Plant Community Composition along the Historic Verde River Irrigation System:

Does Hydrochory Play a Role?

by

Jacqueline Michelle Betsch

A Thesis Presented in Partial Fulfillment
of the Requirements for the Degree
Master's of Science

Approved November 2010 by the
Graduate Supervisory Committee:

Juliet C. Stromberg, Chair
Sharon J. Hall
David M. Merritt

ARIZONA STATE UNIVERSITY

December 2010

ABSTRACT

As an industrial society, humans have increasingly separated agricultural processes from natural ecosystems. Many areas of the Southwestern US, however, maintain traditional practices that link agricultural systems to the natural environment. One such practice, diverting river water into fields via earthen irrigation canals, allows ditch water to recharge groundwater and riparian vegetation to prosper along canal banks. As there is growing interest in managing landscapes for multiple ecosystem services, this study was undertaken to determine if irrigation canals function as an extension of the riparian corridor. I was specifically interested in determining if the processes within semi-arid streams that drive riparian plant community structure are manifested in earthen irrigation ditches.

I examined herbaceous and woody vegetation along the middle Verde River, AZ, USA and three adjacent irrigation ditches across six months. I also collected sieved hydrochores—seeds dispersing through water—within ditches and the river twelve times. Results indicate that ditch vegetation was similar to streamside river vegetation in abundance (cover and basal area) due to surface water availability but more diverse than river streamside vegetation due to high heterogeneity. Compositionally, herbaceous vegetation along the ditch was most similar to the river banks, while low disturbance fostered woody vegetation along the ditches similar to high floodplain and river terrace vegetation.

Hydrochore richness and abundance within the river was dependent on seasonality and stream discharge, but these relationships were dampened in the ditches. Species-specific strategies of hydrochory, however, did emerge in both systems. Strategies include pulse species, which disperse via hydrochory in strict accordance with their restricted dispersal windows, constant species, which are year round hydrochores, and combination species, which show characteristics of both. There was high overlap in the composition of hydrochores in the two systems, with obligate wetland species abundant in both. Upland species were more seasonally constant and abundant in the ditch water than the river. The consistency of river processes and similarity of vegetation suggest that earthen irrigation ditches do function as an extension of the riparian corridor. Thus, these man-made irrigation ditches should be considered by stakeholders for their multiple ecosystem services.

For Grandpa Betsch—thank you for appreciating and acknowledging
my application of your gift.

ACKNOWLEDGEMENTS

I would like to thank Juliet C. Stromberg for always providing new ideas, being an energetic editor, and offering constant assistance. I would also like to thank my other committee members, Sharon J. Hall and David M. Merritt, for their support and guidance through the entire process. Thank you to all land owners and ditch corporations without whom this research would not have been possible: Arizona State Parks, Prescott National Forest, Coconino National Forest, Dianne & Todd Scantlebury, Martha Kaldenbaugh, Frank Geminden, Margaret Edge, Hauser & Hauser Farms, Spur Land & Cattle Company, John McReynolds, and all the owners of the Hickey, Eureka, and Diamond S Ditches.

I would also like to thank Jeanmarie Haney, George Christianson, Less Bovee, Robert Casavant, Sharon Mazek-Lopez, and Ann Smith for knowledge of the Verde Valley and assistance during field work, Liz Makings for help with plant identification, Dave Huber and Jolene Trujillo for answering my many soil questions, Margaret Gibson for assistance with greenhouse space, and Agri Packing for donated supplies.

Thank you to the entire Stromberg Lab and assistants for their field, lab, and greenhouse assistance, helpful comments and opinions, and constant moral support: Meg White, Andrea Hazelton, Natalie Case, Jamie Alcumbrac, Lane Butler, Amanda Suchy, and Frankie Coburn. I would also like to thank Andrea Hazelton for introducing me to my study area and for additional data to strengthen my thesis. Most importantly, I would like to thank Danika Setaro, my fearless companion and friend whose hard work and attitude pulled me through the end of field season and the emergence studies.

I would also like to thank all of my Arizona and Indiana friends and family for their continued support. Thank you Mom and Dad for helping me continue to grow and assisting me in all of my endeavors. Finally, I would like to thank Andrew Kehr, whose field assistance, objective and subjective opinions, and love helped me maintain my sanity.

TABLE OF CONTENTS

Page

CHAPTER

Page

LIST OF TABLES

LIST OF FIGURES

1. INTRODUCTION

Human communities continually interact with the natural environment around them and depend on those ecosystems for a variety of services. Given this interdependence, ecosystems can then be perceived as having two separate components, one part societal and the other ecological (Gallopin, 1991). From this perspective, a socio-ecological system provides services to its human and non-human cohabitants. In the semi-arid Southwestern US, all living organisms have an unavoidable link to river systems—water. Modern societies need fresh water for a variety of domestic, industrial, and agricultural uses (Wallace *et al.*, 2003), but that water is also required by obligate phreatophyte plant species to maintain riparian ecosystems. Gordon and others (2010) have suggested managing water within this socio-ecological framework as a more holistic approach to water management, where both the natural ecosystem and the human population gain services from a multifunctional system.

When considering socio-ecological water management, agriculture is an important focus area because it accounts for 65-75% of the total fresh water used by humans (Wallace *et al.*, 2003). As the agricultural process has become more modernized, it has become increasingly segregated from the natural ecosystem. Many areas of the Southwestern US, however, maintain traditional practices, such as allowing buffer or hedgerow vegetation growth (Hannon and Sisk, 2009; Licht, 1992; Nabhan and Sheridan, 1977), which provide habitat within the agricultural landscape. Traditional earthen irrigation systems that provide river surface water to agricultural fields and are linked to the natural ecosystem through ground water tables (Fernald *et al.*, 2007). The surface water and elevated groundwater provided by earthen irrigation canals also supports vegetation, yet these communities have not been studied.

Agricultural irrigation has altered river systems across the world through water depletion and regulation (Gordon *et al.*, 2010), so water conservation within irrigation is being maximized to lessen its impact on river systems. Lining earthen irrigation systems is one way to conserve water by reducing canal seepage (Fernald *et al.*, 2007). This practice, however, ultimately restricts vegetation from growing along irrigation canals. The growing interest in managing multifunctional systems prompted this study to determine if earthen irrigation canals function as an extension of the riparian corridor. I was specifically interested in determining if processes within semi-arid streams that drive riparian plant community structure, such as seed dispersal, are manifested in earthen irrigation ditches.

This thesis is organized in three parts—part one addresses the vegetation along a semi-arid river and adjacent unlined irrigation canals, part two addresses patterns of seed dispersal through water in a semi-arid river and its relation to seed banks and riparian vegetation, and part three addresses patterns of seed dispersal through water in irrigation canals and its relation to canal seed banks, canal vegetation, and the adjacent river processes.

2. RIVER AND IRRIGATION DITCH VEGETATION

SUMMARY

Agriculture has been a distinct part of human/ecosystem interactions for thousands of years, but agricultural and natural systems have increasingly become segregated in industrial society. Agricultural systems are structured for specific crop/livestock production, but may also provide or support other services of interest such as the provision of habitat. In semi-arid regions, irrigation is imperative to agricultural systems, and irrigation delivery systems are being lined and modernized to increase water efficiency. In unlined irrigation systems, vegetation lines the banks of canals—an attribute lost in lined systems. In this study, we evaluated the vegetation along historic earthen irrigation canals in a semi-arid region to determine its similarity to the natural riparian corridor. We assessed diversity, abundance, and composition of herbaceous and woody vegetation and environmental variables along three irrigation ditches and the adjacent main-stem river across one growing season. In this system, the abundance and unit-area diversity of ditch and river streamside vegetation was similar, but cumulative species number was higher for ditches due to their heterogeneous landscape. Woody vegetation along the irrigation ditches contained common streamside river species, but was dominated by later successional species that require less moisture than river vegetation. Herbaceous vegetation along the ditch also contained species of lower moisture requirements, but ditches were more similar to the streamside river vegetation than to any other location across the riparian zone. These results indicate that irrigation ditches host plant assemblages with some similarities to natural riparian systems. Further evaluation is needed to quantify ecological services these man-made riparian areas provide.

INTRODUCTION

Agriculture has been a part of civilization in the Desert Southwest since prehistoric peoples began farming the land around A.D. 1275 (Fish and Fish, 1994). The Verde River watershed, Arizona, USA, part of the Salt River watershed, is no exception. Prehistoric peoples used a variety of terracing and flooding techniques to irrigate the desert landscape (Fish and Fish, 1994). Agriculture is only possible in this semi-arid area because of irrigation, and well after the prehistoric peoples abandoned the Southwest, European settlers began to irrigate in the region. In the Verde Valley, canals for flood irrigation have been used in agriculture for over 100 years (Hayden, 1940). Surface water is diverted from the Verde River into a series of privately owned unlined irrigation ditches via earthen diversion dams. These irrigation ditches have become a dominant feature on the landscape. In many arid areas irrigation canals have been lined for water conservation (Rahimi and Abbasi, 2008; Ries, 2008), but the Verde Valley irrigation system remains unlined. This system can then be considered a socio-ecological system (Gallopin, 1991). The man-made ditches, the societal portion of the system, are lined with vegetation and ditch water interacts with the groundwater table. Vegetation and groundwater interactions are part of the ecological subsystem.

In a world of human dominated patched landscapes, the expanding interface of urban, agricultural, and wild ecosystems is an area of increasing interest. Urban river restructuring is being evaluated for increased habitat value (Francis and Hoggart, 2008), agricultural buffers and hedgerows are cited as supplying diverse ecosystem functions (Hannon and Sisk, 2009; Licht, 1992; Nabhan and Sheridan, 1977), and the role of water in multifunctional patched landscapes is a suggested avenue of future exploration (Gordon *et al.*, 2010). Agriculture and water use are inseparable—between 65% and 75% of freshwater use by humans is for irrigation (Scanlon *et al.*, 2007; Wallace *et al.*, 2003); riparian trees also have high water needs, thus, the relationship between riparian habitats and agriculture needs to be evaluated.

In industrial agricultural systems, the ecosystem services provided by and associated with crops are often valued higher than types of aesthetic, cultural, and regulatory services (Gordon *et al.*, 2010); the systems are valued mainly for their societal subsystem. Alternatively, Gordon and others (2010) suggest that water can be managed to produce multifunctional agro-ecosystems, emphasizing the entire socio-ecological system. Traditional agricultural systems in arid regions have been shown to provide a variety of ecological and societal services. Traditional agricultural fields in the floodplains of the Rio San Miguel River, Mexico, for example, are lined with riparian trees in order to help stabilize the banks during floods and to provide farmers with timber, an additional crop (Nabhan and Sheridan, 1977). Historic irrigation canals along the Rio Grande, USA, are intimately tied with the groundwater table, increasing water retention in the local community and raising local water tables (Fernald *et al.*, 2007). Vegetation lining agricultural fields in the Western US has also been shown to support bee and bird populations (Berges *et al.*, 2010; Hannon and Sisk, 2009). The plant communities of agricultural irrigation systems as extensions of the riparian ecosystem, however, have been understudied.

In the Desert Southwest, there is a strong relationship between stream flow patterns and plant communities. Certain hydrologic patterns within the river channel are necessary to maintain riparian community structure (Beauchamp *et al.*, 2007; Casanova and Brock, 2000; Stromberg *et al.*, 2007). The perennial Verde River, as with many other southwestern rivers, is dominated by riparian deciduous forests known for their *Populus fremontii* and *Salix gooddingii* populations. These vernal wind- and water-dispersed species germinate and thrive on freshly scoured riverbanks after floods (Canham and Marks, 1985). Floods in riparian areas are a main source of disturbance, which contributes not only to the recruitment of deciduous trees, but also influences the community diversity. Both flood frequency and landscape heterogeneity (due to varying topology) contribute to plant community diversity with intermediate flooding and high heterogeneity leading to high diversity (Pollock *et al.*, 1998).

Nutrient and substrate particle size also influence plant community structure. Soil nutrients and moisture were related to the herbaceous plant community composition along the Verde River, AZ (Beauchamp and Stromberg, 2008). Regulated reaches had lower soil nutrients (nitrate, phosphate, and potassium) and lower richness (Beauchamp and Stromberg, 2008). Low levels of soil extractable phosphorus were associated with higher diversity in another system (Janssens *et al.*, 1998). Other studies found soil moisture and texture correlated to plant community composition, species richness, and species cover (Green and Brock, 1994; Jolley *et al.*, 2010; Nilsson *et al.*, 1991b). Cumulatively, small scale heterogeneity in soil properties and soil/plant interactions increase plant diversity (Ricklefs, 1977). An array of environmental and anthropogenic factors may contribute to plant community structure along the water courses in the Verde Valley, AZ.

The objectives of this study were to determine if plant communities along irrigation ditches are similar to those along a semi-arid river in species diversity, abundance, and composition, and to evaluate the abiotic factors that influence community structure in both systems. Based on differing hydrologic regimes in the irrigation ditches and main stem river (higher flow variability in the river), we expect differences in plant community composition and diversity between the two systems. Specifically, along the river channel we expect more disturbance tolerant species and an increased number of species because of flooding disturbance. On the other hand, we expect irrigation ditches to host both wetland and upland species because of their location cutting across the riparian zone, increasing their diversity; this leads to a competing hypothesis of an increased number of species along the ditches due to landscape heterogeneity (Figure 1).

STUDY SITE

This study was conducted along the middle Verde River near Camp Verde (34° 46', 112° 02'; elevation ca. 950 m) and Cottonwood (34° 31', 111° 50'; elevation ca. 1000 m), Arizona, USA adjacent to and within the Hickey, Eureka, and Diamond S irrigation ditches (Figure 2). Mean annual temperature is 16.7 °C and mean annual precipitation is 29.6 cm. The middle Verde is in the Transition Zone physiographic province, between the Colorado Plateau and the Basin and Range. The river is spring fed at the headwaters and further provided with water by a number of tributaries, including Oak Creek and Beaver Creek. The river flow rate is strongly influenced by monsoon and winter rains and spring snowmelt. Monsoon rains cause annual flooding from late July through September, while winter rains and snowmelt can cause floods through April. The river is characterized by low flow conditions in dry winters and during the dry summer months of May, June, and July.

The middle Verde is influenced by a series of earthen dams that divert surface water into a historic unlined irrigation system. The ditches begin within the river channel and often follow abandoned channels before progressing further out through the floodplain. They maintain almost consistent elevation until they run along the edges of the upper most riparian terraces. Meanwhile, the adjacent river drops in elevation. Three of the Verde Valley ditches, the Eureka, Diamond S, and Hickey, were examined in this study. The ditch system in the Verde Valley was originally developed for irrigation of agriculture, with the Eureka (Hutcheson) Ditch claiming surface water rights in 1893, the Diamond S (Eaman) Ditch claiming surface water rights in 1865 and 1892, and the Hickey Ditch claiming water rights in 1874, 1908, and 1914 (Hayden, 1940). As of 1940, the ditches serviced 417.2, 321.1, and 171.5 acres of agricultural land, respectively (Hayden, 1940). This reach of the Verde

River, between Clarkdale and Camp Verde, irrigated 4099 acres of agricultural land in 1940 (Hayden, 1940). The land use, however, has changed since that time; combined residential, commercial, and industrial land use overtook agricultural use in 1977 (Masek-Lopez and Springer, undated). Lands irrigated for agriculture continue to decline today in the Verde Valley (Masek-Lopez and Springer, undated), as well as across the Southwest United States (Fernald *et al.*, 2007). The Eureka and Diamond S ditches service agricultural crops, predominately alfalfa and sweet corn, pasture land, and pecan orchards, but a majority of the irrigated land on both ditches serves residential users. The Hickey Ditch irrigates pasture, a small-scale organic farm and orchard, and Dead Horse Ranch State Park. The state park, owning a majority of the water rights on the ditch, uses the water to irrigate lawns, irrigate two former tree farms, and feed a series of three lagoons used for recreational fishing.

The Verde River varies in low flow channel width within the study area, ranging from two to fifty meters wide. Flow rates at low flow conditions range from 1.7-2.3 m^3/s north of the Hickey Ditch (Verde River Near Clarkdale, USGS 09504000; <http://waterdata.usgs.gov>) to 1.1-2.3 m^3/s south of the Diamond S Ditch (Verde River Near Camp Verde, USGS 09506000; <http://waterdata.usgs.gov>). The gauge at Camp Verde includes flow from a 10,914 km^2 drainage area. The ditches range from as wide as five meters at the intake to less than one meter wide along the length. Exact flow rates within each ditch are not available, but intake flow based on our bimonthly sampling estimates are as follows: Diamond S Ditch 0.9-1.4 m^3/s, Hickey Ditch 0.1-0.4 m^3/s, and Eureka Ditch 0.1-0.9 m^3/s. Each irrigation ditch is monitored by its ditch company multiple times a week, if not daily, for water level. Monitoring and subsequent action such as return flow adjustments and obstructive vegetation removal by maintenance staff keeps water levels relatively constant within the ditch. The diversion dams, however, do not regulate flow in the Verde River, as only a portion of the surface water in the river is diverted. The river levels fluctuate despite the dams, which are often destroyed and rebuilt after flooding events.

The plant community along the Middle Verde is Sonoran and Interior Riparian Deciduous Forest and Woodland, while Plains and Desert Grassland and Sonoran Desertscrub (Arizona Upland Subdivision) characterize adjacent uplands. The growing season encompasses the warm months of April through October. Average temperatures dip below freezing during the winter months and spring runoff may continue through April, restricting herbaceous growth. A few riparian species begin to set fruit and disperse seeds in May, but the number of species fruiting continues to increase through August. Both fruiting and dispersal then decline in October, with increased senescence.

The river channel is characterized by *Populus fremontii*, *Salix gooddingii,* and *Tamarix chinensis* woodlands or forests. Further from the channel, *Chilopsis linearis*, *S. gooddingii,* and *T. chinensis* shrublands and woodlands or open forblands dominate the floodplain. In many areas old stands of *P. fremontii* are found within areas otherwise devoid of woody vegetation. The ditches begin within the active floodplain (often in an abandoned channel) where they are lined with *P. fremontii*, *S. gooddingii,* and *T. chinensis*, but they soon abut the *Prosopis veluntina* bosques at the edge of the uppermost terrace where they are lined with grasslands, mixed shrublands, woodlands, or forests with a range of riparian and upland species such as *Ephedra* sp., *Celtis laevigata var. reticulata*, *Acacia greggii*, *Simmondsia chinensis*, *Salix gooddingii*, and *Fraxinus velutina*.

METHODS

Experimental design

The basic study design compares vegetation, soils, and stream flows between the main channel and irrigation ditches. Three study areas were located along the river, each corresponding with one irrigation ditch (Figure 3). Six study sites were present per study area: three ditch sites and three adjacent sites in the main channel of the river. The three ditch sites were located as follows: near the diversion dam at the intake, central in the length of the ditch, and near the final return flow. Study sites along both the river and ditches were chosen to have minimal anthropogenic vegetation alteration, where possible.

An additional component of the study design involved comparing ditch vegetation with vegetation sampled in multiple hydrogeomorphic zones within the Verde riparian corridor at three nearby sites. The riparian corridor data were collected by Andrea Hazelton in 2008 (Hazelton, in prep).

Woody Vegetation

Woody vegetation was sampled once (2009) in 5 X 20 m (100 m^2) plots perpendicular to the channel. For the ditches, one plot was randomly located along each edge of the ditch at each site for a total of 18 ditch plots. The river was sampled in zones with distinct vegetation type and cover within 50 m of the river; one plot was placed within each zone resulting in two or three plots per site and a total of 25 river plots. Stem density and basal area by species and total canopy cover were recorded within each plot. Canopy cover was measured with a spherical densiometer at three random points within each plot.

In the riparian corridor, woody vegetation was sampled once (2008): at three study sites, two cross-sectional riparian transects (perpendicular to the valley) were established, separated by 100 m intervals (Hazelton, in prep). Transects from the channel edge extended into the *P. velutina* woodland (if present) on the terrace above the active floodplain on each side of the river. A stratified sampling approach was utilized, wherein one 5 X 20 m 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 25 m of patch width), for a total of 63 plots. Stem density and basal area by species and total canopy cover were recorded within each plot. Canopy cover was measured with a spherical densiometer at three random points within each plot.

Streamside Herbaceous Vegetation

Streamside herbaceous vegetation at the 18 ditch and river sites was assessed April 24-28, June 27-30, and August 18-21, 2009. Herbaceous cover by species was visually estimated in 1 m^2 plots within two meters of the stream edge. Ten plots were randomly located along a 20 m span centered at each study site. Cover was quantified using Braun-Blanquet cover classes (<1, 1-5, 5-25, 50-75, 75-100). Voucher specimens were collected and placed in the Arizona State University herbarium.

Herbaceous vegetation was sampled at additional sites in September 2008 (Hazelton, in prep). The data were collected along two to four transect lines at three sites. Twenty to twenty five 1 m^2 plots were established along each transect line, with ten plots clustered near the stream channel (1m apart) and the remaining plots spaced evenly across the riparian zone, for a total of 179 plots.

Abiotic Variables

At the channel of each of the 18 study sites, width, depth, and flow rate (measured with a Global flow probe FP101) were recorded twice per month (April-September 2009). Soil samples were taken at each site and analyzed for soil moisture (April, June, and August; via gravimetric method; Carter, 1993) texture (April; via Bouyoucos method; Klute, 1986), and macronutrients (April and August; modified from Robertson *et al.*, 1999). Soil samples contained three replicates taken within 1 m^2 from the upper 5 cm of soil. To analyze for macronutrients, exchangeable PO_3^{3-}, NH_4^+, and NO_3^-, soil samples were homogenized, sieved to 2 mm, and then a 5 g portion was mixed with 25 mL of 2 M KCl while a 1.25 g sample was mixed with 25 mL of 0.5 M $NaHCO_3$. Each sample was shaken vigorously and was left to sit overnight. Samples were filtered through pre-leached Whatman #42 filters and refrigerated until analysis. KCl samples were analyzed for NH_4^+, and NO_3^- using a Lachat Quickchem 8000 autoanalyzer; $NaHCO_3$ samples were analyzed for PO_3^{3-} using a Traacs 800 autoanalyzer (Goldwater Environmental Lab at Arizona State University).

Data Analysis

All specimens were identified to species, when possible (Hickman, 1993; Kearney and Peebles, 1951); nomenclature follows http://plants.usda.gov/. Plants were classified into functional groups based on moisture tolerance (http://plants.usda.gov/), wherein obligate and facultative wetland species are hydric, facultative and facultative upland species are mesic, and upland species are xeric. Herbaceous species were also classified based on phylogeny (monocot/eudicot), lifespan (annual/biennial/perennial), and nativity (http://plants.usda.gov/). Woody species were additionally classified into three levels of disturbance tolerance based on published information (http://www.fs.fed.us/database/feis/) and professional opinion. The species are classified as follows: pioneer species colonize newly disturbed habitats and are shade intolerant, facultative pioneers can colonize disturbed or understory habitats, and secondary successional species can establish in understory habitats.

To assess diversity, the Shannon diversity index was calculated using Estimate S 8.2.0 (Magurran, 2004). For woody communities, the average of 18 ditch plots and 18 randomly chosen river streamside plots were assessed. For herbaceous communities, the average of 90 ditch plots and 90 river streamside plots at each sampling period was utilized. To further assess community diversity, species accumulation curves were generated from 90 herbaceous streamside river plots, 90 herbaceous ditch plots, 179 herbaceous riparian corridor plots, 25 woody streamside river plots, 18 woody ditch plots, and 63 woody riparian corridor plots, using expected richness per plot via Sobs (Mao Tau) in Estimate S 8.2.0 (Colwell *et al.*, 2004).

Species richness was compared between systems using Student's t-tests in PASW 18 (Cooper, 1968; Hill, 1970; Taylor, 1970), with experiment wide alpha set at 0.05. For this analysis, the woody species and herbaceous species were each pooled across plots yielding a sample size of 9 river and 9 ditch sites. All data were assessed for normality using histograms and quantile-quantile plots and transformed when necessary. Levene's test for equality of variances was used to test for homogeneity of variances.

Abundances per plot were compared between systems using Student's t-tests. We tested for significant differences in average cover (canopy cover for woody and ground cover for herbaceous), woody basal area, and woody stem density between ditch and river sites (woody plots and herbaceous plots were averaged at each site for a total of 9 river and 9 ditch sites.)

To evaluate community similarity among and between sites and samples, Bray-Curtis similarity index was calculated in Estimate S 8.2.0 (Magurran, 2004). Bray-Curtis similarity index was used to compare presence or absence of individual species and was weighted by species cover. Modified importance values (Curtis and Mcintosh, 1951) for woody species and functional groups were calculated by averaging relative stem density and relative basal area. Weighted-average wetland indicator scores per site were calculated for herbaceous plant communities. The scores were calculated by first summing cover per site by moisture tolerance: obligate wetland, facultative wetland, facultative, facultative upland, and upland. Then each value was weighted (obligate wetland = 1, facultative wetland = 2, facultative = 3, facultative upland = 4, and upland = 5) and averaged. The result was a wetland indicator score between 1 and 5 where sites with highest cover of wetland species have the lowest score.

To identify how environmental factors correlate with herbaceous composition and cover, data were analyzed using non-metric multidimensional scaling in PC-ORD 5. The abiotic factors included in the secondary matrix were flow variation, channel width, thalweg depth, soil nutrients, soil texture, and soil moisture. Woody basal area was analyzed using unconstrained non-metric multidimensional scaling to determine correspondence of the ditch woody plant communities with those of the riparian corridor.

RESULTS

Diversity

The Shannon diversity index showed no differences for either woody or herbaceous streamside vegetation between river and ditch systems at any sampling period (Table I). Species accumulation curves show more woody species in the ditch system than river streamside (Figure 4a). Species accumulation curves for herbaceous sampling (late summer data) show the same trend of more species along the ditch than the river (Figure 4b). The number of both woody and herbaceous species inhabiting the riparian zone, which was composed of multiple hydrogeomorphic zones, was higher than both the river and ditch streamside.

The average number of woody species per streamside site and the average number of herbaceous species per site did not differ between the ditch and the river (Table II). A total of 27 woody species were found within the streamside river and ditch sites, 20 along the ditches and 13 along the river (Table III). 81 herbaceous species were identified along the banks of both the river and ditch systems across three sampling periods, 68 along the ditches and 46 along the river.

Abundance

There was no significant difference in average woody cover, woody stem density, or woody basal area per plot between streamside river and ditch systems (Table II). Average herbaceous cover also did not differ between the river and ditch at any of the three sampling periods (Table II).

Composition

Importance values for woody species across sites showed greater prevalence of secondary successional species along the ditches, while the rivers were dominated by pioneer species (Table III). Also pronounced was the dominance of hydric species such as *S. gooddingii* and *P. fremontii* along the river, while the ditch was characterized by more mesic and xeric species such as *Fraxinus velutina, P. veluntina,* and *Simmondsia chinensis*. Species stem density and basal area show that ditch woody vegetation was most similar to geomorphic surfaces higher within the riparian corridor with respect to species successional class and moisture requirements (Figure 5).

Herbaceous river and ditch streamside systems differed in their moisture requirements; wetland indicator scores showed ditch vegetation required less water than the river vegetation throughout the year (Figure 6). Although the ditch vegetation differed from the streamside river vegetation in 2009, the riparian corridor herbaceous sampling from 2008 showed the ditch to be more similar to the streamside river than any other position across the riparian corridor (Figure 7).

There was dissimilarity between the ditch and river systems in species composition, based on the Bray-Curtis similarity index. Many paired ditch and river sites had no overlapping woody species, and herbaceous similarity was low across all pairs (Table IV). There was, however, a general trend of increasing similarity between ditch and river communities throughout the growing season (Table V). This dissimilarity arose because ditches contained high cover of spring annuals such as *Hordeum murinum, Bromus diandrus*, *Erodium cicutarium*, *Sisymbrium irio*, *Amsinckia intermedia, Clatonia perfoliata*, and *Bromus rubens*, which were uncommon along the river. The river more often contained stands of clonal species such as *Typha domingensis* or *Schoenoplectus acutus*, which ditches generally lack. A variety of obligate and facultative wetland species such as *Ludwigia peploides, Schoenoplectus acutus, Equisetum arvense, Equisetum laevigatum*, and *T. domingensis* were common along the river, while annuals of a wide range of moisture tolerances, such as *Symphyotrichum expansum, Bidens frondosa, Bassia scoparia, Bromus diandrus*, and *Bromus rubens* were common along ditches. *Paspalum distichum, Polypogon monspeliensis, Polypogon viridis, Cynodon dactylon, Melilotus officinalis*, and *Xanthium strumarium* were among the species common to both the river and the ditches (see Appendix I for a complete list of herbaceous species).

There were only two introduced woody species found in this system, *Ailanthus altissima* and *Tamarix chinensis*. Both species were present at ditch and river sites, but *A. altissima* was mostly along ditches and *T. chinensis* was mostly along the river. The nativity of herbaceous cover was different at the two locations. The river had significantly higher average richness and cover of native herbaceous species than introduced species during most sampling times, while the ditch had higher richness and cover of introduced species than native in April (Figure 8). The elevated levels of introduced species along the ditches in April was due primarily to introduced spring annuals such as *Hordeum murinum, Bromus diandrus*, and *Bromus rubens*, while the perennial *Sorghum halepense* kept introduced cover high throughout the year.

The woody and herbaceous vegetation growing along the ditch did not consistently shift down the length of the ditch in terms of moisture requirements (Figure 9, Figure 10). Bray-curtis similarity indices of adjacent river and ditch sites also show that ditch and river sites did not diverge in similarity down the length of the ditch (Table IV). The only shift down the length of the ditch was the amount of woody secondary successional vegetation compared to pioneer vegetation, which increased (Figure 9).

Abiotic Variables and Relation to Vegetation

River flow rate varied across sites and throughout the sampling period, with major peaks in late May, late July, and early September (Figure 11). The variations in ditch flow rates were restricted to much smaller ranges (Figure 11). As expected, we observed a different flow regime in the river and ditches; the river fluctuated with rainfall and snowmelt patterns, while the ditches remained relatively constant in flow rate due to human intervention. The first site on both the Eureka and Diamond S Ditches had higher variation than the rest of the ditch because the first flow regulating gates were downstream of these study sites; without this regulation, the ditch fluctuated with river flows (Figure 12).

The soils along the river had higher silt contents than those along the ditches; most river soils were silts and silt loams, while ditch soils were loams and sandy loams. Average ammonium did not significantly differ between river and ditch sites in April and August, but soil nitrate/nitrite was significantly higher along ditches than the river in April. Average soil phosphate was significantly higher at ditch sites than river sites in August (Table VI). Average soil moisture along the ditches was lower than the river for each month tested (Table VI). Soil moisture along the ditch banks was lower because consistent water levels restricted soil wetting. Additionally, the ditches were man-made channels that had near vertical banks, causing fluctuation in flow to wet only limited additional soil. The riverbanks, on the other hand, were broad and gradually sloping, allowing small variations in flow to wet a much wider surface area. Soil moisture samples were three sub-samples taken within one meter of the water; the ditch samples often contained both dry and moist sub-samples from this steep physical gradient while the river contained all moist samples.

Non-metric multidimensional scaling showed that soil moisture at river sites and soil phosphate levels at ditch sites explained much of the variation in herbaceous composition between the site types (Figure 13). To understand differences within each site type, ditch and river sites were evaluated independently. The herbaceous vegetation assemblages along the river were related mainly to soil texture and moisture (Figure 14), while the ditch herbaceous vegetation was primarily related to soil ammonium and phosphate content (Figure 15). Unconstrained non-metric multidimensional scaling of woody basal area along the ditches and through the riparian corridor showed that sites grouped along axes of successional status and moisture requirements of plants. Ditch sites were most similar to terrace sites at the later successional and drier ends of the axes (Figure 16).

DISCUSSION

Herbaceous vegetation along the ditches was similar to the river streamside, while woody plants along the ditches were more characteristic of the high floodplain and riparian terraces. Average woody and herbaceous cover or richness per plot did not differ between the streamside ditch and river, but species accumulation curves supported our homogeneity hypothesis of increased species along the ditches. Our hypothesis was further supported by the presence of both wetland and upland herbaceous and woody species along the ditches. Differences in flow regime, soil characteristics, and location within the riparian corridor influenced the observed patters.

Flood disturbance typifies the Verde River, but was limited during this study; neither streamside river sites nor ditch sites received scouring disturbance. In fact, the Verde River has not experienced a peak flow to cause major sediment shift and scouring for multiple years prior to 2009; a peak in 2005 may have caused scouring in certain areas (Haney personal communication). The lack of a recent scouring flood along the river allowed time for post flood establishment of woody vegetation, leading to similarities in vegetation abundance between the ditch and the river. This establishment, however, varies across time and intensity of the flooding event (Friedman *et al.*, 1996). After large flooding events, woody streamside vegetation can be cleared leaving large open patches (Latterell *et al.*, 2006), and post flood reestablishment could progress in a variety of spatial and temporal ways. Our river sites remained influenced by recent flooding, evident by pioneer species, such as *Salix exigua* and *Chilopsis linearis*, which thrive in systems of flood disturbance. The ditches, on the other hand, had increased numbers and importance of later successional woody species. The controlled stream flow most likely prevents common river pioneer species such as *P. fremontii* and *S. gooddingii*, as well as the introduced *T. chinensis*, from recruiting on a large scale. The minimally disturbed floodplain terraces contained more secondary successional species, such as *P. velutina,* which were common along the ditches where there was no flooding disturbance. The relative abundance of secondary successional species also increased down the length of the ditches. The patterns of disturbance tolerance suggest that the observed flow consistency in the ditches remains even through floods, restraining the recruitment of large numbers of pioneer species and maintaining a more stable community.

The presence of surface water is a crucial component in riparian communities of the Southwest (Hupp and Osterkamp, 1996). Both the ditches and river had perennial flow, but the ditch and river riparian vegetation differed in species moisture requirements and the ditches were more diverse. The herbaceous species were probably most influenced by the presence of surface water, as ditches contained hydric species whose roots direct touched surface water or resided within a few centimeters, while mesic or xeric herbs were often found on the steep banks within 50 cm of the water's edge. Mesic and xeric species were not found as often along the gradually sloping river streamside. When comparing the ditch streamside to the floodplain herbaceous cover in 2008, it is obvious that the constant surface water provided by the ditches supported the herbaceous community; the ditch herbaceous cover was more similar to the river streamside community than to any geomorphic surface on the floodplain. Thus, the ditch herbaceous vegetation was representing a modified version of streamside riparian vegetation.

Woody species were probably influenced more by the ground water table than the presence of surface water. Both hydric and mesic trees and shrubs grew in strict proximity to the irrigation ditches that were partially located high within the floodplain; we suspect these plants were tapping into a raised water table created by the ditch seepage which increases diversity and maintains high abundance in the system. The ditch-groundwater interactions are unknown for this location, but research in similar systems has shown that irrigation channel seepage raises local groundwater tables. Irrigation water raises the water table in New Mexico because of water seeping from a similar earthen ditch (Fernald *et al.*, 2007). The Cottonwood Ditch, another ditch along the Verde River, corresponds with elevated water tables in the town of Cottonwood, AZ (personal correspondence Masek-Lopez 2010). The presence of woody phreatophytes growing along our ditches suggests our system could be similar. Despite the raised water table, the location of a portion of the ditches within upland systems contributes to their high numbers of xeric species. Xeric species may be capitalizing on the ground water surrounding the ditches, though studies looking at physiology and upland distribution are necessary.

Along with water and disturbance, other environmental factors may be contributing to the observed plant communities. Soil nutrients were consistently higher along the ditches, while the substrate contained more sand. This trend was unexpected, as soil nutrients are often higher in soils with higher clay content (Stromberg *et al.*, 2009), but the plants themselves may be driving the observed trends. Soil nitrate/nitrite were consistently higher in April along ditch sites adjacent to mesquite (*P. veluntina*) bosques. We suspect that high nutrient litter is causing this increase in soil nitrate/nitrite, as total soil nitrogen increases under *Prosopis spp.* in a variety of settings including river terraces (Perroni-Ventura *et al.*, 2006; Schade and Hobbie, 2005). In addition to the increased Nitrogen, phosphate was higher along the river than the ditch. This nutrient increase may also be correlated with the nitrogen fixing *P. velutina*, as nitrogen has been shown to increase the availability of phosphorus within the soil (Houlton *et al.*, 2008). The availability of these added soil nutrients may contribute to alternate suites of species at specific ditch sites.

Service links

Agencies such as the Nature Conservancy and the Arizona State Parks have invested in protecting the diverse riparian areas along the unregulated, perennial upper Verde River for habitat and recreation through land conservation and the protection of in stream flows. Specifically, the Arizona State Parks has created the Verde River Greenway State Natural Area—a stretch of the river that encompasses our study sites—for conservation and recreation (www.pr.state.az.us/parks/VERI/index.html). Tourism brings many visitors to the Verde Valley, and a study of the nearby Hassyampa River Preserve shows the economic benefit of ecotourism to rural areas in Arizona (Crandall, 1992). If maintaining and preserving riparian vegetation for aesthetics and habitat value is a goal, the historic irrigation canals should also be considered as an area of diverse, riparian vegetation.

Agencies have repeatedly focused on the preservation of *P. fremontii* and *S. gooddingii* forests. These forests are intimately linked with natural flow regimes that include floods and high water tables for recruitment and maintenance, but river damming and dewatering in the southwest has lead to their decline in some rivers (Patten, 1998). These coveted pioneer forests provide habitat for many bird species, but the additional riparian forests that thrive along the irrigation systems throughout the valley may be providing similar services. In near-by Sonora Mexico, riparian trees planted within and around agricultural fields increase the total area of riparian trees by an estimated 10% (Swinton *et al.*, 2006). The presence of woody species along man-made channels may provide bird habitat to help support avian populations and the birding industry. A study on a nearby river found that woody cover, regardless of its composition, can support an abundant and diverse avian community not supported by grassland-like agricultural fields (Brand *et al.*, 2008). Another study suggests that the variation in habitat structure found in riparian buffer strips in agricultural areas increase avian diversity, richness, and abundance (Berges *et al.*, 2010). Studies on the Verde River and its tributaries have focused more on specific habitat types found in the valley. A heterogeneous riparian area composed of broad leaf deciduous trees contained higher avian density and diversity than adjacent uplands (Stevens, 1977), but homogeneous *P. fremontii* stands contained higher density and diversity of breading pairs than heterogeneous broad leaf deciduous forests (Carothers, 1974). Studies agree that avian species are specific to habitat type (Mount, 1997; Carothers, 1974; Brand *et al.*, 2008), but since the irrigation ditches are heterogeneous along their length, containing *P. fremontii* and other broad leaf trees, the ditch-specific evaluation of avian communities is needed.

Although the herbaceous vegetation along the ditches is similar to the river streamside, they also host some herbaceous species of interest to stakeholders in the Verde Valley. *S. halepense* is an introduced species of particular interest to farmers using irrigation water because it is considered an agricultural weed. This species is, however, is a perennial grass that may benefit the irrigation corporations. Bank stability in the irrigation ditches is a major concern because sliding banks can decrease water delivery efficiency. Perennial grasses have been shown to have a dense root system, which contributes to bank stability by preventing soil erosion (Gyssels and Poesen, 2003). *S. halepense*, as with other species, has multiple roles within the agroecosystem.

CONCLUSIONS

In support of our first hypothesis, we saw more disturbance tolerant species along the river than along the ditch, but the more variable flow regime of the river did not lead to higher diversity. Our alternative hypothesis relating to heterogeneity and diversity was more strongly supported—a mixture of wetland and upland species were found along the ditches, and the ditches contained more species. Compositionally, the herbaceous vegetation along the ditches was most similar to the river streamside than any location in the riparian zone, and trees, shrubs, and herbaceous vegetation shared similar abundance along the streamside of both systems. The woody vegetation along the ditches was characterized primarily by plants requiring less moisture and less dependent on disturbance for establishment than the river streamside. The heterogeneity due to water availability, soil characteristics, and spatial position of irrigation system appear to drive the composition of this man-made riparian system.

The irrigation system differs from the natural stream in the assemblage of species it supports, but it does support riparian vegetation and habitat along its banks that would not be possible without the irrigation water, or without this now unique unlined structure. The man-made system may provide similar services as natural riparian areas along with its main function of providing water for the local agricultural community. Thus, this historic system should be further evaluated as a multifunctional system, providing services not only to the agricultural users, but also to a variety of stakeholders in the community.

Table I. Shannon's index (H') shows similar diversity of the herbaceous and woody vegetation along the streamside of the Verde River and along the streamside of the adjacent irrigation ditches.

	Herbaceous		Woody	
	River	Ditch	River	Ditch
April	2.78	2.50		
June/July	3.00	2.91	1.79	2.06
August	3.08	3.06		

Table II. There was no significant difference in the average number of species (per m^2 for herbaceous and per 100 m^2 for woody), cover (ground cover for herbaceous and canopy cover for woody), woody basal area, or woody stem density per site between the Verde River and irrigation ditch streamsides (SD = standard deviation, n = 18, alpha = 0.05).

			Herbaceous			Woody		
			Mean	SD	*p*	Mean	SD	*p*
Number of species	April	Ditch	13.0	4.2	0.51			
		River	11.8	3.4				
	June/July	Ditch	14.9	7.5	0.71	4.7	3.0	0.52
		River	15.9	2.4		5.6	2.8	
	August	Ditch	11.1	3.8	0.48			
		River	12.3	3.3				
Cover (%)	April	Ditch	69.3	23.3	0.16			
		River	82.3	11.2				
	June/July	Ditch	72.6	19.9	0.08	41.2	34.4	0.72
		River	86.2	6.4		46.3	22.9	
	August	Ditch	60.8	37.6	0.73			
		River	65.4	12.4				
Basal Area ($m^2/100m^2$)	June/July	Ditch				2.0	1.5	0.4
		River				2.5	1.1	
Stem Density (no./$100m^2$)	June/July	Ditch				8.3	1.5	0.45
		River				8.8	1.2	

Table III. Woody species present along the Verde River and irrigation ditch streamsides in 2009 and across the riparian zone in 2008. Species in the floodplain are divided into geomorphic zones: streamside (SS), lower floodplain (LFP), overflow channel (OC), high floodplain (HFP), and terrace (T). Species are categorized by moisture requirement and successional class. Values shown for the ditch and river species in 2009 are Importance Values.

					Riparian Corridor				
Moisture Class	Successional Status	Species	Ditch	River SS (2009)	River SS (2008)	LFP	OC	HFP	T
Hydric	Pioneer	*Alnus oblongifoli*				X			
		Baccharis salicifolia	5	1	X	X	X	X	
		Platanus wrightii		2					
		Salix exigua		2	X				
		Salix gooddingii	4	19	X	X	X	X	
		Populus fremontii	5	25	X	X	X	X	
	Facultative Pioneer	*Amorpha fruticosa*		1					
Mesic	Pioneer	*Baccharis sarothroides*	< 1				X		
		Chilopsis linearis		3		X	X	X	
		Tamarix chinensis	5	26	X	X		X	
	Facultative Pioneer	*Ailanthus altissima*	13	5		X		X	X
		Fraxinus velutina	8	5		X		X	
	Secondary successional	*Acer negundo*	1		X	X		X	
		Celtis laevigata var. reticulata	4			X	X	X	X
		Forestiera pubescens var. pubescens	< 1			X		X	
		Juglans major		< 1			X	X	X
		Morus sp.		< 1		X			
		Prosopis velutina	32				X	X	X

Table III. (*Continued*)

Moisture Class	Successional Status	Species	Ditch	River SS (2009)	River SS (2008)	LFP	OC	HFP	T
Xeric	Pioneer	*Hymenoclea monogyra*		8			X	X	
	Facultative Pioneer	*Atriplex canescens*	2						
		Ephedra sp.	< 1						
		Robinia neomexicana	1						
	Secondary successional	*Acacia greggii*	7						
		Canotia helocantha	1						
		Juniperus cf. monosperma				X			X
		Larrea tridentata	< 1						
		Mahonia fremontii				X	X		
		Rhus trilobata				X			
		Rhus trilobata	<1						
		Simmondsia chinensis	9						
		Ziziphus obtusifolia var canescens	2					X	X
Total Species			20	13	6	15	10	14	6

Table IV. Bray-Curtis similarity indices for Verde River and adjacent irrigation ditch streamside sites show low similarity between the two systems with respect to both herbaceous and woody vegetation (DSD = Diamond S Ditch, ED = Eureka Ditch, HD = Hickey Ditch; sites are numbered in the downstream direction.)

	Woody	Herbaceous		
	July	April	June	August
DSD1:2	0	0.047	0.126	0.094
DSD3:4	0	0.024	0.202	0.148
DSD5:6	0	0.179	0.096	0.392
ED1:2	0.248	0.476	0.134	0.201
ED3:4	0.016	0.162	0.120	0.120
ED5:6	0.426	0.222	0	0.006
HD1:2	0	0.025	0	0
HD3:4	0	0	0.106	0.007
HD5:6	0.002	0.095	0.144	0.060

Table V. Bray-Curtis similarity indices show that ditch and river herbaceous vegetation, pooled across sites, are dissimilar in all months, but similarity does increase throughout the growing season. Herbaceous vegetation along the river is similar between all months of collection, but ditch vegetation in April is different than ditch vegetation in June and August.

		River			Ditch		
		April	June	August	April	June	August
River	April	1	----	----	----	----	----
	June	0.732	1	----	----	----	----
	August	0.724	0.853	1	----	----	----
Ditch	April	0.175	----	----	1	----	----
	June	----	0.284	----	0.322	1	----
	August	----	----	0.365	0.31	0.711	1

Table VI. Average soil moisture was higher along the river than along the ditches at all months tested. Soil nitrate/nitrite was significantly higher along the ditches in April and soil phosphate was significantly higher in the ditches in August, but soil ammonium did not differ in either month tested (* denotes significance, alpha = 0.05, n = 18).

		April			June			August		
		Mean	SD	p	Mean	SD	p	Mean	SD	p
Soil Moisture	River	0.37	0.19	0.02*	0.38	0.10	0*	0.47	0.26	0.01*
(g/g dry soil)	Ditch	0.18	0.14		0.11	0.1		0.18	0.10	
Nitrate/ite	River	2.43E-7	6.00E-7	0.02*				7.11E-6	3.51E-6	0.14
(g/g dry soil)	Ditch	4.46E-6	4.97E-6					4.92E-6	2.24E-6	
Ammonia	River	5.47E-6	5.57E-6	0.97				2.39E-6	6.45E-6	0.89
(g/g dry soil)	Ditch	4.63E-6	2.27E-6					8.41E-6	8.25E-6	
Phosphate	River	1.02E-5	1.20E-5	0.06				1.06E-5	5.22E-6	0.03*
(g/g dry soil)	Ditch	2.14E-5	1.08E-5					1.75E-5	6.55E-6	

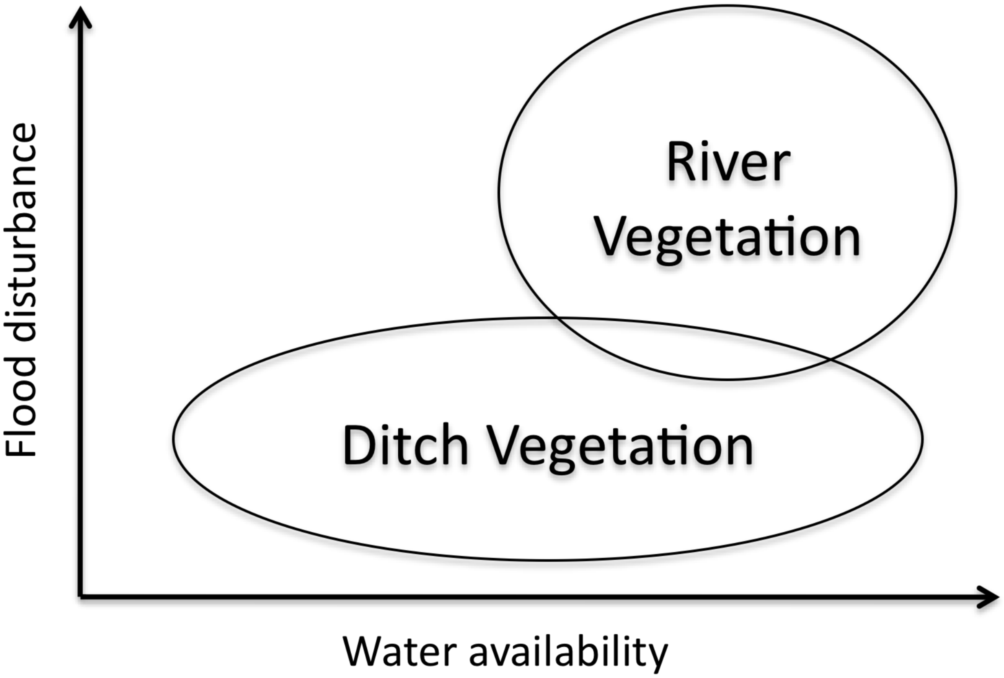


Figure 1. Hypothesized vegetation characteristics along the river and ditch, where the river contains primary successional vegetation with high moisture requirements and the ditch contains later successional vegetation with a range of moisture requirements.

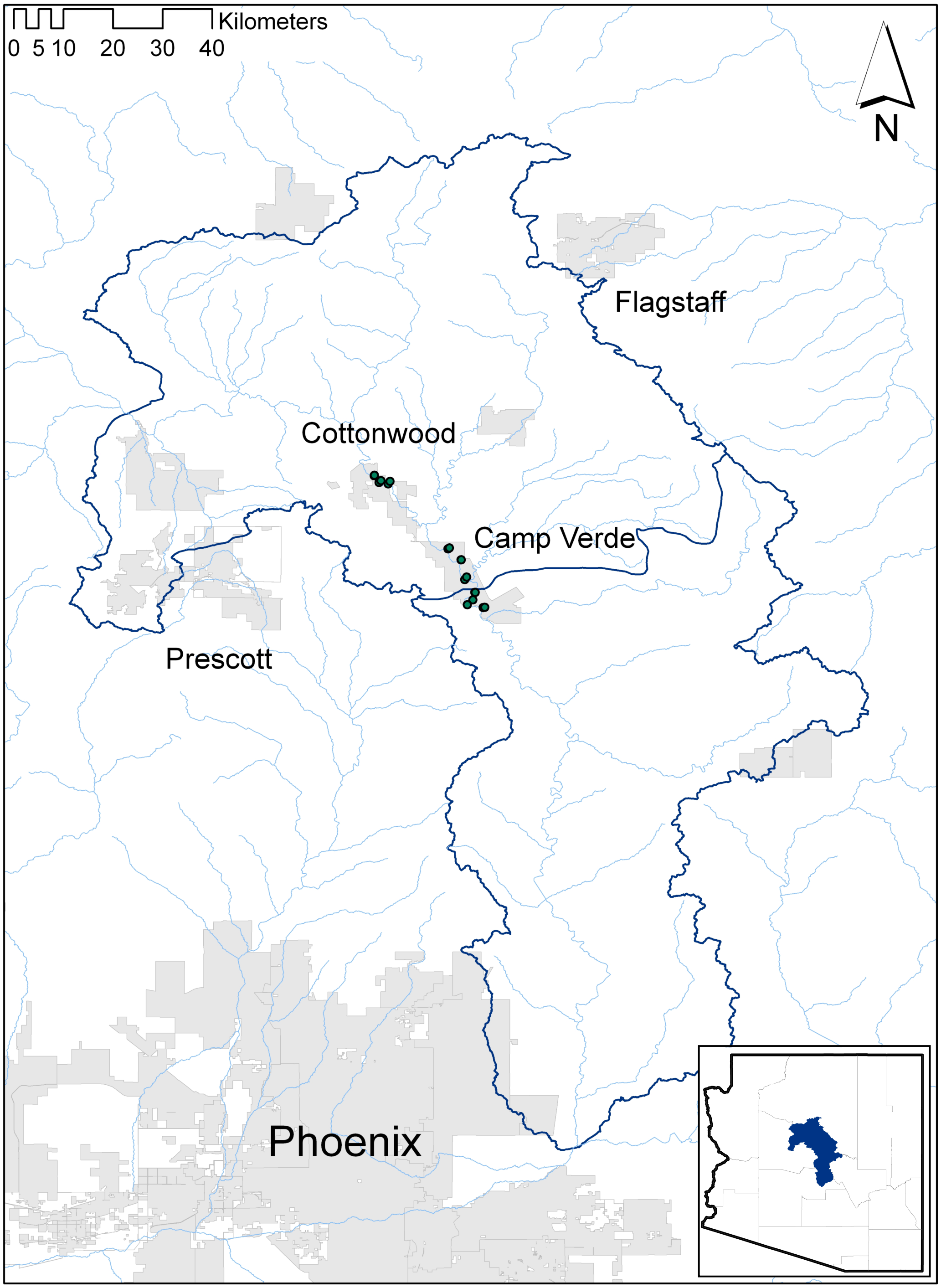


Figure 2. Map with points showing the 18 study sites (9 river, 9 ditch) within the Verde River watershed. Study sites were located between Cottonwood and Camp Verde, AZ, USA.

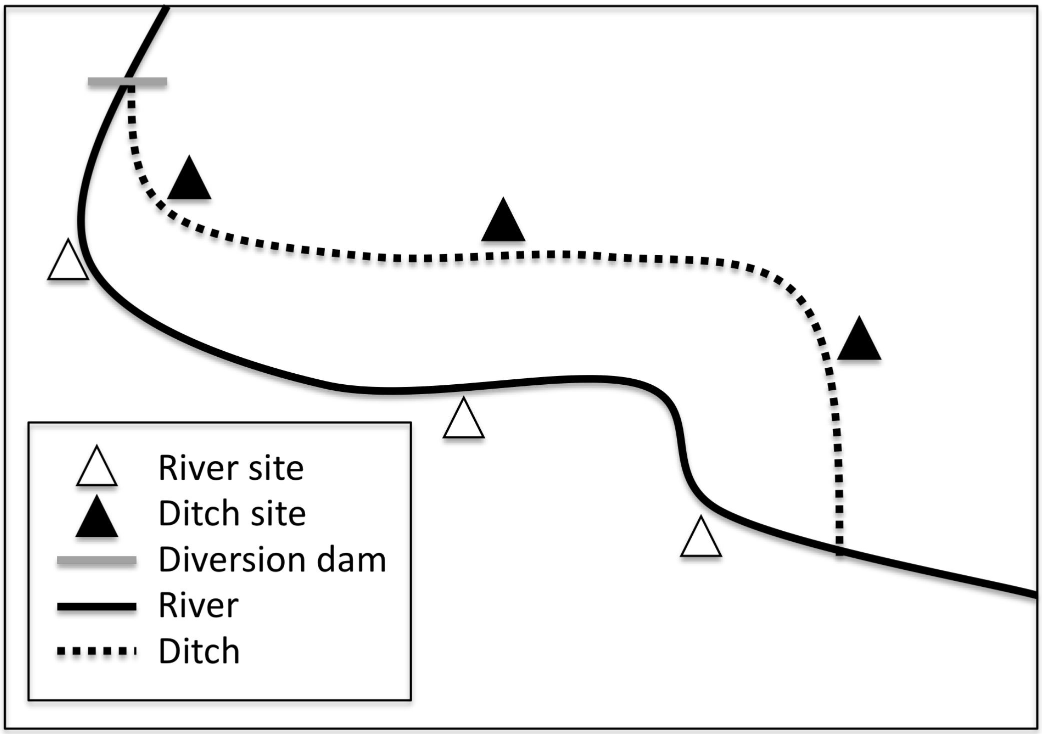


Figure 3. Study sites along each ditch were paired with an adjacent river site. This design was repeated for the three ditches, resulting in a total of 9 ditch study sites and 9 river study sites.

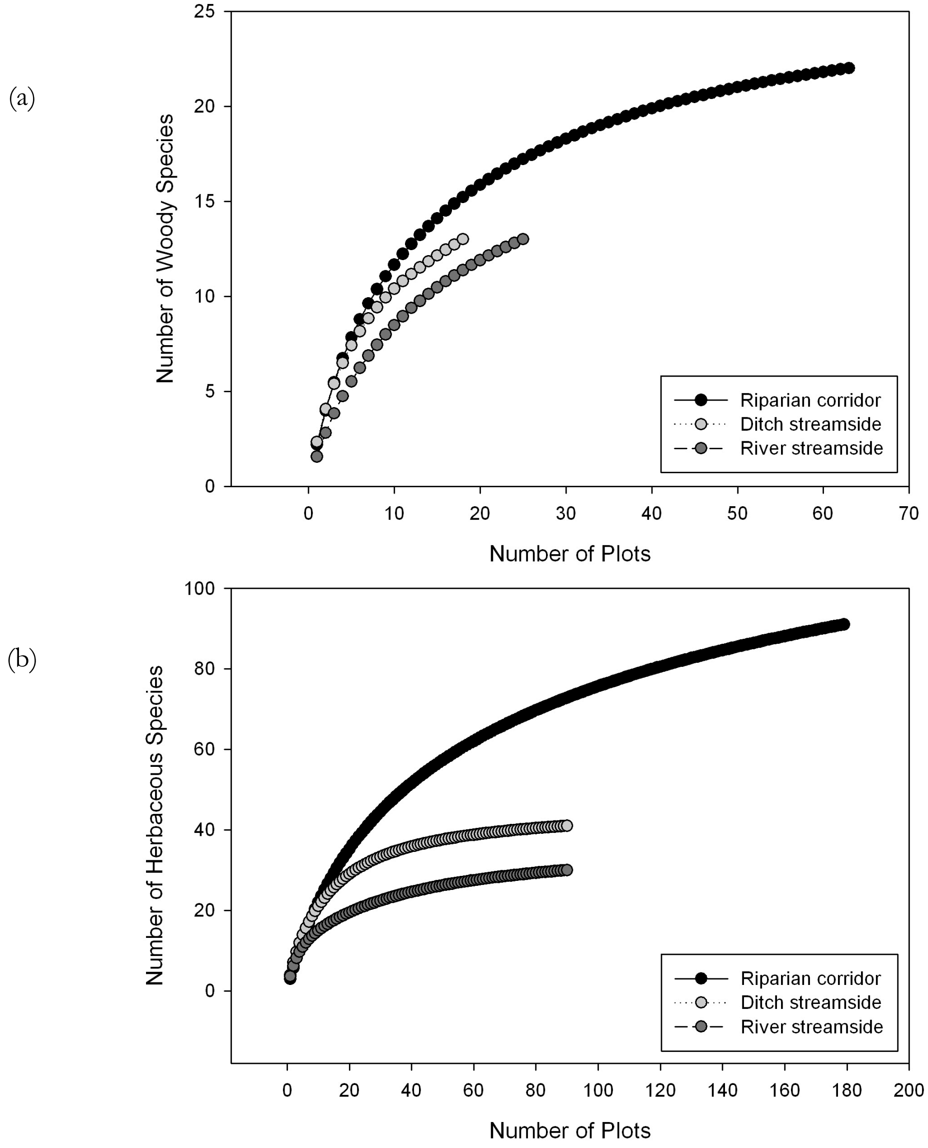
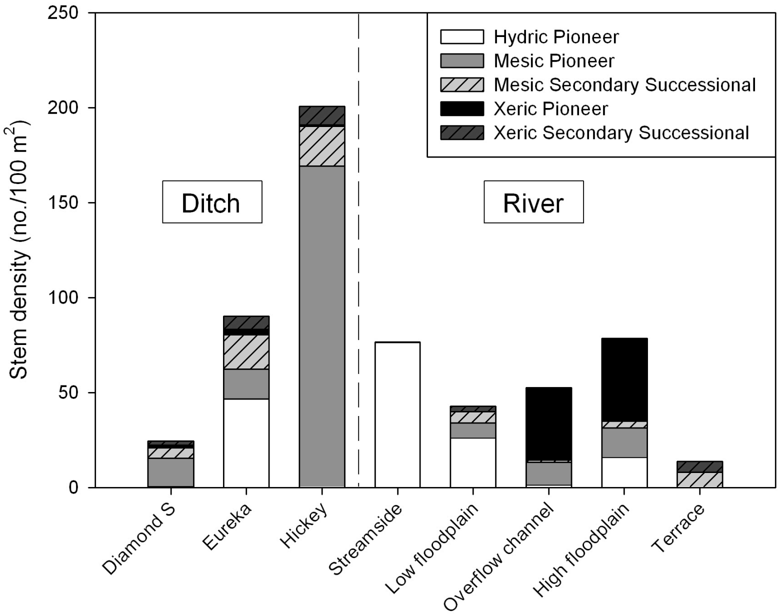


Figure 4. Species accumulation curves for both woody (a; 100 m^2 plots) and herbaceous (b; 1 m^2 plots) show the riparian corridor to have the highest number of species. The ditch streamside supports fewer species than does the entire riparian zone, and the river streamside supports the fewest species.



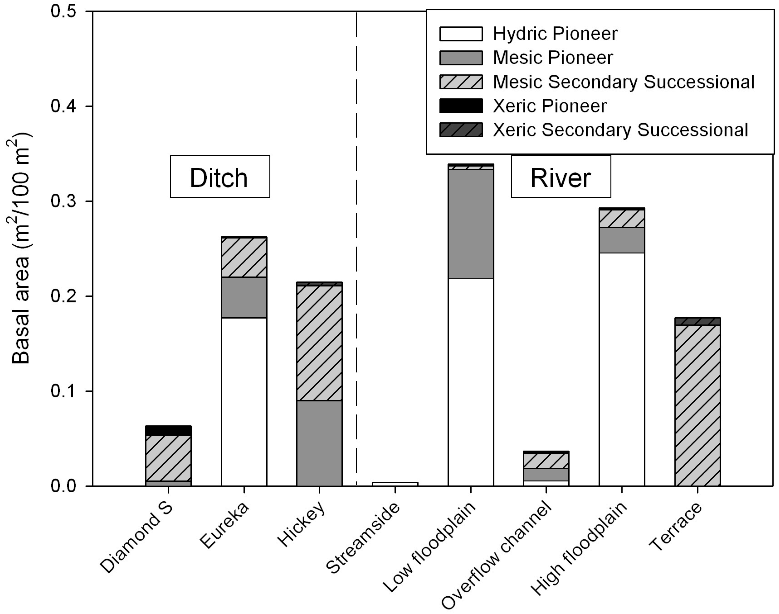


Figure 5. Average woody stem density and basal area, by plant functional group, at each ditch (2009 data) and by hydrogeomorphic zone in the riparian corridor (2008 data) shows the ditches corresponding most strongly with the species found along the high floodplain and terrace.

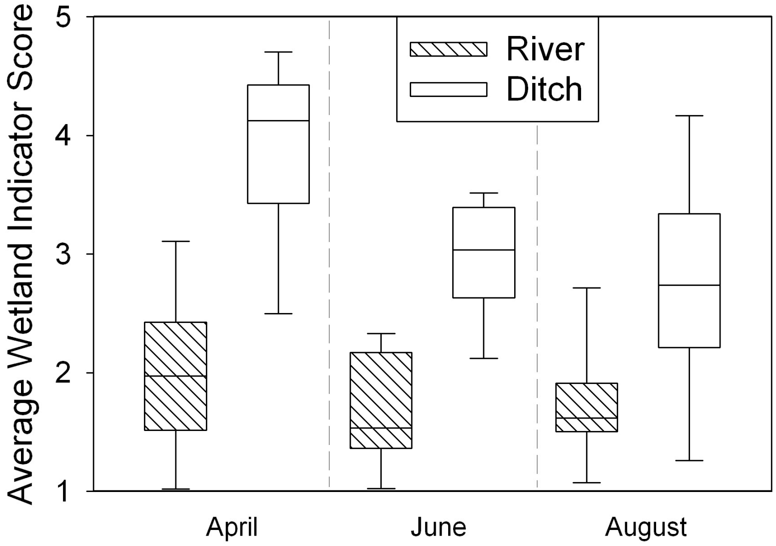


Figure 6. Wetland indicator scores show higher dominance of herbaceous wetland species along the river streamside than along the ditches across all sampling periods (1 = obligate wetland, 5 = upland). Wetland indicator scores were significantly higher along the ditches during all seasons sampled (April $p < 0.001$, June $p < 0.001$, August $p = 0.01$).

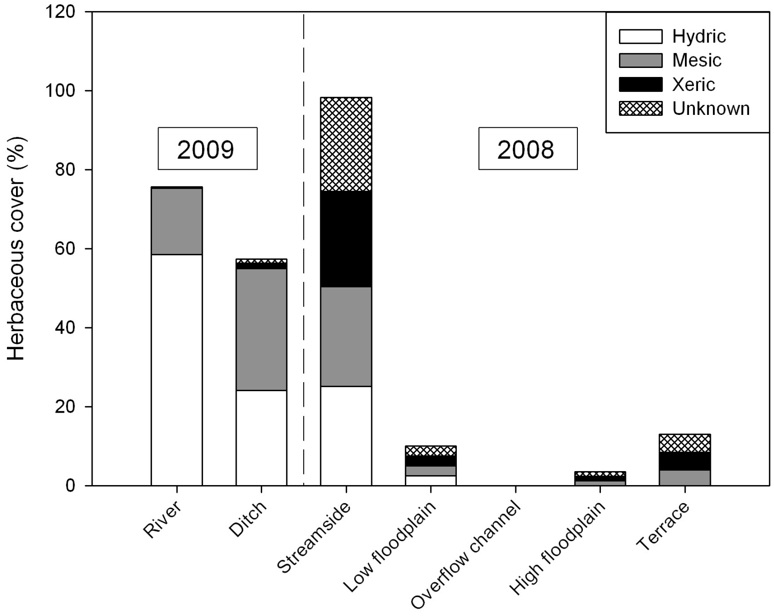
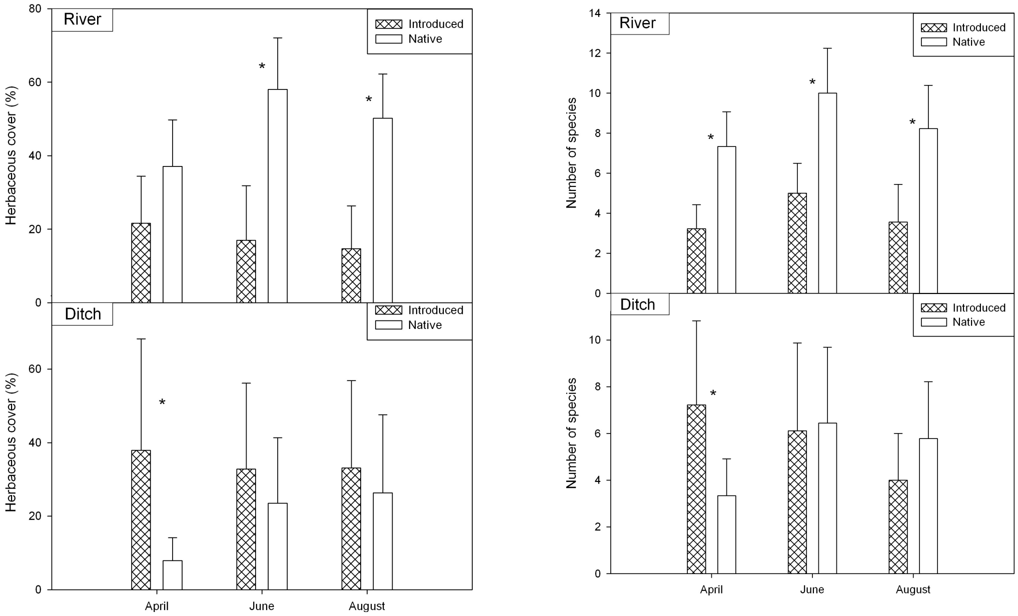


Figure 7. While herbaceous river and ditch streamside vegetation differed in 2009, vegetation along the ditch was more similar to river streamside vegetation than to any other hydrogeomorphic zone within the riparian corridor.



(a) (b)

Figure 8. There was higher cover (a) and richness (b) of native herbaceous species than introduced species per plot along the river at most sampling periods. Ditch communities had higher cover and richness of introduced species than native in April. (* denotes significance, alpha = 0.05)

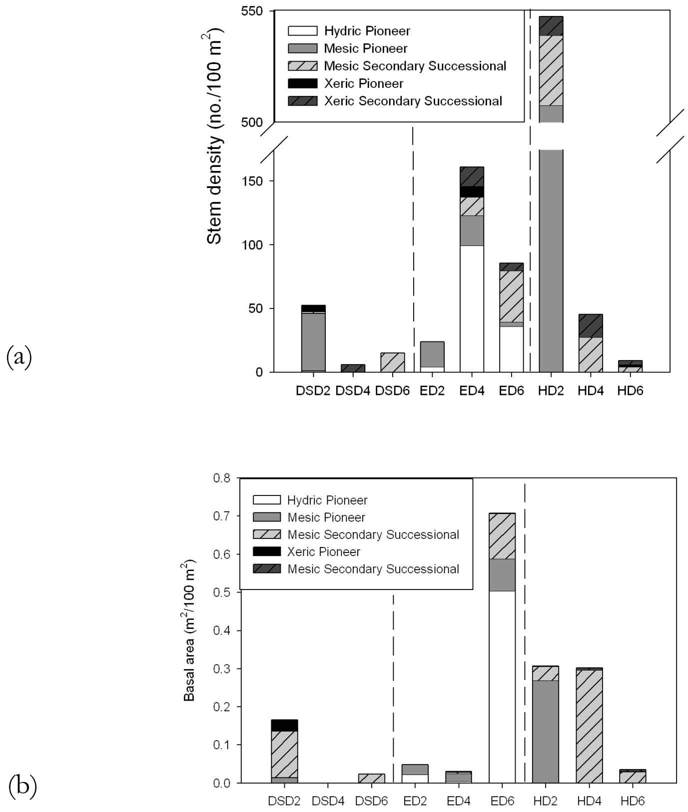


Figure 9. There was no trend of total stem woody density (a) or basal area (b) shifting down the length of the ditches (sites numbered in the downstream direction). There was also no consistent trend of shifts in moisture requirement of species down the length of the ditches. Secondary successional species compared to pioneer species increased down the length of each ditch.

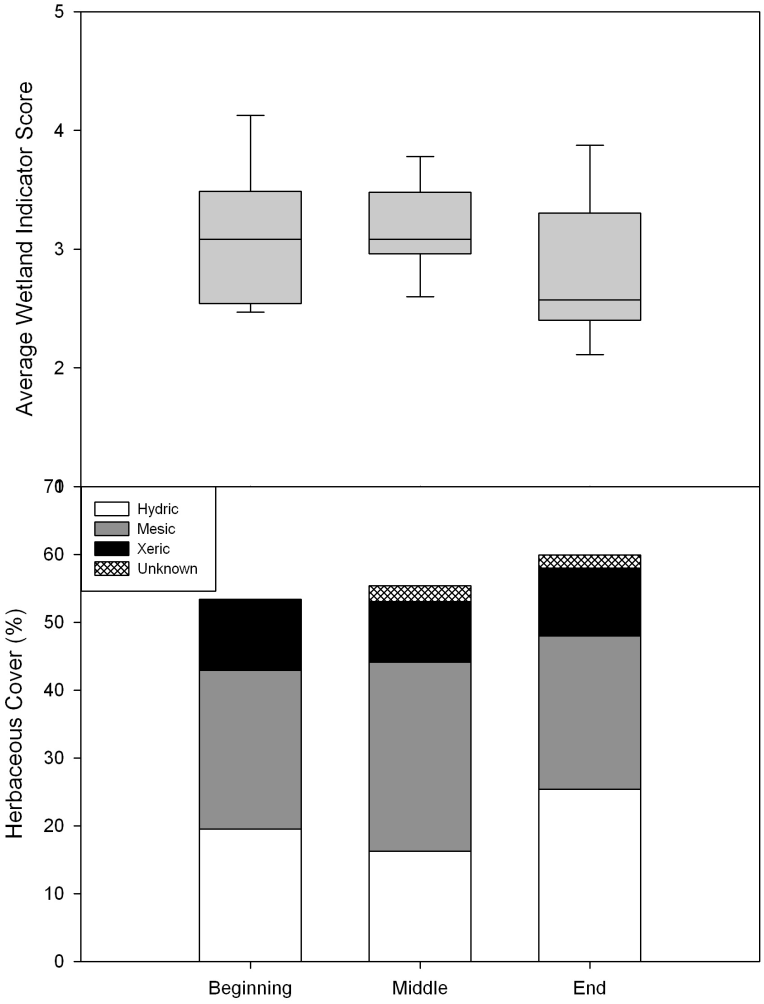


Figure 10. Neither average herbaceous wetland indicator score, nor herbaceous cover by moisture class, differed down the length of the ditch.

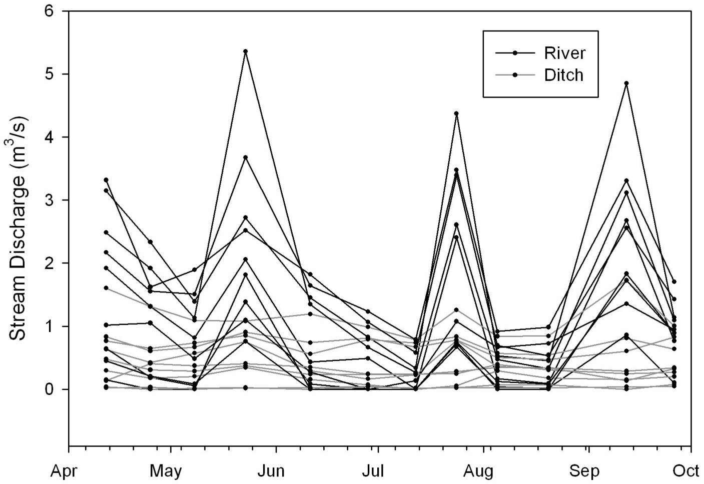


Figure 11. Stream discharge was more seasonally variable in the Verde River than in the irrigation ditches (based on 12 measurements at 18 sites in 2009).

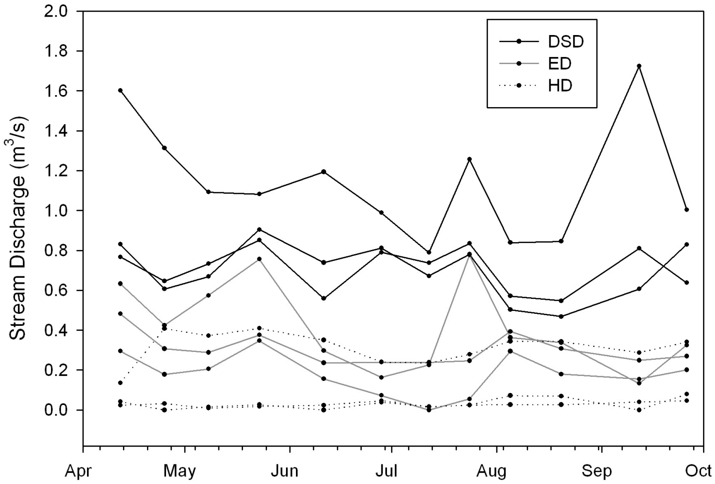


Figure 12. Stream discharge of irrigation ditches; the highly variable Diamond S Ditch (DSD) site and Eureka Ditch (ED) site are the sites nearest to the intake of each ditch. Sites located upstream of the first flow regulating gates showed fluctuation with the river. (HD = Hickey Ditch)

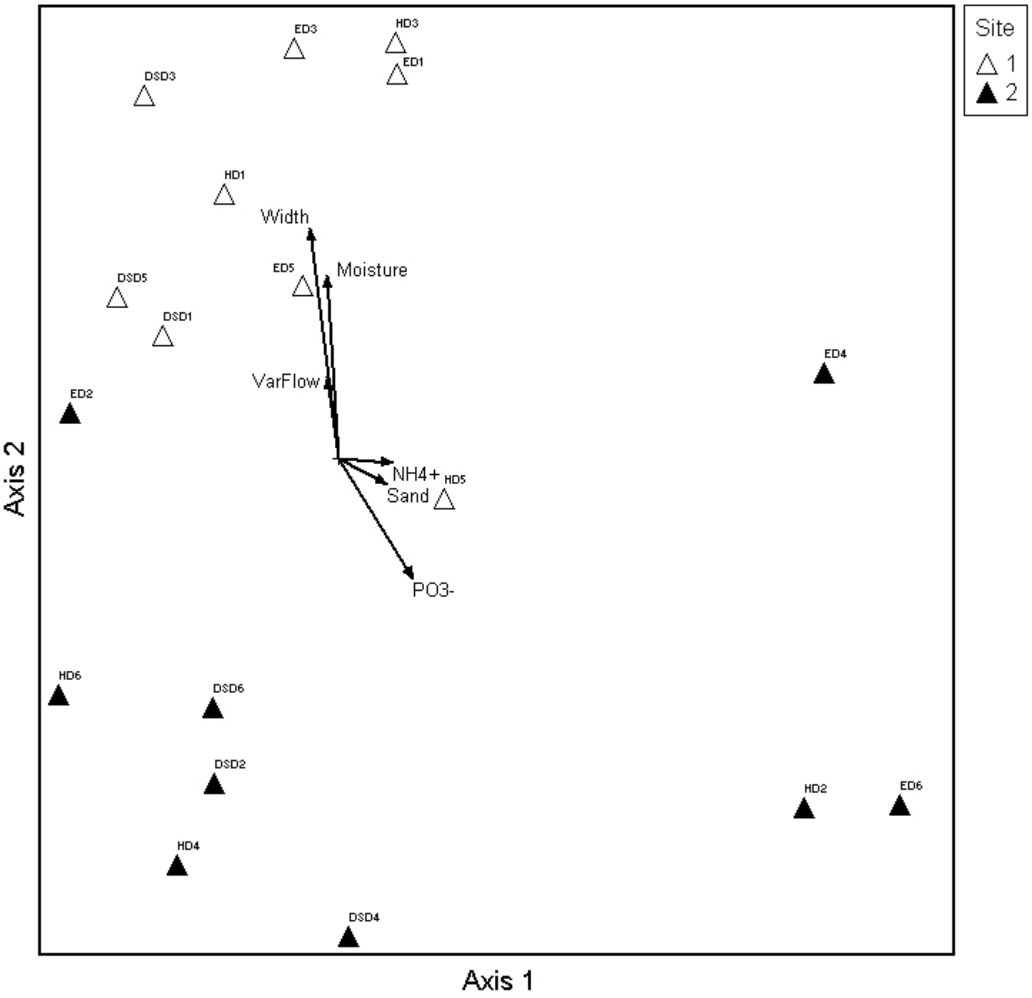


Figure 13. Non-metric multidimensional scaling biplot shows that river (1) and ditch (2) streamside herbaceous vegetation differed along gradients of soil moisture, stream width, flow variation, soil texture, and soil nutrients. River sites had higher soil moisture, while ditches had higher phosphate.

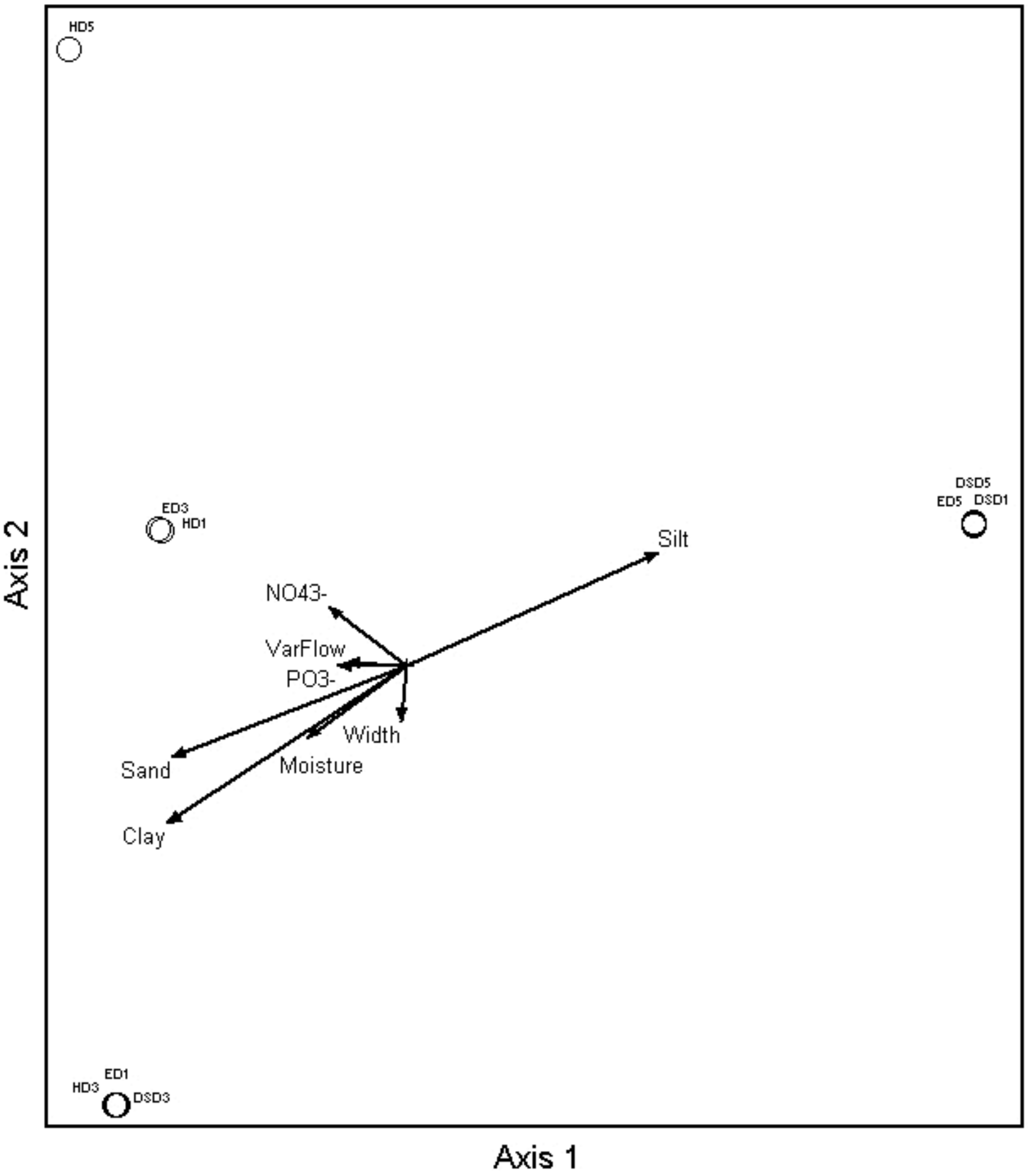


Figure 14. Non-metric multidimensional scaling biplot of river sites shows that differences in soil texture and soil moisture are related to herbaceous vegetation assemblages along the river streamside.

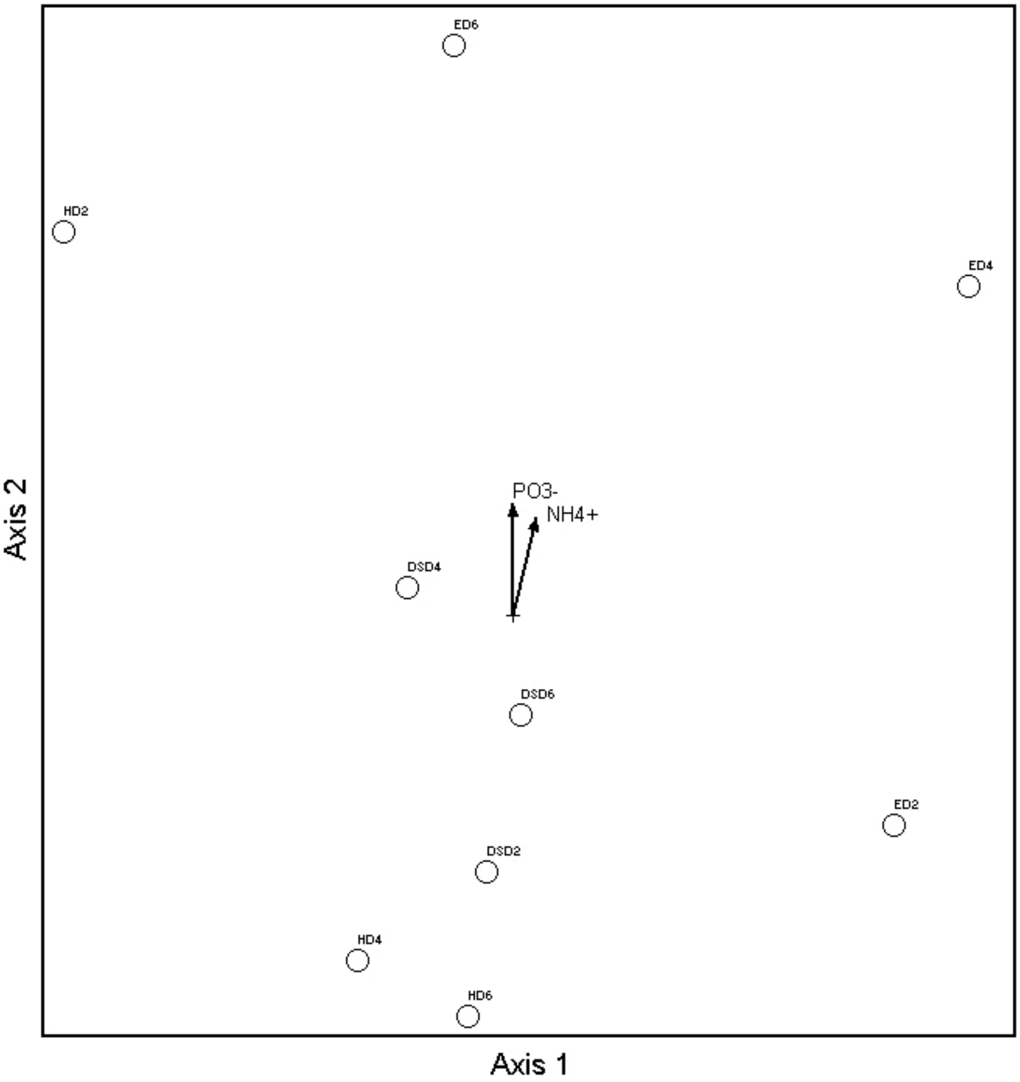


Figure 15. Non-metric multidimensional scaling biplot of ditch sites shows that a gradient of soil ammonium and phosphate is related to herbaceous vegetation assemblages along the ditch streamside.

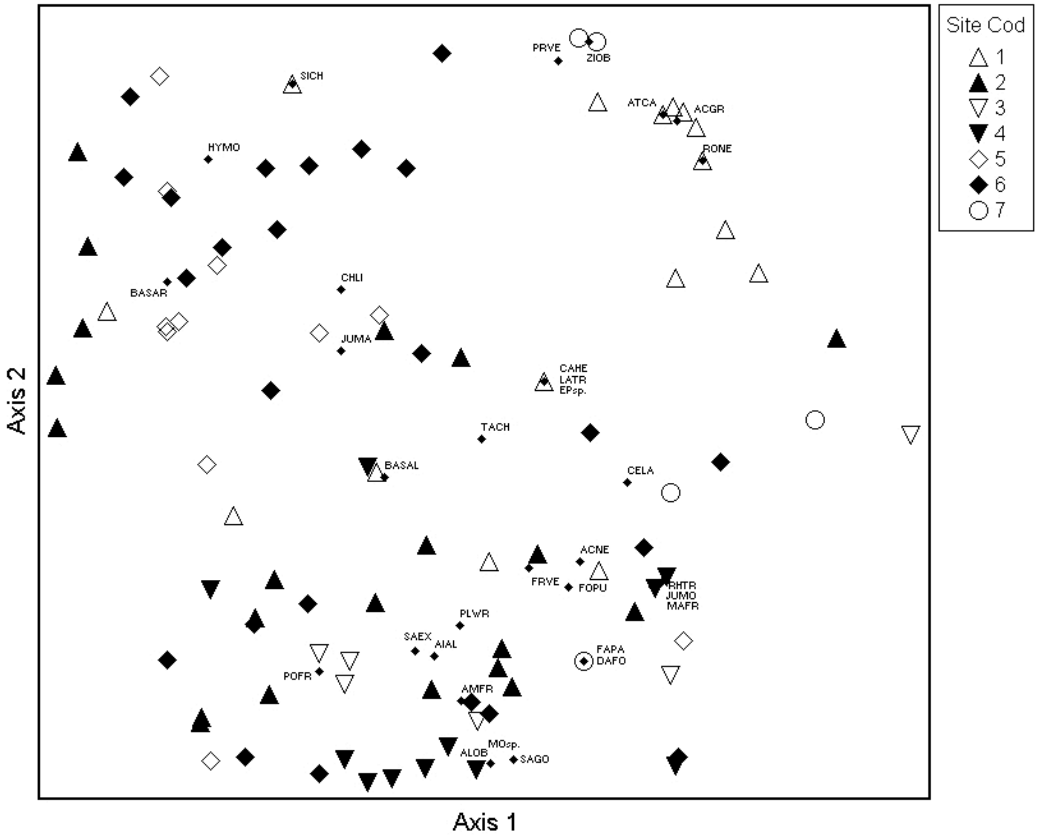


Figure 16. Non-metric multidimensional scaling biplot of ditch streamside and riparian corridor shows sites distributed along an inferred successional axis (Axis 1) and a water availability axis (Axis 2). Many ditch sites fell at the later successional and dry ends of these axes along with terrace plots. Woody species are labeled with four letter abbreviations of scientific name (exceptions: *Bacharis salicifolia* = BACSAL, *B. sarothroides* = BASAR, see Table II for full names). 1 = ditch plots, 2 = river plots (2009), 3 = river streamside plots (2008), 4 = low floodplain plots, 5 = overflow channel plots, 6 = high floodplain plots, 7 = terrace plots.

3. HYDROCHORY IN A SEMI-ARID STREAM

SUMMARY

Hydrochory—the dispersal of seeds via water—is an influential dispersal mechanism for the establishment and maintenance of riparian plant communities. In dynamic semi-arid streams, patterns of hydrochory have been underrepresented in the literature. In this study, we examined how hydrochore abundance, species richness, and composition vary with stream flow rate, time of year, and position within the water column. In addition, we asked how hydrochores relate to seeds deposited on the riverbank and to extant vegetation in the system. We strained hydrochores from the Verde River, AZ, USA across six months of the growing season. Herbaceous and woody vegetation sampling and litter/soil seed bank collections were taken across the same six-month season. Hydrochore richness and abundance were both influenced by seasonality and both increased with stream flow. We observed three species-specific hydrochory strategies for how species are utilizing water for dispersal—pulse species disperse in the water in accordance with their short dispersal phenology, constant species disperse using water throughout the year, and combination species show characteristics of both. Although there was limited similarity between hydrochores and the extant vegetation, our species-specific hydrochory strategies provide evidence for how species utilize seasonal flows for dispersal within the riparian system.

INTRODUCTION

As sessile organisms, plants require specific adaptations to overcome spatial barriers and propagate in safe sites distributed across the landscape (Grubb, 1977; Harper, 1977). Types of dispersal are highly variable within and across species and communities, but one method of dispersal has been increasingly studied within rivers and riparian areas—hydrochory. Hydrochory, the dispersal of diaspores via water, is thought to be a secondary dispersal mechanism derived from modifications for wind dispersal (anemochory) for non-aquatic plants (van der Pijl, 1982). In this riparian context, we are specifically referring to nautohydrochory, dispersal via flowing water, but we use the term hydrochory for simplicity.

High and low river flow pulses are linked to specific seasonal weather patterns, as are the biological processes of flowering, fruiting, dispersal, and germination. Many studies have suggested the important connection of stream flows and dispersal phenology of plants for successful recruitment and establishment (Jansson *et al.*, 2005a; Merritt and Wohl, 2002; Merritt and Wohl, 2006; Staniforth and Cavers, 1976). Discharge peaks are especially important for riparian species that often require scoured or moistened stream banks as safe sites for germination. Flooding has been shown to increase species richness in riparian plant communities because of hydrochore deposition (Jansson *et al.*, 2005b), and certain riparian species even have dispersal from the parent plant coupled to seasonal discharge fluxes (Luzuriaga *et al.*, 2005; Stella *et al.*, 2006). In a swamp forest, predictable shifts in water depth and velocity also correlated with the numbers of trapped hydrochores (Schneider and Sharitz, 1988). In some hydric-region rivers, highest species richness and hydrochore numbers have been documented at highest discharge (Boedeltje *et al.*, 2004), while in others highest species richness and hydrochore numbers occurred at different times of the year than the highest discharge (Moggridge *et al.*, 2009). A working knowledge of the flow regime of a riparian ecosystem is an important component of understanding its influences on dispersal within the system.

Studies have discovered links between stream hydrochores and the extant plant community, suggesting that hydrochory plays an important role in riparian plant community structure (Boedeltje *et al.*, 2003; Johansson *et al.*, 1996; Merritt and Wohl, 2002; Nilsson *et al.*, 1991a). Trapped hydrochores in a European river were related to both the adjacent aquatic and riparian plants, though the relationship was stronger with the aquatic plants (Boedeltje *et al.*, 2003). In an experiment using artificial seeds (wooden cubes), Nilsson and others (1991a) suggest that floating time of hydrochorous seeds may be an important element for structuring riparian plant communities, and longer floating diaspores have indeed been shown to be more prevalent in the extant streamside vegetation (Johansson *et al.*, 1996). While multiple studies have focused on floating ability, the placement of hydrochores within the water column has been largely unstudied. One study noted the prevalence of specific hydrochores with the top of the water column (Staniforth and Cavers, 1976), but a few have discussed transport with respect to river roughness. Turbulent water has been hypothesized (McAtee, 1925) and documented (Merritt and Wohl, 2006) to contain more seeds traveling as submerged than surface hydrochores, but the concept is scarcely documented.

Once deposited in the stream margin or floodplain by flowing water, a seed may germinate or become incorporated into the litter or soil seed bank; colonization can then occur in the future via persistence in the litter or soil seed bank (Menges and Waller, 1983). The variation in longevity of a seed and its likelihood of being buried influence how it will colonize an area. Persistent seeds can live in the soil seed bank for many years, while transient seeds survive less than one year (Thompson and Grime, 1979). After a disturbance, soil seed banks are particularly important as a means of colonization (Luzuriaga *et al.*, 2005).

The first objective of this study was to determine patterns of hydrochory within the Verde River—a semi-arid stream. Specifically, we asked how hydrochore abundance, species richness, and composition vary with stream flow rate, time of year, and position within the water column. We expected to see greater abundance of hydrochores with peak flows from snowmelt in April, and peak flows from monsoon rains in August and/or September. In addition, we expected greater richness during peak flows, due to input of seeds from tributaries, and during seasons with abundant seed maturation. Our second objective was to evaluate the relationships between hydrochory, the litter/soil seed bank, and the extant vegetation. We expected hydrochores to be more similar to the soil/litter seed bank than to the extant vegetation because both hydrochorous and deposited seed banks account for spatial and temporal variability not exhibited in extant vegetation throughout the year.

STUDY SITE

This study was conducted along the middle Verde River near Camp Verde (34° 46', 112° 02'; elevation ca. 950 m) and Cottonwood (34° 31', 111° 50'; elevation ca. 1000 m), Arizona, USA (Chapter 1). Mean annual temperature is 16.7 °C and mean annual precipitation is 29.6 cm. The middle Verde is in the Transition Zone physiographic province, between the Colorado Plateau and the Basin and Range. The river is spring fed at the headwaters and further provided with water by a number of tributaries, including Oak Creek and Beaver Creek. The river flow rate is strongly influenced by monsoon and winter rains and spring snowmelt. Monsoon rains cause annual flooding from late July through September, while winter rains and snowmelt can cause floods through April. The river is characterized by low flow conditions in dry winters and during the dry summer months of May, June, and July.

The Verde River varies in low flow channel width within the study area, ranging from two to fifty meters wide. Flow rates at low flow conditions range from 1.7-2.3 m^3/s

north of Cottonwood (Verde River Near Clarkdale, USGS 09504000; <http://waterdata.usgs.gov>) to 1.1-2.8 m^3/s south of the Camp Verde (Verde River Near Camp Verde, USGS 09506000; <http://waterdata.usgs.gov>). The gauge at Camp Verde includes flow from a 10,914 km^2 drainage area. A series of six earthen dams divert water from the river along the study area for irrigation, but the river is unregulated. The river levels fluctuate despite the dams, which are often destroyed and rebuilt after flooding events.

The plant community along the Middle Verde is Sonoran and Interior Riparian Deciduous Forest and Woodland, while Plains and Desert Grassland and Sonoran Desertscrub (Arizona Upland Subdivision) characterize adjacent uplands. The growing season encompasses the warm months of April through October. Average temperatures dip below freezing during the winter months and spring runoff may continue through April, restricting herbaceous growth. A few riparian species begin to set fruit and disperse seeds in May, but the number of species fruiting continues to increase through August. Both fruiting and dispersal then decline in October, with increased senescence.

The river margins are characterized by *Populus fremontii*, *Salix gooddingii,* and *Tamarix chinensis* woodlands or forests. Further from the channel, *Chilopsis linearis*, *S. gooddingii,* and *T. chinensis* shrublands and woodlands or open forblands dominated the floodplain. In many areas old stands of *P. fremontii* are found within areas otherwise devoid of woody vegetation. Streamside herbaceous vegetation is variable along the river, but often contains stands of obligate and facultative wetland, clonal species such as *Typha domingensis*, *Schoenoplectus acutus*, *Ludwigia peploides, Schoenoplectus acutus, Equisetum arvense,* and *Equisetum laevigatum*.

METHODS

Experimental Design

This descriptive field study compared water-dispersed seeds, the litter/soil seed bank, and streamside vegetation along a semi-arid stream throughout the growing season.

Nine study sites for water-dispersed and litter/soil seed bank collection align with sites for vegetation monitoring (see Chapter 1).

Hydrochory

Water-dispersed seeds were collected twice a month, April through September 2009, using methods modified from Merritt and Wohl (2006). Two seed traps constructed from 0.25 mm polyester mesh were used to capture water-dispersed seeds. The traps have an expanded orifice, with a 120.4 cm^2 opening, which helps decrease the loss of seeds through backflow. Two traps were suspended from a pole held in the thalweg of the channel for 30 minutes at each study site; one trap was floated at the surface while the other was suspended at sixty percent depth.

Soil seed bank

The streamside litter/soil seed bank at each of the nine study sites was sampled in April, June, and August of 2009. Three replicate cores were taken within a 1 m^2 plot per site and combined as one sample. The litter layer and upper layer of soil were collected to the depth of 2.5 cm using a split core sampler, 5 cm diameter.

Seed emergence

Water-dispersed seeds and litter/soil seed bank samples were assessed via the seed emergence method (Roberts, 1981; Thompson *et al.*, 1997). Each sample, including debris, litter, soil, and seeds, was spread over 3-4 cm of sterile (autoclaved) potting soil in 12x16 cm trays, within five days of collection. Trays were placed randomly in a greenhouse with temperatures set to mimic the diurnal and seasonal variation of the Verde Valley. Each sample remained in the greenhouse for one year, and plants were removed once identifiable to species. All specimens were identified to species, when possible (Hickman, 1993; Kearney and Peebles, 1951; nomenclature follows http://plants.usda.gov/). Vouchers were deposited into the Arizona State University Herbarium.

Seed dispersal phenology

Data were collected on the seasonal timing of seed maturation and dispersal for 164 riparian plants species located in the Verde River corridor. These data were collected by Andrea Hazelton (unpublished data) every month for one year.

Data Analysis

To assess how abundance and species richness varied with stream flow and time of year, we used general linear models in SYSTAT 13.0, with an experiment wide alpha of 0.05. Time of year was treated as a categorical variable, with values of 1 through 12. Abundance was analyzed using raw and standardized values. The standardization accounted for variability in flow; the abundance of seeds in each sample was standardized by the flow at collection (seeds/m^3). When flow was below detection limit, the minimum recorded velocity recorded with the instrument across all sampling times (0.046 m/s) was used to standardize the samples. Data were assessed for normality using quantile-quantile plots and histograms and were natural log transformed when necessary.

The average number and richness of surface and submerged hydrochores were compared using paired sample t tests at each collection time to determine if seeds distribution in the water column differed at particular times of the year.

To evaluate similarity between hydrochores, the litter and soil seed bank, and the extant vegetation, Sorensen's similarity index was calculated in Estimate S 8.2.0 (Magurran, 2004). Sorensen's similarity index, a strict comparison of the presence or absence of specific species, was used rather than a weighted similarity coefficient because the number of hydrochores could not be related to the cover of extant species. The species present in hydrochore samples during the month of and the month following seed bank and vegetation sampling were aggregated for this analysis.

RESULTS

Stream discharge

Stream discharge during sample collection peaked at three times during the study—late May, late July, and early September (Figure 17)—which correlated with the three major rainfall events. The abundance and richness of hydrochores both increased with stream discharge, with discharge explaining a significant portion of the variation in each (Figure 18, Figure 19, Table VII). Standardized abundance increased weakly with discharge, indicating that the increase in raw abundance with flow was mainly a factor of a greater volume of water sampled (Figure 18, Table VII). The total number of species collected was highest at the three highest discharge events (Figure 20). Both surface and submerged samples followed the same trends as the total samples (Table VII).

Time of year, dispersal phenology, and position in the water column

General linear models indicate that time of year, separate from discharge, significantly contributed to the variation in abundance, standardized abundance, and richness of hydrochores (Table VII). Abundance of surface hydrochores was greatest in early May, whereas richness peaked in late June (Figure 21, Figure 22). The relative abundance of surface and submerged hydrochores also varied through time, with surface hydrochores more abundant than submerged hydrochores at three of the four abundance peaks (Figure 21).

Presence of species throughout the year was more tightly linked to dispersal phenology for some species than for others. Species varied seasonally based on one of three strategies: pulse species were found in the water in strict accordance with their dispersal phenology, constant species were consistently found in the water despite more restricted and specific dispersal periods, and combination species showed intermediate characteristics (Figure 23). Of the 11 most common hydrochores, we classified 3 as pulse species, 3 as constant species, and 3 as combination strategists; two species could not be categorized because of lack of dispersal phenology data.

The strategists also differed in their patterns of distribution in the water column (Figure 24). Spring dispersed pulse species including obligate wetland *Salix* species were mainly surface dispersed, contributing to the greater abundance of surface hydrochores in early May. *T. chinensis*, a combination strategist, contributed to the high surface hydrochores in early June as it continued to disperse. *Ludwigia peploides*, a combination strategist, was abundant in surface samples during its late July dispersal period, but was also present as a surface and submerged hydrochore throughout the year. The consistent strategist, *Typha domingensis*, was nearly solely responsible for submerged obligate wetland species throughout the study period.

The richness of hydrochores also differed based on the moisture requirements of the species. The richness peak in early September corresponded with the dispersal of a variety of obligate wetland and facultative wetland species, such as *Polypogon monspeliensis* and *Bidens frondosa*. The late July discharge contained the total highest richness, and the highest richness of upland species; all of those upland species were all found in the surface samples (Figure 25). Many of these upland species, such as *Solanum elaegnifolium* and *Ziziphus obtusifolia*, were not actively dispersing in July, so their presence is attributed to headwater wash input during peaks flows. The richness peak in late May included a variety of obligate and facultative wetland species, such as *Ludwigia peploides* and *Cyperus odoratus* that were not actively dispersing; we attribute their presence to resuspension of seeds produced in previous seasons.

Relation to streamside vegetation and the litter/soil seedbank

Hydrochore similarity to vegetation was low across all sampling periods (Table VIII), and surface hydrochores were more similar to vegetation than submerged hydrochores

(Table IX). Of the 62 species present in the extant vegetation throughout across the study, 24 were represented in hydrochore samples and 38 were not. There was higher similarity between the hydrochores and the litter/soil seed bank with Sorensen's values ranging from 0.4 to 0.488 and with 20 of the 26 species in the litter/soil seed bank also found in the hydrochore samples. Similarity values were higher for cumulative occurrences than at any specific sampling time in the year.

When considering only the species found commonly in hydrochore samples, there was greater similarity among hydrochores, litter/soil seed banks, and extant vegetation. Nine (*T. domingensis, L. peploides, T. chinensis, Salix sp., Carex senta, P. monspeliensis, S. acutus, P. fremontii, and Polygonum lapathifolium*) of the eleven most abundant hydrochore species were present in the extant vegetation, but two (*Cyperus odoratus* and *Eclipta prostrata*) were not. Both of these species were present in the litter/soil seed bank, however, indicating that they that *C. odoratus* and *E. prostrata* had been dispersed onto the banks by some means. Of the eleven most abundant hydrochore species, only *Salix sp.* and *P. fremontii* were unrepresented in the litter/soil seed banks, likely owing to collection time not corresponding with dispersal of these short-lived seeds.

DISCUSSION

The temporal patterns of richness and abundance of hydrochore samples in the semi-arid Verde River were dependent on both phenology and the seasonal fluctuation of stream flow. Although it is intuitive that a higher volume of water sampled yields increased total number of species and individuals collected, distinct interactions between discharge, plant phenology, and seed longevity led to multiple patterns of hydrochory. Further, particular patterns of discharge throughout the watershed led to varying outcomes in hydrochore richness and composition.

Contrasts of the three richness peaks indicate the different ways in which high flows and dispersal phenology can influence hydrochore richness and composition. A species richness peak in September was the product of many species dispersing at this time coupled with a discharge peak. At other periods of high flow, notably late July and late May, many hydrochorous species not actively dispersing were captured. The flow pulse in late July originated from rainfall in the headwaters, as many of the lower tributaries did not see increased flow during this period (Table X). The increase in upland species richness with this type of flow event is attributed to wash and headwater input upstream of the study area. High flow events have been shown to be important for bringing in non-local species (Moggridge and Gurnell, 2010). Since flow pulses react differently in headwaters than low floodplains (Tockner *et al.*, 2000), further studies must look at hydrochory in the headwaters to understand their influence on hydrochory throughout this system. The peak flow in May was different in that it was due to local as well as distal tributary input—tributaries throughout the study area contributed to this flow pulse (Table X). The flow contained obligate wetland species that were not actively dispersing at time of collection, so the increased richness was most likely due to resuspension of diaspores from past seasons. A river in Colorado also showed a dispersal peak early in the year from the previous season (Merritt and Wohl, 2006). Hydrochores dispersed through the main channel during high flow pulses from both local and upstream locations, supporting the hypothesis of Nilsson and others (1994) that the river accumulates and transports species longitudinally.

The timing of seed maturation and longevity of seeds influence hydrochory patterns (Boedeltje *et al.*, 2004). From the common species with known phenology, we categorized species into one of three hydrochory strategies: pulse, constant, and combination species. Pulse species were found in the water in strict accordance with their restricted dispersal phenology, a strategy that also seemed to be linked with surface dispersal within the water column. Pulse species also have transient seeds, which are not stored because they are viable for less than one year (Thompson and Grime, 1979). *Salix exigua and Salix gooddingii* (the two possible species comprising our *Salix sp.* hydrochores) and *P. fremontii* have short lived seeds which decrease to 50% viability within 44 days, 44 days, and 54 days, respectively (Stella *et al.*, 2006). The short lived seeds and restricted dispersal windows of *Salix sp.* and *P. fremontii* leads to their presence as hydrochores at specific times relating to dispersal phenology. Sample abundance and richness generally followed similar peaks throughout the season, except when *P. fremontii* and *Salix sp.* dispersed in early May—abundance was at its highest at this sampling period while richness was not highest until late July. Our results were similar to another study where abundance and richness peaks at different times (Moggridge *et al.*, 2009).

P. lapathifolium, another pulse species in our study, is normally dispersed onto the soil surface, where seeds have low overwinter survival if not buried (Staniforth and Cavers, 1976). The winter previous to our study contained no flow pulses between the dispersal period of *P. lapathifolium* and winter that would distribute sediment and burry seeds. Since buried seeds have higher viability (Staniforth and Cavers, 1976), we suggest that the pulse pattern of *P. lapathifolium* in this year is an artifact of seed death from the previous year. Despite the September dispersal period of *P. lapathifolium*, viable seeds were discovered in the August litter and soil seed bank collection. Because no viable seeds were found in the April or June litter and soil seed bank collection, the August seeds may be due to early dispersal. Phenology for many pulse species follows standard seasonal pulse events. This is also evident in other Western US rivers where species disperse in relation to hydrologic fluxes to maximize the probability of establishment (Merritt and Wohl, 2006; Stella *et al.*, 2006). The pulse species observed in this study were found consistently in the surface hydrochore collections, which may relate to the seed morphology—an attribute that we plan to investigate in the future for its tie to hydrochore strategies.

Consistent species such as *T. domingensis*, *C. odoratus*, and *P. monspeliensis* were not only consistent as hydrochores, but were also found in the soil and litter seed bank throughout and beyond their dispersal periods. Thus, consistent hydrochores were also persistent in the litter/soil seed bank, as they remained viable for over a year (Thompson and Grime, 1979). While *T. domingensis* and *P. monspiliensis* were common in the adjacent riparian vegetation, *C. odoratus* was not found in the extant vegetation at any sampling period. All of these species were abundant submerged in the water rather than floating on the river's surface. We expect that these species have long lived seeds that are stored in the stream bed and banks and resuspended throughout the year. As similarly suggested by Merritt and Wohl (2006), these species have important ecological roles as opportunists because their presence throughout the year allows them to be dispersed during flows of any season and thus to colonize after disturbance that occurs at various times throughout the year.

It has been suggested that the ability of hydrochory to influence riparian communities is dependent on fluctuating flows to allow exchange of seeds between the water and adjacent riverbank (Jansson *et al.*, 2005b; Moggridge *et al.*, 2009), so these consistent hydrochores may fill an important niche in riparian communities. Some studies have attributed buoyancy time (i.e. time floating on the surface) as an important factor in how hydrochory influences plant communities (Johansson *et al.*, 1996; Nilsson *et al.*, 1991a), but our study shows that consistent species are transported suspended within the water column. Some of these species are dominant in the extant vegetation, supporting the idea that submerged transport is also important for community structure. Submerged transport may contribute to findings on other rivers where floating ability was not important in community composition (Andersson *et al.*, 2000b).

Species in the combination hydrochore dispersal category, such as *L. peplodies* and *S. acutus* show characteristics of both consistent and pulse hydrochorous species in that they were found throughout the year but also pulsed during their dispersal period. These species were also present in the soil seed bank and vegetation throughout the year. Their apparent extended seed viability allows them to take advantage of seasonal pulses throughout the year like consistent species, but also pulse with dispersal. With these specific species, dispersal phenology aligns with the common flow or flood pulses created by monsoon rains. *Tamarix chinensis* is also in this category because of its long dispersal period throughout the study and its continued presence as a surface hydrochore despite its short-lived seeds (Horton *et al.*, 1960).

The similarity of hydrochores to the extant vegetation was more limited than it was to the litter/soil seed bank. Although hydrochory is still considered important for structuring riparian vegetation, multiple studies, including our own, show limited similarity between hydrochorous dispersal and extant plant communities (Andersson *et al.*, 2000b; Boedeltje *et al.*, 2003). Riparian communities change across space and time, with the extant vegetation representing a single point in time. The litter/soil seed bank, however, encompasses seeds from species dispersed from this or other locations or stored from past seasons. With the addition of flooding, freshly deposited hydrochores and seed bank species have the opportunity to establish (Stromberg *et al.*, 2008). The limited relationships between hydrochory and the litter/soil seed bank and the extant vegetation may shift across a larger timescale with flooding dynamics.

CONCLUSIONS

Richness and abundance of hydrochores increased with stream flow, and the presence of a species as a hydrochore related variably to its dispersal phenology. We recognized three strategies of hydrochory as they related to dispersal phenology in this system: pulse species which were present as hydrochores in synchrony with their limited dispersal phenology, constant species which were found continuously through the study, and combination species which share characteristics of both pulse and continuous species. Although hydrochores were not tightly linked with community extant vegetation in our study, species-specific hydrochory strategies in relation to seasonal flow dynamics may be important for understanding the relationship of hydrochores and vegetation.

Table VII. General linear models show the influence of time of year and discharge on the standardized abundance, abundance, and richness of hydrochore samples. Time of year and discharge account for variation in abundance and richness of samples, but discharge does not account for a significant portion of the variation in standardized abundance (p = 0.05).

			Discharge	Time of Year
	df		1	11
Total	Standardized Abundance	F-Ratio (p)	0.9 (0.4)	3.6 (<0.001*)
	Abundance	F-Ratio (p)	46.7 (<0.001*)	5.6 (<0.001*)
	Richness	F-Ratio (p)	27.1 (<0.001*)	4.2 (<0.001*)
Submerged	Standardized Abundance	F-Ratio (p)	1.3 (0.3)	3.1 (0.001*)
	Abundance	F-Ratio (p)	28.7 (<0.001*)	3.7 (<0.001*)
	Richness	F-Ratio (p)	20.3 (<0.001*)	2.3 (0.02*)
Surface	Standardized Abundance	F-Ratio (p)	0.06 (0.8)	1.9 (0.04*)
	Abundance	F-Ratio (p)	18.1 (<0.001*)	1.9 (0.05*)
	Richness	F-Ratio (p)	11.7 (0.001*)	2.3 (0.01*)

Table VIII. Sorensen's similarity index showing the relationship between extant river streamside vegetation, hydrochores, and the litter and soil seed bank at all three soil sampling periods and cumulatively across all sampling periods. Across the year, there were a total of 62 species in the extant vegetation, 56 hydrochore species, and 26 species in the litter a soil seed bank.

	April		June	
	Hydrochores	Plants	Hydrochores	Plants
Plants	0.303		0.325	
Litter & Soil	0.465	0.262	0.408	0.351

	August		Cumulative	
	Hydrochores	Plants	Hydrochores	Plants
Plants	0.361		0.407	
Litter & Soil	0.4	0.34	0.488	0.364

Table IX. Sorensen's similarity index showing the relationship between the extant river streamside vegetation and the surface and submerged hydrochores. Across the year, there were a total of 62 species in the extant vegetation, 46 surface hydrochore species, and 29 submerged hydrochore species.

	Plants	Surface Hydrochores
Surface Hydrochores	0.453	
Submerged Hydrochores	0.292	0.533

Table X. Daily mean discharge (m^3/s) during the three major sampling discharges (http://waterdata.usgs.gov). The Clarkdale gauge is located upstream of the study sites, while the other three gauges are on tributaries that flow into the river along the length of the study site.

	Gauge Number	Approx. Summer baseflow (m^3/s)	May 23	July 23	September 13
Verde River near Clarkdale	USGS 09504000	2.0	2.4	3.9	2.0
Oak Creek near Cornville	USGS 09504500	0.6	1.6	0.6	0.8
Dry Beaver Creek near Rimrock	USGS 09505350	0.0	0.1	0.0	0.0
Wet Beaver Creek near Rimrock	USGS 09505200	0.2	0.2	0.2	0.2

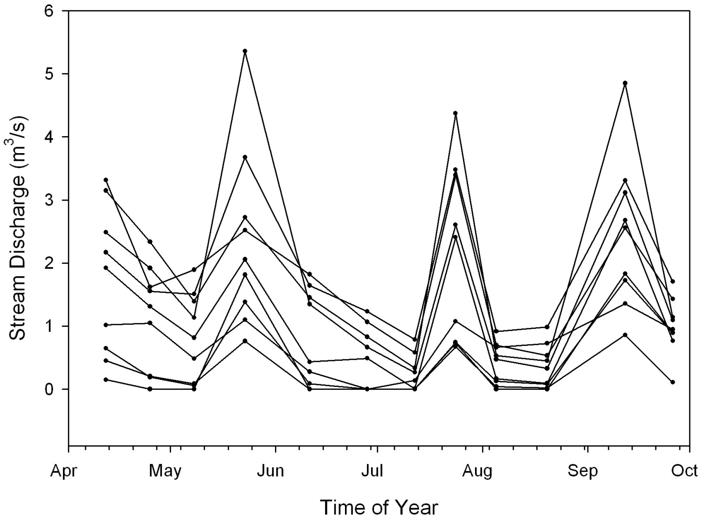


Figure 17. Stream discharge measured at twelve collection times for all nine sites.

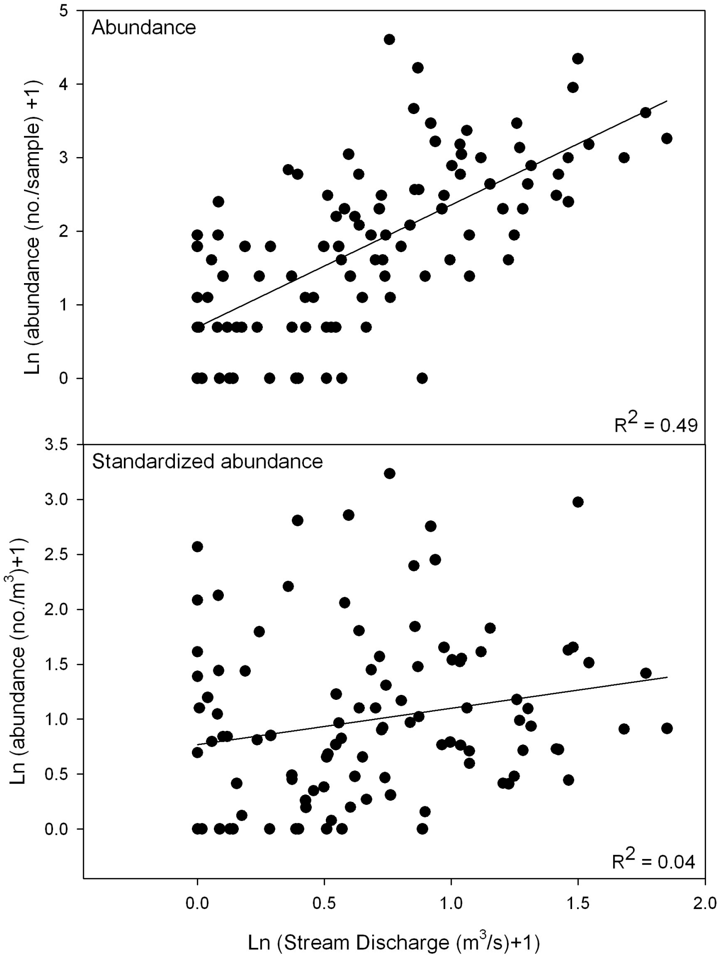


Figure 18. The total abundance (no./sample) of hydrochores increased with stream discharge ($y = 1.66x + 0.69$, $n = 108$, $p = <0.001$). Standardized abundance (no./m^3) of hydrochores related to stream discharge, but the data poorly fit the model ($y = 0.33x + 0.77$, $n = 108$, $p = 0.03$).

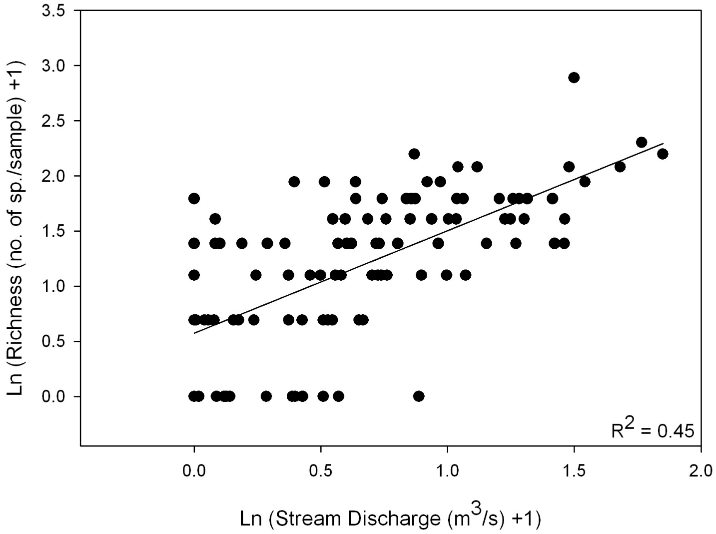


Figure 19. Species richness per sample increased with stream discharge (y = 0.93x + 0.57, n = 108, p = <0.001).

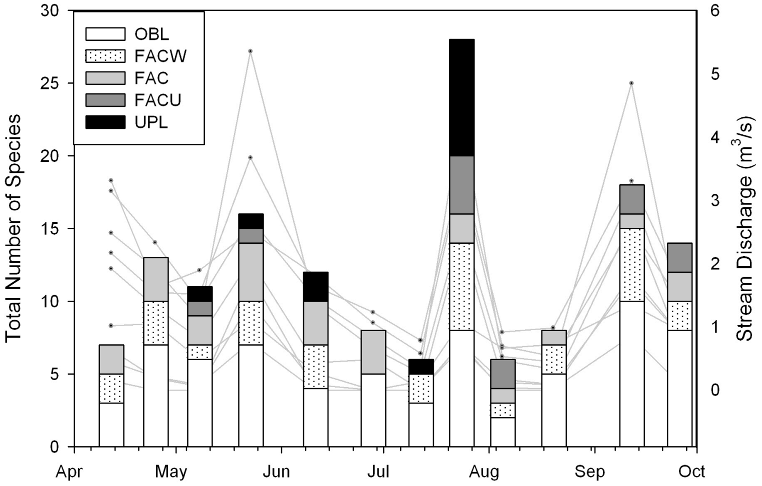


Figure 20. The total number of species collected at each sampling time shows richness corresponding to stream discharge (in grey), with the most species collected in late July. The July peak contained the most upland species. Species broken down by wetland moisture classes: OBL = obligate wetland, FACW = facultative wetland, FAC = facultative, FACU = facultative upland, UPL = upland.

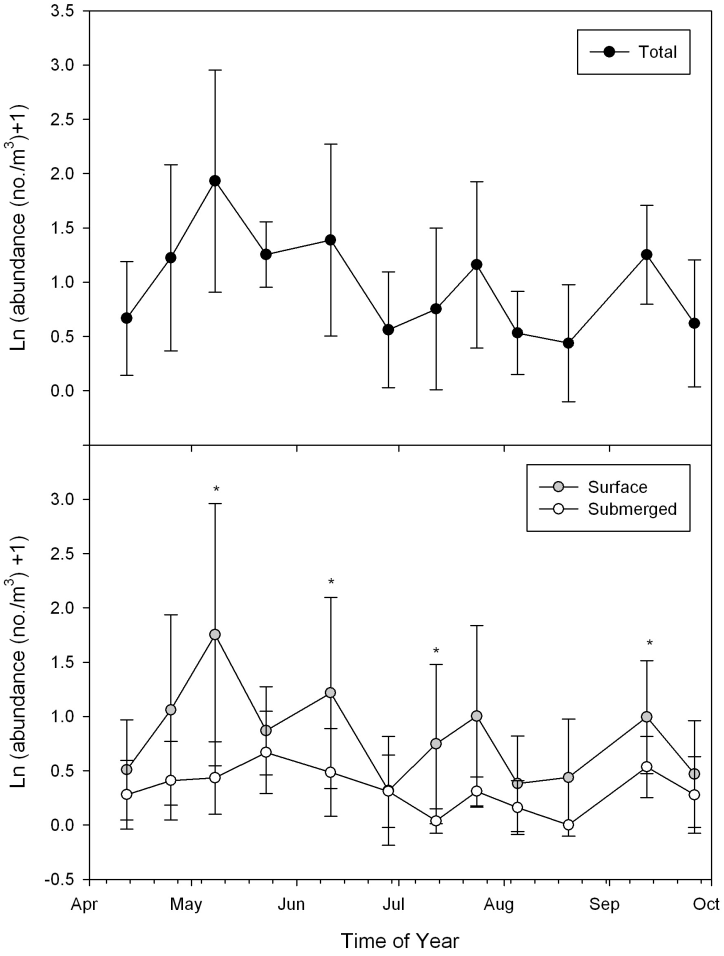


Figure 21. (a) There was a significant effect of time of year on the standardized abundance of hydrochores (no./m^3) ($p < 0.001$), and (b) there were significantly more surface hydrochores than submerged hydrochores (no./m^3) in early May ($p = 0.02$), early June ($p = 0.03$), early July ($p = 0.04$), and early October ($p = 0.02$). (Error bars denote +/- 1 SD; * denotes significant difference in paired sample t test)

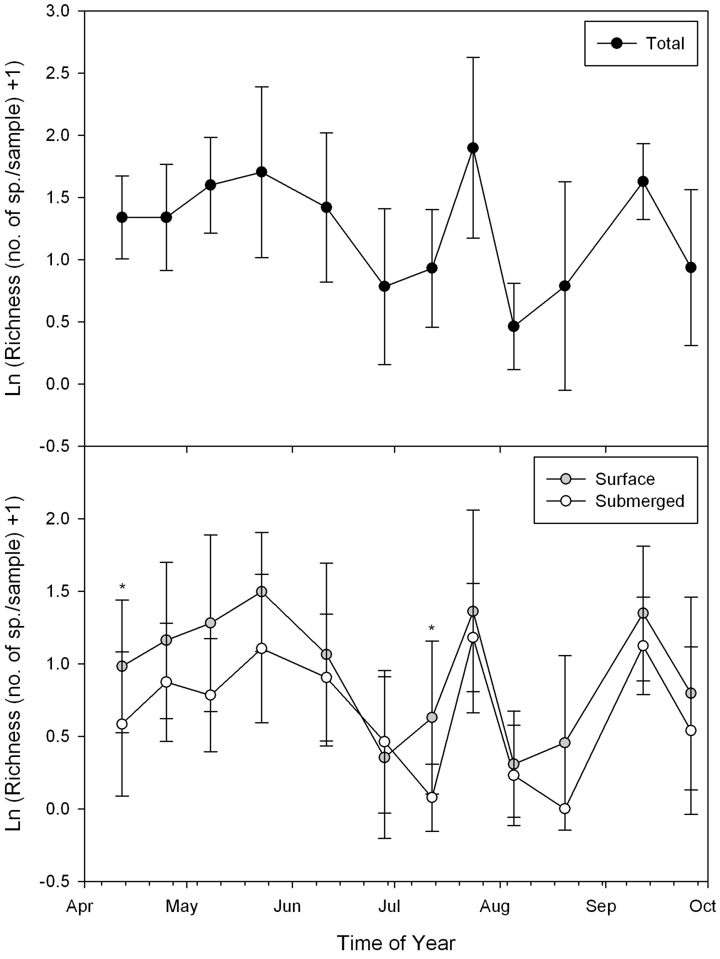


Figure 22. (a) There was a significant effect of time of year on sample richness ($p < 0.001$), and there was significantly higher sample richness in early April ($p = 0.03$) and early July ($p = 0.011$). (Error bars denote +/- 1 SD; * denotes significant difference in paired sample t test).

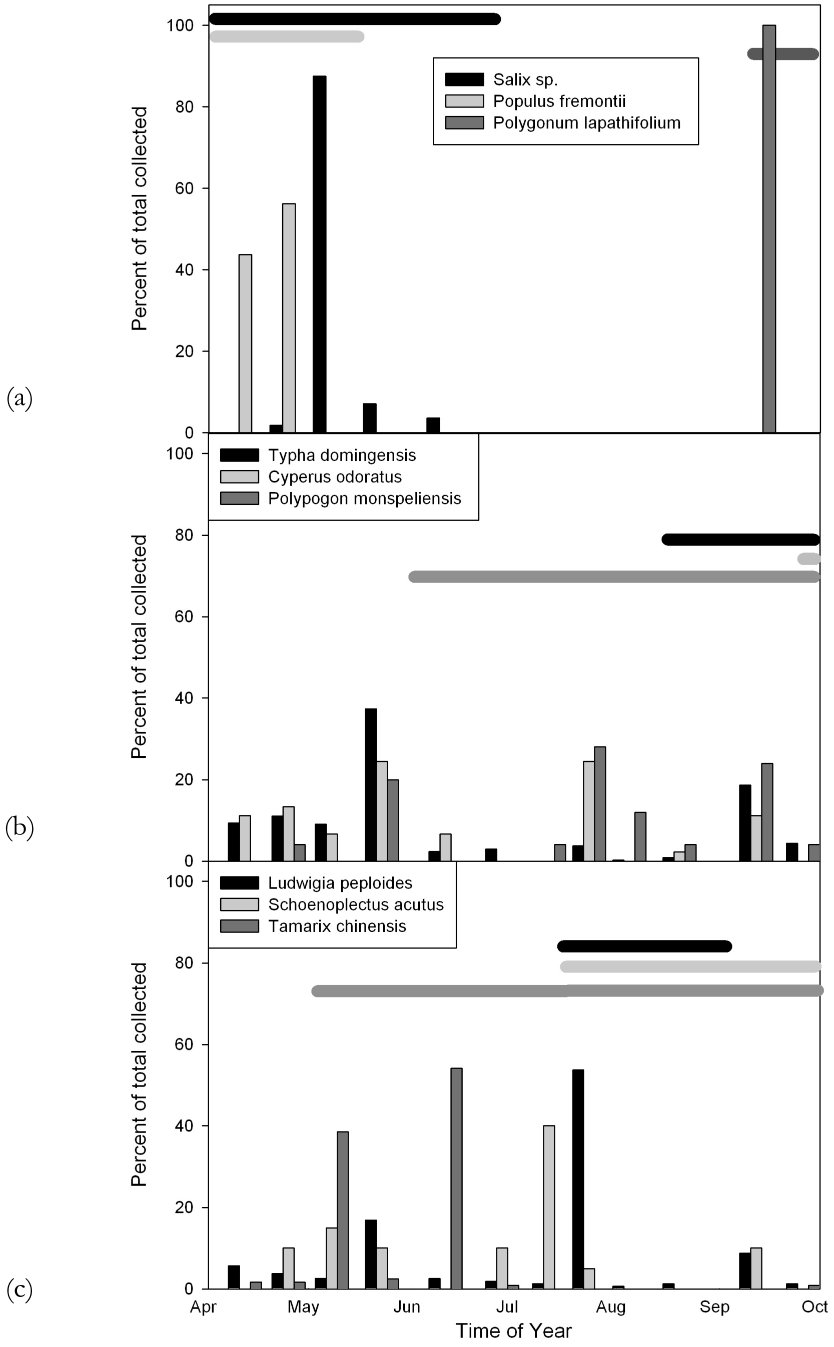


Figure 23. The percent of total hydrochores collected for 9 of the most abundance species at each sampling time shown with the range of their dispersal phenology (*Eclipta prostrata* and *Carex senta* were excluded because dispersal phenology is unknown). (a) *Salix sp.* (n = 112), *Populus fremontii* (n = 16), and *Polygonum lapathifolium* (n = 10) were pulse species. (b) *Typha domingensis* (n = 343), *Cyperus odoratus* (n = 45), and *Polypogon monspeliensis* (n = 25) were continuous species. (c) *Ludwigea peploides* (n = 160), *Tamarix chinensis* (n = 122), and *Schoenoplectus acutus* (n = 20) were combination species.

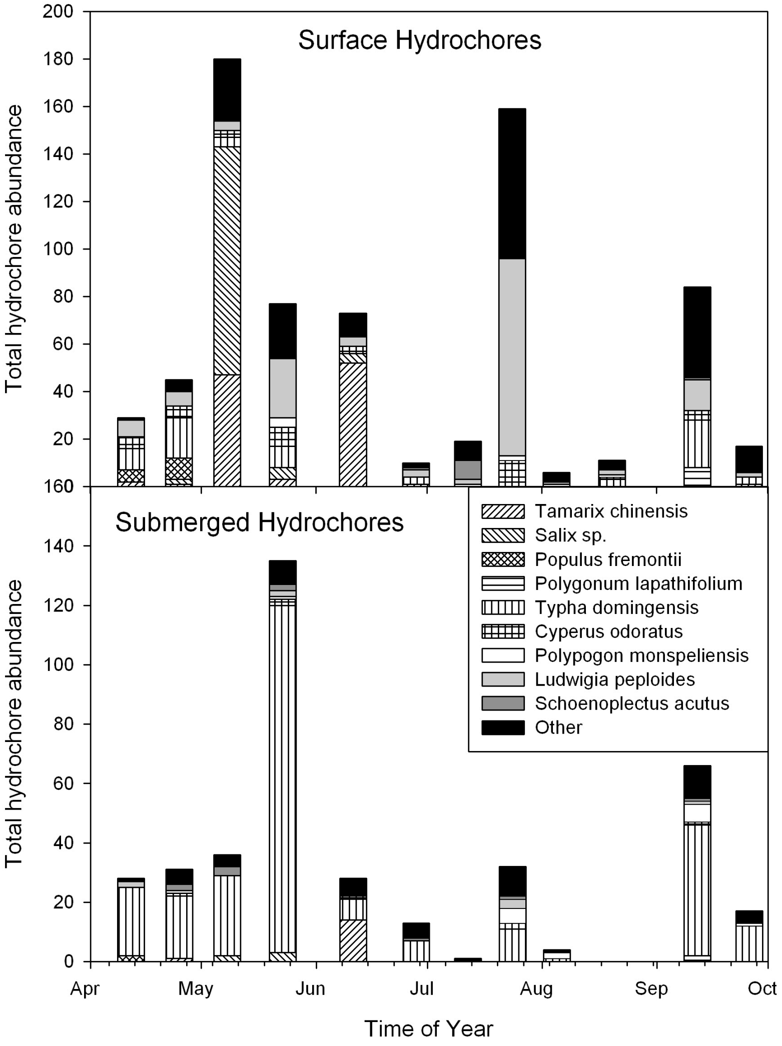


Figure 24. The total abundance of hydrochores across time with nine of the most common species highlighted.

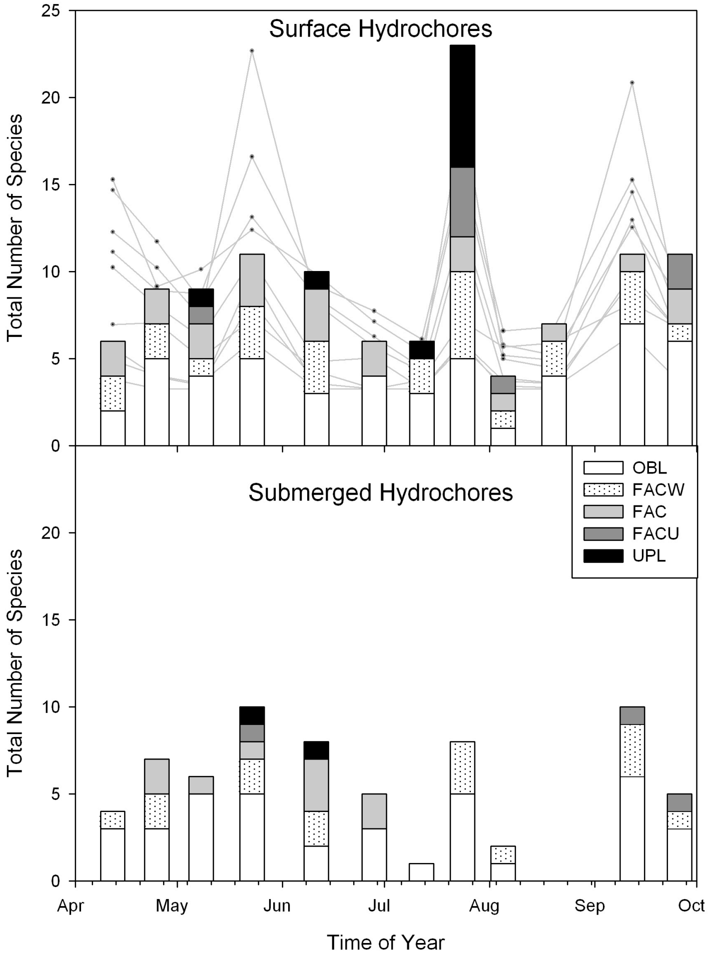


Figure 25. The number of species collected in surface and submerged samples varied through time, with the ratio of surface to submerged species particularly high during the July peak flow (stream discharge in grey). Species broken down by wetland moisture classes: OBL=obligate wetland, FACW=facultative wetland, FAC=facultative, FACU=facultative upland, UPL=upland.

4. DISSEMINATION OF WETLAND SEEDS IN IRRIGATION WATER IN ARIZONA

SUMMARY

Previous studies of hydrochory within the agricultural environment focus on the delivery of unwanted seeds to fields via surface irrigation water, those seeds representing input from ditch bank vegetation. In this study, we are interested in hydrochory as a process that maintains the ditch vegetation as an extension of the riparian corridor. Our objectives were (1) to determine patterns of hydrochory within the irrigation system, (2) to evaluate the relationship between hydrochores, ditch vegetation, and the litter/soil seed bank, and (3) to compare hydrochory within the ditch to the adjacent river. To reach these objectives, we collected hydrochores from the Verde River, AZ, and three adjacent irrigation ditches across six months of the growing season. In addition, we monitored streamside vegetation at each of the study sites across the season. We determined that species-specific hydrochory strategies found in the river were maintained within the ditch system, and the influence of seasonality and stream flow within the irrigation system was similar, but reduced, compared to the river. Comparisons of vegetation and hydrochores within the system suggest that hydrochores within the ditch propagate river wetland vegetation and local ditch vegetation not found along the river. Thus, hydrochory within man-made canals helps maintain both local-ditch vegetation and riparian vegetation characteristic free-flowing rivers.

INTRODUCTION

Agriculture uses 65-75% of the total freshwater consumed by humans (Wallace *et al.*, 2003), and water use for irrigation in the western United States has historically been via flood irrigation (Fernald *et al.*, 2007; Hayden, 1940). Approximately 8 million ha of land in the western US are flood irrigated from water diverted from rivers (Wilson, 1980). Irrigation ditches provide necessary water for agricultural crops, but also deliver unwanted seeds to agricultural fields (Egginton and Robbins, 1920; Wilson, 1980; Hope, 1927) via hydrochory—the dispersal of seeds via water (van der Pijl, 1982). The seeds trapped are generally unwanted because of their competition for nutrients and water with the planted species (Benvenuti, 2007).

Previous studies on hydrochory in agricultural systems examined the input of seeds into the irrigation water. In one of the first studies, Egginton and Robbins (1920) suggest the high input of seeds was a factor of both water entraining seeds previously deposited on the ditch bottom when the ditch was turned on in the spring and input from adjacent ditch vegetation while the ditch was in operation. In addition, high winds may have deposited seeds from adjacent plants into irrigation canals (Hope, 1927). Repetitive trimming of vegetation adjacent to the canals (Hope, 1927) and filtering of irrigation water while it entered fields were suggested for weed management (Egginton and Robbins, 1920; Kelley and Bruns, 1975).

In some regions, traditionally unlined irrigation systems are currently being examined for their capacity to maintain desired riparian vegetation and the ecosystem services they provide, as river water is diverted into manmade canals and returns to the aquifer via multiple avenues (Fernald *et al.*, 2007). Various studies have demonstrated links between stream hydrochores and the extant plant communities along rivers (Boedeltje *et al.*, 2003; Johansson *et al.*, 1996; Nilsson *et al.*, 1991a). The contribution of the river water to the plant communities along irrigation ditches, however, has been understudied.

The first objective of this study was to determine patterns of hydrochory within an irrigation system. Specifically, we asked how hydrochore abundance, species richness, and composition vary with stream flow rate, time of year, and position within the water column. We expected to see greater abundance of hydrochores at periods when bank vegetation has abundant seed maturation, we also expect more surface than submerged hydrochores due to the ditch's consistent elevation. Our second objective was to evaluate the relationships between hydrochory, the litter/soil seed bank, and the extant vegetation. We expected hydrochores to be more similar to the litter/soil seed bank than to the extant vegetation because both hydrochorous and deposited seed banks account for both spatial and temporal variability not exhibited in extant vegetation throughout the year. Our third objective was to compare hydrochory within the ditch to the river. We expected the ditch water to transport similar seeds as are in the river, and to transport additional species arising from the ditch vegetation.

STUDY SITE

This study was conducted along the middle Verde River near Camp Verde (34° 46', 112° 02'; elevation ca. 950 m) and Cottonwood (34° 31', 111° 50'; elevation ca. 1000 m), Arizona, USA adjacent to and within the Hickey, Eureka, and Diamond S irrigation ditches (see Chapter 1). Mean annual temperature is 16.7 °C and mean annual precipitation is 29.6 cm. The middle Verde is in the Transition Zone physiographic province, between the Colorado Plateau and the Basin and Range. The river is spring fed at the headwaters and further provided with water by a number of tributaries, including Oak Creek and Beaver Creek. The river flow rate is strongly influenced by monsoon and winter rains and spring snowmelt. Monsoon rains cause annual flooding from late July through September, while winter rains and snowmelt can cause floods through April. The river is characterized by low flow conditions in dry winters and during the dry summer months of May, June, and July.

The middle Verde is influenced by series of earthen dams that divert surface water into a historic unlined irrigation system. The ditches begin within the river channel and often follow abandoned channels before progressing further out through the floodplain. They maintain almost consistent elevation until they run along the edges of the upper most riparian terraces. Meanwhile, the adjacent river drops in elevation. Three of the Verde Valley ditches, the Eureka, Diamond S, and Hickey, were examined in this study. The ditch system in the Verde Valley was originally developed for irrigation of agriculture, with the Eureka (Hutcheson) Ditch claiming surface water rights in 1893, the Diamond S (Eaman) Ditch claiming surface water rights in 1865 and 1892, and the Hickey Ditch claiming water rights in 1874, 1908, and 1914 (Hayden, 1940). As of 1940, the ditches serviced 417.2, 321.1, and 171.5 acres of agricultural land, respectively (Hayden, 1940). This reach of the Verde River, between Clarkdale and Camp Verde, irrigated 4099 acres of agricultural land in 1940 (Hayden, 1940). The land use, however, has changed since that time; combined residential, commercial, and industrial land use overtook agricultural use in 1977 (Masek-Lopez and Springer, undated). Lands irrigated for agriculture continue to decline today in the Verde Valley (Masek-Lopez and Springer, undated), as well as across the Southwest United States (Fernald *et al.*, 2007). The Eureka and Diamond S ditches service agricultural crops, predominately alfalfa and sweet corn, pasture land, and pecan orchards, but a majority of the irrigated land on both ditches serves residential users. The Hickey Ditch irrigates pasture, a small-scale organic farm and orchard, and Dead Horse Ranch State Park. The state park, owning a majority of the water rights on the ditch, uses the water to irrigate lawns, irrigate two former tree farms, and feed a series of three lagoons used for recreational fishing.

The Verde River varies in low flow channel width within the study area, ranging from two to fifty meters wide. Flow rates at low flow conditions range from 1.7-2.3 m^3/s north of the Hickey Ditch (Verde River Near Clarkdale, USGS 09504000; <http://waterdata.usgs.gov>) to 1.1-2.3 m^3/s south of the Diamond S Ditch (Verde River

Near Camp Verde, USGS 09506000; <http://waterdata.usgs.gov>). The gauge at Camp Verde includes flow from a 10,914 km^2 drainage area. The ditches range from as wide as five meters at the intake to less than one meter wide along the length. Exact flow rates within each ditch are not available, but intake flow based on our bimonthly sampling estimates are as follows: Diamond S Ditch 0.9-1.4 m^3/s, Hickey Ditch 0.1-0.4 m^3/s, and Eureka Ditch 0.1-0.9 m^3/s. Each irrigation ditch is monitored by its ditch company multiple times a week, if not daily, for water level. Monitoring and subsequent action such as return flow adjustments and obstructive vegetation removal by maintenance staff keeps water levels relatively constant within the ditch. The diversion dams, however, do not regulate flow in the Verde River, as only a portion of the surface water in the river is diverted. The river levels fluctuate despite the dams, which are often destroyed and rebuilt after flooding events.

The plant community along the Middle Verde is Sonoran and Interior Riparian Deciduous Forest and Woodland, while Plains and Desert Grassland and Sonoran Desertscrub (Arizona Upland Subdivision) characterize adjacent uplands. The growing season encompasses the warm months of April through October. Average temperatures dip below freezing during the winter months and spring runoff may continue through April, restricting herbaceous growth. A few riparian species begin to set fruit and disperse seeds in May, but the number of species fruiting continues to increase through August. Both fruiting and dispersal then decline in October, with increased senescence.

The river channel is characterized by *Populus fremontii*, *Salix gooddingii,* and *Tamarix chinensis* woodlands or forests. Further from the channel, *Chilopsis linearis*, *S. gooddingii,* and *T. chinensis* shrublands and woodlands or open forblands dominated the floodplain. In many areas old stands of *P. fremontii* are found within areas otherwise devoid of woody vegetation. The ditches begin within the active floodplain (often in an abandoned channel) where they are lined with *P. fremontii*, *S. gooddingii,* and *T. chinensis*, but they soon abut the *Prosopis veluntina* bosques at the edge of the uppermost terrace where they are lined with grasslands, mixed shrublands, woodlands, or forests with a range of riparian and upland species such as *Ephedra* sp., *Celtis laevigata var. reticulata*, *Acacia greggii*, *Simmondsia chinensis*, *Salix gooddingii*, and *Fraxinus velutina*.

Streamside herbaceous vegetation is variable across all river and ditch sites, but within river and within ditch sites do share some similarities. The river more often contains stands of clonal species such as *Typha domingensis* or *Schoenoplectus acutus*, which ditches generally lack. A variety of obligate and facultative wetland species such as *Ludwigia peploides, Schoenoplectus acutus, Equisetum arvense, Equisetum laevigatum*, and *T. domingensis* are common along the river, while annuals of a wide range of moisture tolerances, such as *Symphyotrichum expansum, Bidens frondosa, Bassia scoparia, Bromus diandrus*, and *Bromus rubens* are common along ditches. *Paspalum distichum, Polypogon monspeliensis, Polypogon viridis, Cynodon dactylon, Melilotus officinalis*, and *Xanthium strumarium* are common to both the river and the ditches.

METHODS

Experimental Design

This descriptive field study compared water-dispersed seeds, the litter and soil seed bank, and streamside vegetation along three irrigation ditches in relation to a semi-arid stream (see Chapter 2) throughout the growing season. Eighteen study sites (nine ditch and nine river sites) for water-dispersed and litter/soil seed bank collection align with sites for vegetation monitoring (see Chapter 1).

Hydrochory

Water-dispersed seeds were collected twice a month, April through September 2009, using methods modified from Merritt and Wohl (2006). Two seed traps constructed from 0.25 mm polyester mesh were used to capture water-dispersed seeds. The traps have an expanded orifice, with a 120.4 cm^2 opening, helping to decrease the loss of seeds through backflow. Two traps were suspended from a pole held in the thalweg of the channel for 30 minutes at each study site; one trap was floated at the surface while the other was suspended at sixty percent depth.

Soil seed bank

The streamside litter/soil seed bank at each of the eighteen study sites was sampled in April, June, and August of 2009. Three replicate cores were taken within a 1 m^2 plot per site and combined as one sample. The litter layer and upper layer of soil were collected to the depth of 2.5 cm using a split core sampler, 5 cm diameter.

Seed emergence

Water-dispersed seeds and litter/soil seed bank samples were assessed via the seed emergence method (Roberts, 1981; Thompson *et al.*, 1997). Each sample, including debris, litter, soil, and seeds, was spread over 3-4 cm of sterile (autoclaved) potting soil in 12x16 cm trays, within five days of collection. Trays were placed randomly in a greenhouse with temperatures set to mimic the diurnal and seasonal variation of the Verde Valley. Each sample remained in the greenhouse for one year, and plants were removed once identifiable to species. All specimens were identified to species, when possible ((Hickman, 1993; Kearney and Peebles, 1951); nomenclature follows http://plants.usda.gov/). Vouchers were deposited into the Arizona State University Herbarium.

Seed dispersal phenology

Data were collected on the seasonal timing of seed maturation and dispersal for 164 riparian plants species located in the Verde River corridor. These data were collected by Andrea Hazelton (unpublished data) every month for one year.

Data analysis

To assess how abundance and species richness varied with stream flow and time of year, we used general linear models in SYSTAT 13.0, with an experiment wide alpha of 0.05. Time of year was treated as a categorical variable, with values of 1 through 12. Abundance was analyzed using raw and using standardized values. The standardization accounted for variability in flow; the abundance of seeds in each sample was standardized by the flow at collection (seeds/m^3). When flow was below detection limit, the minimum recorded velocity recorded with the instrument across all sampling times (0.046 m/s) was used to standardize the samples. Data were assessed for normality using quantile-quantile plots and histograms and were natural log transformed when necessary.

The average number and richness of surface and submerged hydrochores were compared using paired sample t tests at each collection time to determine if seeds distribution in the water column differed at particular times of the year.

To evaluate similarity between hydrochores, the litter and soil seed bank, and the extant vegetation, Sorensen's similarity index was calculated in Estimate S 8.2.0 (Magurran, 2004). Sorensen's similarity index, a strict comparison of the presence or absence of specific species, was used rather than a weighted similarity coefficient because the number of hydrochores could not be related to the cover of extant species. The species present in hydrochore samples during the month of and the month following seed bank and vegetation sampling were aggregated for this analysis.

RESULTS

Irrigation ditches

Factors influencing hydrochore richness and abundance. Stream discharge throughout the year was relatively consistent at each ditch study site, although the fluctuations that did occur paralleled river discharge (Figure 12). There was a very weak relationship between stream discharge and abundance of propagules (Figure 26, Table XI). There was a significant effect of discharge on richness, but the model poorly fit the data because of high variation (Figure 27). Despite the variation in the data, discharge explained a significant portion of the variation in total sample richness (Table XI). In addition, discharge explained much of the variation in both the abundance and richness of surface hydrochores, and it explains a significant portion of the variation in the standardized abundance of submerged hydrochores (Table XI).

General linear models indicated that time of year also accounted for some variation in abundance, abundance per m^3, and richness for total, surface, and submerged samples (Table XI). The abundance of surface and submerged hydrochores did not differ at any sampling period (Figure 28), but the number of surface species was significantly higher than the number of submerged species at multiple sampling periods (Figure 29).

Variation among plant groups. Abundance patterns throughout the year differed among species, as abundance was variably linked to dispersal phenology. Species occurrence seasonally based on three strategies described in Chapter 2: pulse species were found in the water in strict accordance with their limited dispersal phenology, constant species were consistently found in the water despite a more restricted and specific dispersal periods, and combination species showed intermediate characteristics (Figure 30). Of the 17 most common hydrochore species, we classified 4 as pulse species, 5 as combination species, and 5 as continuous species.

Relation to streamside vegetation and litter/soil seed bank. Hydrochore similarity to vegetation was low across all sampling periods, as was the similarity of vegetation to the litter/soil seed bank (Table XII). The highest similarity was between the hydrochores and the litter/soil seed bank, with Sorensen's coefficients ranging from 0.3 in April to 0.6 for cumulative data. Similarity values were higher for cumulative occurrences than at any specific time in the year.

Fourteen (*Typha domingensis, Ludwigia peploides, Polypogon monspeliensis, Symphyotrichum expansum, Tamarix chinensis, Salix sp., Polypogon viridis, Populus fremontii, Polygonum lapathifolium, Bidens frondosa, Lactuca serriola, Mimulus guttatus, and Veronica anagallis-aquatica*) of the seventeen most abundant species were found in the extant vegetation, but three species were not (*Eclipta prostrata, Cyperus odoratus,* and *Leersia oryzoides*). These three species were found to a limited degree in the litter/soil seed bank, suggesting that they have been dispersed to the banks by some means. Of the seventeen most abundant hydrochore species, *Salix sp., P. fremontii,* and *Tamarix chinensis* were unrepresented in the litter/soil seed bank, likely owing to collection time not corresponding with dispersal of these short-lived seeds. Across the study, 42 species in the extant vegetation were not found in hydrochore samples, while only five species present in the litter/soil seed bank were not dispersing through hydrochory.

Comparisons between ditch and river hydrochory

Compared to the river, the ditch had much less seasonal variance in flow and in hydrochore abundance and richness through time. In the river, hydrochore abundance per m^3 peaked in early May, while richness peaked in late July, and the total abundance of hydrochores and richness per sample increased strongly with stream discharge (see Chapter 2). The irrigation ditches, however, did not see pronounced peaks throughout the year and did not vary clearly with discharge. One trend that was similar between the two systems was the increased richness of surface hydrochores compared to submerged hydrochores at multiple sampling periods (Figure 29). Though not significant in the ditch, there were also more surface than submerged hydrochores per volume in both systems (Figure 28).

The ditches contained more total species and numbers of hydrochores across the study: the river contained 56 species and 1111 total hydrochores, while the ditch contained 74 species and 2332 hydrochores (see Appendix II for complete species list). Both systems had high numbers of wetland species (Figure 31), and these species were common to both systems (Figure 32). The higher total number of hydrochore species in the ditch system was due to unique species across all moisture requirements (Figure 32), but high numbers of ditch species per sampling period was due to unique species of higher drought tolerance (Figure 31).

Common species in the ditch and river were similar and species maintained consistent hydrochorous dispersal classifications in both systems. Two of the most common species, *Lactuca serriola* and *Pseudognaphalium luteoalbum* (both facultative wetland), were more prevalent as hydrochores in the ditches than the river.

Wetland indicator scores of hydrochores within the ditches and river show higher abundance of wetland species dispersing within the river than the ditch (Figure 33). This same pattern was seen in the streamside vegetation, but the difference in wetland indicator scores was more pronounced within the vegetation (Figure 33).

DISCUSSION

Hydrochory patterns in the ditches were similar in several respects to those in the river, indicating that irrigation ditches function as an extension of the river. The species-specific hydrochory strategies found within the river system remained consistent within the ditches, demonstrating that the man-made irrigation canals exhibit similar riverine processes. In addition, the river and ditches both had increased richness of surface hydrochores compared to submerged hydrochores and generally higher abundance of surface hydrochores than submerged. The same pulse species remained dominant on the surface of the water in both systems and did not appear in the litter/soil seed bank. The constant species *Typha domingenesis* remained dominant in the seed bank throughout the year and dispersed suspended in the water column in both systems.

In other respects, the ditch had a distinct hydrochory signature. Both discharge peaks and dispersal period influenced the abundance and richness of hydrochores in the river, but the ditch did not show these patterns as strongly. Similar to other studies (Wilson, 1980; Kelley and Bruns, 1975), we found more total species in the ditch systems than the adjacent river. We speculate that the higher number of hydrochore species in the ditch compared to the river is a function of the size of the vegetated band relative to the size of the receiving stream (narrow for the ditch, wide for the river). The flow consistency within the ditches also reduced richness peaks seen in the river due to consistent volumes of water sampled within the ditches.

The hydrochores within the irrigation canal were a combination of both river and local sources. In the man-made ditch system located throughout the riparian corridor, many of the same wetland hydrochores found in the river remained dominant in the ditches. Despite the difference in flow consistency, streamside herbaceous vegetation along the ditches was similar to the main stem river in that they both supported species of high moisture requirements (Chapter 1). The river was most likely led to the establishment of wetland species in the extant vegetation along the ditches. The dispersal of seeds within both systems occurs via not only water, but also via wind and animals from distant and local communities (Benvenuti 2007; van der Pijl 1982). It is the connectivity of the river water, however, that ties the plant communities along irrigation ditches to the river.

Input of seeds from ditch banks and other local vegetation lead to the increased representation of species with lower moisture requirements within the ditch hydrochores. The vegetation along the ditches, containing both wetland and upland species, contributed seeds to the irrigation water. The river contained fewer of these upland and facultative upland hydrochores across the sampling period, with specific peaks of drought-tolerant hydrochores correlating with flow peaks. The difference between the abundance and richness of species of different moisture requirements in ditch and river further supports the idea that hydrochores represent local vegetation in regulated systems (Andersson *et al.*, 2000a). This input from local vegetation is common in other flood irrigation systems (Kelley and Bruns, 1975; Li and Qiang, 2009; Egginton and Robbins, 1920), and dispersal via wind is considered a main contributor to additional ditch hydrochores (Hope, 1927). Two of our most abundant ditch hydrochore species, *Lactuca serriola* and *Pseudognaphalium luteoalbum,* are wind-dispersed species not commonly found in the river water—another example of the ditches being influenced by the local community.

CONCLUSIONS

Patterns of hydrochory in man-made, regulated irrigation ditches were similar in several respects to those in the semi-arid Verde River. The maintenance of riverine processes within the irrigation system suggests they are ecologically an extension of the river. Species-specific patterns of hydrochory remained consistent in the river and ditches, but there was limited influence of discharge and seasonality on richness and abundance within the ditch was owing to flow consistency. Ditch vegetation is not only influenced by the presence of river surface water for growth, but also by the input of hydrochorous seeds from the river that maintain the wetland vegetation.

Table XI. General linear model shows that discharge was more important than time of year in explaining the variation in the abundance, standardized abundance, and richness of hydrochore samples (alpha = 0.05).

			Discharge	Time of Year
	df		1	11
Total	Standardized Abundance	F-Ratio (p)	0.007 (0.9)	0.7 (0.7)
	Abundance	F-Ratio (p)	3.6 (0.06)	0.9 (0.5)
	Richness	F-Ratio (p)	7.4 (0.008*)	0.9 (0.5)
Submerged	Standardized Abundance	F-Ratio (p)	7.7 (0.007*)	1.5 (0.1)
	Abundance	F-Ratio (p)	2.5 (0.1)	1.0 (0.1)
	Richness	F-Ratio (p)	2.0 (0.2)	0.6 (0.9)
Surface	Standardized Abundance	F-Ratio (p)	2.2 (0.1)	1.0 (0.4)
	Abundance	F-Ratio (p)	6.8 (0.01*)	1.5 (0.1)
	Richness	F-Ratio (p)	16.3 (<0.001*)	1.5 (0.1)

Table XII. Sorensen's similarity index showing the relationship between extant ditch streamside vegetation, hydrochores, and the litter/soil seed bank at all three sampling periods and cumulatively across all sampling periods. Across the year, there were a total of 86 species in the extant vegetation, 74 hydrochore species, and 37 species in the litter/soil seed bank.

	April		June	
	Hydrochores	Plants	Hydrochores	Plants
Plants	0.368		0.452	
Litter & Soil	0.314	0.214	0.492	0.257
	August		**Cumulative**	
	Hydrochores	Plants	Hydrochores	Plants
Plants	0.482		0.534	
Litter & Soil	0.522	0.333	0.627	0.427

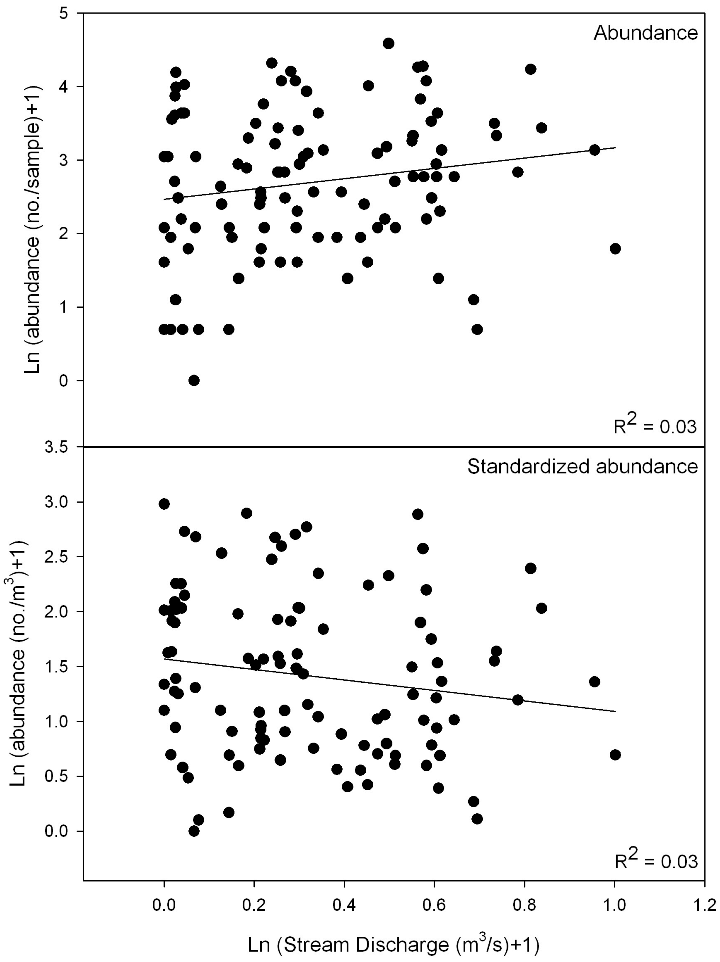


Figure 26. Neither abundance (no./sample) nor standardized abundance (no./m^3) of hydrochores related to stream discharge (y = 0.70x + 2.47, n = 108, p = 0.07; y = -0.47x + 1.57, n = 108, p = 0.1).

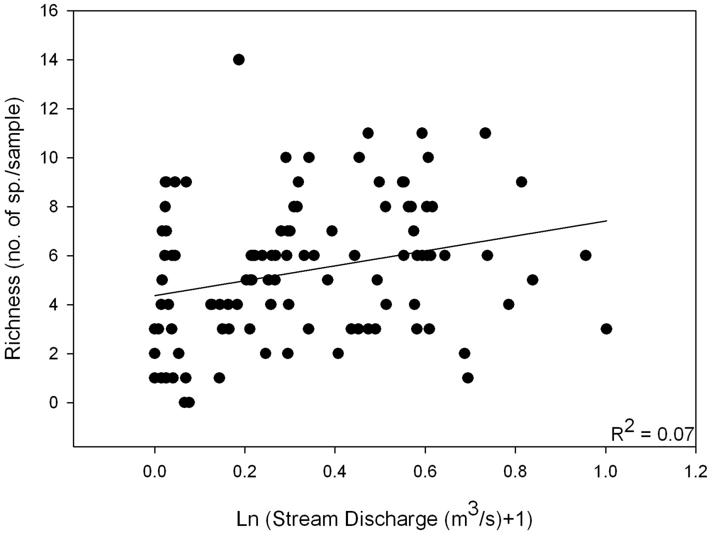


Figure 27. Sample richness per sample increased with stream discharge (y = 3.05x + 4.36, n = 108, p = 0.005), but the data were highly variable and poorly fit the model.

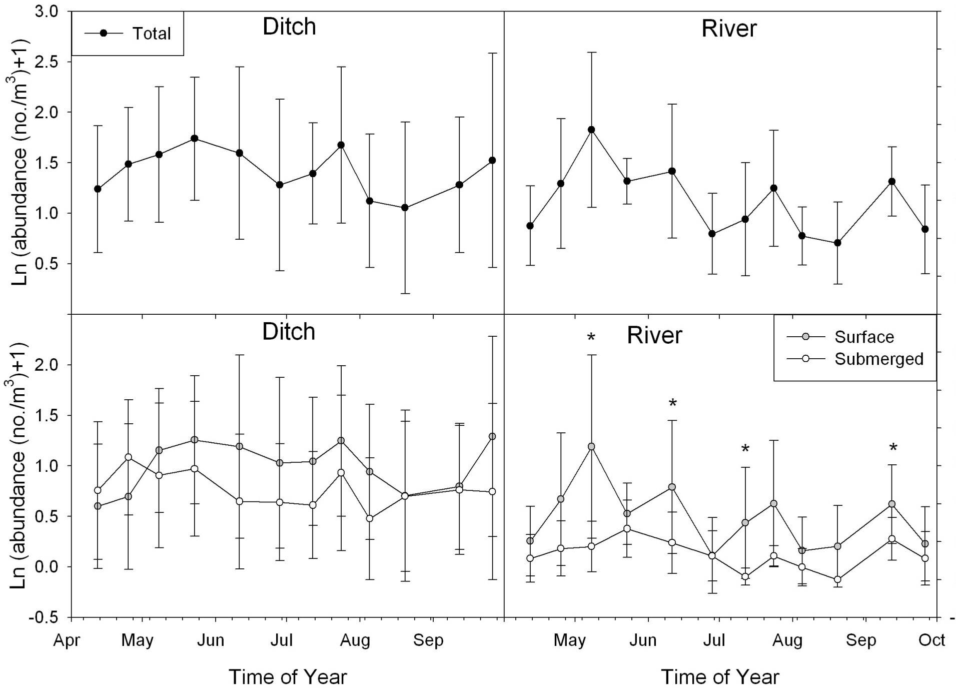


Figure 28. The standardized abundance (no./m^3) of surface and submerged hydrochores did not differ at any sampling period in the ditch, but there were more surface hydrochores at some periods in the river (Error bars denote +/- 1 SD;
*denotes significance in a paired t test).

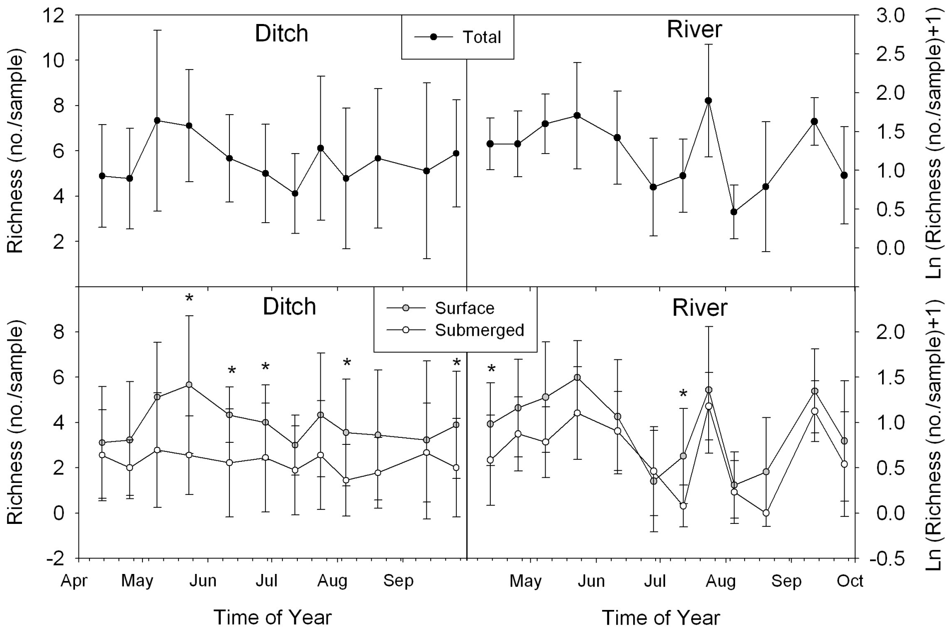


Figure 29. There were significantly more surface than submerged hydrochore species per sample in the ditch in late May (p = 0.03), early and late June (p = 0.04, p = 0.04), early August (p = 0.05), and late September (p = 0.05). (Error bars denote +/- 1 SD; * denotes significant difference in paired sample t test)

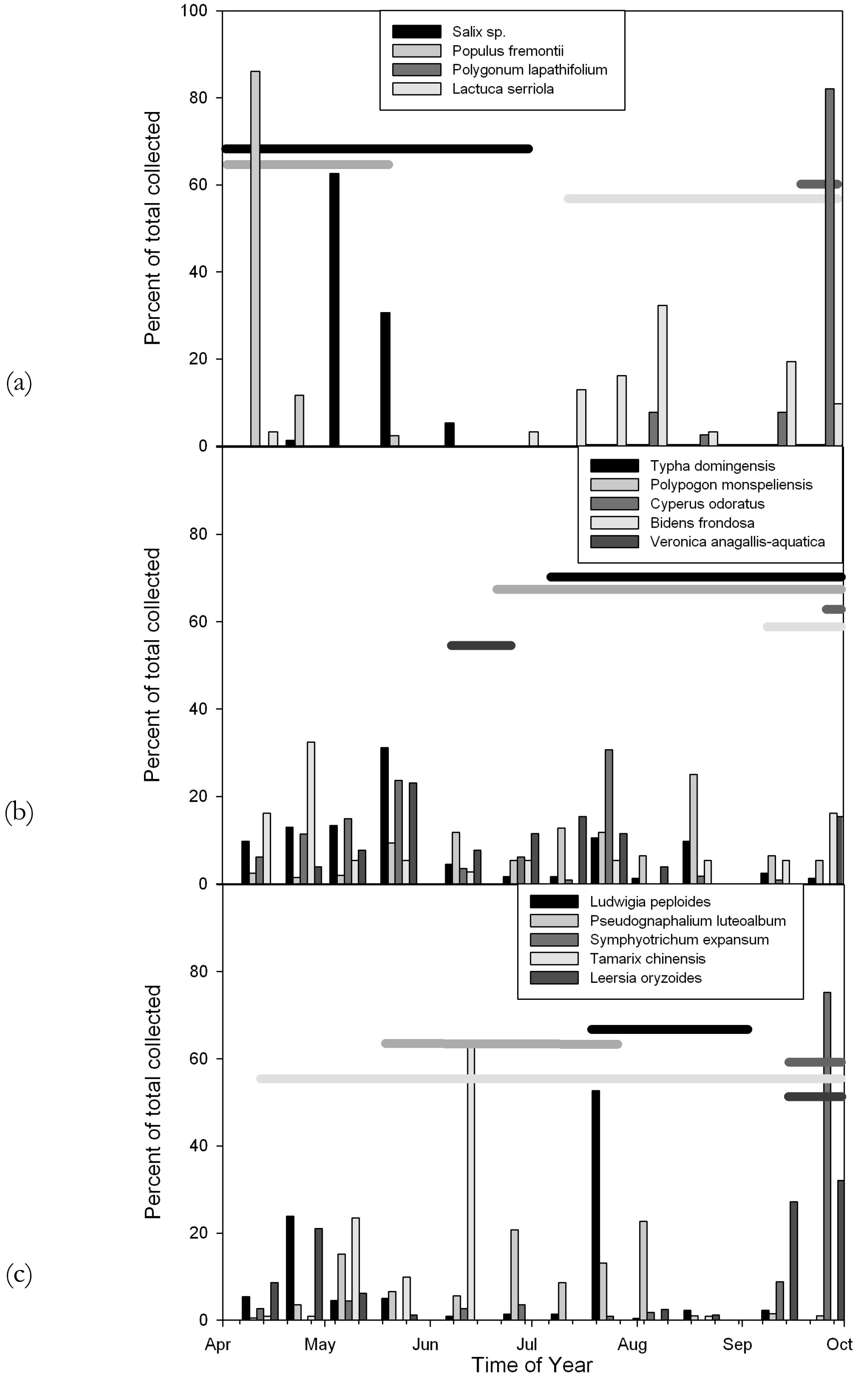


Figure 30. The percent of total hydrochores collected for 14 of the most abundant species at each sampling time shown with the range of their dispersal phenology. (a) *Salix sp.* (n = 75), *Populus fremontii* (n = 43), *Polygonum lapathifolium* (n = 39), and *Lactuca serriola* (n = 31) were pulse species. (b) *Typha domingensis* (n = 247), *Polypogon monspeliensis* (n = 204), *Cyperus odoratus* (n = 114), *Bidens frondosa* (n = 37), and *Veronica anagallis-aquatica* (n = 26) were continuous species. (c) *Ludwigia peploides* (n = 222), *Pseudognaphalium luteoalbum* (n = 198), *Symphyotricum expansum* (n = 113), *Tamarix chinensis* (n = 111), *Leersia oryzoides* (n = 81), and were combination species.

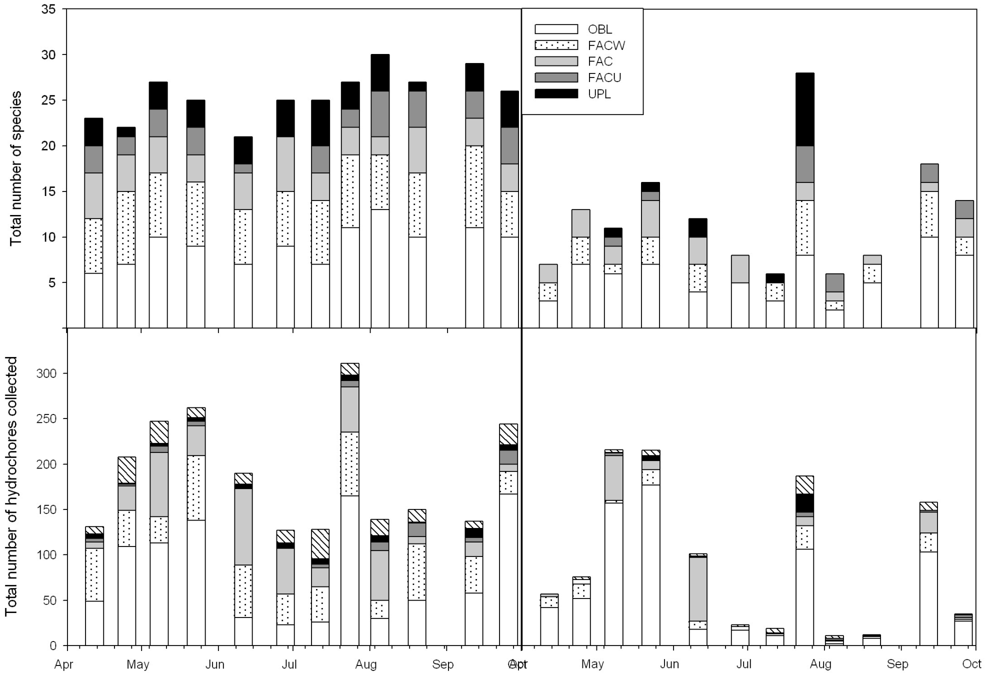


Figure 31. Total hydrochore richness and relative proportion of species of different moisture requirements across time remained steady in the ditches, while the river fluctuated. In addition, total hydrochore abundance was increased in the ditch due mainly to increased hydrochores of higher moisture requirements.

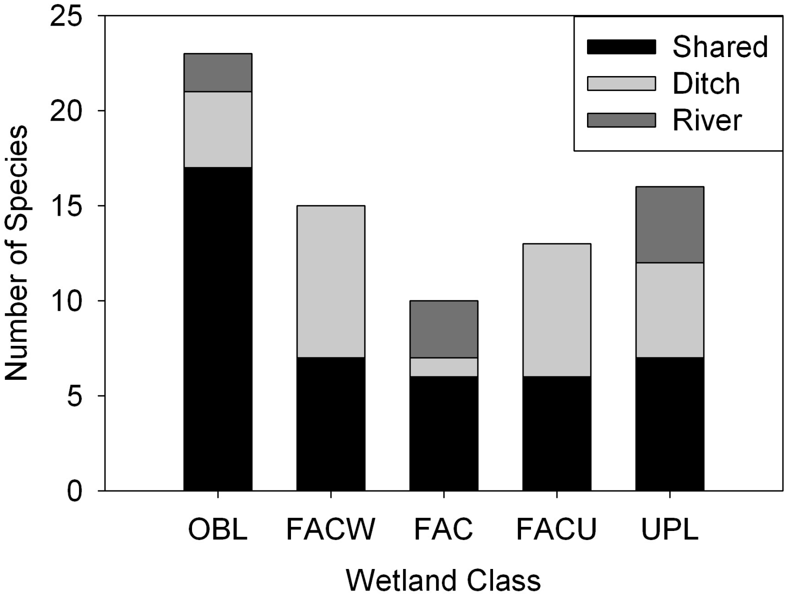
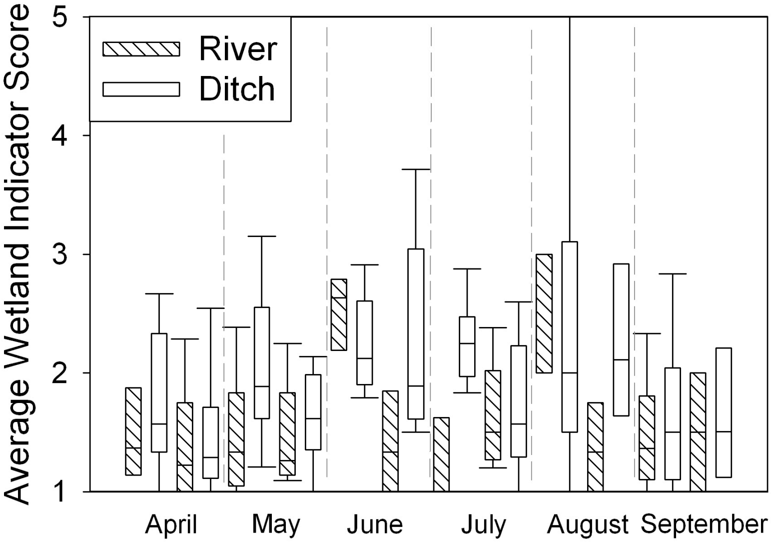


Figure 32. The number of shared hydrochore species was high across all moisture classes (46 species), but the ditch contained more unique species (27 species) than the river (9 species). There were relatively more shared obligate wetland species than species of higher drought tolerance (OBL = obligate wetland, FACW = facultative wetland, FAC = facultative, FACU = facultative wetland, UPL = upland).

(a)



(b)

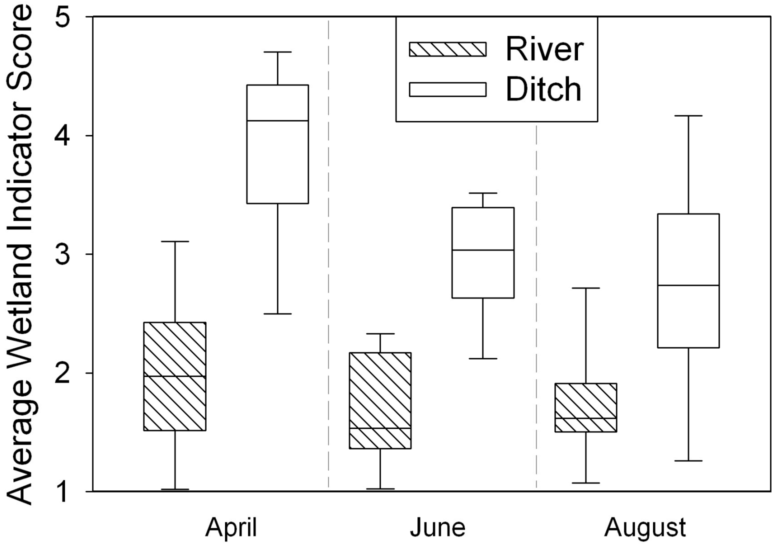


Figure 33. Average wetland indicator scores for hydrochores (a) and herbaceous vegetation (b) show the consistent pattern of species requiring more water dispersing through river the water and present in the river streamside vegetation than the ditch (1 = obligate wetland, 5 = upland).

5. CONCLUSIONS

Human constructed earthen irrigation canals function as a modified riparian system. Streamside vegetation along the canals is similar to the adjacent river in abundance (cover and basal area), but the canal vegetation is higher in diversity than the adjacent river. Compositionally, canal vegetation is indicative of both river streamside herbaceous vegetation and high flood plain and terrace woody vegetation. Similar patterns of hydrochory within the irrigation system and adjacent river contribute to the maintenance of riparian vegetation within the man-made irrigation system.

The vegetation that lines the irrigation system would not be possible without the irrigation water in this now unique unlined structure. Thus, this agricultural system is actually a multifunctional system contributing to both the societal and ecological components of the ecosystem. The irrigation system's main service of providing water for agriculture inadvertently supports a man-made riparian system. This type of novel riparian system should be further evaluated for the specific goals of various stakeholders, but the observed vegetation patterns and processes documented by this study reveal promising riparian habitat value.

REFERENCES

Andersson E, Nilsson C, Johansson ME. 2000a. Effects of river fragmentation on plant dispersal and riparian flora. *Regulated Rivers-Research & Management* **16**: 83-89.

Andersson E, Nilsson C, Johansson ME. 2000b. Plant dispersal in boreal rivers and its relation to the diversity of riparian flora. *Journal of Biogeography* **27**: 1095-1106.

Beauchamp VB, Stromberg JC, Stutz JC. 2007. Flow regulation has minimal influence on mycorrhizal fungi of a semi-arid floodplain ecosystem despite changes in hydrology, soils, and vegetation. *Journal of Arid Environments* **68**: 188-205.

Beauchamp VB, Stromberg JC. 2008. Changes to herbaceous plant communities on a regulated desert river. *River Research and Applications* **24**: 754-770.

Benvenuti S. 2007. Weed seed movement and dispersal strategies in the agricultural environment. *Weed Biology and Management* **7**: 141-157.

Berges SA, Moore LAS, Isenhart TM, Schultz RC. 2010. Bird species diversity in riparian buffers, row crop fields, and grazed pastures within agriculturally dominated watersheds. *Agroforestry Systems* **79**: 97-110.

Boedeltje G, Bakker JP, Bekker RM, Van Groenendael JM, Soesbergen M. 2003. Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of the species in the species pool. *Journal of Ecology* **91**: 855-866.

Boedeltje G, Bakker JP, Ten Brinke A, Van Groenendael JM, Soesbergen M. 2004. Dispersal phenology of hydrochorous plants in relation to discharge, seed release time and buoyancy of seeds: the flood pulse concept supported. *Journal of Ecology* **92**: 786-796.

Brand LA, White GC, Noon BR. 2008. Factors influencing species richness and community composition of breeding birds in a desert riparian corridor. *Condor* **110**: 199-210.

Canham CD, Marks PL. 1985. The Response of Woody Plants to Disturbance: Patterns of Establishment and Growth. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press: San Diego, CA; 197-216.

Carothers SW, Johnson RR, Aitchison SW. 1974. Population structure and social organization of Southwestern riparian birds. *American Zoologist* **14**: 97-108.

Carter MR (ed). 1993. Soil Sampling and Methods of Analysis. Lewis publishers: Ann Arbor.

Casanova MT, Brock MA. 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities?. *Plant Ecology* **147**: 237 250.

Colwell RK, Mao CX, Chang J. 2004. Interpolating, extrapolating, and comparing incidence based species accumulation curves. *Ecology* **85**: 2717-2727.

Cooper BE. 1968. Algorithm AS 3: The integral of Student's t distribution. *Applied Statistics* **17**: 189-190.

Crandal K, Colby B, Rait KA. 1992. Valuing riparian preserves: A Southwestern case study. *Rivers* **3**: 88-98.

Curtis JT, Mcintosh RP. 1951. An Upland Forest Continuum in the Prairie-Forest Border Region of Wisconsin. *Ecology* **32**: 476-496.

Egginton GE, Robbins WW. 1920. Irrigation water as a factor in the dissemination of weed seeds. Colorado Agricultural Experiment Station Bulletin: Fort Collins, Colorado.

Fernald AG, Baker TT, Guldan SJ. 2007. Hydrologic, riparian, and agroecosystem functions of traditional Acequia irrigation systems. *Journal of Sustainable Agriculture* **30**: 147-171.

Fish SK, Fish PR. 1994. Prehistoric Desert Farmers of the Southwest. *Annual Review of Anthropology* **23**: 83-108.

Francis RA, Hoggart SPG. 2008. Waste not, want not: The need to utilize existing artificial structures for habitat improvement along urban rivers. *Restoration Ecology* **16**: 373 381.

Friedman JM, Osterkamp WR, Lewis WM. 1996. Channel narrowing and vegetation development following a Great Plains flood. *Ecology* **77**: 2167-2181.

Gallopin GC. 1991. Human Dimensions of Global Change - Linking the Global and the Local Processes. *International Social Science Journal* **43**: 707-718.

Gordon LJ, Finlayson CM, Falkenmark M. 2010. Managing water in agriculture for food production and other ecosystem services. *Agricultural Water Management* **97**: 512-519.

Green DM, Brock JH. 1994. Chemical Status of Soils in 4 Urban Riparian Plant Communities. *Landscape and Urban Planning* **28**: 121-127.

Grubb p. 1977. Maintenance of species-richness in plant communities-importance of regeneration niche. *Biological reviews of the Cambridge Philosophical Society* **52**: 107-145.

Gyssels G, Poesen J. 2003. The importance of plant root characteristics in controlling concentrated flow erosion rates. *Earth Surface Processes and Landforms* **28**: 371-384.

Hannon LE, Sisk TD. 2009. Hedgerows in an agri-natural landscape: Potential habitat value for native bees. *Biological Conservation* **142**: 2140-2154.

Harper JL. 1977. *Population Biology of Plants*. Academic Press: New York.

Hayden TA. 1940. *Irrigation on Upper Verde River Watershed from Surface Waters*.

Hickman JC. 1993. *The Jepson Manual: Higher Plants of California*. University of California Press: Berkely, CA.

Hill GW. 1970. Algorithm 396: Student's t-quantiles. *Communications of the ACM* **13**: 619-620.

Hope A. 1927. The dissemination of weed seeds by irrigation water in Alberta. *Scientific Agriculture* **7**:268-276.

Horton JS, Mounts FC, Kraft JM. 1960. Seed germination and seedling establishment of phreatophyte species. Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO.

Houlton BZ, Wang YP, Vitousek PM, Field CB. 2008. A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature* **454**: 327-330.

Hupp CR, Osterkamp WR. 1996. Riparian vegetation and fluvial geomorphic processes. *Geomorphology* **14**: 277-295.

Janssens F, Peeters A, Tallowin JRB, Bakker JP, Bekker RM, Fillat F, Oomes MJM. 1998. Relationship between soil chemical factors and grassland diversity. *Plant and Soil* **202**: 69-78.

Jansson R, Zinko U, Merritt DM, Nilsson C. 2005a. Hydrochory increases riparian plant species richness: a comparison between a free-flowing and a regulated river. *Journal of Ecology* **93**: 1094-1103.

Jansson R, Zinko U, Merritt DM, Nilsson C. 2005b. Hydrochory increases riparian plant species richness: a comparison between a free-flowing and a regulated river. *Journal of Ecology* **93**: 1094-1103.

Johansson ME, Nilsson C, Nilsson E. 1996. Do rivers function as corridors for plant dispersal?. *Journal of Vegetation Science* **7**: 593-598.

Jolley RL, Lockaby BG, Cavalcanti GG. 2010. Changes in riparian forest composition along a sedimentation rate gradient. *Plant Ecology* **210**: 213-224.

Kearney TH, Peebles RH. 1951. *Arizona Flora*. University of California Press: Berkely, CA, USA.

Kelley AD, Bruns VF. 1975. Dissemination of Weed Seeds by Irrigation Water. *Weed Science Society of America* **23**: 486-493.

Klute A. 1986. *Methods of Soil Analysis Part 1: Physical & Mineralogical Methods*. Soil Science of America, Inc.: Madison, WI, USA.

Latterell JJ, Bechtold JS, O'Keefe TC, Van Pelt R, Naiman RJ. 2006. Dynamic patch mosaics and channel movement in an unconfined river valley of the Olympic Mountains. *Freshwater Biology* **51**: 523-544.

Li RH, Qiang R. 2009. Composition of floating weed seeds in lowland rice fields in China and the effects of irrigation frequency and previous crops. *Weed Research* **49**: 417-427.

Licht LA. 1992. Salicaceae Family Trees in Sustainable Agroecosystems. *Forestry Chronicle* **68**: 214-217.

Luzuriaga AL, Escudero A, Olano JM, Loidi J. 2005. Regenerative role of seed banks following an intense soil disturbance. *Acta Oecologica-International Journal of Ecology* **27**: 57-66.

Magurran AE. 2004. *Measuring biological diversity*. Blackwell Publishing: Oxford.

Masek-Lopez S, Springer AE. Assessment of human influence on riparian change in the Verde Valley, Arizona. *Arizona Water Protection Fund Report.*

McAtee WL. 1925. Notes on drift, vegetable balls, and aquatic insects as a food product of inland waters. *Ecology* **6**: 288-302.

Menges ES, Waller DM. 1983. Plant Strategies in Relation to Elevation and Light in Floodplain Herbs. *American Naturalist* **122**: 454-473.

Merritt DM, Wohl EE. 2002. Processes governing hydrochory along rivers: hydraulics, hydrology, and dispersal phenology. *Ecological Applications* **12**: 1071-1087.

Merritt DM, Wohl EE. 2006. Plant dispersal along rivers fragmented by dams. *River Research and Applications* **22**: 1-26.

Moggridge HL, Gurnell AM. 2010. Hydrological Controls on the Transport and Deposition of Plant Propagules within Riparian Zones. *River Research and Applications* **26**: 512 527.

Moggridge HL, Gurnell AM, Mountford JO. 2009. Propagule input, transport and deposition in riparian environments: the importance of connectivity for diversity. *Journal of Vegetation Science* **20**: 465-474.

Mount, J. 1997. Description of cottonwood habitats utilized by neotropical migratory birds along the upper Verde River. Arizona State University MS Thesis.

Nabhan GP, Sheridan TE. 1977. Living Fencerows of Rio San Miguel, Sonora, Mexico Traditional Technology for Floodplain Management. *Human Ecology* **5**: 97-111.

Nilsson C, Gardfjell M, Grelsson G. 1991a. Importance of hydrochory in structuring plant communities along rivers. *Canadian Journal of Botany* **69**: 2631-2633.

Nilsson C, Ekbald A, Dynesius M, Backe S, Gardfjell M, Bjorn C, Hellqviist S, Roland J. A comparison of species richness and traits of riparian plants between a main river channel and its tributaries. *The Journal of Ecology* **82**: 281-295.

Nilsson C, Ekblad A, Gardfjell M, Carlberg B. 1991b. Long-Term Effects of River Regulation on River Margin Vegetation. *Journal of Applied Ecology* **28**: 963-987.

Patten DT. 1998. Riparian ecosystems of semi-arid North America: Diversity and human impacts. *Wetlands* **18**: 498-512.

Perroni-Ventura Y, Montana C, Garcia-Oliva F. 2006. Relationship between soil nutrient availability and plant species richness in a tropical semi-arid environment. *Journal of Vegetation Science* **17**: 719-728.

Pollock MM, Naiman RJ, Hanley TA. 1998. Plant species richness in riparian wetlands – A test of biodiversity theory. *Ecology* **79**: 94-105.

Rahimi H, Abbasi N. 2008. Failure of concrete canal lining on fine sandy soils: A case study for the Saveh project. *Irrigation and Drainage* **57**: 83-92.

Ricklefs RE. 1977. Environmental Heterogeneity and Plant Species-Diversity - Hypothesis. *American Naturalist* **111**: 376-381.

Ries N. 2008. The (Almost) All-American Canal: Consejo de Desarrollo Economico de Mexicali v. United States and the Pursuit of Environmental Justice in Transboundary Resource Management. *Ecology Law Quarterly* **35**: 491-529.

Roberts HA. 1981. Seed banks in the soil. *Advances in Applied Biology* **6**: 1-55.

Robertson PG, Coleman DE, Bledsoe CS, Sollins P. 1999. Standard Soil Methods for Long Term Ecological Research. *Long-Term Ecological Research Network Series* **2**.

Scanlon BR, Jolly I, Sophocleous M, Zhang L. 2007. Global impacts of conversions from natural to agricultural ecosystems on water resources: Quantity versus quality. *Resources Research* **43**.

Schade JD, Hobbie SE. 2005. Spatial and temporal variation in islands of fertility in the Sonoran Desert. *Biogeochemistry* **73**: 541-553.

Schneider RL, Sharitz RR. 1988. Hydrochory and regeneration in a bald cypress-water tupelo swamp forest. *Ecology* **69**: 1055-1063.

Staniforth RJ, Cavers PB. 1976. Experimental-Study of Water Dispersal in Polygonum Spp. *Canadian Journal of Botany-Revue Canadienne De Botanique* **54**: 2587-2596.

Stella JC, Battles JJ, Orr BK, McBride JR. 2006. Synchrony of seed dispersal, hydrology and local climate in a semi-arid river reach in California. *Ecosystems* **9**: 1200-1214.

Stevens LE, Brown BT, Simpson JM, Johnson RR. 1977. Importance, preservation and management of riparian habitat: A symposium. USDA Forest Service General Technical Report: Tuscon, AZ. RM-43; 156-164.

Stromberg JC, Lite SJ, Dixon JD, Tiller RL. 2009. Riparian Vegetation. *Ecology and Conservation of the San Pedro River*: The University of Arizona Press: Tuscon, AZ. 13-36.

Stromberg JC, Beauchamp VB, Dixon MD, Lite SJ, Paradzick C. 2007. Importance of low flow and high-flow characteristics to restoration of riparian vegetation along rivers in and south-western United States. *Freshwater Biology* **52**: 651-679.

Stromberg JC, Boudell JA, Hazelton AF. 2008. Differences in seed mass between hydric and xeric plants influence seed bank dynamics in a dryland riparian ecosystem. *Functional Ecology* **22**: 205-212.

Swinton SM, Lupi F, Robertson GP, Landis DA. 2006. Ecosystem Services from Agriculture: Looking beyond the Usual Suspects. *American Journal of Agricultural Economics* **88**: 1160-1166.

Taylor GAR. 1970. Algorithm AS 27: The integral of Student's t-distribution. *Applied Statistics* **19**: 113-114.

Thompson, K, Bakker, J, Bekker, R. 1997. The soil seed banks of North West Europe: methodology, density and longevity. Cambridge University Press: Cambridge, UK.

Thompson K, Grime JP. 1979. Seasonal-Variation in the Seed Banks of Herbaceous Species in 10 Contrasting Habitats. *Journal of Ecology* **67**: 893-921.

Tockner K, Malard F, Ward JV. 2000. An extension of the flood pulse concept. *Hydrological Processes* **14**: 2861-2883.

van der Pijl L. 1982. *Principles of Dispersal in Higher Plants*. Springer-Verlag: New York.

Wallace JS, Acreman MC, Sullivan CA. 2003. The sharing of water between society and ecosystems: from conflict to catchment-based co-management. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **358**: 2011-2026.

Wilson RG. 1980. Dissemination of Weed Seeds by Surface Irrigation Water in Western Nebraska. *Weed Science* **28**: 87-92.

APPENDIX I

HERBACEOUS SPECIES PRESENCE

					River	River	River
		DSD	ED	HD	DSD	ED	HD
Berula erecta	OBL						X
Bidens laevis	OBL						X
Carex senta	OBL		X		X	X	X
Hydrocotyle verticillata	OBL				X	X	X
Juncus articulatus	OBL					X	X
Ludwigia peploides	OBL		X		X	X	X
Mimulus guttatus	OBL			X			
Nasturtium officinale	OBL	X			X		X
Paspalum distichum	OBL	X	X	X	X	X	X
Polygonum lapathifolium	OBL	X					
Polygonum punctatum	OBL				X		X
Samolus valerandi ssp. parviflorus	OBL					X	
Schoenoplectus acutus	OBL	X	X		X	X	X
Schoenoplectus americanus	OBL		X		X	X	X
Symphyotrichum expansum	OBL	X	X	X		X	X
Typha domingensis	OBL	X	X		X	X	X
Veronica anagallis-aquatica	OBL	X		X	X	X	X
Agrostis exarata	FACW					X	
Ambrosia trifida	FACW	X	X			X	
Arundo donax	FACW						X
Bidens frondosa	FACW	X	X	X	X	X	
Calibrachoa parviflora	FACW				X		
Chloracantha spinosa	FACW	X					
Claytonia perfoliata	FACW			X			
Echinochloa colona	FACW					X	
Echinochloa crus-galli	FACW		X	X		X	X
Equisetum arvense	FACW					X	X
Equisetum laevigatum	FACW	X			X	X	X
Juncus torreyi	FACW	X	X			X	X
Mentha arvensis	FACW	X		X	X		

					River	River	River
		DSD	ED	HD	DSD	ED	HD
Mentha spicata	FACW	X					
Plantago major	FACW	X		X	X	X	X
Poa nemoralis ssp. interior	FACW	X	X	X			X
Polygonum aviculare	FACW		X				
Polygonum persicaria	FACW	X	X		X	X	
Polypogon monspeliensis	FACW	X	X	X	X	X	X
Polypogon viridis	FACW	X	X	X	X	X	X
Rumex crispus	FACW			X			X
Rumex salicifolius var. mexicanus	FACW	X		X	X		
Sonchus asper	FACW	X	X				
Ambrosia psilostachya	FAC		X	X	X	X	X
Bassia scoparia	FAC	X	X				
Funastrum cynanchoides ssp. cynanchoides	FAC	X		X			
Helianthus annuus	FAC	X		X		X	
Lactuca serriola	FAC	X	X	X			X
Marrubium vulgare	FAC	X		X			
Plantago lanceolata	FAC						X
Pseudognaphalium luteoalbum	FAC			X			
Schedonorus phoenix	FAC		X		X	X	X
Sphenopholis obtusa	FAC		X				
Convolvulus arvensis	FACU			X			
Conyza canadensis	FACU		X	X			
Cynodon dactylon	FACU	X	X		X	X	X
Elymus glaucus	FACU			X			
Galium aparine	FACU			X			
Gaura mollis	FACU	X	X	X			
Melilotus indicus	FACU			X			
Melilotus officinalis	FACU	X	X	X	X	X	X
Parthenocissus quinquefolia	FACU		X				
Sonchus oleraceus	FACU		X				

		DSD	ED	HD	River DSD	River ED	River HD
Sorghum halepense	FACU	X	X	X	X	X	X
Xanthium strumarium	UP	X	X	X	X	X	X
Amsinckia sp.	UP			X			
Artemisia ludoviciana	UP	X					
Bromus arizonicus	UP	X	X			X	
Bromus arvensis	UP			X			
Bromus catharticus	UP	X	X	X			
Bromus diandrus	UP	X	X	X			X
Bromus rubens	UP	X	X	X			
Centaurea melitensis	UP			X			
Chamaesyce sp.	UP	X					
Chenopodium sp.	UP	X	X				
Chorispora tenella	UP			X			
Corydalis aurea	UP				X		
Erodium cicutarium	UP			X			
Gutierrezia sp.	UP		X				
Hordeum murnium ssp. glaucum	UP	X		X			
Ipomoea sp.	UP			X			
Lepidium lasiocarpum var. lasiocarpum	UP	X					
Sisymbrium irio	UP	X		X		X	
Solanum elaeagnifolium	UP			X			
Verbascum thapsus	UP			X			
Ambrosia sp.	UP	X	X	X		X	X
Apium sp.	UP						X
Convolvulaceae sp.	UP	X					
Cyperaceae sp.	UP	X		X	X	X	
Juncus sp.	UP	X				X	X
Lamium amplexicaule	UP			X			
Schizachyrium sp.	UP		X				
Torilis arvensis	UP			X			

APPENDIX II

HYDROCHORE PRESENCE

		HD	ED	DSD	River HD	River ED	River DSD
Berula erecta	OBL			X	X		
Bidens laevis	OBL		X				X
Carex senta	OBL	X	X	X	X	X	X
Cyperus acuminatus	OBL					X	
Hydrocotyle verticillata	OBL	X	X	X	X		X
Juncus articulatus	OBL	X	X	X	X		
Leersia oryzoides	OBL	X	X	X	X	X	
Ludwigia peploides	OBL	X	X	X	X	X	X
Mimulus guttatus	OBL	X	X	X	X	X	X
Nasturtium officinale	OBL				X		
Paspalum distichum	OBL		X	X			
Polygonum lapathifolium	OBL	X	X	X	X	X	X
Polygonum punctatum	OBL		X	X	X	X	
Polypogon interruptus	OBL	X		X	X		
Rorippa palustris	OBL		X	X			
Schoenoplectus acutus	OBL		X	X		X	X
Symphyotrichum divaricatum	OBL			X			
Symphyotrichum expansum	OBL	X	X	X	X		
Typha domingensis	OBL	X	X	X	X	X	X
Veronica americana	OBL	X		X			X
Veronica anagallis-aquatica	OBL	X	X	X	X	X	X
Veronica peregrina	OBL		X				
Salix sp.	OBL	X	X	X	X	X	X
Bidens frondosa	FACW	X	X	X	X	X	
Calibrachoa parviflora	FACW		X	X			
Cyperus odoratus	FACW	X	X	X	X	X	X
Echinochloa colona	FACW	X					
Echinochloa crus-galli	FACW	X	X				
Juglans major	FACW	X	X				
Juncus torreyi	FACW		X	X			
Mentha arvensis	FACW			X			
Muhlenbergia asperifolia	FACW		X				
Plantago major	FACW	X	X	X			
Polypogon monspeliensis	FACW	X	X	X	X	X	X
Polypogon viridis	FACW	X	X	X	X	X	X
Populus fremontii	FACW	X	X	X	X	X	X
Rumex violascens	FACW			X			X
Sonchus asper	FACW	X	X	X		X	X
Bassia scoparia	FAC		X	X		X	
Eclipta prostrata	FAC	X	X	X	X	X	X
Fraxinus velutina	FAC		X				
Lactuca serriola	FAC	X	X	X		X	X
Plantago lanceolata	FAC				X		

		HD	ED	DSD	River HD	River ED	River DSD
Poa annua	FAC						X
Sphenopholis obtusa	FAC		X	X		X	
Sporobolus contractus	FAC					X	
Tamarix chinensis	FAC	X	X	X	X	X	X
Amaranthus palmeri	FACU		X				
Conyza canadensis	FACU	X	X	X	X	X	
Cynodon dactylon	FACU			X		X	
Gaura mollis	FACU			X			
Melilotus indicus	FACU	X					
Melilotus officinalis	FACU	X	X			X	X
Nicotiana obtusifolia var. obtusifolia	FACU		X				
Solidago canadensis	FACU			X			
Sonchus oleraceus	FACU	X	X	X	X	X	X
Sorghum halepense	FACU		X	X		X	
Sporobolus cryptandrus	FACU		X				
Taraxacum officinale	FACU			X			
Prosopis sp.	FACU	X	X			X	
Bothriochloa laguroides ssp. torreyana	UPL		X	X		X	
Bouteloua barbata	UPL		X				
Bromus arizonicus	UPL	X	X	X			X
Bromus arvensis	UPL		X	X			X
Bromus catharticus	UPL			X			
Bromus diandrus	UPL	X	X	X			
Bromus rubens	UPL	X	X	X		X	
Chenopodium pratericola	UPL	X					
Descurainia pinnata	UPL					X	
Descurainia sophia	UPL			X		X	
Erigeron divergens	UPL	X	X	X			
Erodium cicutarium	UPL		X				
Gilia sinuata	UPL					X	
Hordeum murnium ssp. glaucum	UPL			X		X	
Plantago patagonica	UPL					X	
Solanum elaeagnifolium	UPL					X	
Verbascum thapsus	UPL	X		X		X	
Ziziphus obtusifolia	UPL		X			X	
Baccharis sp.	Unknown		X	X			X
Morus sp.	Unknown			X		X	
Vitex sp.	Unknown		X				