$

Table 14. Spearman's  $\rho$  values measuring correlations between the plant functional traits used in Westoby's (1999) method and environmental variables characterizing each species' habitat for 14 Verde River taxa in June 2008 and 15 Verde River taxa in September 2008.

Environmental Variable	June 2008			September 2008		
	SLA	Plant Height	Seed Mass	SLA	Plant Height	Seed Mass
<i>Resource Availability</i>						
Silt	0.09	-0.16	0.22	-0.01	-0.27	0.52 *
Clay	0.09	0.30	0.01	-0.13	0.19	0.16
Soil moisture	0.08	0.38	-0.07	0.14	0.08	0.14
Overstory cover	0.67 *	-0.49 †	0.24	0.49 †	-0.28	0.10
Max depth to groundwater	0.20	-0.50 †	0.09	-0.07	-0.23	0.26
<i>Disturbance Intensity/ Frequency</i>						
Flood recurrence interval	0.04	-0.55 *	0.11	-0.19	-0.22	0.13
Time since most recent flood	0.18	-0.68 *	0.04	-0.23	-0.19	0.20
Shear stress- 2008 flood	0.01	0.40	-0.05	0.27	0.00	-0.17

\*  $p \leq 0.05$

†  $0.05 \leq p \leq 0.1$

Table 15. Spearman's  $\rho$  values measuring correlations between plant functional traits used in Hodgson et al.'s (1998) method and environmental variables characterizing each species' habitat for 14 Verde River taxa in June 2008.

Environmental Variable	Canopy height	Lateral Spread	Leaf dry matter content	Leaf dry mass	Specific leaf area	Flowering duration	Flowering start	Seed mass
<i>Resource Availability</i>								
Silt	-0.16	-0.16	-0.3	0.38	0.09	0.36	-0.37	0.22
Clay	0.3	0	-0.57 *	0.48 †	0.09	0.15	-0.2	0.01
Soil moisture	0.38	-0.16	-0.32	0.68 *	0.08	-0.14	-0.29	-0.07
Overstory cover	-0.49 †	0.02	0.27	0.26	0.67 *	0	-0.50 †	0.24
Max depth to groundwater	-0.50 †	-0.22	0.33	-0.44	0.2	-0.33	-0.06	0.09
<i>Disturbance Intensity/ Frequency</i>								
Flood recurrence interval	-0.55 *	-0.22	0.32	-0.52 †	0.04	-0.14	-0.07	0.11
Time since most recent flood	-0.68 *	-0.35	0.33	-0.55 *	0.18	-0.11	-0.26	0.04
Shear stress- 2008 flood	0.4	0.42	-0.14	0.44	0.01	0.07	0.13	-0.05

\*  $p \leq 0.05$

†  $0.05 \leq p \leq 0.1$

Table 16. Spearman's  $\rho$  values measuring correlations between plant functional traits used in Hodgson et al.'s (1998) method and environmental variables characterizing each species' habitat for 15 Verde River taxa in September 2008.

Environmental Variable	Canopy height	Lateral spread	Leaf dry matter content	Leaf dry mass	Specific leaf area	Flowering duration	Flowering start	Seed mass
<i>Resource Availability</i>								
Silt	-0.27	-0.48 †	-0.16	0.35	-0.01	0.16	0.49 †	0.52 *
Clay	0.19	-0.37	-0.28	0.27	-0.13	-0.15	-0.12	0.16
Soil moisture	0.08	-0.48 †	-0.01	0.4	0.14	-0.19	-0.05	0.14
Overstory cover	-0.28	0.12	0.25	0.06	0.49 †	-0.13	-0.39	0.1
Max depth to groundwater	-0.23	0.14	0.09	-0.25	-0.07	0.25	-0.35	0.26
<i>Disturbance Intensity/ Frequency</i>								
Flood recurrence interval	-0.22	0.13	0.24	-0.36	-0.19	0.29	-0.39	0.13
Time since most recent flood	-0.19	0.06	0.16	-0.29	-0.23	0.24	-0.29	0.2
Shear stress- 2008 flood	0	0.1	-0.08	0.13	0.27	-0.1	0.43	-0.17

\*  $p \leq 0.05$

†  $0.05 \leq p \leq 0.1$

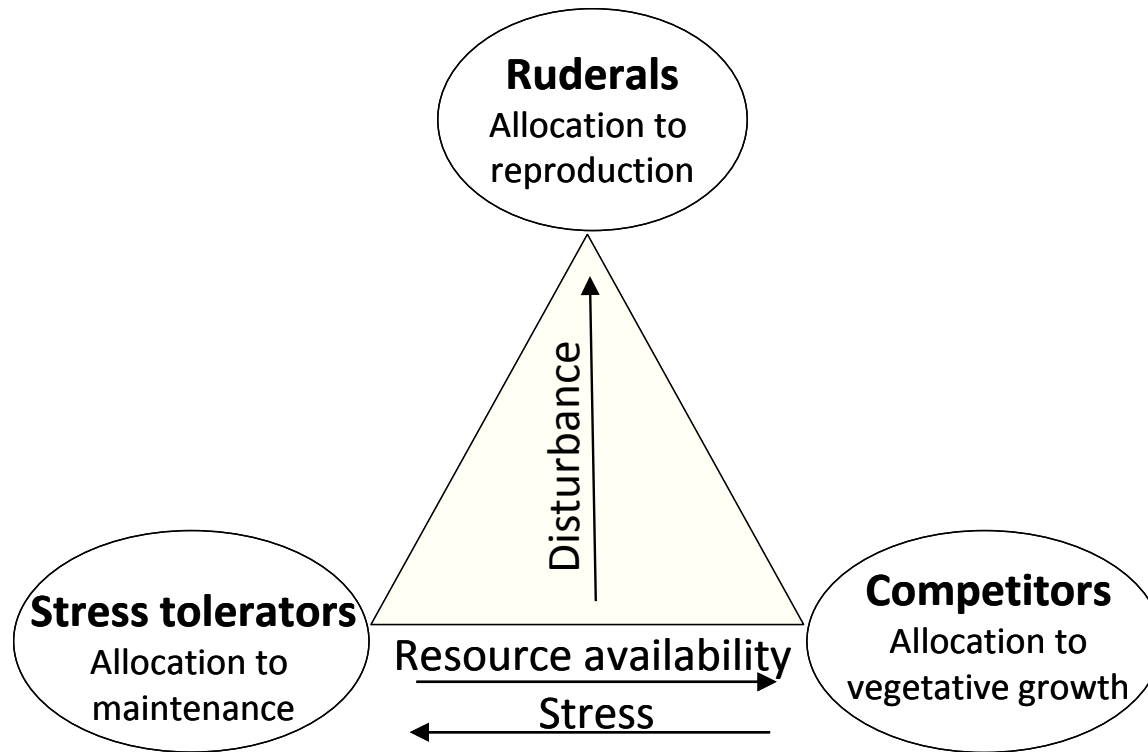


Figure 8. Resource allocation and habitat characteristics for the three primary life history strategies proposed by Grime (1974, 1977).

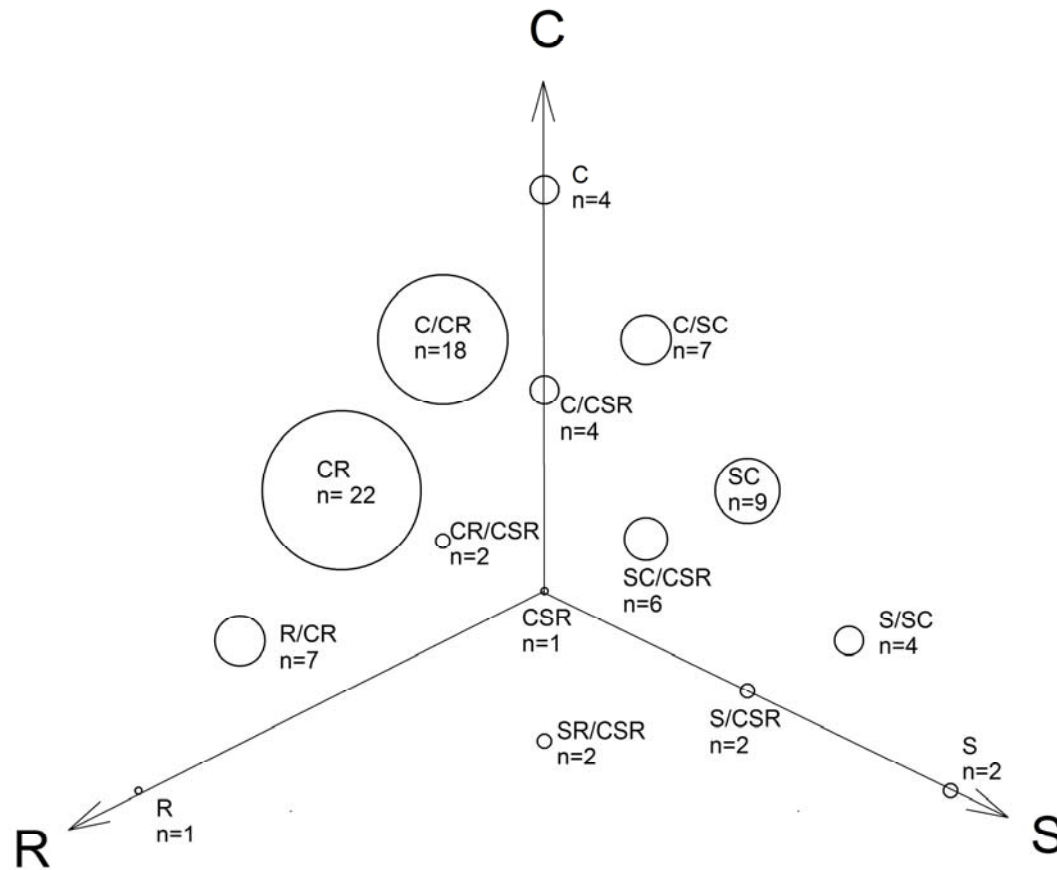


Figure 9. Number of taxa classified into each CSR strategy according to methods described in Hodgson et al. (1998). Only herbaceous taxa (both monocots and dicots) were used to test the method.

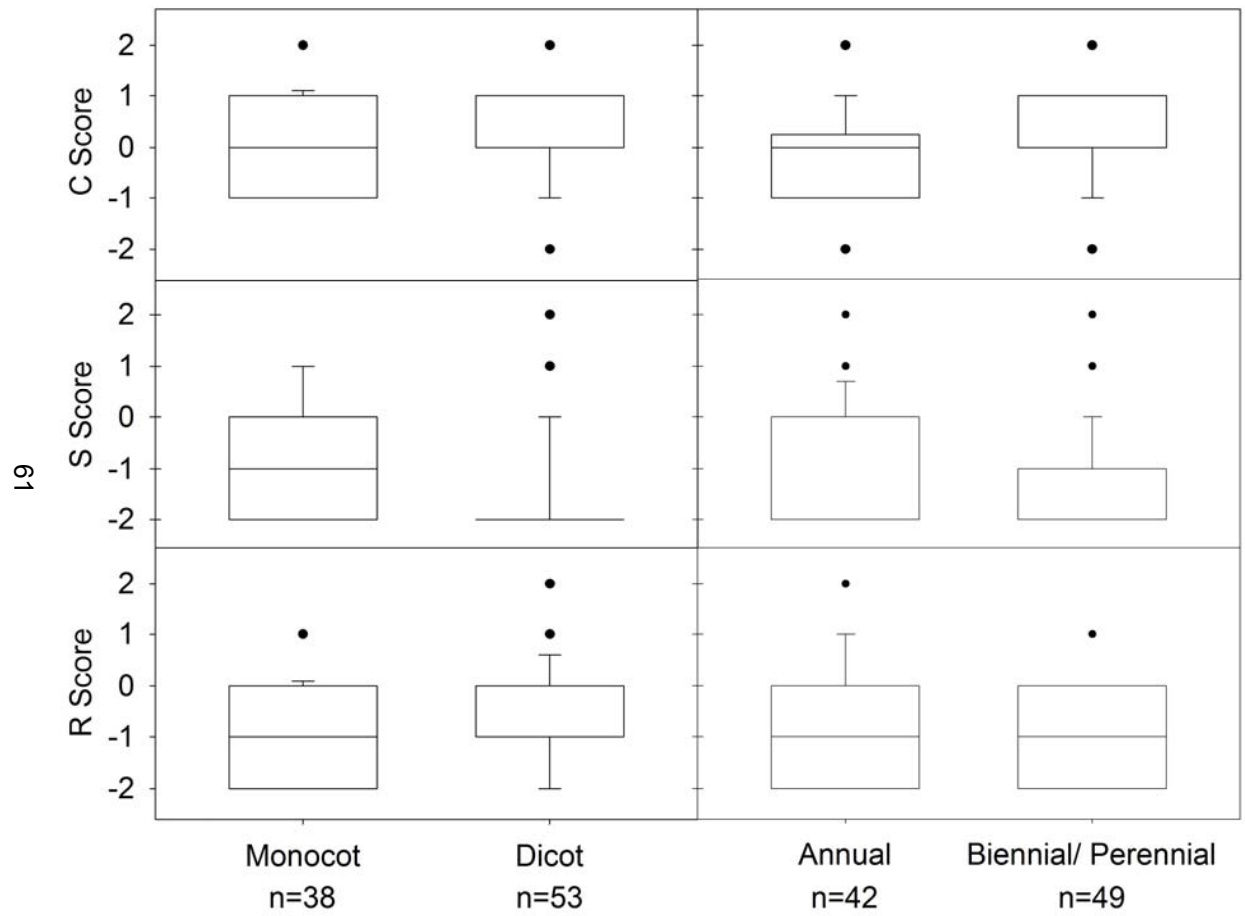


Figure 10. Median, quartile divisions, and outliers of C-, S-, and R-scores for monocots vs dicots and annual vs. perennial plants.



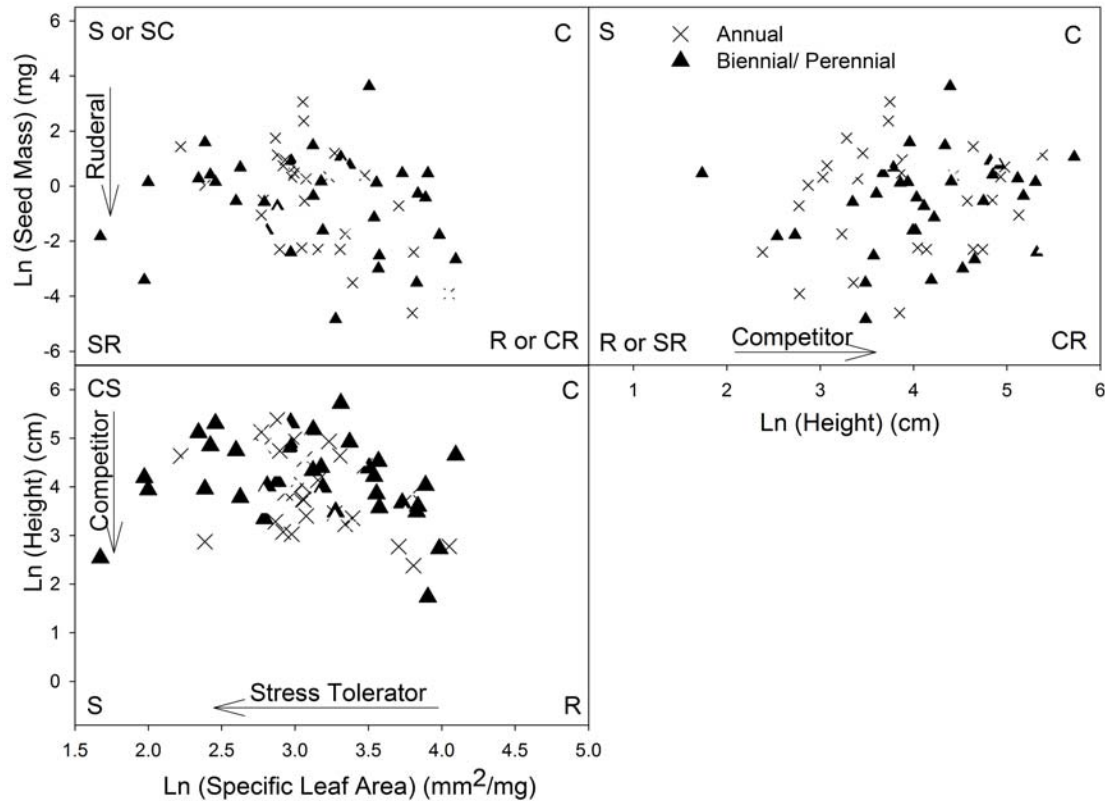


Figure 11. Positions of 91 Verde River herbaceous taxa in three dimensional leaf-height-seed space, according to Westoby's (1999) method of assessing plant life history strategies. Taxa are coded according to longevity (annual vs. perennial). Plants with the capability of completing a biennial life cycle are coded as perennials. Labels interpreting the functional traits according to Grime's (1974, 1977) CSR theory are included just inside the axes.

#### 4. CONCLUSION

Results of both papers highlight the ways in which vegetation changes along hydrologic gradients. Chapter 2 examines plant community change in terms of shifts in dominance and changes in species richness and cover. The results of this correlative study suggest that if conditions along the Verde River become drier, certain drought-adapted species will increase in abundance, at the expense of marshland vegetation and species richness. If the frequency of large floods increases, the age structure of riparian forests will likely shift to a higher density of younger trees and shrubs.

The functional groups in chapter 2, particularly those describing drought tolerance, were designated based primarily on expert opinion. That expert opinion was that of the authors in some cases, and that of U.S. Department of Agriculture employees in other cases. Unfortunately, there is not always enough autecological information available to assign some species to functional groups. This can sometimes limit analysis to the dominant species, at the expense of understanding the diverse forest understory. Ideally, functional groups could be defined based on characteristics of the plant itself. There are numerous options for functional group classification systems, but many are specific to certain habitats or climates. Those that claim to be universal are for the most part unproven as such.

Chapter 3 looks at changes in plant functional traits along the same hydrologic gradients that were analyzed in chapter 2, plus the additional environmental factor of overstory cover. Instead of describing changes according to species, or a priori-described functional groups, this chapter describes vegetation change in terms of traits such as leaf mass, plant height, and flowering duration. The same data set is also used to test the "universality" of two methods of quantifying plant strategies. While neither method was a resounding success, relationships were found between some functional traits and environmental variables. In particular, the "leaf economics" strategic tradeoff was supported by this data set. The "leaf economics" concept refers to a suite of leaf traits that co-vary consistently in plant species worldwide. Strategically, the concept

translates to a trade-off between the capacity for rapid growth in response to pulses of resources, and the ability to conserve resources by retaining leaves for a longer period of time.

The lessons of chapter 2 may be interpreted in the context of the results of chapter 3. It is not clear how increased flooding might change the morphological characteristics of the average floodplain plant. However, it is clear that drought conditions will lead to a shift from plants with characteristics of the "rapid growth" strategy to those of the resource conserving strategy. This corresponds to a shift to plants with smaller, denser leaves and shorter stature. This could manifest as a dominance shift from trees to shrubs, annuals to perennials, or plants with broad leaves to those with small leaves, needles, or otherwise reduced leaves. This is consistent with predictions that river drying would lead to a decline in Fremont cottonwood and Goodding's willow, two tall tree species with broad, deciduous leaves, and an increase in saltcedar and desert willow, tree-shrub species with smaller leaves.

These results have implications that are pertinent to applied and theoretical ecology. From the applied perspective, it is useful for land managers to know what vegetation changes to expect from climate change and certain anthropogenic land uses. Furthermore, if the changes described in this paper are deemed undesirable, wise management of groundwater and surface water use could prevent some of the vegetation changes from occurring. From a theoretical perspective, these results contribute further support for the leaf economics gradient representing the primary gradient of plant strategies.

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APPENDIX A

LIST OF TAXA USED IN THE STUDY AND CORRESPONDING LIFE SPAN, CSR  
RESULTS, AND LHS VALUES

Taxa Name	Family	Monocot/ Dicot	Life Span	CSR category	SLA	Height	Seed Mass
<i>Acalypha neomexicana</i>	Euphorbiaceae	dicot	annual	SC	40.7	16.0	0.49
<i>Amaranthus palmeri</i>	Amaranthaceae	dicot	annual	CR	18.1	52.0	0.30
<i>Ambrosia acanthacarpa</i>	Asteraceae	dicot	annual	CR/CSR	17.6	26.7	5.72
<i>Ambrosia psilostachya</i>	Asteraceae	dicot	perennial	C/CR	21.5	66.3	6.60
<i>Ambrosia trifida</i>	Asteraceae	dicot	annual	C	66.0	243.3	14.50
<i>Aristida purpurea</i>	Poaceae	monocot	perennial	S/SC	7.4	51.3	1.16
<i>Arundo donax</i>	Poaceae	monocot	perennial	C/SC	13.8	246.7	0.10
<i>Berula erecta</i>	Apiaceae	dicot	perennial	C/CR	46.4	36.7	0.76
<i>Bidens frondosa</i>	Asteraceae	dicot	annual	C/CR	31.8	115.0	2.67
<i>Bidens laevis</i>	Asteraceae	dicot	perennial	C/CR	29.1	137.3	2.14
<i>Boerhavia coccinea</i>	Nyctaginaceae	dicot	perennial	C/CR	11.0	39.8	2.12
<i>Bouteloua aristidoides</i>	Poaceae	monocot	annual	R/CR	34.6	25.3	1.11
<i>Bouteloua barbata</i>	Poaceae	monocot	annual	SR/CSR	28.3	25.3	0.18
<i>Bouteloua curtipendula</i>	Poaceae	monocot	perennial	CR	48.9	56.3	0.66
<i>Bouteloua eriopoda</i>	Poaceae	monocot	perennial	S/SC	5.5	29.7	0.34
<i>Bromus catharticus</i>	Poaceae	monocot	perennial	CR	42.5	51.3	7.70
<i>Bromus diandrus</i>	Poaceae	monocot	annual	S/SC	21.3	41.7	10.66
<i>Bromus rubens</i>	Poaceae	monocot	annual	SC/CSR	22.8	41.9	2.90
<i>Bromus tectorum</i>	Poaceae	monocot	annual	CR/CSR	26.3	31.7	3.30
<i>Calibrachoa parviflora</i>	Solanaceae	dicot	annual	R	38.0	10.0	0.05
<i>Carex praegracilis</i>	Cyperaceae	monocot	perennial	S/CSR	16.3	28.4	0.56
<i>Carex senta</i>	Cyperaceae	monocot	perennial	SC	11.4	87.0	0.50
<i>Chamaesyce hyssopifolia</i>	Euphorbiaceae	dicot	annual	S/SC	32.3	84.0	1.48
<i>Chenopodium fremontii</i>	Chenopodiaceae	dicot	annual	CR	16.0	168.3	0.35
<i>Chloris virgata</i>	Poaceae	monocot	annual	SR/CSR	29.3	27.7	0.20

Taxa Name	Family	Monocot/ Dicot	Life Span	CSR category	SLA	Height	Seed Mass
<i>Cleome lutea</i>	Capparaceae	dicot	annual	C/CR	17.8	216.7	3.10
<i>Conyza canadensis</i>	Asteraceae	dicot	annual	CR	25.8	130.7	0.07
<i>Corydalis aurea</i>	Fumariaceae	dicot	perennial	CR	32.3	22.9	1.09
<i>Cynadon dactylon</i>	Poaceae	monocot	perennial	CSR	24.3	54.2	0.20
<i>Cyperus odoratus</i>	Cyperaceae	monocot	annual	SC	21.0	57.0	0.11
<i>Datura wrightii</i>	Solanaceae	dicot	perennial	CR	33.3	80.7	37.50
<i>Descurainia pinnata</i>	Brassicaceae	dicot	annual	SC/CSR	15.6	37.0	0.10
<i>Echinochloa colona</i>	Poaceae	monocot	annual	C/CR	35.5	64.0	1.20
<i>Elymus canadensis</i>	Poaceae	monocot	perennial	C/SC	22.7	76.3	4.40
<i>Eragrostis pectinacea</i>	Poaceae	monocot	annual	S/CSR	12.3	34.3	0.15
<i>Eriochloa acuminata</i>	Poaceae	monocot	annual	SC	19.4	84.0	1.80
<i>Erodium cicutarium</i>	Geraniaceae	dicot	annual	SC	18.5	21.6	2.10
<i>Euphorbia dentata</i>	Euphorbiaceae	dicot	annual	R/CR	30.0	25.3	1.99
<i>Evovulus nuttallianus</i>	Solanaceae	dicot	perennial	S	5.6	7.7	4.95
<i>Funastrum cynanchoides</i> ssp. <i>cynanchoides</i>	Asclepiadaceae	dicot	perennial	C/CR	27.4	305.0	2.89
<i>Gaura hexandra</i> ssp <i>gracilis</i>	Onagraceae	dicot	annual	SC	21.2	42.3	21.40
<i>Helianthus annuus</i>	Asteraceae	dicot	annual	C/CR	11.5	203.0	42.80
<i>Heterotheca subaxillaris</i>	Asteraceae	dicot	annual	C/CR	16.2	127.0	0.60
<i>Hordeum jubatum</i>	Poaceae	monocot	perennial	SC/CSR	27.8	49.3	2.12
<i>Hordeum murinum</i>	Poaceae	monocot	annual	SC/CSR	23.4	50.8	3.24
<i>Hydrocotyle verticillata</i>	Apiaceae	dicot	perennial	R/CR	49.6	5.7	1.59
<i>Hymenothrix loomisii</i>	Asteraceae	dicot	perennial	C/CR	13.4	115.3	0.58
<i>Juncus articulatus</i>	Juncaceae	monocot	perennial	SC/CSR	16.1	36.4	0.02
<i>Juncus bufonius</i>	Juncaceae	monocot	annual	R/CR	57.4	16.1	0.02

Taxa Name	Family	Monocot/ Dicot	Life Span	CSR category	SLA	Height	Seed Mass
<i>Juncus mexicanus</i>	Juncaceae	monocot	perennial	SC	7.2	66.0	0.03
<i>Juncus torreyi</i>	Juncaceae	monocot	perennial	SC	9.5	85.3	0.01
<i>Kochia scoparia</i>	Chenopodiaceae	dicot	annual	C/SC	17.2	136.7	0.54
<i>Lactuca serriola</i>	Asteraceae	dicot	annual	CR	21.4	97.0	0.58
<i>Leersia oryzoides</i>	Poaceae	monocot	perennial	C/CSR	35.0	47.3	1.13
<i>Ludwigia peploides</i>	Onagraceae	dicot	perennial	C/CR	23.7	43.3	102.35
<i>Machaeranthera gracilis</i>	Asteraceae	dicot	annual	S	12.9	15.7	0.31
<i>Matthiola longipetala</i>	Brassicaceae	dicot	perennial	C/CR	16.6	55.7	0.20
<i>Melilotus officinalis</i>	Fabaceae	dicot	perennial	C/CR	12.5	135.0	2.70
<i>Mentha spicata</i>	Lamiaceae	dicot	perennial	CR	35.5	92.3	0.05
<i>Mentzelia multiflora</i>	Loasaceae	dicot	perennial	CR	8.4	75.3	0.77
<i>Nasturtium officinale</i>	Brassicaceae	dicot	perennial	R/CR	53.7	15.3	0.17
<i>Oenothera elata ssp hirsutissima</i>	Onagraceae	dicot	perennial	CR	34.9	112.3	0.28
<i>Paspalum dialatum</i>	Poaceae	monocot	perennial	C/CSR	25.5	82.1	1.50
<i>Phalaris arundinacea</i>	Poaceae	monocot	perennial	C	22.7	177.0	0.70
<i>Plantago lanceolata</i>	Plantaginaceae	dicot	perennial	CR	16.4	35.7	1.30
<i>Polanisia dodecandra</i>	Capparaceae	dicot	annual	CR	14.3	87.7	2.59
<i>Polygonum aviculare</i>	Polygonaceae	dicot	annual	SC	21.7	30.0	1.30
<i>Polygonum lapathifolium</i>	Polygonaceae	dicot	annual	CR	21.6	84.0	1.24
<i>Polypogon monspeliensis</i>	Poaceae	monocot	annual	CR	27.3	103.3	0.10
<i>Polypogon viridis</i>	Poaceae	monocot	perennial	R/CR	35.7	35.6	0.08
<i>Pseudognaphalium luteoalbum</i>	Asteraceae	dicot	annual	R/CR	44.7	47.0	0.01
<i>Ranunculus cymbalaria</i>	Ranunculaceae	dicot	perennial	CR	24.2	19.5	0.07
<i>Rumex crispus</i>	Polygonaceae	dicot	perennial	CR	30.8	94.7	1.50

Taxa Name	Family	Monocot/ Dicot	Life Span	CSR category	SLA	Height	Seed Mass
<i>Salsola tragus</i>	Chenopodiaceae	dicot	annual	CR	12.3	86.7	1.87
<i>Samolus valerandi</i> ssp. <i>parviflorus</i>	Primulaceae	dicot	perennial	CR	46.0	32.6	0.03
<i>Schedonorus phoenix</i>	Poaceae	monocot	perennial	C/CR	20.9	103.3	2.40
<i>Schoenoplectus acutus</i>	Cyperaceae	monocot	perennial	C	11.7	201.3	1.16
<i>Schoenoplectus americanus</i>	Cyperaceae	monocot	perennial	C	21.6	131.2	2.49
<i>Schoenoplectus</i> <i>tabernaemontani</i>	Cyperaceae	monocot	perennial	C/SC	10.4	166.3	1.32
<i>Setaria macrostachya</i>	Poaceae	monocot	perennial	C/SC	17.8	76.0	0.40
<i>Sisymbrium irio</i>	Brassicaceae	dicot	annual	C/CR	23.5	62.7	0.10
<i>Solanum elaeagnifolium</i>	Solanaceae	dicot	perennial	SC/CSR	10.9	52.3	4.90
<i>Sonchus asper</i>	Asteraceae	dicot	annual	CR	30.2	103.7	0.28
<i>Sorghum halapense</i>	Poaceae	monocot	perennial	C/CSR	18.8	182.0	3.80
<i>Sphaeralcea</i> cf. <i>fendleri</i>	Malvaceae	dicot	perennial	C/CSR	24.0	81.7	1.19
<i>Sporobolus contractus</i>	Poaceae	monocot	perennial	C/SC	15.9	121.7	0.15
<i>Symphiotrichium expansum</i>	Asteraceae	dicot	annual	C/CR	18.1	114.3	0.10
<i>Typha domingensis</i>	Typhaceae	monocot	perennial	C/SC	5.5	218.4	0.10
<i>Verbesina encelioides</i>	Asteraceae	dicot	annual	CR	19.9	144.7	2.00
<i>Veronica anagallis-aquatica</i>	Scrophulariaceae	dicot	perennial	CR	60.0	105.0	0.07
<i>Xanthium strumarium</i>	Asteraceae	dicot	annual	C/CR	15.7	195.3	68.90

APPENDIX B

SPEARMAN CORRELATIONS AMONG THE ENVIRONMENTAL VARIABLES



June 2008

Environmental Variable	<i>Resource Availability</i>					<i>Disturbance Intensity/ Frequency</i>		
	Silt	Clay	Soil moisture	Overstory cover	Max depth to groundwater	Flood recurrence interval	Time since most recent flood	Shear stress- 2008 flood
<i>Resource Availability</i>								
Silt	1	0.73	0.34	0.06	-0.26	-0.29	-0.14	-0.02
Clay	0.73	1	0.73	0.07	-0.42	-0.59	-0.49	0.27
Soil moisture	0.34	0.73	1	0.31	-0.64	-0.8	-0.73	0.65
Overstory cover	0.06	0.07	0.31	1	0.09	-0.06	0	0.31
Max depth to groundwater	0.26	-0.42	-0.64	0.09	1	0.91	0.88	-0.8
<i>Disturbance Intensity/ Frequency</i>								
Flood recurrence interval	0.29	-0.59	-0.8	-0.06	0.91	1	0.94	-0.87
Time since most recent flood	0.14	-0.49	-0.73	0	0.88	0.94	1	-0.86
Shear stress- 2008 flood	0.02	0.27	0.65	0.31	-0.8	-0.87	-0.86	1

September 2008

Environmental Variable	<i>Resource Availability</i>					<i>Disturbance Intensity/ Frequency</i>		
	Silt	Clay	Soil moisture	Overstory cover	Max depth to groundwater	Flood recurrence interval	Time since most recent flood	Shear stress- 2008 flood
<i>Resource Availability</i>								
Silt	1	0.74	0.64	0.31	-0.07	-0.17	-0.15	-0.04
Clay	0.74	1	0.79	0.16	-0.34	-0.49	-0.44	0.16
Soil moisture	0.64	0.79	1	0.26	-0.70	-0.73	-0.73	0.39
Overstory cover	0.31	0.16	0.26	1	-0.08	-0.17	-0.25	0.20
Max depth to groundwater	-	-	-	-	1	0.90	0.95	-0.71
<i>Disturbance Intensity/ Frequency</i>								
Flood recurrence interval	0.17	-0.49	-0.73	-0.17	0.90	1	0.97	-0.78
Time since most recent flood	0.15	-0.44	-0.73	-0.25	0.95	0.97	1	-0.75
Shear stress- 2008 flood	0.04	0.16	0.39	0.20	-0.71	-0.78	-0.75	1