

DISSERTATION

MULTI-SCALE DRIVERS OF RIPARIAN VEGETATION FORM AND FUNCTION
IN EPHEMERAL STREAM NETWORKS OF THE SONORAN DESERT

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ABSTRACT

MULTI-SCALE DRIVERS OF RIPARIAN VEGETATION FORM AND FUNCTION IN EPHEMERAL STREAM NETWORKS OF THE SONORAN DESERT

To identify the drivers of riparian vegetation form and function throughout ephemeral watersheds of the Sonoran Desert, I investigated factors that condition plant responses to hydrologic fluxes across spatial scales ranging from watersheds to shrub canopies. Community composition and tree water relations were examined within the framework of a hydrogeomorphic stream classification defined by channel planform, boundary materials, and lateral confinement. The cover and density of perennial plant species and functional groups differed among stream types. Compositional differences between stream classes corresponded to variation in channel gradient, highlighting the role of fluvial disturbance in structuring riparian plant communities. Seasonal patterns of water stress and subsurface water sources for the four most abundant tree species also differed among stream types. Water stress was most severe and persistent in headwater streams, where thin alluvium limited water storage. Periodic flood recharge was stored in deep alluvium (>1 m) along downstream channel segments, reducing seasonal water stress for extended periods. In these stream types, riparian trees relied on shallow water sources (≤ 50 cm) throughout much of the year, but accessed deeper water sources during summer droughts. Subsurface water sources were more variable in headwater stream types. Ecohydrological processes in these arid stream networks were driven by rainfall and streamflow pulses, but mediated by alluvial characteristics.

I also conducted a two-year factorial field experiment to understand the factors limiting riparian tree establishment, and clarify how facilitative mechanisms vary with annual rainfall.

Seedling survival was most strongly dependent on herbivore protection provided by nurse shrubs, regardless of precipitation amounts. In contrast, the importance of facilitation through canopy shading varied with increasing annual rainfall. Despite strong effects on survival, seedling growth rates were insensitive to annual rainfall.

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TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	iv
TABLE OF CONTENTS.....	vi
LIST OF TABLES.....	ix
LIST OF FIGURES.....	x
1 Introduction.....	1
2 Does a Hydrogeomorphic Stream Classification Explain Riparian Plant Community Composition?.....	4
2.1 Introduction.....	4
2.2 Methods.....	7
2.3 Results.....	10
2.3.1 Species Cover.....	10
2.3.2 Species Density.....	11
2.3.3 Functional Group Cover.....	11
2.3.4 Functional Group Density.....	12
2.3.5 Reach Scale Geomorphic Drivers of Community Composition.....	12
2.4 Discussion.....	13
2.4.1 Species Composition.....	14
2.4.2 Functional Group Composition.....	15
2.4.3 Reach Scale Geomorphic Drivers of Community Composition.....	17
2.4.4 Application of the Hydrogeomorphic Stream Classification.....	18

3	Seasonal Ecohydrology of Riparian Trees in Ephemeral Stream Networks Differs Among Hydrogeomorphic Stream Types	32
3.1	Introduction	32
3.2	Methods	34
3.2.1	Seasonal Water Stress	35
3.2.2	Seasonal Water Sources	35
3.2.3	Daily Water Use	37
3.2.4	Statistical Analyses	37
3.3	Results	38
3.3.1	Seasonal Water Stress	39
3.3.2	Seasonal Water Sources	41
3.3.3	Daily Water Use	43
3.4	Discussion.....	44
4	Relative Importance of Abiotic and Biotic Limitations to Seedling Establishment	62
4.1	Introduction	62
4.2	Methods	64
4.3	Results	67
4.3.1	Seedling Survival	68
4.3.2	Seedling Growth.....	70
4.4	Discussion.....	71
5	Synthesis	89
5.1	Implications for a Changing Climate.....	92
5.2	Management Implications	93

5.3	Restoration Implications.....	94
6	References.....	96
7	Appendix.....	118
7.1	Designation of Plant Functional Groups	118

LIST OF TABLES

2.1. <i>A priori</i> plant functional groups.....	20
2.2. Tests for global differences among stream types in riparian plant community composition (PerMANOVA) and compositional variance (PermDISP).....	21
2.3. Pairwise comparisons for differences in riparian plant community composition (PerMANOVA) among stream types.....	22
2.4. Pairwise comparisons for differences in riparian plant community compositional variance (PermDISP) among stream types.....	23
2.5. Ranked subsets of reach scale abiotic variables corresponding to differences in riparian plant community composition among stream types.....	24
3.1. Effects of season, stream type, and watershed on predawn water potential during 2012 and 2013.....	49
3.2. Effects of season, stream type, and watershed on relative $\delta^{18}\text{O}$ during 2012 and 2013	50
4.1. Seedling initial stem heights (cm) after planting	75
4.2. Effects of treatment, irrigation, and plant size on seedling survival during the first year	76
4.3. Effects of treatment, irrigation, and plant size on seedling survival during the second year	77
4.4. Effects of shade, irrigation and seedling initial height on relative growth rates during the first year.....	78
4.5. Effects of shade, irrigation and seedling initial height on relative growth rates during the second year.....	79
7.1. Plant species and <i>a priori</i> plant functional groups.....	118

LIST OF FIGURES

2.1. Location of study reaches at Yuma Proving Ground and Barry M. Goldwater Range, in the Sonoran Desert of southern Arizona, USA.....	25
2.2. Nonmetric Multidimensional Scaling ordination of (A) species relative cover (stress = 0.145), and (B) species relative density (stress = 0.169)	26
2.3. Ranked contribution of species relative cover to Bray-Curtis dissimilarity between stream types (A), and similarity within stream types (B).....	27
2.4. Ranked contribution of species relative density to Bray-Curtis dissimilarities between stream types (A), and similarity within stream types (B).....	28
2.5. Nonmetric Multidimensional Scaling ordination of (A) functional group relative cover (stress = 0.132), and (B) functional group relative density (stress = 0.111).....	29
2.6. Ranked contribution of functional group relative cover to Bray-Curtis dissimilarities between stream types (A), and similarity within stream types (B).....	30
2.7. Ranked contribution of functional group relative density to average Bray-Curtis dissimilarities between stream types (A), and similarity within stream types (B)	31
3.1. Rainfall (P), relative water content (θ_R) and predawn plant water potential (Ψ_{PD}) in Mohave Wash during 2012 and 2013	51
3.2. Rainfall (P), relative water content (θ_R) and predawn plant water potential (Ψ_{PD}) in Mohave Wash during 2012 and 2013	52
3.3. Seasonal variation in predawn plant water potential (Ψ_{PD}) of species across stream types ..	53
3.4. Seasonal variation in predawn plant water potential (Ψ_{PD}) between species within stream types	54
3.5. Isotopic composition of waters from riparian tree xylem, shallow (<50 cm) and deep (>50	

cm) alluvium, and precipitation during 2012 and 2013.....	55
3.6. $\delta^{18}\text{O}$ profiles beneath the active channels of incised alluvium and braided reaches	56
3.7. Rainfall (P), relative water content (θ_R) and $\delta^{18}\text{O}$ values in Mohave Wash during 2012 and 2013.....	57
3.8. Rainfall (P), relative water content (θ_R) and $\delta^{18}\text{O}$ values in Yuma Wash during 2012 and 2013.....	58
3.9. Seasonal differences in relative $\delta^{18}\text{O}$ within species across stream types	59
3.10. Seasonal differences in relative $\delta^{18}\text{O}$ between species within stream types.....	60
3.11. Rainfall (P), relative water content (θ_R) and relative sap velocity (RSV) in Mohave Wash from January 2013 to May 2014.....	61
4.1. Potential evapotranspiration (PET) and cumulative precipitation at experimental plots during 2012 and 2013.....	80
4.2. Survival rates of <i>Olneya tesota</i> seedlings in experimental plots from January 2012 to January 2014.....	81
4.3. Survival rates of <i>Parkinsonia microphylla</i> seedlings in experimental plots from January 2012 to January 2014	82
4.4. Survival rates of <i>Parkinsonia florida</i> seedlings in experimental plots from January 2012 to January 2014.....	83
4.5. Comparison of survival rates for (A) <i>O. tesota</i> , (B) <i>P. microphylla</i> and (C) <i>P. florida</i> across treatment and irrigation levels during the first year.....	84
4.6. Comparison of survival rates for (A) <i>O. tesota</i> , (B) <i>P. microphylla</i> and (C) <i>P. florida</i> across experimental factors during the first year	85
4.7. Comparison of survival rates for (A) <i>O. tesota</i> , (B) <i>P. microphylla</i> and (C) <i>P. florida</i> across treatment and irrigation levels during the second year	86

4.8. Comparison of survival rates for (A) *O. tesota*, (B) *P. microphylla* and (C) *P. florida* across experimental factors during the second year 87

4.9. Relative growth rates of (A) *O. tesota*, (B) *P. microphylla*, and (C) *P. florida* during the first year as a function of initial height (cm) 88

1 Introduction

Classification systems across a range of spatial scales are widely used in the study and management of physical processes in stream networks (Church 1992, Thorne 1997, Montgomery and Buffington 1998). Differences in hydrogeomorphic processes among stream types are believed to produce distinctive ecological dynamics (Montgomery 1999, Thorp et al. 2006), but this hypothesis is rarely tested (Naiman et al. 1992).

A hydrogeomorphic stream classification for ephemeral streams in arid mountainous watersheds described five channel types: piedmont headwater, bedrock, bedrock with alluvium, incised alluvium, and braided (Sutfin et al. 2014). These stream types were defined by differences in channel planform, composition of boundary materials, and degree of lateral confinement. Bedrock streams are incised into cohesive rocks, and lack persistent alluvium. These steep and tightly confined channels drain mountain slopes, and support sparse vegetation. Bedrock with alluvium streams are also confined between bedrock valley walls, but they contain thin (typically < 1 m) alluvium that forms persistent lateral and point bars. Larger bedrock with alluvium channels may contain discontinuous narrow floodplain benches. These streams occupy narrow montane valleys, where riparian vegetation occurs in narrow bands along channel margins. Piedmont headwater streams are incised into consolidated Plio-Pleistocene alluvium. Lateral confinement is moderate to high, and channels contain thin (<50 cm) modern alluvium. Riparian vegetation on the bed and banks of these channels grades into open shrublands on adjacent upland surfaces. Incised alluvium streams are entrenched into piedmont surfaces and montane valley floors. These channels contain thick (> 1 m) alluvial deposits, with overbank surfaces ranging from narrow benches to wide floodplains, depending on lateral confinement. Riparian vegetation forms dense bands along channel margins and lower floodplain surfaces,

which grades into more open and xeric communities on outer floodplain surfaces. Braided streams contain multiple channels underlain by deep alluvium. They exhibit low to moderate confinement, and occupy alluvial valley floors. Extensive floodplain surfaces occur on channel margins and island tops. Vegetation is concentrated along the banks and lower floodplains, but dense patches of shrubs and trees occur on channel beds.

The five hydrogeomorphic stream types possess distinctive geomorphic and hydraulic characteristics (Sutfin et al. 2014), as well as alluvial depth and stratigraphic structure (Harry et al., *in prep*). Variation among stream types in the magnitude, frequency, and timing of streamflow (Faulconer et al. *in prep*.) interact with alluvial characteristics to produce different subsurface moisture dynamics (Kampf et al., *in review*). Riparian ecological dynamics are driven by interactions between hydrologic regimes (Fisher et al. 2007, Larned et al. 2010) and geomorphic disturbance (Gregory et al. 1991, Montgomery 1999, Benda et al. 2004). Therefore, the five stream types may support distinctive ecological properties and processes (Montgomery 1999, Thorp et al. 2006).

The distribution of trees in arid environments is extremely limited (Shreve and Wiggins 1964, Shmida and Burgess 1988, Gibson 1996), but has profound effects on physical and biological processes. Riparian trees in the Sonoran Desert provide habitats for numerous plant and animal taxa, and influence physical and ecological processes across a range of spatial scales (Burquez and Quintana 1994, Suzan et al. 1996, Drezner 2010). Understanding the limitations to tree ecophysiological performance and regeneration is critical to management and restoration of desert landscapes (Merritt and Bateman 2012).

I tested the ecological significance of an ephemeral stream hydrogeomorphic classification by comparing spatial patterns in riparian vegetation and riparian tree water relations across stream types in arid watersheds of the Sonoran Desert. This classification

framework was used to identify reach-scale physical drivers of plant community composition and ecohydrological dynamics. A two-year factorial field experiment was performed to identify the limitations to riparian tree establishment, and understand how facilitative mechanisms vary with annual rainfall.

2 Does a Hydrogeomorphic Stream Classification Explain Riparian Plant Community Composition?

2.1 Introduction

Stream channel classifications have been widely used in geomorphology (Church 1992, Montgomery and Buffington 1998, Montgomery 1999) and aquatic ecology (Newson and Newson 2000, Thorp et al. 2006), but few riparian ecologists have adopted this approach. Studies of riparian ecosystems have focused on the roles of lateral and longitudinal physical gradients in shaping spatial patterns of vegetation (Junk et al. 1989, Ward and Stanford 1995), as well as hydrogeomorphic processes that support riparian plant establishment and persistence (Hupp and Osterkamp 1996, Scott et al. 1996, Bendix and Hupp 2000). While abiotic gradients form the habitat templates that constrain ecological processes, incorporating generalizable stream reach types into riparian ecology can facilitate the understanding, management, and restoration of these ecosystems (Gregory et al. 1991, Naiman et al. 1992, Newson and Newson 2000).

Existing channel classifications have been developed largely from analyses of perennial rivers in temperate regions, with a focus on rivers draining forested mountainous terrain (Naiman et al. 1992). Dryland ephemeral streams are the most common, but least studied fluvial environment on earth (Bull and Kirkby 2002, Nanson et al. 2002). However, a recent channel classification for ephemeral stream networks identified five distinctive geomorphic environments in the Sonoran Desert (Sutfin et al. 2014). Increased focus on dryland riparian ecosystems in recent years has led to a growing global data set, but a broader understanding of longitudinal biotic patterns has been hampered by a lack of a conceptual framework for interpreting these data. Application of process-based hydrogeomorphic stream typologies to the analysis of riparian

vegetation dynamics can clarify the physical drivers of ecological processes, and provide context to biotic patterns (Newson and Newson 2000).

Stream networks may be divided into stream types (also known as functional process zones or process domains), which exhibit similar hydrogeomorphic processes and patterns (Montgomery 1999, Thorp et al. 2006). The abundance and spatial arrangement of stream types within watersheds are determined by many factors, including geologic discontinuities and network structure (Montgomery 1999, Benda et al. 2004, Thorp et al. 2006, Poole 2010). Differences in the magnitude, frequency, and duration of sediment and water fluxes among reach types produce fluvial environments with distinctive landforms, hydraulics, and alluvial characteristics (Montgomery and Buffington 1998, Montgomery 1999, Benda et al. 2004). These properties affect the frequency and duration of hydrologic connections, which ultimately determine nutrient cycling dynamics, erosion and deposition of geomorphic surfaces, and subsurface moisture regime (Gregory et al. 1991, Fisher et al. 2007, Poole 2010, Larned et al. 2011).

Ecological patterns and processes within dryland stream networks are shaped by the spatial and temporal distributions of hydrologic fluxes (Fisher et al. 2007, Larned et al. 2010) and geomorphic disturbance (Gregory et al. 1991, Montgomery 1999, Benda et al. 2004). Hydrologic connections govern the availability of water and nutrients, influencing the distribution of resources for plant growth (Poole 2010, Larned et al. 2010). Fluvial disturbances produce habitat heterogeneity, drive plant community succession, and modify population dynamics (Gregory et al. 1991, Thorp et al. 2006, Larned et al. 2010). The spatial distribution of riparian plants within stream networks reflect differing tolerances along gradients of water availability and disturbance, in addition to the diffusive effects of biotic interactions (Hupp and Osterkamp 1996, Bendix and Hupp 2000). Compositional shifts in relation to these abiotic

drivers lead to distinctive community types associated with particular hydrogeomorphic settings (Bendix 1994, Shaw and Cooper 2008, Angiolini et al. 2011).

While species are the fundamental units in plant ecology, analysis of plant functional traits can provide additional insight into ecological processes and yield more broadly applicable relationships (Shmida and Burgess 1988, Merritt et al. 2010). Plant growth forms (e.g. tree, shrub, grass) characterize broad differences in woodiness, canopy architecture, and root distributions that relate to patterns of spatial resource partitioning (Shmida and Burgess 1988, Stromberg 2013). Differences in rooting depth and lateral spread among growth forms (Canadell et al. 1996, Schenk and Jackson 2002a) correspond to distinctive patterns of water use (Davis and Mooney 1986, Shmida and Burgess 1988). Such morphological groups also exhibit differences in flood disturbance tolerance (Sandercock and Hooke 2010), and have distinctive regeneration niches (Cornelissen et al. 1996, Flores et al. 2004, Butterfield and Briggs 2011). Subdivisions of growth forms based on photosynthetic habit and leaf phenology (e.g. evergreen, winter deciduous, drought deciduous) reflect differences in physiological rates and responses to variation in resource availability that relate primarily to temporal partitioning of niches (Chabot and Hicks 1982, Smith et al. 1997, Sperry and Hacke 2002).

Identifying the reach-scale hydrogeomorphic drivers that influence plant community characteristics among stream types can clarify ecological patterns and processes occurring at watershed and landscape scales (Newson and Newson 2000, Thorp et al. 2006). Framing these relationships in terms of plant functional groups can enhance their utility (Shmida and Burgess 1988, Merritt et al. 2010). Process-based hydrogeomorphic stream types are expected to correspond to distinctive spatiotemporal biotic patterns (Montgomery 1999, Thorp et al. 2006), but these linkages are rarely tested (Naiman et al. 1992). To determine if differences in physical environments among stream types produce distinctive riparian vegetation (Thorp et al. 2006), I

assessed the ecological significance of an arid ephemeral stream classification (Sutfin et al. 2014). I addressed the following questions: (1) Does reach-scale species and functional group composition of perennial riparian plant communities differ among hydrogeomorphic stream types? (2) Which geomorphic characteristics drive variation in ephemeral stream riparian community composition at the reach scale?

2.2 Methods

The composition of perennial riparian vegetation was measured in 86 stream reaches at US Army Yuma Proving Ground (YPG) and 15 reaches at US Air Force Barry M. Goldwater Range (BMGR), in the Sonoran Desert of southwestern Arizona, USA (Figure 2.1). Regional topography consists of low igneous mountain ranges with gently sloping piedmonts, separated by broad alluvial valleys (Shreve and Wiggins 1964, McAuliffe 1999). Study watersheds at YPG range from 60 to 845 m, and those at BMGR range from 260 to 1250 m. Modern alluvium is gravel to cobbles in a sandy matrix, while piedmont surfaces are consolidated Plio-Pleistocene alluvium (Eberly and Stanley 1978, McAuliffe 1994). Biseasonal rainfall is derived from Pacific frontal storms from November to March, and convective thunderstorms that occur from July to September (Sellers and Hill 1974). Mean annual precipitation increases with elevation, and ranges from 93 to 103 mm at YPG, and from 156 to 213 mm at BMGR (NCDC station IDs #29654, 26865, 23393, 20080). Temperatures throughout the region are more uniform, with mean annual daily minima and maxima of 13°C and 32°C. Aside from the allogenic Colorado and Gila rivers, streamflow throughout the region is ephemeral. Upland vegetation consists of scattered microphyllous shrubs and subshrubs, primarily *Larrea tridentata* (creosote) and *Ambrosia dumosa* (white bursage) (Shreve and Wiggins 1964, Turner and Brown 1994). Riparian plant communities are dominated by xerophytic shrubs such as *Acacia* spp., *Ambrosia* spp., *Lycium* spp., *Encelia farinosa* (brittlebush), and *L. tridentata*. Common riparian trees

include *Olneya tesota* (ironwood), *Parkinsonia microphylla* (foothills paloverde), and *Parkinsonia florida* (blue paloverde), while *Psoralea argophylla* (smoketree) and *Prosopis velutina* (velvet mesquite) are locally abundant along larger alluvial streams. Except *P. spinosus*, these trees occupy upland surfaces within wetter portions of their ranges (Turner et al. 1995, Smith et al. 1997).

Study reaches were selected to maximize geographic distribution and represent the range of geomorphic conditions within accessible areas, without regard to vegetation characteristics. Reach lengths were scaled to four channel widths in braided streams and twelve channel widths in all others. Vegetation was surveyed throughout the entire active fluvial corridor of smaller reaches. In larger reaches (primarily braided), 10 m wide belt transects spanning the fluvial corridor were surveyed along two to four cross sections. Surveyed areas ranged from 50 m² to 1700 m². Variably-sized sample areas were necessary to adequately sample plant communities in proportion to plant density and physiognomy. In small bedrock or piedmont headwater reaches, fluvial corridor widths were as small as 2 m, while channel characteristics and stream type often changed over distances of <50 m. Conversely, patchy vegetation and variable landforms within large braided reaches were not adequately characterized in plots sized for headwater reaches (<100 m²). In alluvial streams, the active fluvial corridor consisted of channel and floodplain surfaces below relict terraces. Active fluvial corridors of streams incised into bedrock or piedmont surfaces were delineated by the elevation of fluvial landforms or staining on bedrock canyon walls.

Individuals of all perennial plant species were counted on each active fluvial surface (bed, bank, floodplain/overbank), and the percentage of total canopy coverage by species was obtained by averaging visual estimates from two independent observers. To standardize errors in counting rhizomatous grasses and shrubs, plants were considered to be individuals when

separated by at least 1 m for discrete patches of grass and shrubs and 3 m for trees, unless connecting lateral roots or prostrate stems indicated otherwise. Abundances (densities) were derived by dividing counts by sampled area. Vegetation surveys were conducted during full leaf-out in spring months (March-May) in 2011 and 2012.

I derived 18 *a priori* plant functional groups consisting of major growth forms subdivided on the basis of photosynthetic habit and leaf phenology (Table 1), similar to those of Shreve and Wiggins (1964), Lavorel et al. (1997) and Scholes et al. (1997). These groupings comprise functional trait combinations affecting resource acquisition and use, and should therefore exhibit distinctive responses to disturbance and resource availability (Petchey and Gaston 2006). Functional groups were assigned based on published species accounts and field observations over two years (Appendix 1).

Geomorphic and hydraulic characteristics provided by Sutfin et al. (2014) were derived from topographic surveys along four equally-spaced cross sections in each study reach. Variables included channel gradient and entrenchment ratio (Rosgen 1994), as well as bankfull measures of width:depth, boundary shear stress, and stream power. Mean elevation was derived from 30 m DEMs, and Solar Analyst in ArcMap 10.1 was used to estimate total annual insolation (Fu and Rich 1999).

Differences in community composition among stream types were assessed using nonparametric permutational MANOVA (PerMANOVA) and distance-based tests of homogeneity of multivariate dispersion (PermDISP) (Anderson 2001, 2006). These tests were performed on Bray-Curtis similarity matrices relativized by sample unit totals for both cover and densities of species and functional groups. Relative cover and density values were arcsine-square root transformed, and rare species occurring in less than 5 % of sites were omitted (McCune and Grace 2002). Nonmetric Multidimensional Scaling ordinations were used to illustrate

multivariate differences in location and dispersion among reach types (Kruskal and Wish 1978). Species and functional groups responsible for compositional dissimilarity among stream types, and similarity within stream types, were identified by partitioning variance components of similarity matrices with the SIMPER procedure (Clarke 1993). Abiotic drivers of compositional differences among stream types were identified as the subset of variables from the environmental similarity matrix that optimized the Spearman rank correlation with biotic matrices (Clarke and Ainsworth 1993). The environmental matrix was calculated from Euclidean distances on \log_{10} transformed and normalized abiotic variables. Environmental gradients were illustrated as vectors on ordinations, scaled proportionally to correlations with axis scores.

2.3 Results

A total of 88 perennial plant species were observed in the study reaches. The 86 study reaches at YPG contained 72 species, and 60 species were found in the 15 reaches at BMGR. Only one exotic species (*Tamarix aphylla*) was found, consisting of one individual each in two braided reaches. Twenty-three species occurred in less than 5 % of study reaches, and were not used in the statistical analyses.

2.3.1 Species Cover

The composition and variability of species cover differed significantly among the five stream types (Table 2.2; Figure 2.2A). Bedrock, piedmont headwater, and braided streams each had distinctive floristic composition. However, the vegetation of incised alluvium and bedrock with alluvium streams was similar (Table 2.3). Variability was highest in bedrock streams and lowest in braided streams, but similar in other stream types (Table 2.4). Differences in the relative cover of eight species drove 53 % of the dissimilarity among stream types (Figure 2.3A). *Olneya tesota* and *Parkinsonia microphylla* produced the largest sources of variation, while *Encelia farinosa*, *Larrea tridentata*, *Ambrosia dumosa*, *Lycium torreyi*, *Hyptis emoryi*, and

Acacia greggii each contributed 7.9 to 4.9 % of compositional dissimilarity. Although they did not substantially contribute to differences between other stream types, *Parkinsonia florida* and *Ambrosia salsola* were useful in distinguishing braided streams. Relative cover of *P. microphylla*, *E. farinosa*, *L. tridentata*, *O. tesota*, and *A. dumosa*, provided 70 % of compositional similarity within stream types, although *Acacia greggii* was also important in braided streams (Figure 2.3B).

2.3.2 Species Density

The composition and dispersion of species density differed between stream types (Table 2.2; Figure 2.2B). Each stream type exhibited a unique composition (Table 2.3), and bedrock streams had significantly greater variability than other stream types (Table 2.4). Floristic patterns of species density were largely driven by *E. farinosa*, which provided 9.9 % of dissimilarity among stream types (Figure 2.4A) and 27 % of similarity within stream types (Figure 2.4B). *Larrea tridentata*, *A. dumosa*, *Fagonia laevis*, and *L. torreyi* contributed 6.3 to 4.8 % of overall dissimilarity. Braided streams were also distinguished by relative densities of *A. salsola* (5.7 %) and *Bebbia juncea* (5.3 %), while bedrock streams were differentiated by *Sphaeralcea ambigua* (4.3 %) and *P. microphylla* (4.2 %). In addition to contributions from *E. farinosa*, similarity within stream types was driven by varying densities of *A. dumosa* (13 %), *L. tridentata* (12%), and *P. microphylla* (6.8 %).

2.3.3 Functional Group Cover

Community composition defined by the relative cover of functional groups differed among stream types (Table 2.2; Figure 2.5A). Bedrock with alluvium and incised alluvium streams were not significantly different, but all other stream types had unique vegetation (Table 2.3). Beta diversity was highest in bedrock streams and lowest in braided streams, but was similar among other stream types (Table 2.4). The relative cover of evergreen trees,

photosynthetic stem trees, and drought deciduous subshrubs each contributed 14 % to compositional differences among stream types (Figure 2.6A). Shrubs with evergreen, drought deciduous, and winter deciduous foliage provided 11 to 10 % of dissimilarity. Relative cover of drought deciduous subshrubs provided 26% of compositional similarity within stream types, followed by evergreen shrubs (18 %), photosynthetic stem trees (17 %), and evergreen trees (13 %) (Figure 2.6B).

2.3.4 *Functional Group Density*

Stream types were significantly different in the composition and dispersion of functional group densities (Table 2.2; Figure 2.5B). Relative densities of functional groups in bedrock with alluvium streams was similar to that of bedrock and incised alluvium streams, but all other pairwise comparisons were significantly different (Table 2.3). Beta diversity was similar among all stream types, except for bedrock streams, which had the greatest dispersion (Table 2.4). Relative density of drought deciduous subshrubs provided 19 % of compositional differences among stream types, and much of the remaining dissimilarity was caused by drought deciduous shrubs (13 %), evergreen shrubs (11 %), herbaceous plants (9.2 %), and photosynthetic stem trees (8.2 %) (Figure 2.7A). Similarity within stream types arose primarily from the density of drought deciduous subshrubs (47 %), with lesser contributions from evergreen shrubs (15 %) and drought deciduous shrubs (13%) (Figure 2.7B).

2.3.5 *Reach Scale Geomorphic Drivers of Community Composition*

Compositional variation in the cover and density of species and functional groups occurred primarily along co-varying gradients of channel slope and width:depth (Figures 2.2 and 2.5). Piedmont headwater, incised alluvium, and bedrock with alluvium streams occupied similar portions of this gradient, but distinctive community composition of piedmont headwater streams was associated with lower stream power. Channel slope occurred in all of the highest-ranked

subsets of abiotic variables corresponding to floristic differences among stream types (Table 2.5). Variation in species cover was best explained by channel slope and reach elevation ($r_s = 0.51$). The most parsimonious subset of predictors for differences in species density consisted of channel slope, width:depth, and elevation ($r_s = 0.48$), since the inclusion of stream power or shear stress yielded negligible improvements. Similarly, channel slope provided the most explanatory power for variation in functional group cover ($r_s = 0.46$). Differences in functional group densities among stream types were best explained by channel slope and width:depth ($r_s = 0.47$).

2.4 Discussion

The five hydrogeomorphic stream types supported distinctive riparian plant composition. Relative cover and density of species and functional groups differed substantially between braided, bedrock, and piedmont headwater streams. Incised alluvium and bedrock with alluvium streams, while different from other stream types, supported similar vegetation that was distinguishable only by species density. A comparison of channel geometry and hydraulic variables showed a comparable pattern of distinctive physical environments occurring in braided, bedrock, and piedmont headwater streams, while incised alluvium and bedrock with alluvium streams were similar (Sutfin et al. 2014).

The distinctive physical environments and perennial plant composition of braided, bedrock, and piedmont headwater streams correspond to their placement as end-members along the fluvial continuum of ephemeral watersheds in the Sonoran Desert. Braided streams within the study area occur in flat lowlands, where wide, low-gradient channels have low erosive potential (Sutfin et al. 2014). Bedrock streams represent the opposite end of the continuum, with steep and highly-confined channels draining mountainous uplands. Piedmont headwater streams possess moderate gradients that reflect the topography of mountain pediments, but small discharges in

these headwater segments generate low stream power and sediment transport capacity. Similar physical environments and plant communities in bedrock with alluvium and incised alluvium streams arise from their co-occurrence along the transition zone from mountainous uplands to lowland valleys.

Despite general similarities among bedrock with alluvium and incised alluvium channels, fundamental differences in boundary materials suggest differing sensitivities to disturbance, processes of geomorphic adjustment, and ecohydrological dynamics that warrant separate treatment. Channel incision and lateral adjustment of bedrock with alluvium streams is largely constrained by resistant channel boundaries. In contrast, flood disturbance and more gradual changes in sediment and streamflow regimes could result in bed incision, channel widening, and avulsion within incised alluvium streams (Knighton 1998). The thickness of alluvial deposits within bedrock with alluvium streams is typically less than those of incised alluvium channels (Harry et al. *in prep*), and would likely induce different rates of streamflow transmission losses (Goodrich et al. 1997) and subsurface moisture dynamics (Shaw and Cooper 2008, Kampf et al. *in review*). The resulting disparity in the magnitude and frequency of streamflow, and patterns of root zone water availability, are expected to produce differences in the timing and extent of plant establishment and mortality, and water relations. Aggregation of abiotic and biotic characteristics across the reach scale may have precluded the detection of geomorphic and ecological differences among these stream types that occur at finer scales.

2.4.1 *Species Composition*

Differences in floristic composition between stream types within the study area are driven by the most common species in the regional flora of the northern Sonoran Desert, *Ambrosia dumosa*, *E. farinosa*, and *L. tridentata* (Shreve and Wiggins 1964, Turner et al. 1995). These were among the most influential components of variation between riparian vegetation of all

stream types. *Encelia farinosa* commonly occurs on rocky slopes (Parker 1988, Smith et al. 1997), and its tolerance for the low water availability typical of coarse thin sediments allows it to attain the greatest relative cover in bedrock streams. In contrast, *A. dumosa* and *L. tridentata* occupy sandy soils and alluvial sediments (Shreve and Wiggins 1964), resulting in their higher abundance in piedmont headwater, and braided and incised alluvium streams, respectively. *Olneya tesota* and *P. microphylla* are the most abundant and widespread trees in xeroriparian communities of the Lower Colorado Valley, and commonly occur on upland surfaces in less xeric portions the northern Sonoran Desert (Shreve and Wiggins 1964, Turner et al. 1995). Their prevalence throughout the studied watersheds reflect the ability to inhabit a wide range of substrates and geomorphic settings (Parker 1988), but their scarcity in bedrock streams is likely due to lower moisture availability during dry seasons. Although occurring at lower densities than other species, the larger stature of these trees heavily impacted relative cover in all stream types. Secondary differences among stream types arise from more localized species occurrences, according to their affinity for specific substrates and facilitative interactions. Species typical of braided and incised alluvium streams such as *B. juncea*, *A. salsola*, *P. florida* and *P. spinosus* are found on thick unconsolidated sediments and active alluvium throughout their ranges (Campbell and Green 1968, Turner et al. 1995, Baldwin et al. 2002).

2.4.2 *Functional Group Composition*

The dominance of drought deciduous subshrubs throughout ephemeral watersheds of the northern Sonoran Desert, particularly in the more xeric bedrock and piedmont headwater streams, results from their ability to rapidly utilize brief moisture pulses and minimize water demands during drought periods by shedding photosynthetic tissue (Shreve and Wiggins 1964, Smith et al. 1997). A similar strategy for coping with environmental variations in herbaceous perennials is reflected by a comparable spatial pattern of relative abundance. While larger

drought deciduous shrubs follow the same temporal pattern of resource acquisition as their subshrub counterparts, they were most abundant in downstream alluvial portions of stream networks, suggesting that greater rooting depth enables them to access moisture in deeper strata (Davis and Mooney 1986, Shmida and Burgess 1988). Gas exchange and growth rates of woody evergreen and photosynthetic stem plants are lower than those of drought deciduous growth forms, but they require more persistent soil moisture to meet the metabolic demands of maintaining photosynthetic tissue throughout the year (Smith et al. 1997). The greater importance of these functional groups within incised alluvium and braided streams suggests that lower rates of resource acquisition provides a competitive advantage in lower network positions, where infrequent flow events may only recharge deep alluvium once every one or two years. In dryland settings, cacti of all sizes and perennial grasses are most abundant where reliable warm-season moisture occurs (Shmida and Burgess 1988, Smith et al. 1997), which probably explains their relative scarcity within ephemeral watersheds in a region of highly variable monsoon rainfall.

Differences in the frequency and intensity of periodic flood disturbance among the channel types corresponds to variation in the relative density of growth forms. Intense flood disturbance associated with high channel gradient and bankfull shear stress in bedrock streams favors the compact and flexible canopies of subshrubs. In contrast, the greater aboveground biomass and rigid stems of arborescent growth forms makes them more susceptible to flood damage, and slower growth rates could limit their ability to recolonize between floods. Although the flexible and multi-stemmed canopies of shrubs are less susceptible than trees to flood disturbance (Sandercock and Hooke 2010), both growth forms exhibited similar spatial distributions. This pattern suggests that access to stable water supplies in deep alluvium exerts greater influence than disturbance regime on the occurrence of larger woody plants in arid

watersheds (Shreve and Wiggins 1964, Balding and Cunningham 1974, Shmida and Burgess 1988, Lite and Stromberg 2005).

2.4.3 Reach Scale Geomorphic Drivers of Community Composition

Channel slope was the primary reach-scale driver of riparian community composition in ephemeral stream networks of the Sonoran Desert. The influence of channel slope on riparian ecological patterns arises from direct effects on disturbance potential, and indirect effects on alluvial storage and subsurface water availability. As the primary determinant of streamflow velocity and sediment transport capacity (Knighton 1998), channel gradient governs channel and floodplain hydraulics, and the associated disturbance regimes that directly shape riparian communities (Hupp 1982, Baker 1989, Bendix 1997). Spatial variation in sediment transport and deposition controls the distribution and character of fluvial landforms, indirectly influencing patterns of flood inundation that are associated with the distributions of plant species and riparian community types (Hupp 1982, 1986, Bendix 1994, Bendix and Hupp 2000). At larger spatial scales, channel slope and related covariates (e.g., stream power, width:depth) determine sediment deposition, and the thickness and extent of active alluvium. Sediment thickness limits subsurface moisture storage capacity, and is a fundamental control on desert plant community composition (Kassas and Imam 1954, Shreve and Wiggins 1964, McAuliffe 1999).

Stream reach elevation was a secondary determinant of species composition. Similar patterns have been recognized in mountainous semi-arid watersheds of higher relief (Baker 1989, Bendix 1994, Sieben et al. 2009), but the limited range of elevations among the study reaches (460 m) is unlikely to create substantial zonation in temperature or rainfall regimes. Instead, elevation likely serves as a proxy for changes in substrate type. Within the study area, bedrock streams occur at the highest elevations and piedmont headwaters occur at moderate elevations, while incised alluvium and braided streams are found at the lowest elevations. Insolation or heat

load, typically quantified by indices of slope aspect, strongly influences soil moisture dynamics and plant community composition in upland desert environments (Shreve and Wiggins 1964, Noy-Meir 1973, Parker 1988). The finding that total annual insolation did not covary with riparian composition likely reflects compensation for evapotranspirational losses, due to substantial run-on water subsidies from contributing watersheds and tree canopy shading, which is not typically available in upland sites.

2.4.4 Application of the Hydrogeomorphic Stream Classification

Although the hydrogeomorphic stream types presented here have not been previously applied in vegetation studies, analogous patterns of riparian species and functional group composition occur in dryland stream networks around the world. Distinctive plant community types in the equivalents of bedrock, incised alluvium, and braided streams have been widely observed in ephemeral watersheds throughout Saudi Arabia (Al Wadie 2002, Alatar et al. 2012, Al-Rowaily et al. 2012, Abdel Khalik et al. 2013, El Ghazali et al. 2013), Egypt (Kassas and Imam 1954, Ali et al. 2000), and Algeria (Benhouhou et al. 2003), as well as along perennial and intermittent rivers in South Africa (Van Coller et al. 1997) and Italy (Angiolini et al. 2011, Nucci et al. 2012). Bedrock with alluvium and incised alluvium streams in the study area support broadly similar vegetation, but compositional differences among the equivalents of these stream types have been recognized in other ephemeral stream networks of the southwestern USA (Shaw and Cooper 2008) and northern Africa (Kassas and Imam 1954, Benhouhou et al. 2003). While specific physical and biological attributes vary with regional climate, geology, and biogeography, considerable evidence indicates that these stream types comprise distinctive hydrogeomorphic and ecological process domains.

The ephemeral stream classification of Sutfin et al. (2014) characterizes spatial patterns of riparian plant communities and physical drivers of ecological dynamics at the stream reach

scale, and has many potential applications in research, management, and restoration. The classification can be used to select appropriate reference sites for restoration targets, and to identify suitable controls and replicates in manipulative experiments. In observational studies, it can provide a defensible basis for sample stratification, and be used to identify portions of fluvial gradients for process-based investigations. Since these stream types appear to be broadly relevant to dryland fluvial environments around the world, they may facilitate scientific communication as concise and meaningful descriptors of physical and biological process domains. Although the specific attributes of these stream types will likely vary between regions, this typology has the potential to provide rich physical and biological information from simple visual inspection of qualitative features.

Table 2.1. *A priori* plant functional groups. Functional groupings for each species and associated references are in Appendix 1.

Functional Group	Species	Examples
Evergreen Trees	4	<i>Olneya tesota</i> ; <i>Condalia globosa</i>
Photosynthetic Stem Trees	3	<i>Parkinsonia</i> spp.; <i>Psoralea spinosa</i>
Winter Deciduous Trees	2	<i>Prosopis</i> spp.; <i>Chilopsis linearis</i>
Columnar Cacti	1	<i>Carnegiea gigantea</i>
Evergreen Shrubs	6	<i>Larrea tridentata</i> ; <i>Simmondsia chinensis</i>
Drought Deciduous Shrubs	13	<i>Lycium</i> spp.; <i>Fouquieria splendens</i>
Photosynthetic Stem Shrubs	6	<i>Krameria</i> spp.; <i>Ephedra aspera</i>
Winter Deciduous Shrubs	4	<i>Acacia</i> spp.; <i>Colubrina californica</i>
Shrubby Cacti	5	<i>Cylindropuntia</i> spp.; <i>Opuntia</i> spp.
Evergreen Subshrubs	2	<i>Ambrosia ambrosioides</i> ; <i>Tiquilia canescens</i>
Drought Deciduous Subshrubs	19	<i>Encelia farinosa</i> ; <i>Ambrosia dumosa</i>
Photosynthetic Stem Subshrubs	2	<i>Carlowrightia arizonica</i> ; <i>Porophyllum gracile</i>
Winter Deciduous Subshrubs	1	<i>Ayenia microphylla</i>
Low Cacti	5	<i>Mammillaria</i> spp.; <i>Opuntia basilaris</i>
Vines	2	<i>Sarcostemma cynanchoides</i> ; <i>Cottia gracilis</i>
Herbaceous	7	<i>Sphaeralcea ambigua</i> ; <i>Eriogonum inflatum</i>
Grasses	6	<i>Hilaria rigida</i> ; <i>Aristida purpurea</i>
Epiphytic Parasites	1	<i>Phoradendron californicum</i>

Table 2.2. Tests for global differences among stream types in riparian plant community composition (PerMANOVA) and compositional variance (PermDISP).

Source	PerMANOVA			PermDISP	
	R²	F	P	F	P
Species Cover	0.239	6.27	<0.001	12.0	<0.001
Species Density	0.230	5.96	<0.001	7.84	<0.001
Functional Group Cover	0.252	6.73	<0.001	13.8	<0.001
Functional Group Density	0.284	7.94	<0.001	5.85	0.002

Table 2.3. Pairwise comparisons for differences in riparian plant community composition (PerMANOVA) among stream types. Bold P-values are significant at $\alpha = 0.05$.

Comparison	Species Cover		Species Density		Functional Group Cover		Functional Group Density	
	t	P	t	P	t	P	t	P
Bedrock vs Bedrock with Alluvium	1.75	0.004	1.55	0.024	2.13	<0.001	1.53	0.064
Bedrock vs Incised Alluvium	2.43	<0.001	2.07	0.001	2.82	<0.001	2.27	0.004
Bedrock vs Piedmont Headwater	2.50	<0.001	2.35	<0.001	2.14	0.002	1.59	0.041
Bedrock vs Braided	3.41	<0.001	3.22	<0.001	3.71	<0.001	4.20	<0.001
Bedrock with Alluvium vs Incised Alluvium	1.40	0.079	1.44	0.033	1.42	0.087	1.41	0.092
Bedrock with Alluvium vs Piedmont Headwater	2.48	<0.001	2.53	<0.001	2.01	0.002	1.88	0.007
Bedrock with Alluvium vs Braided	2.81	<0.001	2.91	<0.001	2.45	<0.001	3.87	<0.001
Incised Alluvium vs Piedmont Headwater	2.22	<0.001	2.26	0.001	2.56	<0.001	2.58	<0.001
Incised Alluvium vs Braided	2.32	0.002	2.34	<0.001	2.34	<0.001	3.04	<0.001
Piedmont Headwater vs Braided	3.67	<0.001	3.73	<0.001	4.07	<0.001	5.22	<0.001

Table 2.4. Pairwise comparisons for differences in riparian plant community compositional variance (PermDISP) among stream types. Bold P-values are significant at $\alpha = 0.05$.

Comparison	Species Cover		Species Density		Functional Group Cover		Functional Group Density	
	t	P	t	P	t	P	t	P
Bedrock vs Bedrock with Alluvium	2.72	0.021	2.08	0.049	2.71	0.023	2.31	0.043
Bedrock vs Incised Alluvium	4.54	0.001	3.43	0.001	5.10	<0.001	3.30	0.004
Bedrock vs Piedmont Headwater	4.17	0.002	4.21	0.001	3.46	0.008	3.58	0.002
Bedrock vs Braided	7.44	<0.001	5.50	<0.001	7.98	<0.001	4.89	<0.001
Bedrock with Alluvium vs Incised Alluvium	1.80	0.11	1.30	0.25	1.88	0.087	0.851	0.42
Bedrock with Alluvium vs Piedmont Headwater	1.66	0.14	2.12	0.052	0.619	0.59	1.06	0.31
Bedrock with Alluvium vs Braided	4.55	<0.001	3.16	0.005	4.56	<0.001	2.17	0.035
Incised Alluvium vs Piedmont Headwater	0.007	0.99	0.849	0.45	1.25	0.27	0.192	0.86
Incised Alluvium vs Braided	2.71	0.016	1.86	0.084	3.70	0.002	1.39	0.21
Piedmont Headwater vs Braided	2.30	0.051	0.933	0.40	4.10	0.002	1.22	0.27

Table 2.5. Ranked subsets of reach scale abiotic variables corresponding to differences in riparian plant community composition among stream types. r_s = Spearman rank correlation. All correlations were significant at $\alpha = 0.01$.

	Variable Subset	r_s
Species Cover	Slope, Elevation	0.505
	Slope, Shear Stress, Elevation	0.504
	Slope, Stream Power, Elevation	0.504
	Slope, Shear Stress, Stream Power, Elevation	0.501
	Slope, Width:Depth, Shear Stress, Elevation	0.501
Species Density	Slope, Width:Depth, Stream Power, Elevation	0.485
	Slope, Width:Depth, Elevation	0.482
	Slope, Width:Depth, Shear Stress, Elevation	0.474
	Slope, Width:Depth, Shear Stress, Stream Power, Elevation	0.468
	Width:Depth, Shear Stress, Elevation	0.455
Functional Group Cover	Slope, Shear Stress	0.461
	Slope, Shear Stress, Elevation	0.460
	Slope	0.460
	Slope, Shear Stress, Stream Power, Elevation	0.451
	Slope, Elevation	0.444
Functional Group Density	Slope, Width:Depth	0.468
	Slope, Width:Depth, Stream Power	0.458
	Slope, Width:Depth, Shear Stress	0.445
	Slope, Width:Depth, Stream Power, Elevation	0.443
	Slope, Width:Depth, Elevation	0.442

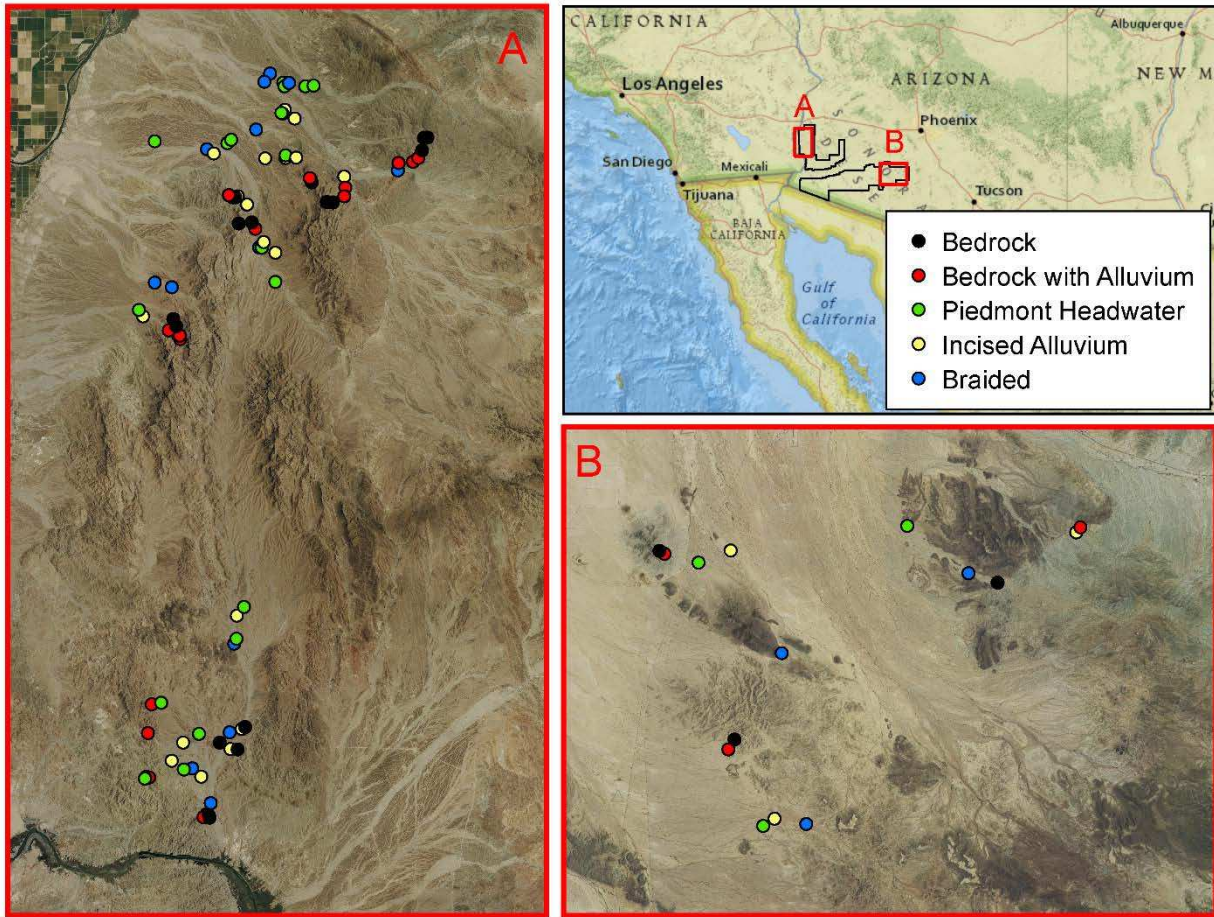


Figure 2.1. Location of study reaches at Yuma Proving Ground and Barry M. Goldwater Range, in the Sonoran Desert of southern Arizona, USA.

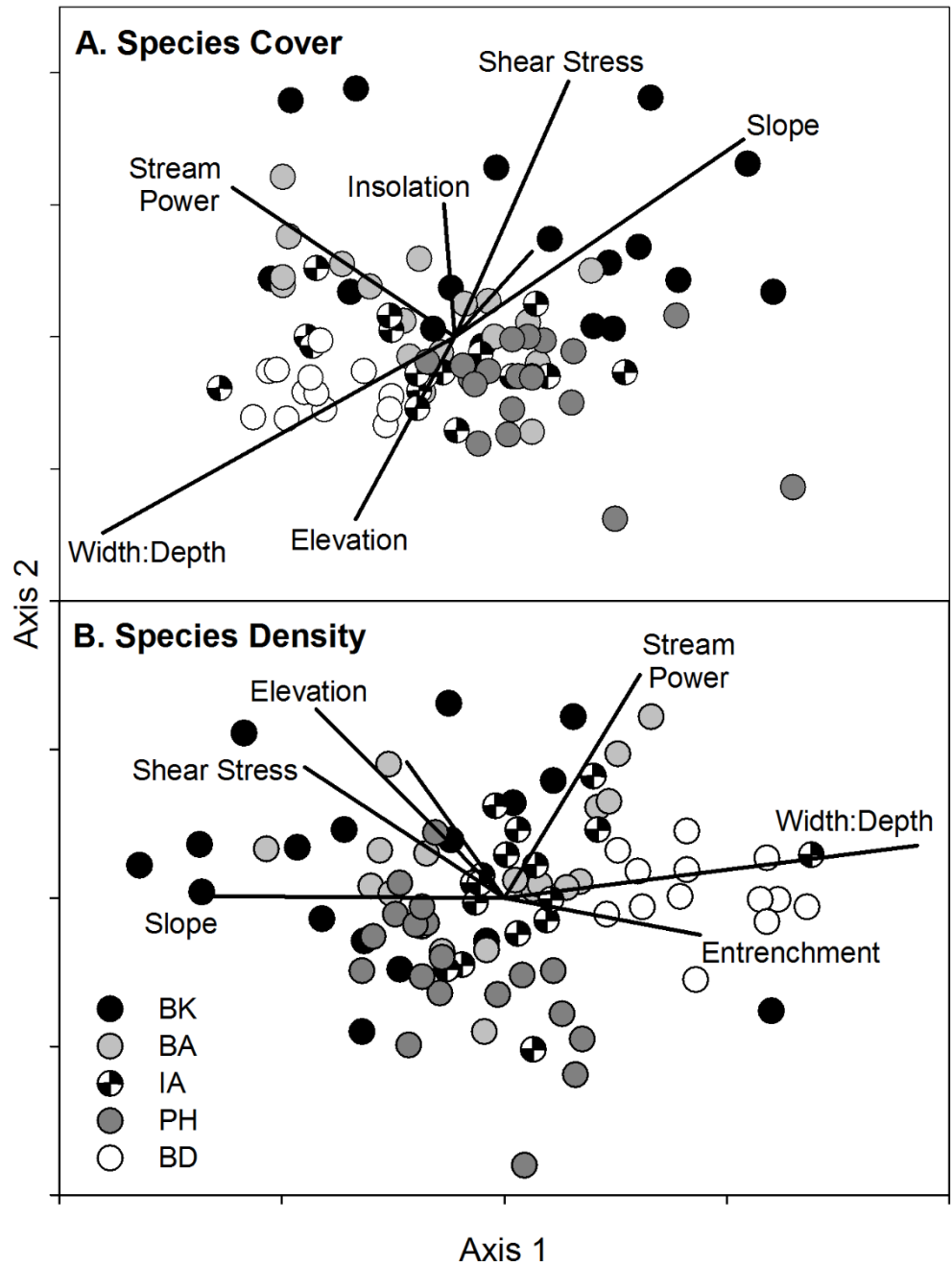


Figure 2.2. Nonmetric Multidimensional Scaling ordination of (A) species relative cover (stress = 0.145), and (B) species relative density (stress = 0.169). BK = bedrock; BA = bedrock with alluvium; IA = incised alluvium; PH = piedmont headwater; BD = braided.

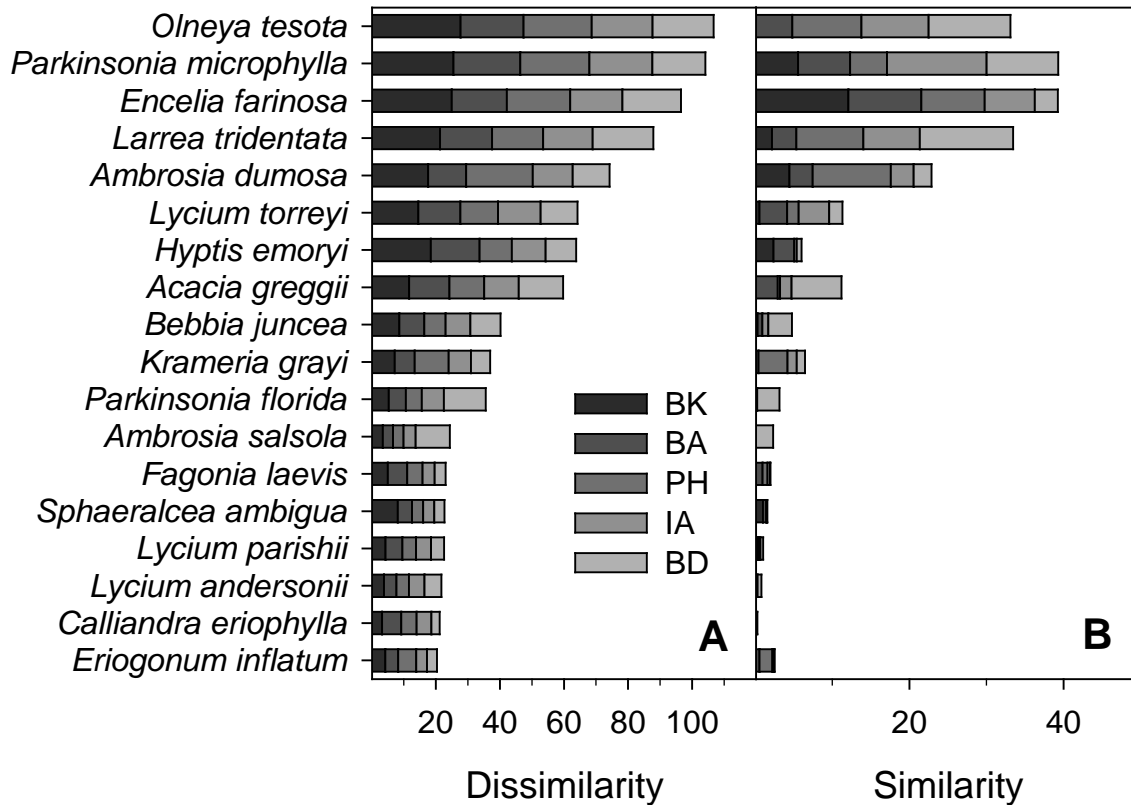


Figure 2.3. Ranked contribution of species relative cover to Bray-Curtis dissimilarity between stream types (A), and similarity within stream types (B). Only the 18 highest-ranked species are shown. BK = bedrock; BA = bedrock with alluvium; IA = incised alluvium; PH = piedmont headwater; BD = braided.

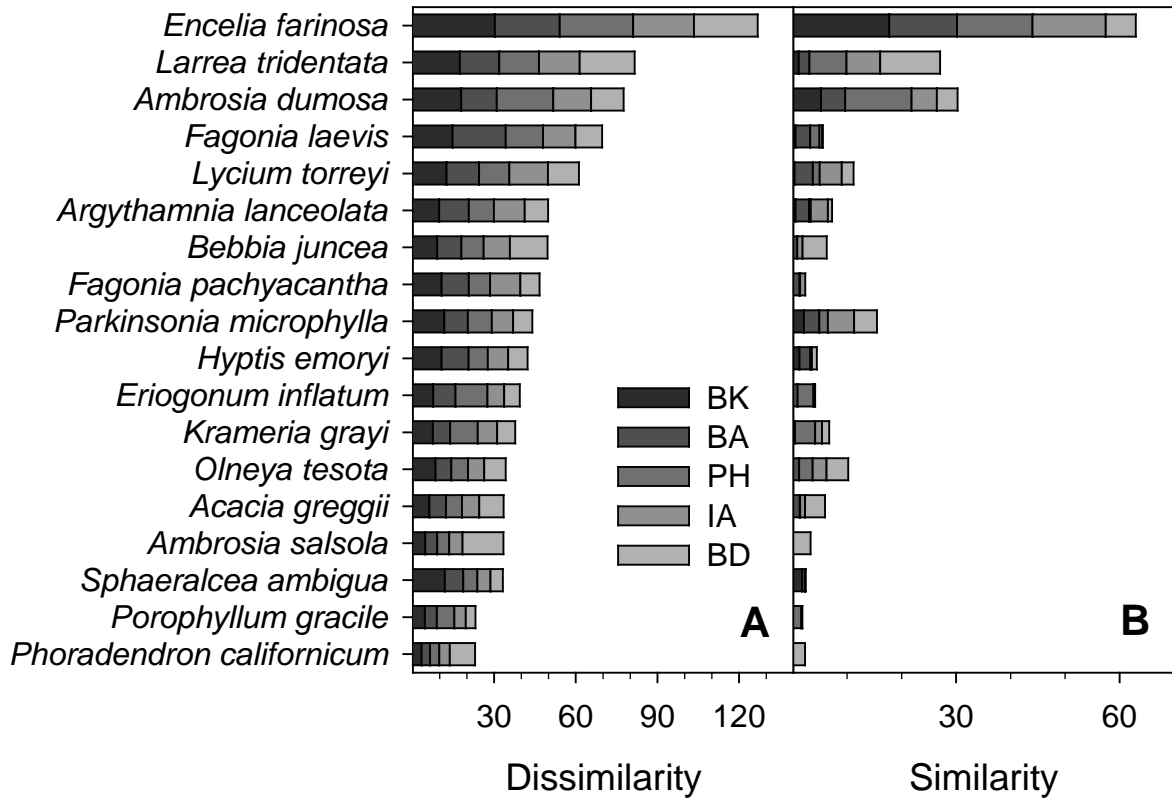


Figure 2.4. Ranked contribution of species relative density to Bray-Curtis dissimilarities between stream types (A), and similarity within stream types (B). Only the 18 highest-ranked species are shown. BK = bedrock; BA = bedrock with alluvium; IA = incised alluvium; PH = piedmont headwater; BD = braided.

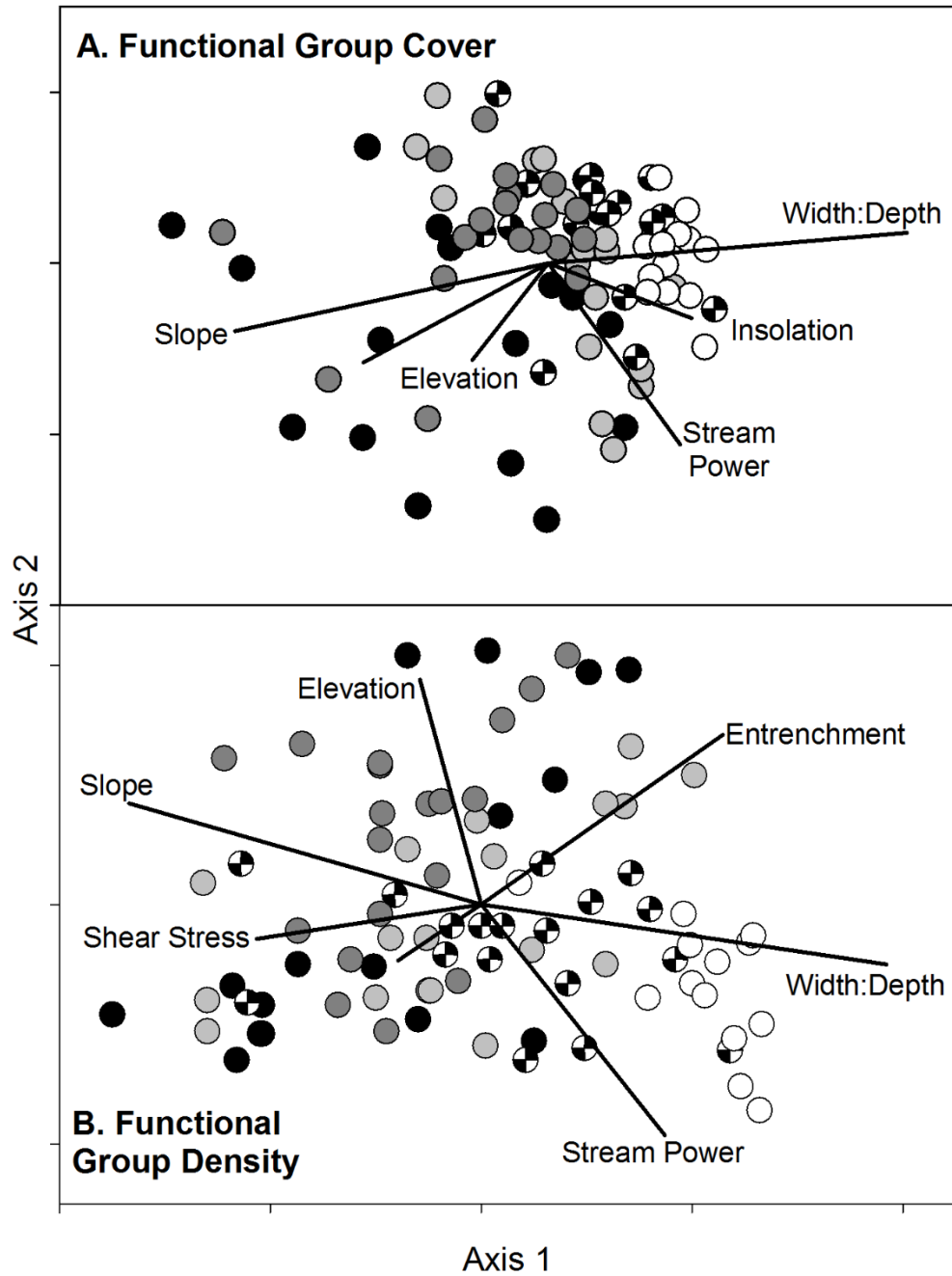


Figure 2.5. Nonmetric Multidimensional Scaling ordination of (A) functional group relative cover (stress = 0.132), and (B) functional group relative density (stress = 0.111). See Figure 2.2 caption for symbols.

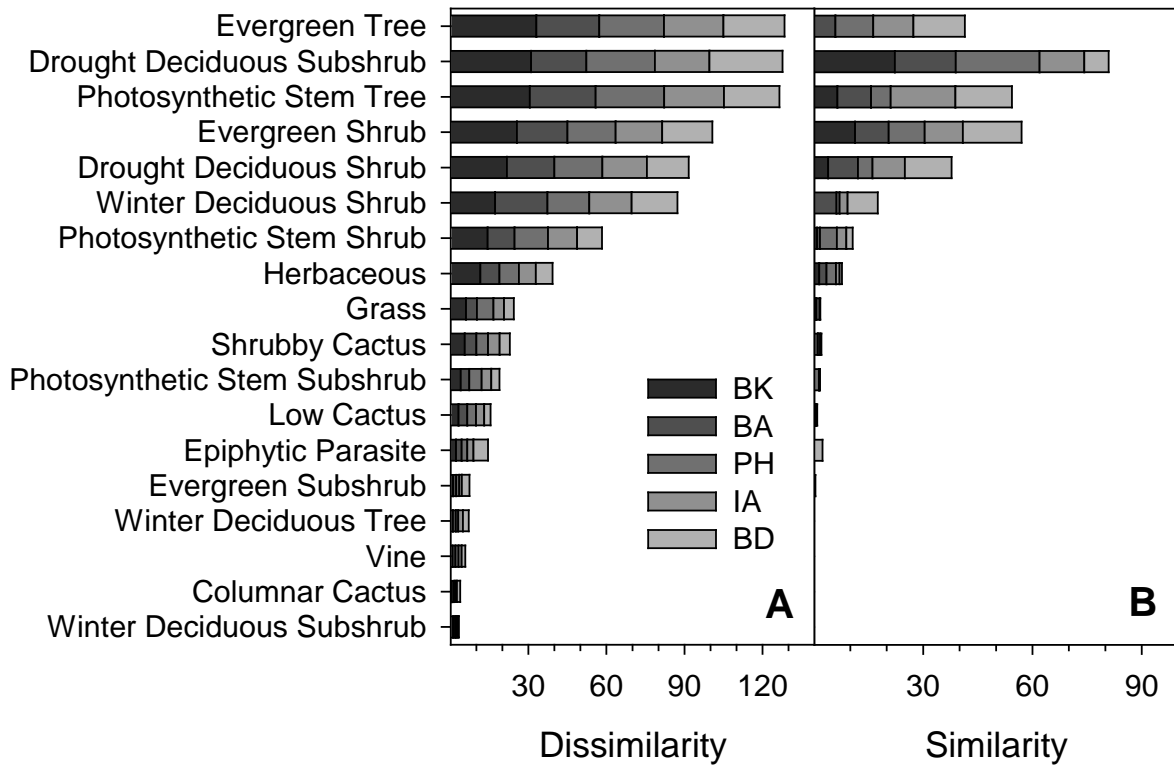


Figure 2.6. Ranked contribution of functional group relative cover to Bray-Curtis dissimilarities between stream types (A), and similarity within stream types (B). BK = bedrock; BA = bedrock with alluvium; IA = incised alluvium; PH = piedmont headwater; BD = braided.

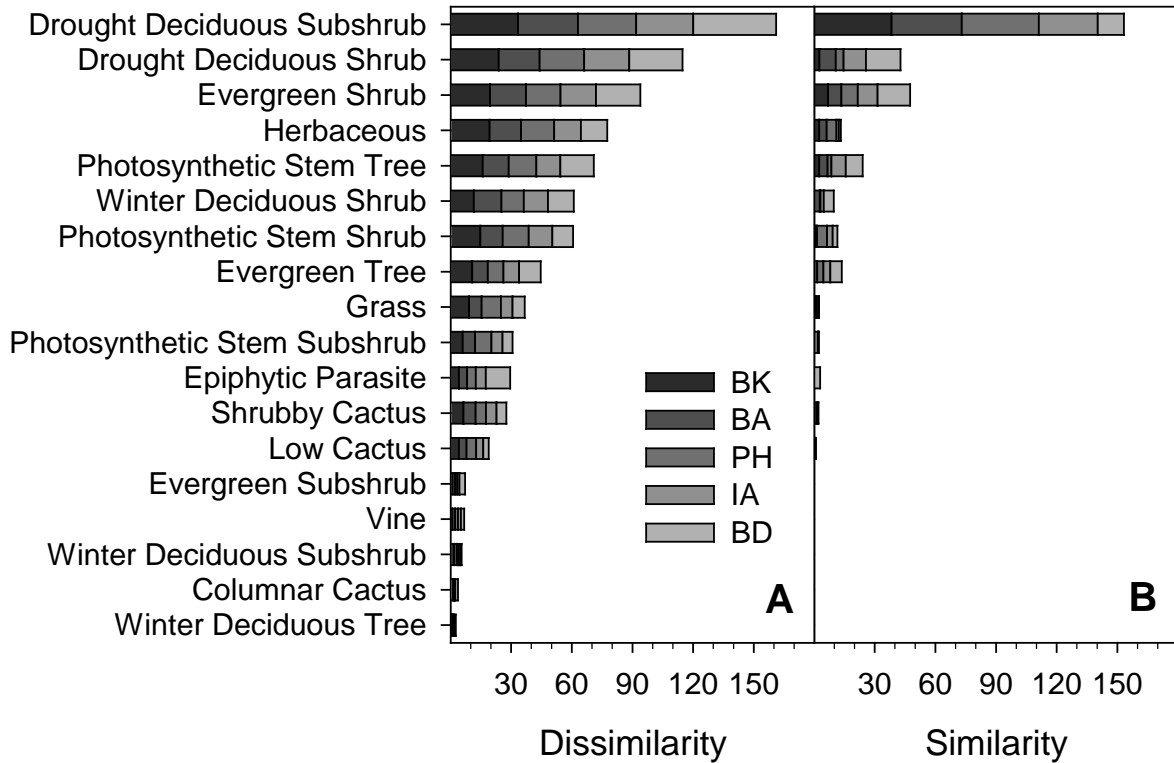


Figure 2.7. Ranked contribution of functional group relative density to average Bray-Curtis dissimilarities between stream types (A), and similarity within stream types (B). BK = bedrock; BA = bedrock with alluvium; IA = incised alluvium; PH = piedmont headwater; BD = braided.

3 Seasonal Ecohydrology of Riparian Trees in Ephemeral Stream Networks Differs Among Hydrogeomorphic Stream Types

3.1 Introduction

Substrate properties and geomorphic setting profoundly influence plant water availability in arid regions. Fine-textured sediments and shallow soil profiles magnify plant water stress during drought periods, while deep unconsolidated alluvium and fractured bedrock can provide persistent water supplies (Shreve and Wiggins 1964, McAuliffe 1994, 1999, Busch and Smith 1995). Numerous studies from upland settings have shown that differences in sediment depth and subsurface hydraulic properties among geomorphic surfaces produce divergent patterns of water stress at seasonal to multi-year timescales (Halvorson and Patten 1974, McAuliffe 1994, 1999, Smith et al. 1995, Hamerlynck et al. 2002). These processes suggest that variations in streamflow regime and subsurface water storage capacity throughout ephemeral stream networks give rise to distinctive patterns of water stress and water use. Additional support for this hypothesis comes from comparisons of foliar $\delta^{13}\text{C}$ along an intermittent desert stream, which showed that yearly water stress in riparian trees declines with increasing drainage area and flow permanence (Sponseller and Fisher 2006).

The dominant riparian tree species in ephemeral watersheds of the Sonoran Desert have photosynthetic stems or evergreen leaves that remain photosynthetically active throughout the year, despite chronic water limitation and intense summer droughts (Szarek and Woodhouse 1977, 1978, Nilsen et al. 1989). These include *Olneya tesota* (desert ironwood) and *Parkinsonia microphylla* (foothills paloverde) which occur throughout stream networks, and localized populations of *Parkinsonia florida* (blue paloverde) and *Psoralea argemone* (smoketree) along larger alluvial streams. All of these trees have extensive root systems, thought to be

capable of accessing both shallow and deep water sources (Turner and Brown 1994, Turner et al. 1995, Gibson 1996), although their maximum rooting depths are unknown (Stromberg 2013). Previous investigators have speculated that these trees maintain high water potentials and active transpiration during drought periods by using deep vadose (Smith et al. 1997) or phreatic water sources (Nilsen et al. 1984, Gibson 1996). However, populations of *O. tesota* and *P. microphylla* occurring along headwater streams with thin alluvium underlain by bedrock or consolidated sediments may not have access to deep water sources. Identifying seasonal water sources, particularly during droughts, and how these sources are partitioned among dominant species, remain key topics in dryland ecohydrology (Smith et al. 1998).

Physiological functioning of riparian trees may be tightly coupled to streamflow events where subsurface water availability is limited (Horton et al. 2001, Gazal et al. 2006). The few studies that have investigated the water sources of riparian trees in ephemeral streams focused on groundwater use by phreatophytes (Kolb et al. 1997, Snyder and Williams 2000, Costelloe et al. 2008), and no information is available on seasonal water sources of riparian trees where shallow groundwater does not occur. Upland woody plants in arid settings rely primarily on deep soil water, but can opportunistically use shallow water sources following warm-season rainfall (Williams and Ehleringer 2000, Schwinning et al. 2002, 2003, West et al. 2007b). These observations support the assumption that riparian trees along ephemeral desert streams rely primarily on deep water sources (Smith et al. 1997).

Understanding the variation in ecohydrological relations of riparian trees throughout ephemeral stream networks is necessary for informed management and restoration, and predicting potential responses to changing climate and land use. Distinctive patterns of plant water stress and physiological functioning among stream types can be used to identify the relative sensitivities of different species to hydrologic alterations. Understanding the relative

importance of seasonal water sources may shed light on how tree populations will respond to changing precipitation patterns. To clarify these issues, I examined the ecohydrological relationships of the four most abundant riparian tree species in ephemeral watersheds of the western Sonoran Desert. *Olneya tesota*, *P. microphylla*, and *P. florida* occur throughout the northern Sonoran Desert and occupy upland surfaces within less arid portions of their ranges (Shreve and Wiggins 1964, Turner and Brown 1994, Turner et al. 1995). In contrast, *P. spinosus* is an obligate riparian species endemic to the arid Lower Colorado Valley of the Sonoran Desert. Differences in the geographic ranges of these species (Turner et al. 1995), and their distributions within ephemeral stream networks of the study area (Shaw and Cooper *in prep.*), suggest that they occupy distinctive hydrologic niches. I tested four hypotheses to understand the ecohydrological dynamics of riparian trees in dryland ephemeral streams. H₁: Seasonal patterns of water stress and water use for each species differ among hydrogeomorphic stream types, corresponding to variations in alluvial characteristics. H₂: Seasonal water relations differ among species within stream types, with widespread facultative riparian species exhibiting greater variability and localized obligate riparian species occupying habitats that exert minimal water stress. H₃: Riparian trees along arid ephemeral streams lacking shallow groundwater rely primarily on deep water sources that are stable over time. H₄: Water sources are partitioned among co-occurring species to minimize competition.

3.2 Methods

Ecohydrological dynamics of *O. tesota*, *P. microphylla*, *P. florida*, and *P. spinosus* were examined at eight stream reaches within two ephemeral watersheds, Yuma and Mohave washes, on the U.S. Army Yuma Proving Ground in southwestern Arizona, USA. To characterize the gradient of fluvial environments supporting riparian trees, study reaches in each watershed were located within representative hydrogeomorphic stream types described by Sutfin et al. (2014):

piedmont headwater, bedrock with alluvium, incised alluvium, and braided streams. These stream types epitomize longitudinal variation in geomorphic character (Sutfin et al. 2014), alluvial thickness (Harry et al. *in prep.*), streamflow and subsurface moisture regimes (Faulconer et al. *in prep.*; Kampf et al. *in review*), and riparian plant composition (Shaw and Cooper, *in prep.*) found in mountainous desert terrain. Seasonal ecophysiological measurements were performed during winter (January), spring (March), summer (June), and fall (September) in 2012 and 2013, on five permanently-marked mature individuals of each species in reaches where they occurred. Concurrent measurements of alluvial volumetric water content, stream stage, and rainfall were recorded at 15 minute intervals in each reach (Kampf et al. *in review*).

3.2.1 *Seasonal Water Stress*

Xylem water potential was measured with a Model 1505D pressure chamber (PMS Instruments Inc., Albany, OR), using 3-5 actively-growing terminal shoots for each plant. Predawn water potential was measured between 0:00 and 4:00 during 2012 and 2013. Midday water potential was measured in 2013, using shoots collected from sunlit branches between 12:00 and 16:00. Samples were refrigerated in sealed plastic bags containing moistened paper towels until analysis (≤ 30 min).

3.2.2 *Seasonal Water Sources*

Isotopic composition of xylem and alluvial waters were used to determine plant water sources. Fully suberized terminal shoots (~2 cm diameter) were taken from actively-growing branches (Ehleringer and Osmond 1989). Plant samples were stored in glass vials sealed with Parafilm-wrapped Teflon caps. Concurrent with plant tissue collection, depth-integrated samples of shallow alluvium were taken from the upper 50 cm of the active channel. At incised alluvium and braided channels, where alluvial fill is at least 4 m deep (Harry et al. *in prep.*), isotopic profiles were developed from trenches dug in January and September 2012, and May 2013.

During trenching, depth-integrated alluvium samples were collected at 50 cm intervals, to a maximum depth of 4 m. Alluvium samples were stored in 1 L Nalgene bottles sealed with Parafilm. Plant and sediment samples were frozen until analysis.

Azeotropic distillation of xylem and alluvial waters was performed at the EcoCore Stable Isotope Laboratory at Colorado State University, using the distillation apparatus and methods outlined in Revesz and Woods (1990) and Revesz et al. (2012). Since isotopic fractionation likely occurs within photosynthetic tissue beneath the bark of suberized stems in *Parkinsonia* spp. and *P. spinosus*, the bark and cambium of all plant samples were removed prior to distillation. Isotopic composition of extracted waters was determined using a Thermo Scientific Delta V Plus run in continuous mode, connected to a high-temperature conversion elemental analyzer (TCEA) via a Conflo IV. A Thermo AI 1310 autosampler injected three 1.0 μl aliquots of each sample into the TCEA column, and the measurements were averaged. Results were normalized using a linear equation derived from three laboratory reference materials, and reported as $\delta^2\text{H}$ and $\delta^{18}\text{O}$ relative to V-SMOW (Gonfiantini 1978, Coplen 1988). Long-term 2σ uncertainties for $\delta^2\text{H}$ and $\delta^{18}\text{O}$ using this procedure are $\pm 5.0\text{‰}$ and $\pm 0.8\text{‰}$, respectively. Isotopic analyses were performed at the University of Wyoming Stable Isotope Facility.

Similarity of alluvial isotopic compositions at depths >50 cm allowed us to lump these samples into one water source (Phillips et al. 2005). Results showed that xylem waters were at times more enriched than the corresponding depth-integrated shallow alluvial waters, suggesting that plants were using water from surficial sediments. Since the alluvial samples do not represent discrete end-members, quantitative mixing models (e.g. Phillips and Gregg 2001) were not used to determine the proportions of water sources used by plants. Instead, isotopic composition of xylem waters relative to shallow alluvial waters ($\delta^{18}\text{O}_{\text{Rel}} = \delta^{18}\text{O}_{\text{xylem}} - \delta^{18}\text{O}_{\text{shallow alluvium}}$) was

analyzed. Since root water uptake by *O. tesota* and other woody xerophytes can fractionate $\delta^2\text{H}$ (Ellsworth and Williams 2007), only $\delta^{18}\text{O}$ was analyzed.

3.2.3 Daily Water Use

Daily water use was characterized with sap velocity measurements at the four reaches in Mohave Wash, from January 2013 to May 2014. One sensor was installed in an *O. tesota* and *P. microphylla* at each reach, and in a *P. florida* and *P. spinosus* in the braided reach. Sap velocity was quantified using 3-needle sensors (East 30 Sensors, Pullman, WA). The outer needles measured temperature differentials at 5, 18, and 30 mm below bark, above and below a heat pulse introduced by a line heater within the center needle. Measurements were averaged from 60 to 100 s following an 8 s heat pulse, and stored at 15 minute intervals using AM16/32B multiplexers and CR1000 data loggers (Campbell Scientific, Logan, UT). In order to standardize errors from insolation and circumferential variation in flow rates, sensors were installed within 1 m of the ground under insulated housings on the north side of stems. Two increment cores collected from each tree in May 2014 were used to estimate sapwood depth and moisture content. Thermal diffusivity was estimated following Vandegehuchte and Steppe (2012), and sap velocity was calculated using the Heat Ratio Method (Burgess et al. 2001). Sap flow rates in individual trees vary circumferentially due to complex xylem architecture, hydraulic redistribution, and variable refilling of stem capacitance (Burgess and Bleby 2006, Kume et al. 2012, Shinohara et al. 2013). Because these sources of variation can introduce considerable errors in whole-tree sap flux estimated from a single sensor, seasonal patterns of water use across species and stream types were compared using relative sap velocities.

3.2.4 Statistical Analyses

Seasonal variations in water potential and $\delta^{18}\text{O}_{\text{Rel}}$ were compared using repeated-measures ANOVAs. Separate analyses for *O. tesota*, *P. microphylla*, and *P. florida* included the

effects of season, stream type, watershed, and all interactions. Since *P. spinosus* occurred in multiple stream types only in Mohave Wash, the effects of season and stream type were examined only for that watershed. Interspecific differences in water potential and isotopic composition were examined using 2-way ANOVAs for each study reach, with season and species as factors. Factors in all models were considered fixed effects, while individual plants were treated as random effects. The covariance structures of repeated observations within individuals were modeled with heterogeneous compound-symmetry, and multiple comparisons used Tukey-Kramer adjusted confidence intervals.

3.3 Results

Annual rainfall at study reaches in Mohave Wash ranged from 130 to 165 mm in 2012, and 145 to 192 mm in 2013. In Yuma Wash, annual rainfalls were 136 to 161 mm in 2012, and 96 to 108 mm in 2013. Different patterns of rainfall, streamflow, and alluvial water content occurred in each watershed. Monsoon storms produced three streamflow events at all sites in Mohave Wash, during July and September 2012, and September 2013 (Figure 3.1). Streamflow was more frequent in the piedmont headwater reach, where eight events occurred (Figure 3.1A). The upper 50 cm of alluvium in all reaches was saturated for less than one day after each flow event. Relative water content in shallow alluvium was most variable at the bedrock with alluvium reach, and ranged from 7 to 30 % (Figure 3.1C). Water content below 50 cm at the braided reach was more stable, and only varied in response to streamflow recharge (Figure 3.1G). A siltstone aquitard underlying the incised alluvium reach maintained near-saturated conditions at ~200 cm depth from July 2012 to December 2013 (not shown).

Greater variation in streamflow frequency occurred between stream types in Yuma Wash (Figure 3.2). On 14 July 2012, monsoon thunderstorms produced up to 86 mm of rainfall, resulting in overbank flooding in all study reaches. In the following month, two floods occurred

in the piedmont headwater and bedrock with alluvium reaches, but only one flow occurred at the incised alluvium and braided sites. These monsoon floods and smaller winter storms maintained relative water contents in the upper 50 cm of alluvium between 20 and 35 % through the following spring. A modest streamflow event occurred during July 2013 at the piedmont water, incised alluvium, and braided reaches, raising shallow alluvial water contents for less than one month.

3.3.1 Seasonal Water Stress

Predawn plant water potentials followed a similar seasonal pattern at all stream types in Mohave Wash (Figure 3.1). Minimum water potentials occurred during June in both years, but increased water availability following monsoon rainfall and streamflow reduced plant water stress in late summer and fall months. Winter streamflow events improved plant water status through the following spring at the piedmont headwater reach, where predawn water potentials ranged from -2.3 to -1.2 MPa (Figure 3.1B). Greater variability occurred at the bedrock with alluvium reach, where water potentials ranged from -2.2 to -1.0 MPa for *O. tesota* and -3.0 to -1.1 MPa for *P. microphylla* (Figure 3.1D). Predawn water potentials varied between -1.7 and -0.3 MPa at the incised alluvium reach, and seasonal variation was comparable among species (Figure 3.1F). Similar dynamics occurred at the braided reach, and water potentials ranged from -2.0 to -0.6 MPa (Figure 3.1H).

The stream types in Yuma Wash exhibited divergent seasonal patterns of water stress, but species within sites followed broadly similar patterns (Figure 3.2). Predawn water potentials ranged from -2.1 to -0.8 MPa at the piedmont headwater reach (Figure 3.1B), and -2.5 to -0.8 MPa at the bedrock with alluvium reach (Figure 3.1D). At these sites, plant water status remained high throughout the winter and spring of 2013, but did not recover from summer drought during fall 2013. In contrast, recharge from monsoon floods in 2012 and 2013

maintained elevated water potentials at the incised alluvium and braided reaches for at least one year. Water potentials ranged from -2.2 to -0.8 MPa at the incised alluvium reach (Figure 3.2F) and -2.4 to -0.4 MPa at the braided reach (Figure 3.2H).

Seasonal patterns of water stress for all species differed among stream types, but differing rainfall and streamflow inputs caused these patterns to vary between watersheds (Table 3.1; Figure 3.3). In both watersheds, the greatest disparities among stream types occurred during summer drought periods. *Olneya tesota* within Mohave Wash experienced similar water stress in all reaches during winter, but had significantly higher water potentials at the incised alluvium reach during summer and fall (Figure 3.3A). Water status of *O. tesota* did not differ among stream types during winter and spring in Yuma Wash, but summer water potentials in braided and incised alluvium reaches exceeded those in piedmont headwater and bedrock with alluvium reaches (Figure 3.3B). Across all seasons, *O. tesota* in both watersheds experienced similar water stresses in bedrock with alluvium and piedmont headwater streams. *Parkinsonia microphylla* in Mohave Wash experienced the greatest water stress in bedrock with alluvium and piedmont headwater reaches during summer and fall respectively (Figure 3.3C), while the piedmont headwater reach in Yuma Wash had the lowest water potentials in these seasons (Figure 3.3D). Water potentials of *P. florida* were similar across stream types in both watersheds during fall and winter months (Figure 3.3E, F), but water stress in the Yuma bedrock with alluvium reach was greater than other stream types during summer.

Interspecific differences in seasonal water stress occurred within most of the study reaches (Figure 3.4). *Olneya tesota* experienced lower predawn water potentials than *P. microphylla* along piedmont headwater streams in Mohave ($p = <0.001$) and Yuma Wash ($p = 0.014$). These differences varied seasonally in Mohave Wash ($p = 0.042$), and were greatest during winter. In bedrock with alluvium streams, seasonal water status was similar among

species in Mohave Wash, but *O. tesota* had lower water potentials than *P. florida* in Yuma Wash ($p = 0.031$). Water stress differed among species ($p = <0.001$) and followed different seasonal patterns for species ($p = 0.011$) at the Mohave Wash incised alluvium reach. Predawn water potentials were consistently highest for *P. spinosus* and lowest for *P. microphylla*. In contrast, no interspecific variation in water stress was detected at the Yuma incised alluvium reach ($p = 0.094$). At the braided reach in Mohave Wash, species water stress differed ($p = <0.001$) but followed similar temporal patterns. Except during summer, *Psorothamnus spinosus* had the highest water potentials, while *O. tesota* had the lowest.

3.3.2 Seasonal Water Sources

Isotopic composition of deep alluvium samples (>50 cm) from incised alluvium and braided reaches were similar to precipitation samples, indicating that deeper alluvial waters were recharged by rapid infiltration (Figure 3.5). Shallow alluvial waters (≤ 50 cm) showed greater variation in $\delta^{18}\text{O}$ and $\delta^2\text{H}$ due to evaporative enrichment. Xylem waters of the four species were all within the range of shallow and deep alluvium, suggesting that plants were not accessing exogenous water sources (e.g. the regional aquifer). Profiles of $\delta^{18}\text{O}$ from deep alluvial waters varied by less than 4 ‰ before and after monsoon flooding in 2012, and reflected minimal evaporative enrichment below 50 cm depth between samples (Figure 3.6).

Seasonal variation in $\delta^{18}\text{O}$ of shallow alluvium differed between stream types within each watershed. In Mohave Wash, the most positive $\delta^{18}\text{O}$ values typically occurred during summer in all reaches (Figure 3.7). Shallow alluvium at Yuma Wash exhibited greater variability, particularly in spring and fall samples from piedmont headwater and bedrock with alluvium sites (Figure 3.8). During the winter and spring after the large September 2012 flood, $\delta^{18}\text{O}$ of shallow alluvium from the Yuma braided and incised alluvium reaches were similar to deep alluvium.

In both watersheds, seasonal variation in isotopic composition of xylem waters was similar among species in each reach. In Mohave Wash, xylem $\delta^{18}\text{O}$ values frequently equaled or exceeded those of shallow alluvium, but xylem waters from braided and incised alluvium reaches were 3 to 11 ‰ lower than shallow alluvium during summers (Figures 3.7F, H). Seasonal dynamics were considerably different at Yuma Wash. At the piedmont headwater reach, xylem $\delta^{18}\text{O}$ exceeded shallow alluvium by 5 ‰ during the winter of 2013, but were otherwise 3 to 11 ‰ lower (Figure 3.8B). Xylem waters were 9 to 12 ‰ lower than shallow sediments at the bedrock with alluvium reach, but were within 3 ‰ of shallow alluvium from September 2012 to March 2013 (Figure 3.8D). Xylem $\delta^{18}\text{O}$ values from the incised alluvium and braided reaches were similarly less enriched prior to the September 2012 flood, but equaled or exceeded shallow alluvium until the following summer (Figures 3.8F, H).

Differences between $\delta^{18}\text{O}$ of xylem and shallow alluvium ($\delta^{18}\text{O}_{\text{Rel}}$) varied seasonally among stream types for all species (Table 3.2). Across both watersheds, *O. tesota* and *P. microphylla* in piedmont headwater streams used more water from deep strata during fall, and from surficial sediments during winter, than conspecifics in other stream types. During summer, *O. tesota* and *P. microphylla* relied more heavily on deep alluvial waters in braided reaches than other sites. Seasonal variation in water sources among stream types also differed between watersheds (Figure 3.9). *Olneya tesota* in piedmont headwater and bedrock with alluvium reaches in Yuma Wash accessed water sources below 50 cm, but trees in these reaches at Mohave Wash used shallow alluvium. *Parkinsonia microphylla* $\delta^{18}\text{O}_{\text{Rel}}$ values in piedmont headwater and incised alluvium reaches were lower throughout the warm season at Yuma Wash than at Mohave Wash, indicating a stronger dependence on deep water sources. A similar pattern occurred for *P. florida* along incised alluvium streams. Although water sources differed among stream types for each species, $\delta^{18}\text{O}_{\text{Rel}}$ values indicated that co-occurring species did not use

different water sources (Figure 3.10). None of the 2-way ANOVAs for $\delta^{18}\text{O}_{\text{Rel}}$ in each study reach contained significant effects for species or season*species.

3.3.3 Daily Water Use

Sap velocities measured from January 2013 to May 2014 illustrate differing temporal patterns of water use across stream types in Mohave Wash (Figure 3.11). Patterns of water use by *O. tesota* and *P. microphylla* was similar at the piedmont headwater reach, where summer streamflow resulted in two sustained transpiration pulses (Figure 3.11B). Maximum daily sap velocities for *O. tesota* (6.0 cm h^{-1}) and *P. microphylla* (3.2 cm h^{-1}) occurred two weeks after the first summer flow event. Regardless of season, relative sap velocities fell below 10 % for *O. tesota* and 20 % for *P. microphylla* after two months without precipitation. At the bedrock with alluvium reach, maximum sap velocities of *O. tesota* (3.5 cm h^{-1}) and *P. microphylla* (1.9 cm h^{-1}) also occurred after monsoon streamflow (Figure 3.11D). Higher subsurface storage capacity allowed *O. tesota* to maintain relative sap velocities up to 60 % of maximum through the following spring, despite a lack of rainfall. Water use of both species was less than 20 % of maximum during summer droughts. Temporal water use patterns differed between species at the incised alluvium site (Figure 3.11F). *Olneya tesota* sap velocities were more uniformly distributed, ranging from 50 to 90 % of maximum (13 cm h^{-1}) throughout much of the study period. Maximum daily sap velocity of *P. microphylla* (1.1 cm h^{-1}) occurred after the September 2013 flood, and water use through the following spring averaged 60 %.

Bimodal patterns of water use occurred at the braided reach in Mohave Wash (Figure 3.11H). Relative sap velocities of both *Parkinsonia* species and *P. spinosus* exceeded 90 % of maximum after rainfall events in winter and summer. Maximum daily sap velocities of *P. microphylla* (1.6 cm h^{-1}) and *P. spinosus* (3.2 cm h^{-1}) occurred during spring, while those of *O. tesota* (14 cm h^{-1}) and *P. florida* (14 cm h^{-1}) occurred after the September 2013 flow. Water use

of *P. microphylla* and *P. spinosus* declined to less than 20 % during the following winter and spring, but *O. tesota* and *P. florida* maintained relative sap velocities between 30 and 50 %.

3.4 Discussion

Seasonal patterns of drought stress and water sources of riparian trees in Sonoran Desert ephemeral streams differed among the hydrogeomorphic stream types. Plants growing in bedrock with alluvium and piedmont headwater channels experienced the greatest seasonal water stress, despite more frequent rainfall and streamflow inputs, while braided and incised alluvium streams provided more mesic habitats for riparian trees. Relative sap velocities indicated that water use and gas exchange were episodic and more strongly limited by seasonal water availability in piedmont headwater and bedrock with alluvium streams than in braided and incised alluvium channels. Differences among stream types were most pronounced during summer droughts, but were minimal during the comparatively mild winter and spring months. Periods of reduced plant water stress after large floods also persisted longer in incised alluvium and braided streams. These disparities in riparian tree water status among stream types paralleled differences in seasonal water sources. Plants in braided reaches accessed the deepest subsurface water sources during summer drought periods. During winter months, trees growing along piedmont headwater streams foraged from the upper-most surficial sediments, while conspecifics in other stream types relied on water down to 50 cm depth.

Differences in seasonal water relations among stream types correspond to variation in alluvial characteristics along the riverine continuum. Deeper unconsolidated alluvium in braided and incised alluvium channels provides greater subsurface storage capacity than in headwater stream segments (Harry et al. *in prep.*, Kampf et al. *in review*). Low infiltration rates and water-holding capacity of consolidated sediments underlying piedmont headwater streams lead to higher water stress during summer droughts, compared to plants growing on unconsolidated

alluvium (McAuliffe 1994, Smith et al. 1995, Hamerlynck et al. 2002). Despite more frequent streamflow events in piedmont headwater and bedrock with alluvium reaches (Faulconer et al. *in prep.*), limited subsurface storage resulted in greater seasonal water stress and episodic water use that was tightly coupled to moisture inputs. Differences in channel morphology and hydraulic properties among stream types (Sutfin et al. 2014) interact with these ecohydrological dynamics to produce distinctive riparian plant communities (Shaw and Cooper, *in prep.*).

Riparian trees in alluvial stream reaches relied primarily on water from the upper 50 cm of active alluvium during winter and spring months. They accessed deeper water sources during summer droughts and rainless autumn months. Following winter and spring rainfall, and occasionally after late-summer floods, all species extracted enriched water from the surficial sediments. Studies from less arid regions have described temporary uptake of shallow soil water after summer rainfall by woody plants that rely primarily on water from deep soil layers (Williams and Ehleringer 2000, Schwinning et al. 2002, 2003, West et al. 2007b). Similar opportunistic use of shallow soil water by dryland woody phreatophytes have been reported from ephemeral stream (Kolb et al. 1997, Snyder and Williams 2000) and valley floor settings (Chimner and Cooper 2004, Kray et al. 2012). In all cases, these shifts have been attributed to increased water potential in near-surface sediments following infiltration. However, riparian trees at some sites used shallow water sources despite higher water availability in underlying sediments.

Water use from shallow and surficial alluvium may allow woody plants to maximize nutrient uptake. Desert soils typically have low N content, and nutrient availability is highest in near-surface sediments (Noy-Meir 1973, Collins et al. 2008). Streamflow pulses provide N and labile C inputs to ephemeral stream ecosystems, through stimulation of microbial activity as well as nutrient imports from throughout the watershed (Belnap et al. 2005, Harms and Grimm 2010,

Larned et al. 2010, Collins et al. 2014). Although nitrogen-fixing bacteria can occupy root nodules in *O. tesota* (Felker and Clark 1981) and *P. spinosus* (Jenkins et al. 1988), nutrient pulses associated with periodic floods may provide critical resource subsidies.

Riparian tree water sources were more variable in bedrock with alluvium and piedmont headwater streams. Trees in piedmont headwater reaches, where active alluvium is typically <50 cm deep, relied more heavily on deep water sources. Since low infiltration rates minimize deep wetting of consolidated sediments in these landforms (McAuliffe 1994, 1999, Smith et al. 1995, Hamerlynck et al. 2002), it seems unlikely that increased water availability promotes deeper foraging. Instead, accumulation of windblown salts or elevated surface temperatures may limit shallow root development (McAuliffe 1994). Seasonal water sources and drought stress were most variable between bedrock with alluvium reaches, likely due to differing lithologies of the underlying bedrock. Trees experienced greater water stress and relied exclusively on shallow alluvium at the Mohave Wash site, but plants in Yuma Wash maintained higher water potentials and used deeper water sources for much of the year. Alluvium at the Mohave Wash site is underlain by thick rhyolite sequences, while the Yuma Wash bedrock with alluvium channel is bounded by faulted granodiorite and gneiss (Eberly and Stanley 1978, Tosdal et al. 1989). More extensive bedrock fracturing at the Yuma Wash site may have allowed greater access to deeper water sources underlying the active alluvium.

There was no evidence for water source partitioning among co-occurring species. The similarity of hydrologic niches among species at each site is at odds with the differences in spatial distribution and seasonal water status. Extreme droughts or other periodic conditions not present during the study may contribute to distributional differences.

Despite similar water sources, interspecific differences in water relations within stream types were apparent. *Psorothamnus spinosus* experienced the highest predawn water potentials,

likely due to lower water demands associated with small leaf areas (Nilsen et al. 1984, 1989) and dense leaf hairs (Gibson 1996). *Olneya tesota* maintains the greatest leaf area throughout the year, and typically had lower water potentials than co-occurring photosynthetic stem trees at sites with shallow alluvium. *Parkinsonia microphylla* had the lowest predawn water potentials of all species in braided and incised alluvium streams. Differences in water status at reaches with deep alluvium may correspond to the spatial distribution of species within the fluvial corridor. *Psorothamnus spinosus* occurs exclusively on active channel sediments, while *P. microphylla* are often restricted to higher floodplain positions. Differing recharge and water-holding capacity of shallow sediments between fluvial surfaces may underlie the divergent seasonal patterns of water stress among species at these sites.

Minimum observed predawn water potentials for the species in these study sites were comparable to values reported from other locations. Mean summer predawn water potentials of *P. spinosus* fell to -1.9 MPa, and trees from similar habitats in southern California regularly experienced predawn water potentials as low as -2.0 MPa (Nilsen et al. 1984). *Olneya tesota* leaves lose turgor at -3.7 MPa (Monson and Smith 1982, Nilsen et al. 1984), and minimum reported predawn water potentials in field studies range from -2.7 to -3.3 MPa (Szarek and Woodhouse 1977, Monson and Smith 1982, Nilsen et al. 1984). This species experienced predawn water potentials down to -2.3 MPa in piedmont headwater reaches. *Parkinsonia microphylla* maintains positive assimilation at predawn water potentials above -3.1 MPa (Szarek and Woodhouse 1978), and experiences complete xylem embolism at -6.0 MPa (Pockman and Sperry 2000). In upland settings, *P. microphylla* withstands predawn water potentials of -3.6 MPa (Halvorson and Patten 1974). At study sites in Mohave and Yuma Wash, mean predawn water potentials during summer ranged from -2.5 to -2.0 MPa. Differences between observed

water status and estimated physiological tolerances suggest that these species were not strongly limited by water availability in any stream type where they occurred.

Woody plant mortality during historic droughts in the Sonoran Desert was highest in marginal habitats that experienced chronic water stress (Bowers and Turner 2001, 2002). Within the study area, severe or prolonged droughts are most likely to cause tree mortality in xeric piedmont headwater and bedrock with alluvium streams. In all stream types, late-summer streamflow exerted stronger and more persistent effects on ecophysiological performance than winter storms. Changes to monsoon precipitation patterns will likely be a critical determinant in riparian tree responses to climatic variation.

Table 3.1. Effects of season, stream type, and watershed on predawn water potential during 2012 and 2013. Bold p-values are significant at $\alpha = 0.05$. *2-way ANOVA for Mohave Wash only.

Effect	<i>O. tesota</i>			<i>P. microphylla</i>			<i>P. florida</i>			<i>P. spinosus*</i>		
	df	F	p	df	F	p	df	F	p	df	F	p
Season (T)	3	47.0	<0.001	3	42.0	<0.001	3	38.0	<0.001	3	35.3	<0.001
Stream Type (S)	3	40.0	<0.001	3	9.18	<0.001	2	13.0	<0.001	1	23.1	<0.001
Watershed (W)	1	82.0	<0.001	1	60.3	<0.001	1	24.2	<0.001			
T * S	9	5.18	<0.001	9	5.96	<0.001	6	2.70	0.023	3	2.03	0.15
T * W	3	4.20	0.009	3	1.65	0.19	3	5.16	0.004			
S * W	3	8.04	<0.001	2	9.92	<0.001	1	17.1	<0.001			
T * S * W	9	2.28	0.024	6	1.61	0.16	3	5.00	0.004			

Table 3.2. Effects of season, stream type, and watershed on relative $\delta^{18}\text{O}$ during 2012 and 2013. Bold p-values are significant at $\alpha = 0.05$. *2-way ANOVA for Mohave Wash only.

Effect	<i>O. tesota</i>			<i>P. microphylla</i>			<i>P. florida</i>			<i>P. spinosus</i> *		
	df	F	p	df	F	p	df	F	p	df	F	p
Season (T)	3	52.7	< 0.001	3	25.5	< 0.001	3	157	< 0.001	3	44.0	< 0.001
Stream Type (S)	3	3.01	0.034	3	15.2	< 0.001	2	3.26	0.045	1	16.2	< 0.001
Watershed (W)	1	7.30	0.008	1	14.8	< 0.001	1	0.78	0.38			
T * S	9	28.7	< 0.001	9	34.7	< 0.001	6	5.11	< 0.001	3	18.8	< 0.001
T * W	3	1.46	0.23	3	1.83	0.15	3	6.68	< 0.001			
S * W	3	6.29	< 0.001	2	38.3	< 0.001	1	8.62	0.005			
T * S * W	9	9.69	< 0.001	6	7.85	< 0.001	3	2.21	0.10			

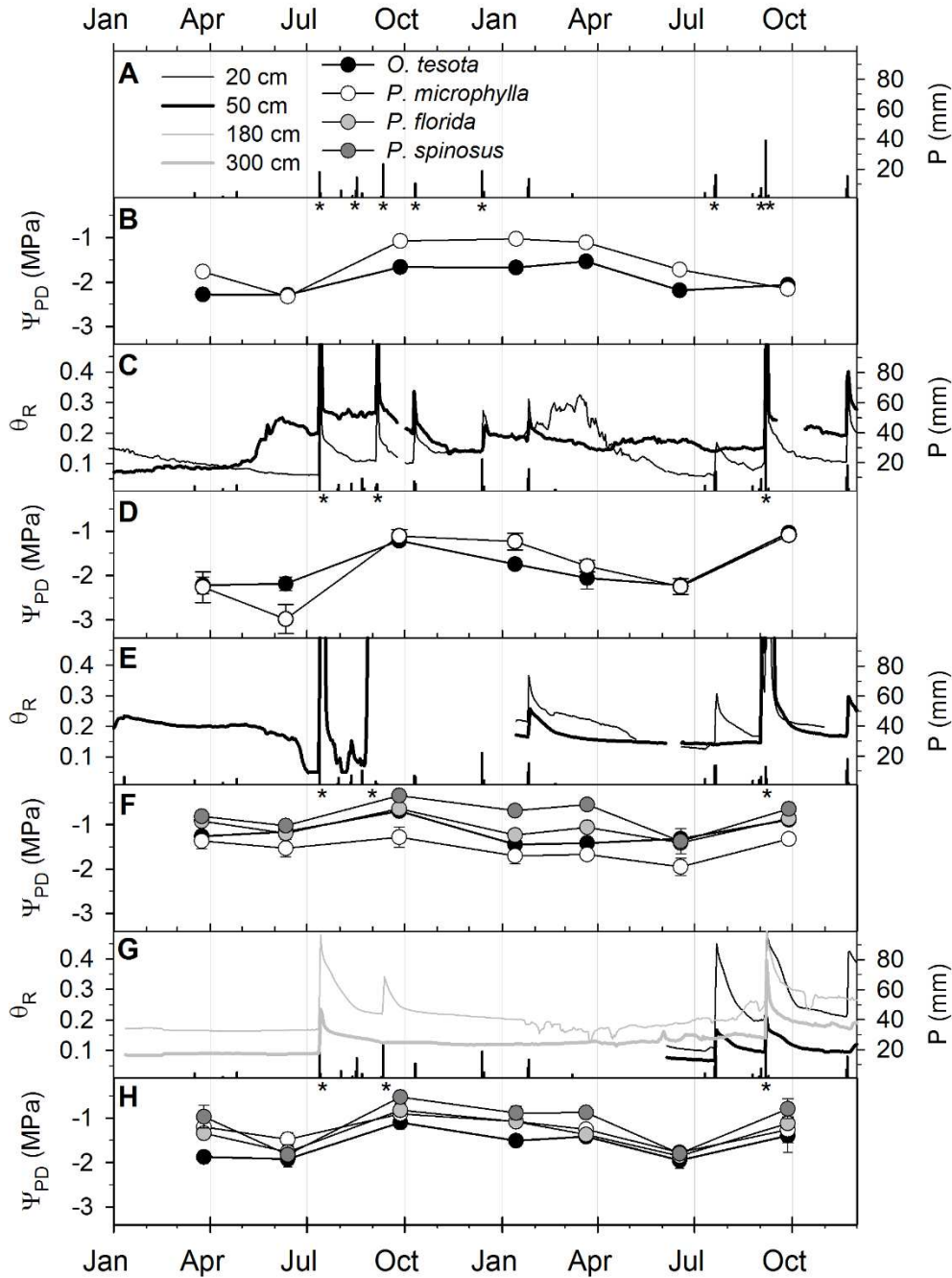


Figure 3.1. Rainfall (P), relative water content (θ_R) and predawn plant water potential (Ψ_{PD}) in Mohave Wash during 2012 and 2013. Rainfall at piedmont headwater (A); predawn water potential at piedmont headwater (B); rainfall and water content at bedrock with alluvium (C); predawn water potential at bedrock with alluvium (D); rainfall and water content at incised alluvium (E); predawn water potential at incised alluvium (F); rainfall and water content at braided (G); predawn water potential at braided (H). Points are means for each species and error bars are 1 S.E. Asterisks indicate streamflow events.

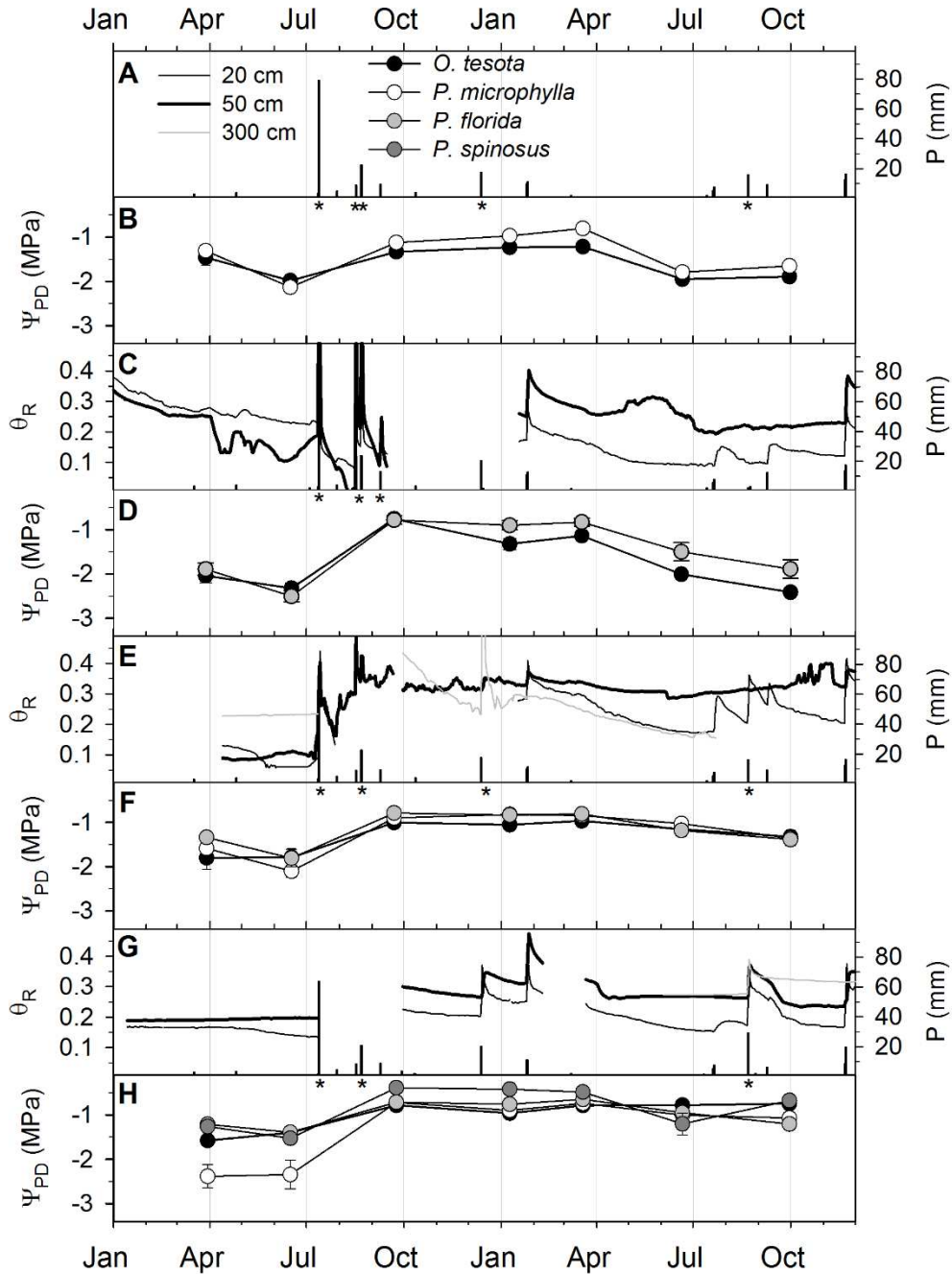


Figure 3.2. Rainfall (P), relative water content (θ_R) and predawn plant water potential (Ψ_{PD}) in Yuma Wash during 2012 and 2013. Rainfall at piedmont headwater (A); predawn water potential at piedmont headwater (B); rainfall and water content at bedrock with alluvium (C); predawn water potential at bedrock with alluvium (D); rainfall and water content at incised alluvium (E); predawn water potential at incised alluvium (F); rainfall and water content at braided (G); predawn water potential at braided (H). Points are means for each species and error bars are 1 S.E. Asterisks indicate streamflow events.

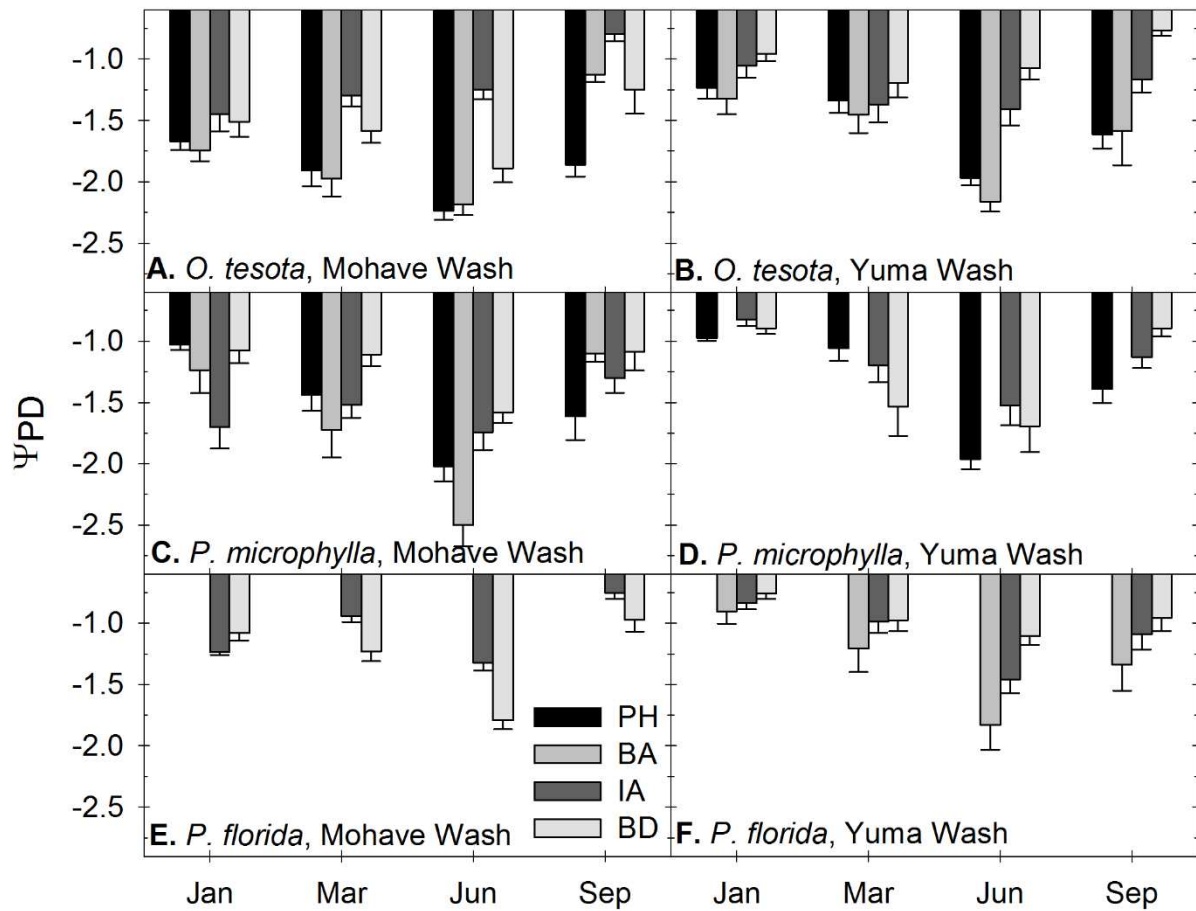


Figure 3.3. Seasonal variation in predawn plant water potential (Ψ_{PD}) of species across stream types. Points are means of each species and error bars are 1 S.E. PH = piedmont headwater, BA = bedrock with alluvium, IA = incised alluvium, BD = braided.

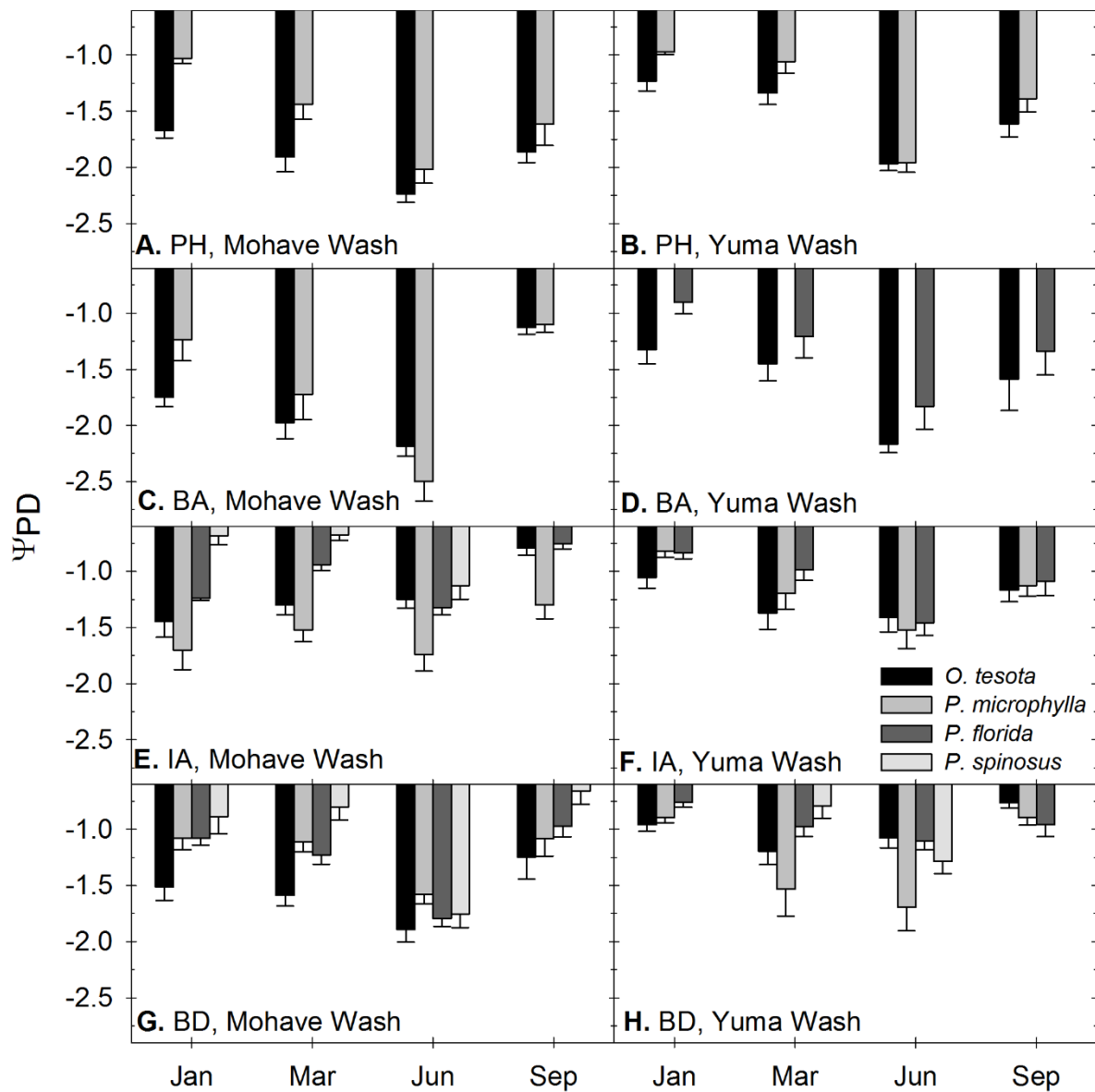


Figure 3.4. Seasonal variation in predawn plant water potential (Ψ_{PD}) between species within stream types. Points are means of each species and error bars are 1 S.E. PH = piedmont headwater, BA = bedrock with alluvium, IA = incised alluvium, BD = braided.

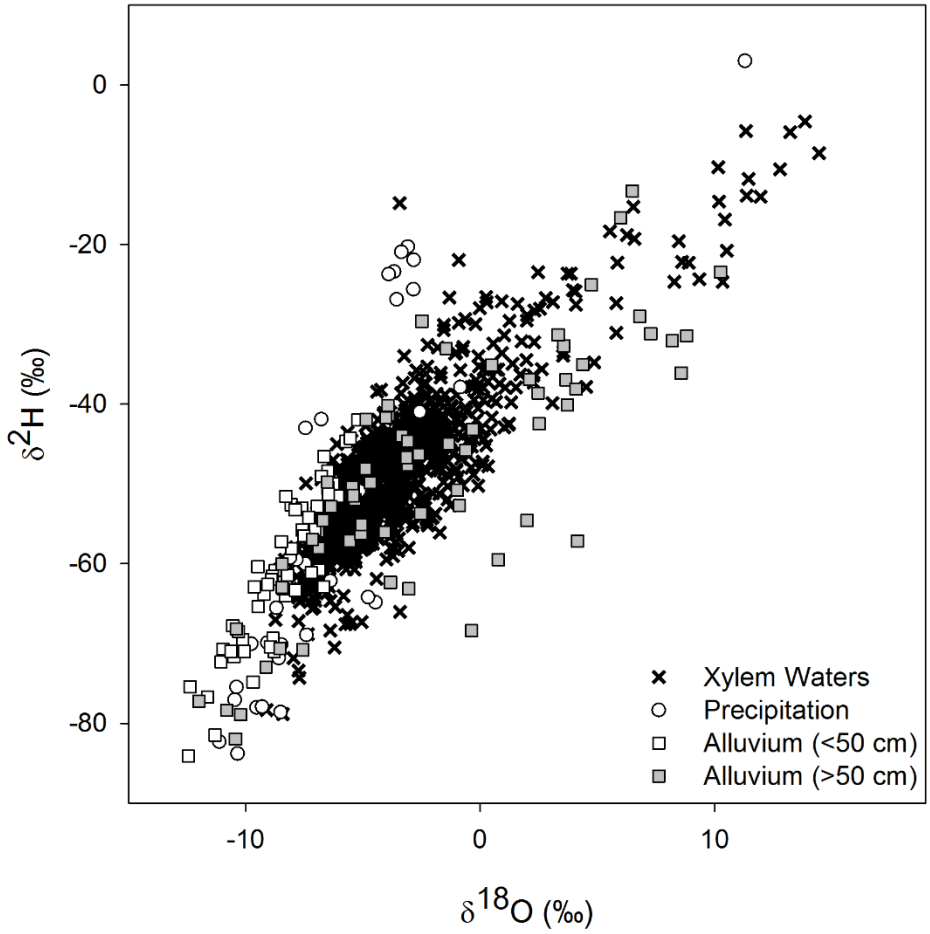


Figure 3.5. Isotopic composition of waters from riparian tree xylem, shallow (<50 cm) and deep (>50 cm) alluvium, and precipitation during 2012 and 2013.

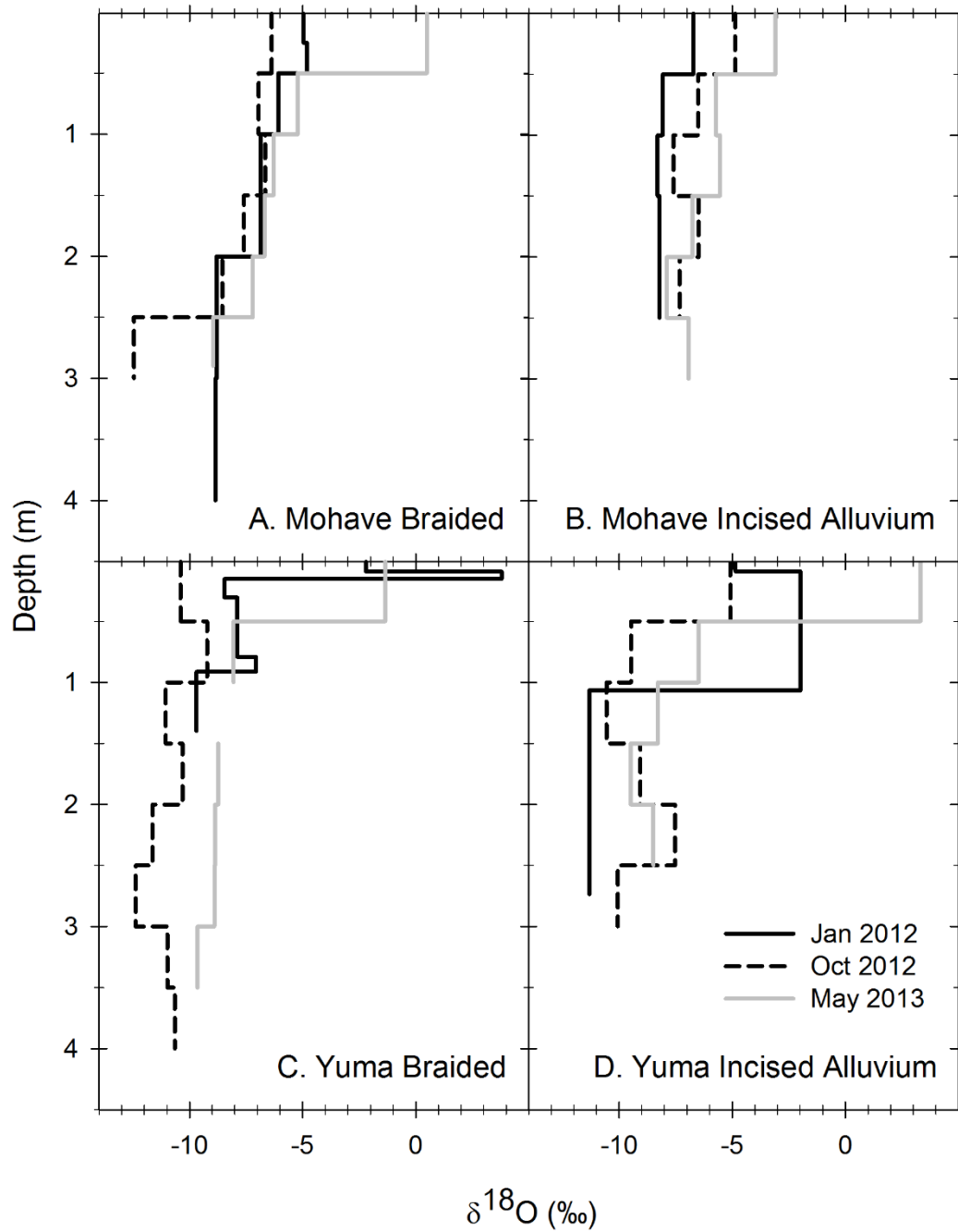


Figure 3.6. $\delta^{18}\text{O}$ profiles beneath the active channels of incised alluvium and braided reaches.

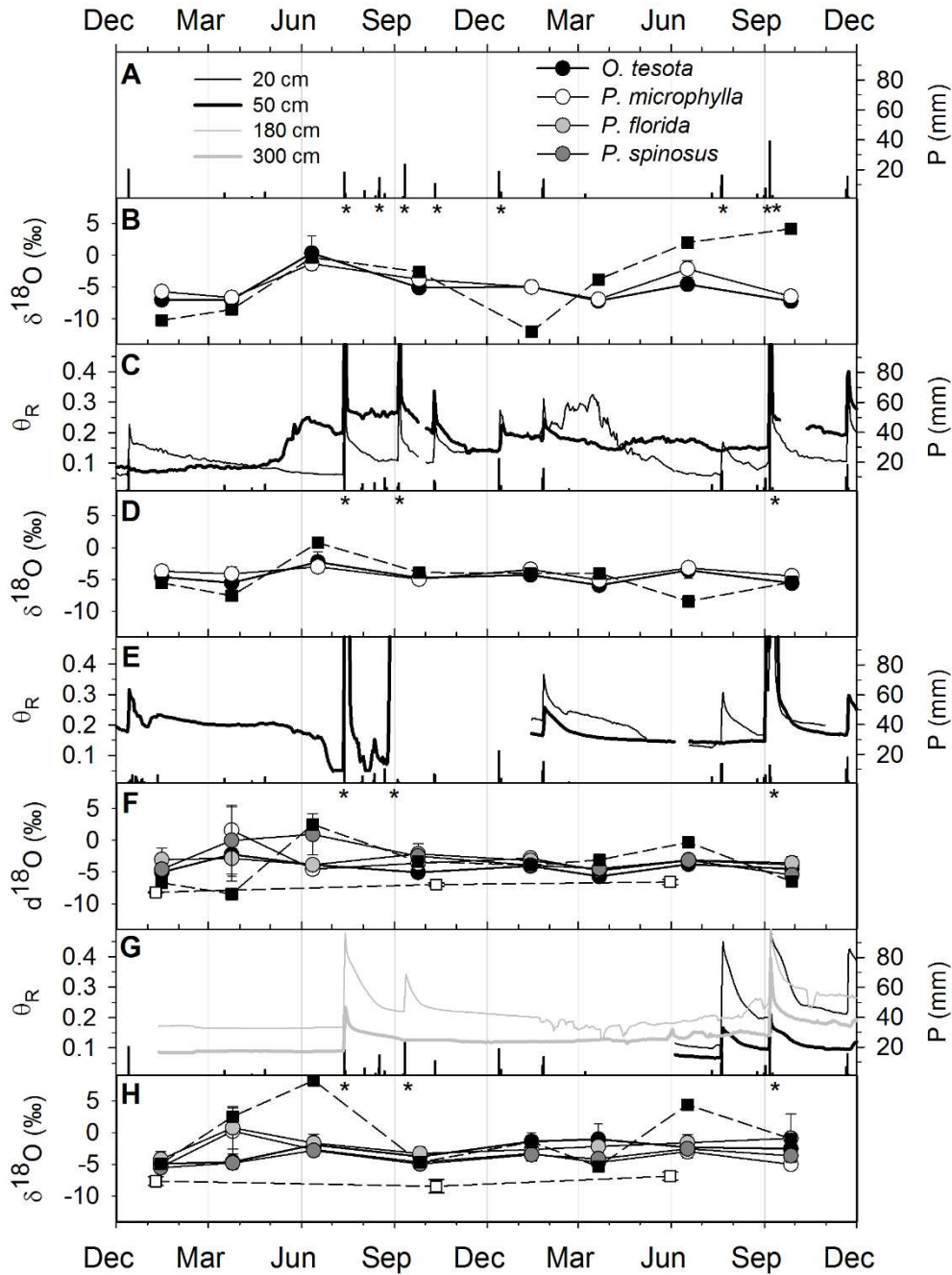


Figure 3.7. Rainfall (P), relative water content (θ_R) and $\delta^{18}\text{O}$ values in Mohave Wash during 2012 and 2013. Rainfall at piedmont headwater (A); $\delta^{18}\text{O}$ at piedmont headwater (B); rainfall and water content at bedrock with alluvium (C); $\delta^{18}\text{O}$ at bedrock with alluvium (D); rainfall and water content at incised alluvium (E); $\delta^{18}\text{O}$ at incised alluvium (F); rainfall and water content at braided (G); $\delta^{18}\text{O}$ at braided (H). Points are means for each species and error bars are 1 S.E. Filled squares indicate shallow (<50 cm) alluvium, open squares indicated deep (>50 cm) alluvium. Asterisks indicate streamflow events.

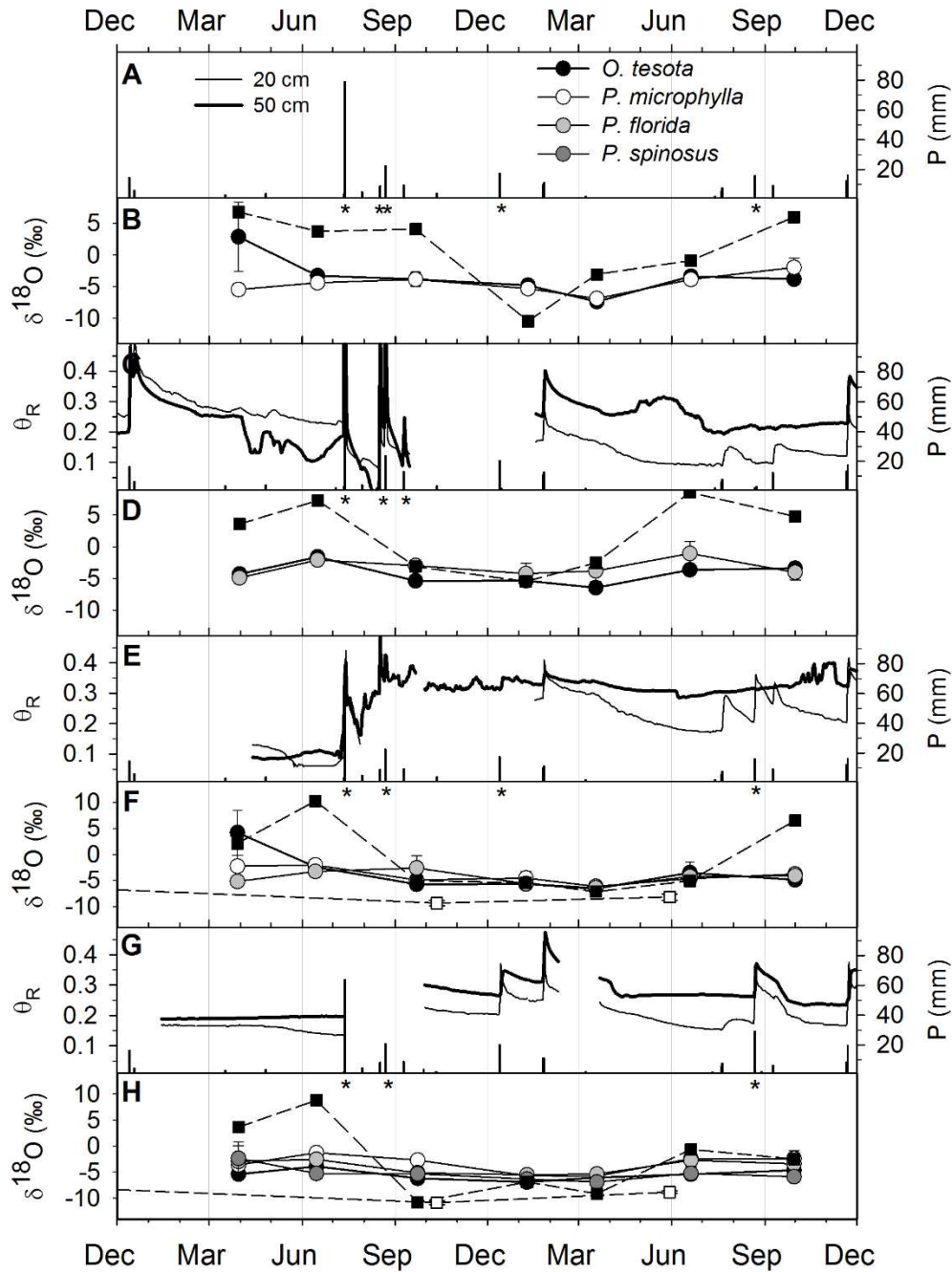


Figure 3.8. Rainfall (P), relative water content (θ_R) and $\delta^{18}\text{O}$ values in Yuma Wash during 2012 and 2013. Rainfall at piedmont headwater (A); $\delta^{18}\text{O}$ at piedmont headwater (B); rainfall and water content at bedrock with alluvium (C); $\delta^{18}\text{O}$ at bedrock with alluvium (D); rainfall and water content at incised alluvium (E); $\delta^{18}\text{O}$ at incised alluvium (F); rainfall and water content at braided (G); $\delta^{18}\text{O}$ at braided (H). Points are means for each species and error bars are 1 S.E. Filled squares indicate shallow (<50 cm) alluvium, open squares indicated deep (>50 cm) alluvium. Asterisks indicate streamflow events.

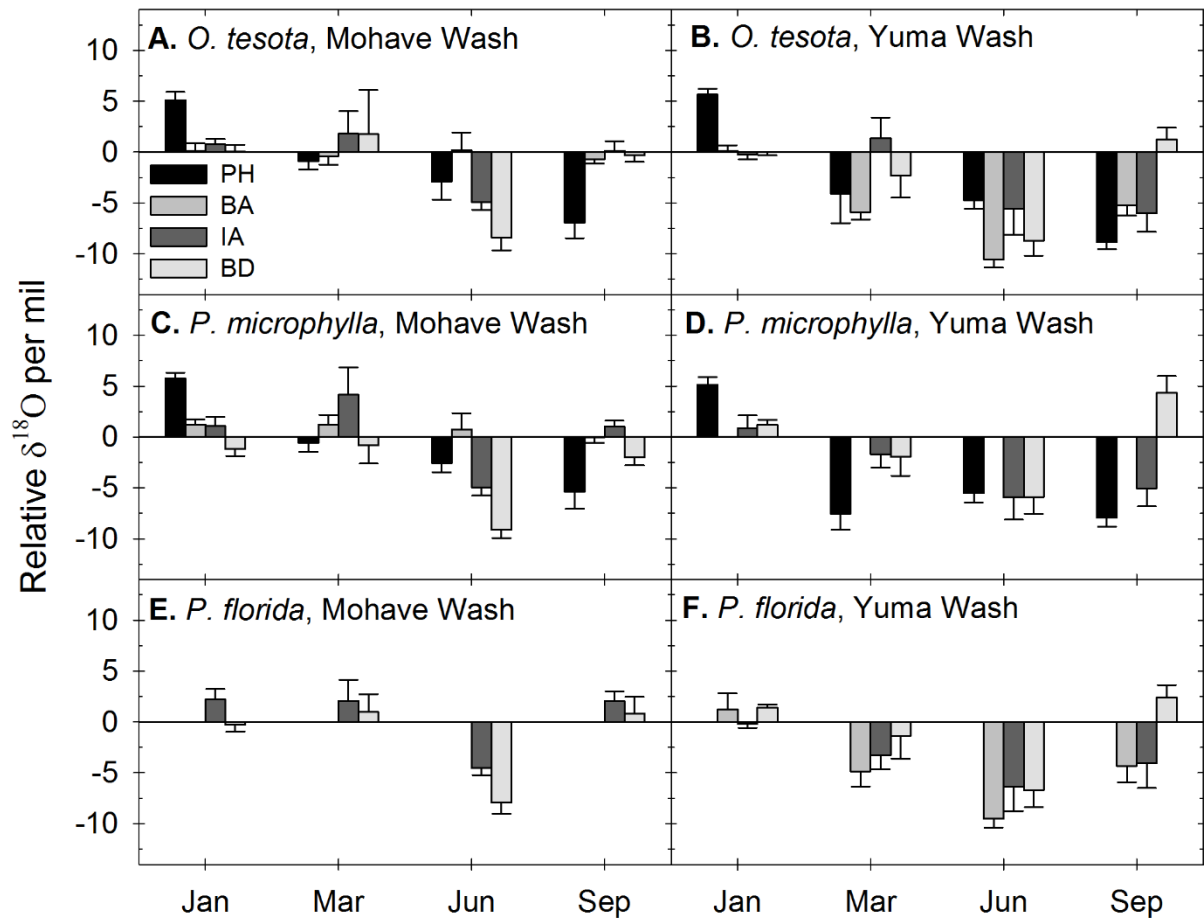


Figure 3.9. Seasonal differences in relative $\delta^{18}\text{O}$ within species across stream types. Bars are means of each species and error bars are 1 S.E. Positive values are more enriched than shallow alluvium (< 50 cm). PH = piedmont headwater, BA = bedrock with alluvium, IA = incised alluvium, BD = braided.

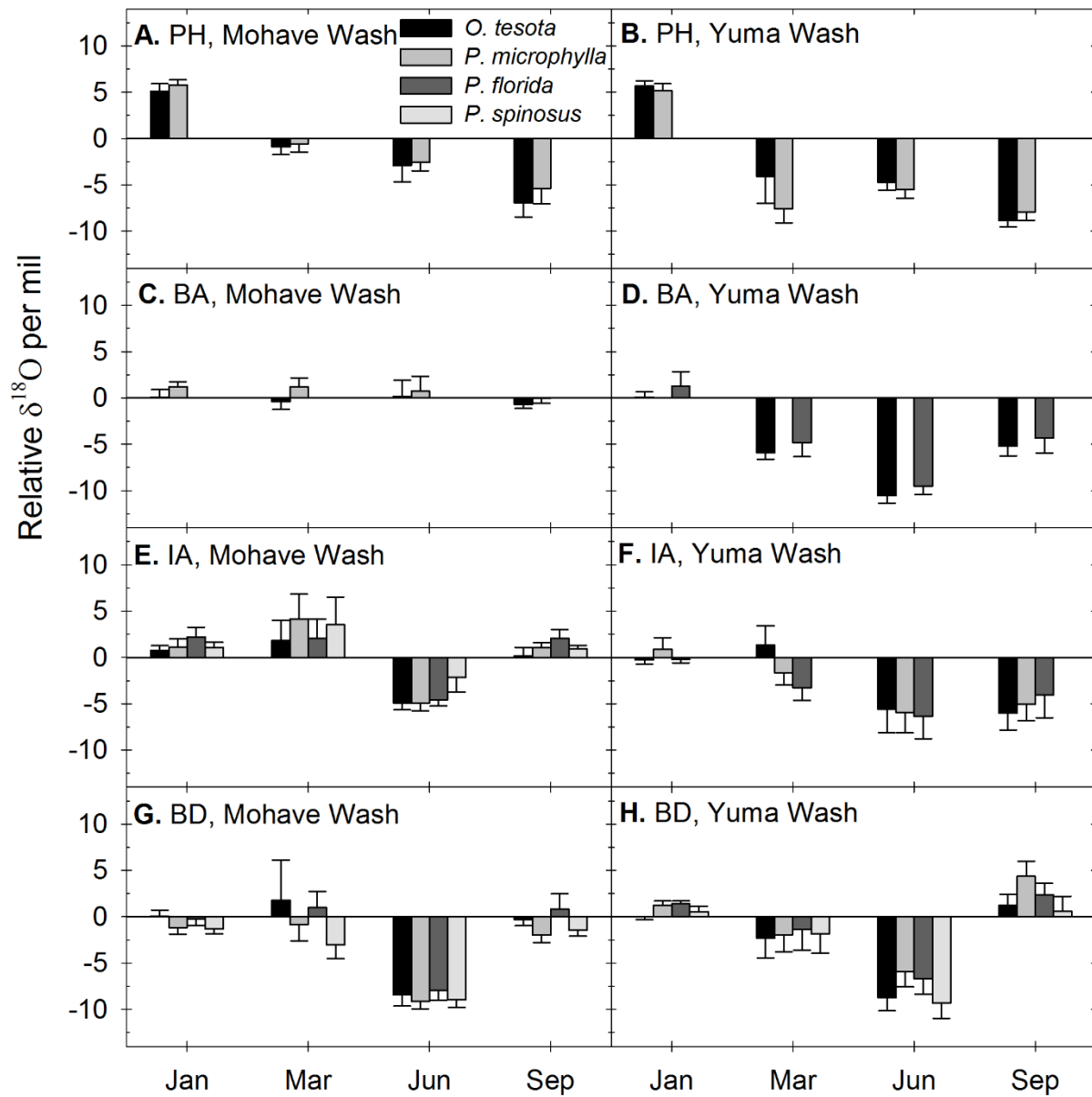


Figure 3.10. Seasonal differences in relative $\delta^{18}\text{O}$ between species within stream types. Bars are means of each species and error bars are 1 S.E. Positive values are more enriched than shallow alluvium (< 50 cm). PH = piedmont headwater, BA = bedrock with alluvium, IA = incised alluvium, BD = braided.

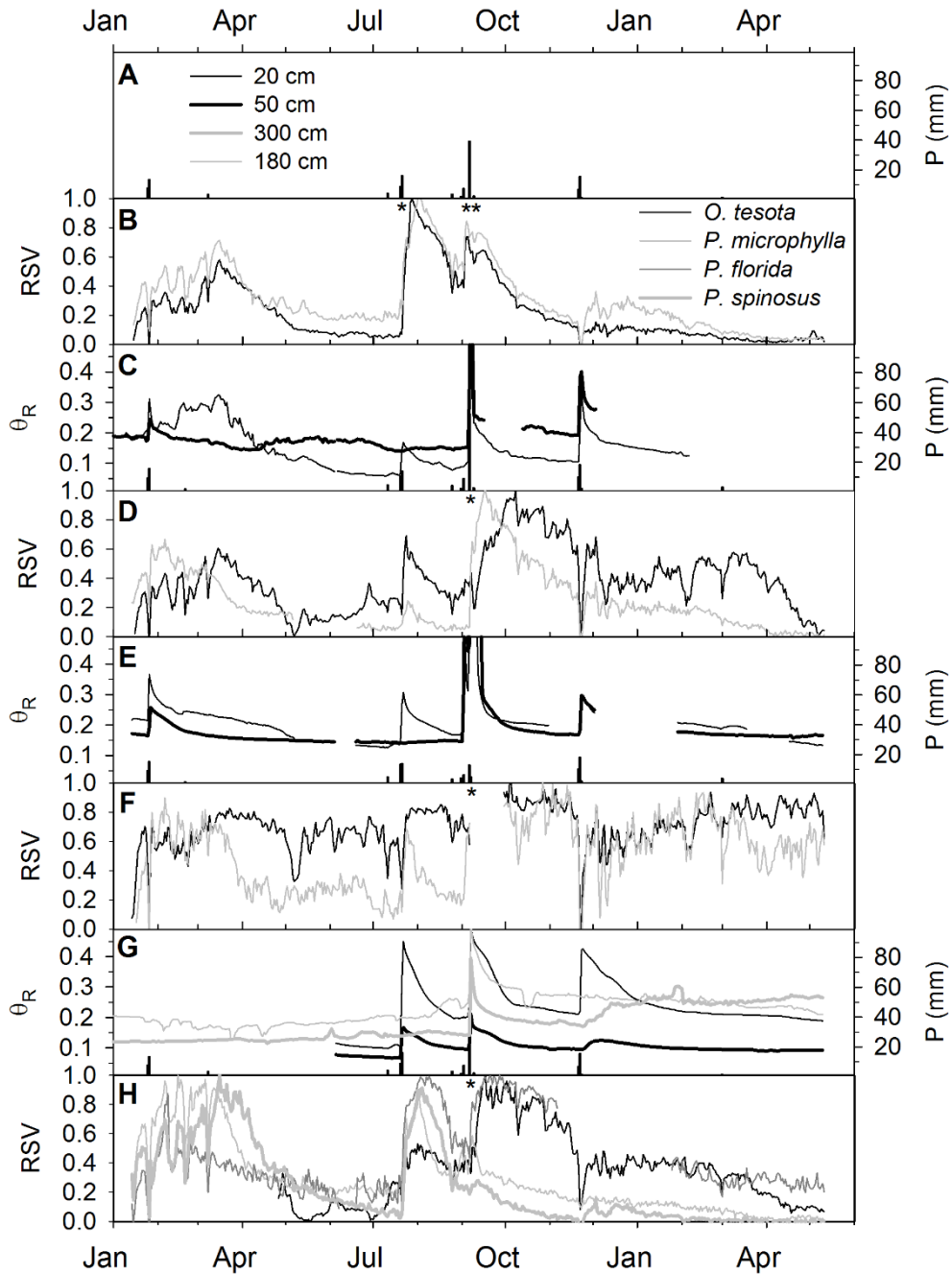


Figure 3.11. Rainfall (P), relative water content (θ_R) and relative sap velocity (RSV) in Mohave Wash from January 2013 to May 2014. Rainfall at piedmont headwater (A); RSV at piedmont headwater (B); rainfall and water content at bedrock with alluvium (C); RSV at bedrock with alluvium (D); rainfall and water content at incised alluvium (E); RSV at incised alluvium (F); rainfall and water content at braided (G); RSV at braided (H). Asterisks indicate streamflow events.

4 Relative Importance of Abiotic and Biotic Limitations to Seedling Establishment

4.1 Introduction

Facilitation of seedling establishment by nurse plants is a widely reported phenomenon in dryland ecosystems (Holmgren et al. 1997, Flores and Jurado 2003, Gómez-Aparicio 2009). However, understanding the importance of this process along gradients of environmental stress in arid regions has stimulated considerable debate (Maestre et al. 2005, 2006, Lortie and Callaway 2006). Addressing this controversy requires quantifying the effects of facilitative mechanisms in alleviating environmental stresses, including abiotic resource stress (e.g., water limitation), abiotic non-resource stress (e.g., excessive solar insolation) and biotic stress from herbivory (Maestre et al. 2009, Soliveres et al. 2014). Further clarification can be gained by separate consideration of important fitness measures such as survival and growth (Maestre et al. 2005, He et al. 2013).

Advancing our understanding of the mechanisms that facilitate woody plant establishment in drylands requires knowledge of the relative effects of biotic and abiotic stressors and their interactions, but relatively few studies have addressed more than one environmental stressor (Smit et al. 2009, Soliveres et al. 2014). Previous field experiments have found that canopy shading is the dominant facilitative mechanism for woody plant establishment in semiarid grassland and forest communities (Callaway 1992, Castro et al. 2004, Gómez-Aparicio et al. 2008, Good et al. 2014), but herbivory was identified as the primary limitation on seedling survival in a semiarid Australian woodland (Maher et al. 2010). Other studies have not produced definitive results (Flores et al. 2004, Louthan et al. 2014). No manipulative experiments have assessed the relative importance of abiotic and biotic limitations on woody

plant establishment in desert plant communities, where intense herbivory and chronic water limitation create extreme environmental stresses.

In drylands around the world, pulses of woody plant recruitment occur during rainy years that are driven by periodic climate events such as El Niño-Southern Oscillation (Swetnam and Betancourt 1998, Holmgren et al. 2006b). In the most arid regions, anomalous wet periods may be the only opportunities for perennial plant establishment (León et al. 2011). Increased water availability can modulate seedling survival responses to herbivore pressure (Holmgren et al. 2006a) and nurse plant shading (Tielbörger and Kadmon 2000, Barchuk et al. 2005, Padilla and Pugnaire 2009, Butterfield et al. 2010). However, little is known about the potentially complex three-way interactions between herbivory, shade, and rainfall.

Survival and growth rates of woody plant seedlings often respond differently to abiotic stress (Maestre et al. 2005, He et al. 2013). In dryland settings where shading led to increased seedling survival rates, growth responses have been highly variable (Hastwell and Facelli 2003, Castro et al. 2004, Gómez-Aparicio et al. 2005, Jefferson and Pennacchio 2005, Good et al. 2014). Similarly, the reported effects of annual rainfall on growth rates have varied considerably (Holmgren et al. 2006a, Squeo et al. 2007, Matías et al. 2012). Variation in growth responses to abiotic stress may be driven by functional traits of both nurse and protégé species, abiotic stress levels, and age of the protégé (Callaway and Walker 1997, Holmgren et al. 1997).

The Sonoran Desert of North America is an ideal system for investigating the relative importance of environmental stressors on woody plant seedling survival and growth. Facilitation by nurse plants has been studied for decades in this region and is known to be critical to the reproduction of many plant taxa (Flores and Jurado 2003, Butterfield et al. 2010). As in other deserts, nurse plants reduce extreme solar insolation and thermal stress, and ameliorate chronic

water stress for protégé seedlings (Callaway 2007). Herbivory by leporids (McAuliffe 1986, 1988) and ungulates (Abella 2008) may also limit seedling survival.

To understand the processes limiting woody plant establishment and the relative importance of facilitative mechanisms in arid ecosystems, I addressed the following questions: (1) Is microclimatic amelioration through shading, or protection from herbivores, the dominant facilitative mechanism for seedling survival and growth? (2) How do infrequent wet years interact with shade and herbivory to affect seedling survival and growth? (3) What is the relative importance of herbivory by large and small mammals? (4) How does seedling size influence survival and growth responses to biotic and abiotic stressors? I answered these questions through a two-year factorial field experiment examining the relative importance of herbivory, shade, rainfall, and seedling size to the survival and growth of three common xeroriparian tree species of the Sonoran Desert: *Olneya tesota* A. Gray (desert ironwood), *Parkinsonia microphylla* (Torrey) Rose & I.M. Johnston (foothills paloverde), and *Parkinsonia florida* (Benth. ex A. Gray) S. Watson (blue paloverde). To isolate the effects of facilitative mechanisms from competitive interactions and localized substrate alterations, artificial nurse plants were constructed to mimic the shade and herbivore protection provided by natural benefactors (Callaway 2007).

4.2 Methods

Experimental plots were established on unvegetated floodplain surfaces along an ephemeral tributary of the lower Colorado River in southwestern Arizona, USA (N 33.456123°, E -114.492205°; 210 m elevation). The study area is located on the U.S. Army Yuma Proving Ground within the Lower Colorado Valley subdivision of the Sonoran Desert, the most arid portion of the Sonoran Desert (Shreve and Wiggins 1964, Turner and Brown 1994). Mean annual precipitation ranges from 93 to 103 mm and mean daily temperatures range from 13 to 32° C at

nearby climate stations (NCDC cooperative stations 29654, 26865). In this hyperthermic arid region, monthly potential evapotranspiration exceeds precipitation throughout the year (Sellers and Hill 1974). Seasonal rainfall is derived from Pacific frontal storms from November to March, while convective thunderstorms of the North American Monsoon may occur from July to September. Upland surfaces are sparsely vegetated by low shrubs, but ephemeral streams support comparatively dense xeroriparian communities containing diverse herbaceous plants, shrubs and trees (Shreve and Wiggins 1964, Turner and Brown 1994).

Experimental factors of shade and herbivory were applied in a randomized complete block design, with four replicate blocks located on separate floodplain surfaces. Blocks consisted of eight 24 m² plots, where all treatment levels of herbivory and shade were crossed. Herbivory treatments consisted of three levels, which excluded: (i) only small animals such as *Lepus californicus* (black-tailed jackrabbits) and *Silvilagus audubonii* (desert cottontail rabbits); (ii) only large mammals such as *Equus asinus* (feral asses), *Equus ferus caballus* (feral horses), and *Odocoileus hemionus* (mule deer); (iii) all animals; and a control. Small animal enclosures consisted of 60 cm tall fencing (6 mm mesh) around plot perimeters, buried 30 cm below ground, following Brown and Munger (1985). Large animals were excluded by suspending polypropylene deer fencing (Tenax Corp., Baltimore, MD, USA) from 60 to 150 cm above ground. Full enclosures used both types of fencing. Shading was accomplished by covering plots with 90 % shade cloth on wooden frames suspended 2.4 m above the ground. The shade treatment level was determined by averaging photosynthetically active radiation measurements (n = 20) under two regionally common nurse shrubs, *Bebbia juncea* var. *aspera* Greene (sweetbush) and *Ambrosia salsola* (Torrey & A. Gray) Strother & B.G. Baldwin (cheesebush).

Each plot was split among two irrigation treatment levels, randomly assigned as irrigated and ambient rainfall. Irrigation was applied by hand watering as monthly additions to ambient

rainfall in 2012, to achieve an annual total of 175 mm, corresponding to approximately a 6 year recurrence interval. This amount was determined by frequency analysis of annual rainfall totals from a 55-year record (1908-2013) in Quartzsite, Arizona (NCDC ID 26865; 265 m elevation) located 33 km northwest of the study site, and was distributed following average monthly proportions of annual rainfall for those years. Irrigated subplots received a total of 44 mm in addition to ambient rainfall, applied on 19 February (12 mm), 11 March (6 mm), 25 April (14 mm), and 16 August (12 mm). During 2013, all seedlings received ambient rainfall. Rainfall and other meteorological variables were measured within 1 km of the experimental blocks.

Olneya tesota, *P. microphylla*, and *P. florida* were randomly assigned to species rows within each subplot. Eight large seedlings (655 ml pots) and 24 small seedlings (164 ml pots) were inter-planted in each species row, allowing 900 cm² and 225 cm² for each large and small seedling, respectively. Seeds collected from the study area were sown in equal parts composted wood byproduct, peat, and perlite (Gro-Well Brands, Inc., Tempe, AZ) at a nearby nursery (Signature Botanica, Morristown, AZ). Large seedlings were grown for five months in D40 deepots, while small seedlings were grown for four months in SC10 conetainers. Mean initial heights of each plant size are shown in Table 4.1. All plants received two applications of 21-5-20 fertilizer and one application of mycorrhizal inoculum (Myco-Drench, Tri-C Enterprises, Chino, CA) while at the nursery.

A total of 6144 plants were installed into the experimental plots during 11-14 January 2012, consisting of 512 large and 1536 small seedlings of each species. To minimize transplanting shock, all seedlings were watered in with 11 mm over three days following planting, after which time the irrigation treatments were imposed. Survival rates were recorded during approximately monthly censuses between January 2012 and January 2014. Browsing by leporids immediately after planting affected all seedlings in unprotected plots, so initial stem

heights were measured only for seedlings within small animal and full exclosures ($n = 3072$).

Changes in stem height were measured annually during January 2013 and 2014. Camera traps in each study block were used to document the principle agents of herbivory.

Experimental effects on seedling survival and growth were assessed by comparing least-squares means of generalized linear mixed models using Proc GLIMMIX in SAS 9.4 (SAS Institute Inc., Carey, NC, USA). Analyses of yearly survival and relative growth rates (change in stem height \div initial height at the beginning of each year) were performed separately for each species. Categorical variables of ‘treatment’ (shade \times herbivory), irrigation, and seedling size were used to model the logit of binomial survival responses, allowing for up to three-way interactions. Since growth rates typically vary with plant size, relative growth rates were compared in ANCOVA models using the covariate of initial height (pooled across size classes), measured at the beginning of each year. Low survival rates resulted in few replicates within most treatments, so seedlings were pooled into ‘shaded’ and ‘unshaded’ plots to maximize degrees of freedom for growth comparisons. This decision was supported by preliminary analyses showing that ‘treatment’ was not significantly related to relative growth rates of any species ($p > 0.54$). In both analyses, experimental factors were considered fixed effects, while study blocks and their interactions with experimental factors were treated as random effects. Multiple comparisons were made using Tukey-Kramer adjusted confidence intervals, and all reported differences were significant at $\alpha = 0.05$.

4.3 Results

Ambient precipitation during 2012 was 130 mm, corresponding to a long-term recurrence interval of 2.2 yr (exceedance probability, $P = 0.46$; Figure 4.1). A lack of winter and spring rainfall caused the first half of 2012 to be abnormally dry, but monsoon thunderstorms raised cumulative precipitation above the long-term median after July. In irrigated subplots, monthly

additions to rainfall during the dry winter and spring months resulted in an annual total of 175 mm, with a recurrence interval of 5.5 yr ($P = 0.18$). A streamflow event lasting 1 hour occurred on 13 July 2012, but stage indicators showed that none of the experimental plots were inundated. In 2013, when irrigation treatments stopped and all seedlings received ambient rainfall, precipitation followed a more typical annual distribution and totaled 136 mm ($P = 0.43$), and no streamflow occurred at the study sites. Total potential evapotranspiration, calculated using the Penman-Monteith method (Allen et al. 1998), was about 2500 mm in each year.

4.3.1 Seedling Survival

Overall survival rates after one year were 3.6 % for *Olneya tesota*, 6.3 % for *Parkinsonia microphylla* and 6.6 % for *P. florida*. The effects of herbivory, shade, irrigation and plant size on survival rates over time were similar among species (Figures 4.2-4.4). Small mammal herbivory killed the majority of seedlings that were accessible soon after planting. Where small animals were excluded, desiccation-induced mortality during spring and summer constrained first-year survival.

Regardless of irrigation treatment or plant size, intense herbivory by leporids killed all seedlings in plots accessible to small animals during the first year. Seedlings in unshaded plots open to small animals were all dead by June 2012, while those in shaded plots died by January 2013. No large animal herbivory occurred in any of the experimental plots, and 3187 photographs from camera traps indicated that seedlings were consumed exclusively by *Lepus californicus* and *Silvilagus audubonii*.

Shading significantly increased first-year survival of all species ('treatment' effect, Table 4.2). Overall survival rates ranged from 20 to 31 % in shaded small animal exclosures, while only 0 to 3.1 % of seedlings survived in unshaded plots. Survival in shaded full exclosures was lower for *O. tesota* (9.0 %) and *P. florida* (18 %) than in shaded small animal exclosures.

Mean survival rates in irrigated subplots exceeded those in ambient rainfall subplots by a factor of 2.7 to 3.0 (Table 4.2). Significant treatment \times irrigation effects indicate that annual rainfall modified the survival responses of all species to shading (Figure 4.5). The highest survival rates occurred in irrigated subplots within shaded small animal exclosures (*O. tesota*, 32 %; *P. microphylla*, 38 %; *P. florida*, 50 %), which exceeded survival of unirrigated seedlings in the same plots by factors of 3.6 for *O. tesota*, 1.7 for *P. microphylla*, and 3.0 for *P. florida*. Comparable increases occurred within shaded full exclosures. In unshaded plots, no seedlings lived beyond the first summer without irrigation, while up to 6.3 % of irrigated seedlings survived.

Survival rates were higher for large *O. tesota* and *P. florida* seedlings compared to small seedlings, and plant size mediated the effects of irrigation and shade on all species (Table 4.2). In ambient rainfall subplots, survival of large *O. tesota* and *P. microphylla* seedlings exceeded that of small seedlings by factors of 5.0 and 1.8. Differences among size classes were lower in irrigated subplots, but large seedling survival was still 56 to 120 % higher. Survival rates of large seedlings were always higher than small seedlings in shaded plots, but differences were less consistent in unshaded plots. Treatment \times irrigation \times size effects were significant for each species (Figure 4.6). Survival of large seedlings was generally highest in all treatment combinations, while unirrigated small seedlings had the lowest survival rates.

Overall survival rates were substantially higher during the second year, and 85 % of the remaining *O. tesota* (n = 74), 84 % of *P. florida* (n = 135), and 80 % of *P. microphylla* (n = 128) lived until January 2014. Since the surviving seedlings were protected from small herbivores, mortality was caused exclusively by desiccation during summer (Figures 4.2-4.4). Species survival responses to experimental factors diverged during the second year, with much of the mortality occurring in plots with high first-year survival.

Survival rates of each species differed among shade treatments during the second year (Table 4.3). In unshaded exclosures, all of the remaining *O. tesota* (n = 1) and *P. florida* (n = 9) seedlings survived, but only 29 % of *P. microphylla* survived (n = 7). Seedling survival in shaded exclosures was between 78 and 91 %, and all *O. tesota* and *P. florida* mortality occurred in these plots.

Overall *O. tesota* and *P. florida* survival was not affected by irrigation during the previous year, but *P. microphylla* survival was 13 % lower in irrigated subplots (Table 4.3). Interactions between first-year irrigation and shade differed among species (Figure 4.7). Survival rates of irrigated *O. tesota* and *P. florida* seedlings was highest in unshaded plots, but irrigated *P. microphylla* survival was 65 % lower in unshaded plots.

As during the first year, overall survival of large seedlings was higher than small seedlings (Table 4.3). Relative to small seedlings, large seedling survival differed by < 3 % in shaded plots for *O. tesota*, but was 10 to 12 % higher for *P. microphylla* and up to 23 % higher for *P. florida*. Significant treatment × irrigation × size effects for each species describe complex variation in survival responses among experimental factors, but lack of replicates allowed only coarse distinctions within multiple comparisons (Figure 4.8).

4.3.2 Seedling Growth

Mean stem height of surviving *P. florida* seedlings (n = 135) increased by 109 ± 6.2 % (mean ± SE) during the first year, while *O. tesota* (n = 74) and *P. microphylla* (n = 128) heights increased by 79.8 ± 7.8 % and 47.4 ± 4.1 %. Unlike survival rates, first-year growth rates of all species were unaffected by supplemental irrigation (Table 4.4). The mean relative growth rate of *P. florida* in shaded plots (1.13) was twice as large as in unshaded plots (0.553), but shading did not affect *P. microphylla* growth. The effect of shade on *O. tesota* growth was not evaluated, since only one seedling survived in unshaded plots. Relative growth rates of *O. tesota* and *P.*

microphylla declined at similar rates with increasing initial height (Figure 4.9A, 4.9B).

Significant shade × initial height interaction reflected differences in size-dependent growth rates between shaded and unshaded plots (Table 4.4). Growth of *P. florida* seedlings decreased with initial height in shaded plots, but growth rates increased slightly with seedling height in unshaded plots (Figure 4.9C).

During the second year, relative growth rates of the remaining seedlings were substantially lower and similar among species. Mean stem height increased by 19.2 ± 3.6 % for *O. tesota* (n = 63), 21.7 ± 2.7 % for *P. florida* (n = 113), and 17.7 ± 2.6 % for *P. microphylla* (n = 102). Irrigation during the previous year did not affect growth of any species (Table 4.5). In contrast to the first year, growth rates of *P. florida* seedlings were not influenced by shade, and the effect of shade on *O. tesota* and *P. microphylla* growth was not tested due to scarcity of seedlings in unshaded plots (n = 1 and 2, respectively). Seedling height at the beginning of the second year was not related to growth rates of any species in ANCOVA models containing interactions.

4.4 Discussion

Variation in annual rainfall can influence the relative importance of abiotic and biotic stressors on woody plant seedling survival in arid environments. Under approximately median annual rainfall, 100 % mortality occurred in plots lacking shade or protection from small herbivores, reflecting equal influence among abiotic and biotic stressors. In contrast, biotic stress from herbivory outweighed abiotic resource stress (water limitation) and non-resource stress (excessive solar insolation) under conditions of enhanced rainfall. Previous work has described seasonal variation in the relative importance of biotic and abiotic facilitative mechanisms to tree establishment in semiarid to subhumid Mediterranean forests (Perea and Gil 2014). This study

expands our understanding of these processes by documenting the role of annual rainfall on facilitative mechanisms in an arid xeroriparian ecosystem.

The stress-gradient hypothesis suggests that facilitation becomes increasingly important as environmental stress increases (Bertness and Callaway 1994). The greater importance of shade to seedling survival under higher abiotic stress (lower annual rainfall) supports this notion. It has also been suggested that associational resistance is weaker under high abiotic stress, and becomes increasingly important as abiotic stress declines (Smit et al. 2009). My data contradict this assertion, by showing the critical need for herbivore protection under contrasting abiotic stress levels. The use of artificial nurse plants to provide shade and herbivore protection neglects potential negative plant interactions, such as competition for water. Outcomes of pairwise interactions with living nurse plants may be less positive with higher rainfall, since competition likely increases with lower abiotic stress (Callaway and Walker 1997, Holmgren et al. 1997).

Periodic years with above-average precipitation are critical windows for woody plant establishment in the Sonoran Desert (Butterfield et al. 2010) and other dryland regions (Swetnam and Betancourt 1998, Holmgren et al. 2006b). For all species, enhanced precipitation during the first year increased survivorship under shade and allowed the survival of unshaded seedlings, which otherwise died. Previous work has also highlighted the role of rainfall in modulating the facilitative effect of nurse plant shading (Kitzberger et al. 2000, Tielbörger and Kadmon 2000, Barchuk et al. 2005, Padilla and Pugnaire 2009). However, intense herbivory by leporids precluded seedling survival regardless of rainfall amounts, and the interactions between climate, shade and plant size were only apparent when these abundant herbivores were excluded. This finding is supported by work in South American drylands showing that high herbivore pressure can limit tree establishment even during infrequent rainy years (Holmgren et al. 2006a). The

overwhelming importance of herbivory in constraining tree seedling establishment has also been reported from less xeric regions in the Sonoran Desert (McAuliffe 1986, Bowers et al. 2004).

In contrast to the initially positive effects of shade and irrigation, these factors led to slight reductions in *O. tesota* and *P. florida* survival during the second year. Low replication due to very high first year mortality, particularly in unshaded plots, may have limited my understanding of second year effects. However, lower root : shoot ratios and other physiological tradeoffs in shade-acclimated seedlings may have made them more susceptible to subsequent drought stress (Smith and Huston 1989, Holmgren et al. 1997).

Lepus californicus and *Silvilagus audubonii* appear to be the primary biotic agents of tree seedling mortality within the most arid portion of the Sonoran Desert. These common leporids of North American drylands consume woody vegetation during droughts and in winter months, when preferred grass and herbaceous forage is unavailable (Hayden 1966, Westoby 1980, Anderson and Shumar 1986, Hoagland 1992, Wansi et al. 1992). McAuliffe (1986) also observed that leporid herbivory was a primary constraint on *P. microphylla* seedling survival, and leporid exclosures in the Chihuahuan Desert significantly increased survival rates of woody plant seedlings (Martínez and López-Portillo 2003, Roth et al. 2007). Leporid population densities can vary due to disease and predation (Lightfoot et al. 2010), but there was no evidence that leporid abundance was abnormally high during the study. Although native and feral ungulates commonly browse larger saplings and mature trees within the study area (J. Shaw, unpublished data), they had no effect on seedling survival in the experimental plots. *Olneya tesota* and *Parkinsonia* spp. are known to be important dietary components for native *Odocoileus hemionus* (Marshall et al. 2004, 2012, Alcalá-Galvan and Krausman 2012) and feral *Equus asinus* (Abella 2008, Marshall et al. 2012). The lack of ungulate herbivory on seedlings may reflect their vertical browsing preferences for taller vegetation (Crawley 1983, Ward 2006).

Growth responses to rainfall and shade diverged considerably from seedling survival (Maestre et al. 2005, Brooker et al. 2008, He et al. 2013). While enhanced rainfall improved survival rates of all species, it did not affect above-ground relative growth rates. A similar lack of sensitivity in growth rates to annual rainfall, despite significant effects on survival, has been observed in woody plants from the Spanish Mediterranean (Matías et al. 2012) and the Atacama Desert (Squeo et al. 2007). Shading resulted in a doubling of first-year stem growth in *Parkinsonia florida*, but its congener *P. microphylla* grew at similar rates in open and shaded plots. In contrast to the substantial interspecific variation in mean stem growth rates during the first year, all species exhibited similarly low stem growth rates during the second year. The declining effects of facilitative mechanisms on survival and growth during the second year may reflect ontogenetic shifts in sensitivity to abiotic stressors (Callaway and Walker 1997, Callaway 2007).

The spatial distribution and ranges of the three dominant tree species differ in these xeroriparian communities (Shreve and Wiggins 1964, Turner et al. 1995), but my analyses suggest that they possess broadly similar regeneration niches. Seedling survival in all three species is strongly dependent on the shade and herbivore protection afforded by nurse plants. Interspecific differences in stem growth rates did not persist into the second year, suggesting that above-ground growth rate does not comprise a substantial axis of differentiation among regeneration niches. Recruitment rates are likely greatest during years of high precipitation, when fewer seedlings are killed by abiotic stressors.

Table 4.1. Seedling initial stem heights (cm) after planting.

Species	Size	Mean	S.E.
<i>O. tesota</i>	Large	21.4	0.72
	Small	12.1	0.44
<i>P. florida</i>	Large	31.9	0.84
	Small	17.8	0.33
<i>P. microphylla</i>	Large	20.1	0.46
	Small	13.6	0.36

Table 4.2. Effects of treatment, irrigation, and plant size on seedling survival during the first year. Bold p-values are significant at $\alpha = 0.05$.

Effect	df	<i>O. tesota</i>		<i>P. microphylla</i>		<i>P. florida</i>	
		F	p	F	p	F	p-value
Treatment (T)	9	2.39E5	<0.0001	957	<0.0001	4.30E5	<0.0001
Irrigation (I)	12	1.04E5	<0.0001	4.14E3	<0.0001	1.93E6	<0.0001
T × I	12	3.71E3	<0.0001	1.64E3	<0.0001	1.12E5	<0.0001
Size (S)	984	4.01E4	<0.0001	0.00	0.99	Infty	<0.0001
T × S	984	68.6	<0.0001	25.3	<0.0001	Infty	<0.0001
I × S	984	1.34E3	<0.0001	158	<0.0001	Infty	<0.0001
T × I × S	984	110	<0.0001	98.7	<0.0001	Infty	<0.0001

Table 4.3. Effects of treatment, irrigation, and plant size on seedling survival during the second year. Bold p-values are significant at $\alpha = 0.05$.

Effect	<i>O. tesota</i>			<i>P. microphylla</i>			<i>P. florida</i>		
	df	F	p	df	F	p	df	F	P
Treatment (T)	2	Infty	< 0.0001	4	1.77E4	< 0.0001	3	62.3	0.0042
Irrigation (I)	2	4.05	0.18	5	3.33E3	< 0.0001	3	2.30	0.23
T × I	2	Infty	< 0.0001	5	40.4	0.0014	3	Infty	< 0.0001
Size (S)	57	28.0	< 0.0001	105	2.87E3	< 0.0001	115	80.8	< 0.0001
T × S	57	Infty	< 0.0001	105	17.1	< 0.0001	115	Infty	< 0.0001
I × S	57	Infty	< 0.0001	105	Infty	< 0.0001	115	4.03	0.047
T × I × S	57	Infty	< 0.0001	105	Infty	< 0.0001	115	Infty	< 0.0001

Table 4.4. Effects of shade, irrigation and seedling initial height on relative growth rates during the first year. Samples were pooled across shaded and unshaded plots and plant sizes, with initial height (H, cm) as a covariate. Bold p-values are significant at $\alpha = 0.05$.

Effect	<i>O. tesota</i>			<i>P. microphylla</i>			<i>P. florida</i>		
	df	F	p	df	F	p	df	F	p
Shade (Sh)	*			116	0.41	0.52	123	6.34	0.013
Irrigation (I)	3	1.80	0.27	3	0.07	0.80	3	0.00	0.97
Initial Height (H)	41	10.7	0.002	116	5.79	0.018	123	0.53	0.47
Sh \times H	*			116	1.01	0.32	123	3.92	0.050
I \times H	24	0.82	0.37	116	0.07	0.79	123	0.00	0.97

* shade effect excluded due to lack of replicates in unshaded plots.

Table 4.5. Effects of shade, irrigation and seedling initial height on relative growth rates during the second year. Samples were pooled across shaded and unshaded plots and plant sizes, with initial height for second year (H₂, cm) as a covariate.

Effect	<i>O. tesota</i>			<i>P. microphylla</i>			<i>P. florida</i>		
	df	F	p	df	F	p	df	F	p
Shade (Sh)	*			*			1	0.22	0.72
Irrigation (I)	2	0.06	0.83	3	0.24	0.66	3	0.17	0.71
Initial Height (H ₂)	54	1.75	0.19	92	2.02	0.16	100	2.27	0.14
Sh × H ₂	*			*			100	0.02	0.88
I × H ₂	54	0.19	0.66	92	0.07	0.79	100	0.15	0.70

* shade effect excluded due to lack of replicates in unshaded plots.

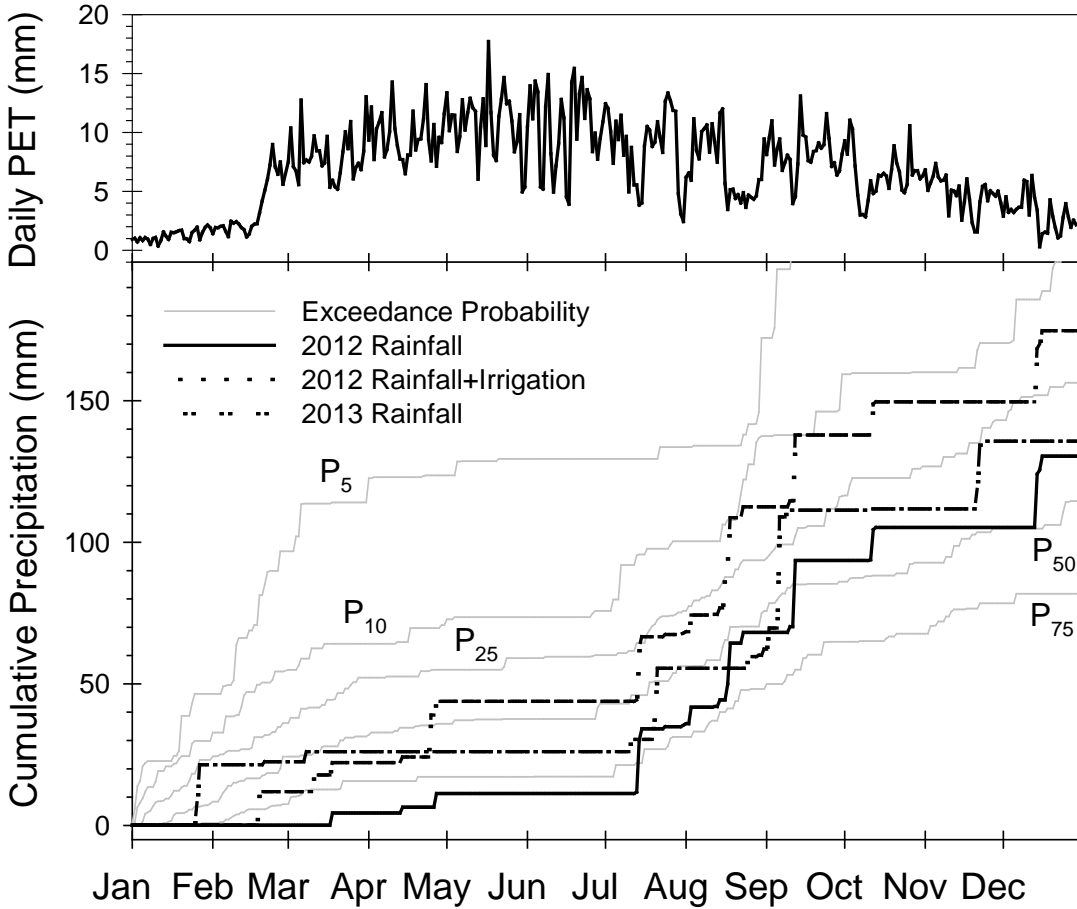


Figure 4.1. Potential evapotranspiration (PET) and cumulative precipitation at experimental plots during 2012 and 2013. Exceedance probabilities are based on 55 yr record at Quartzsite, AZ.

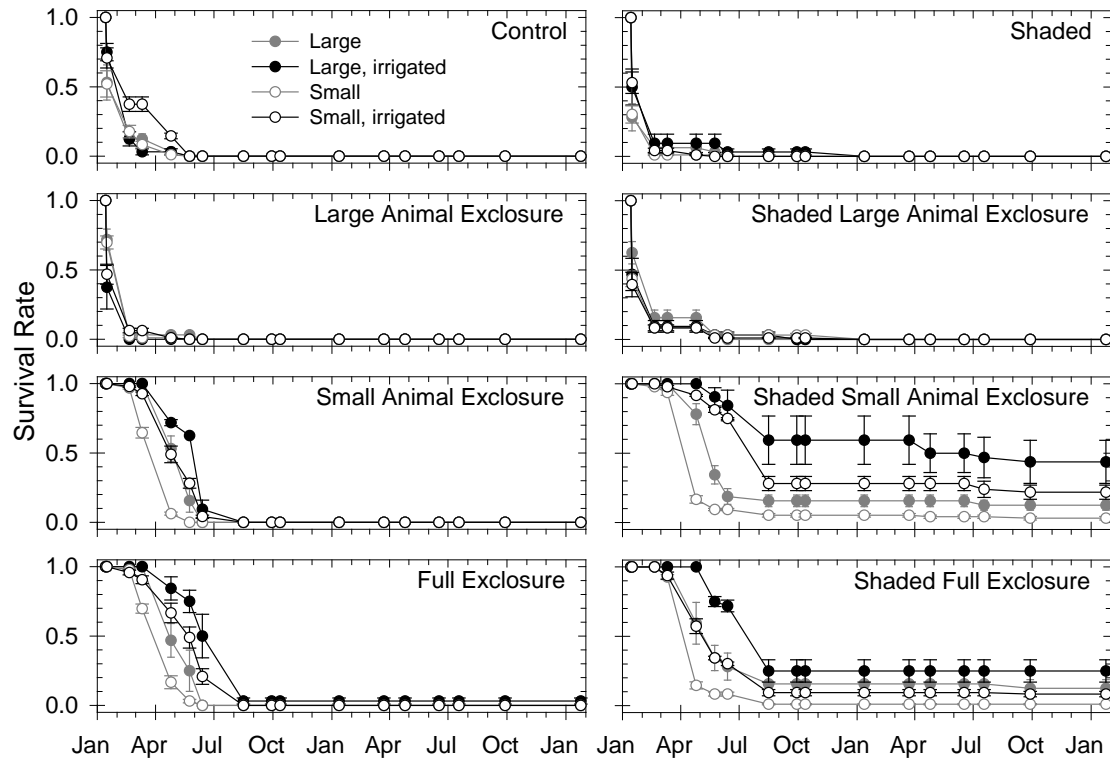


Figure 4.2. Survival rates of *Olneya tesota* seedlings in experimental plots from January 2012 to January 2014.

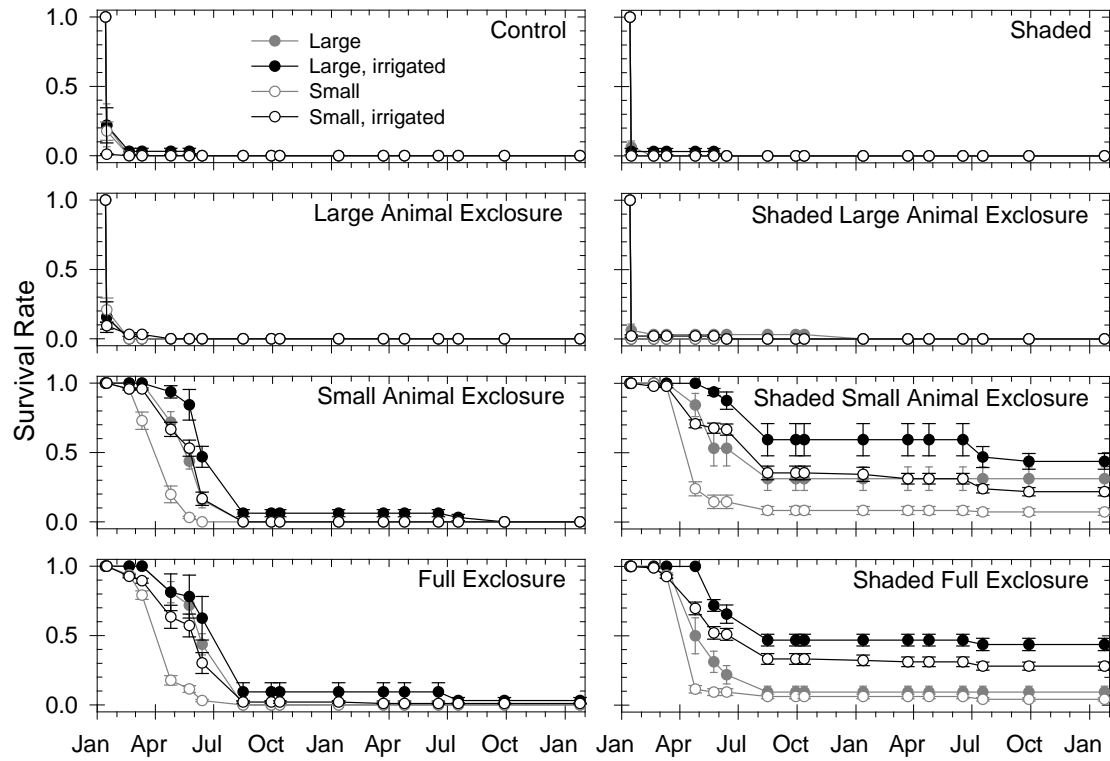


Figure 4.3. Survival rates of *Parkinsonia microphylla* seedlings in experimental plots from January 2012 to January 2014.

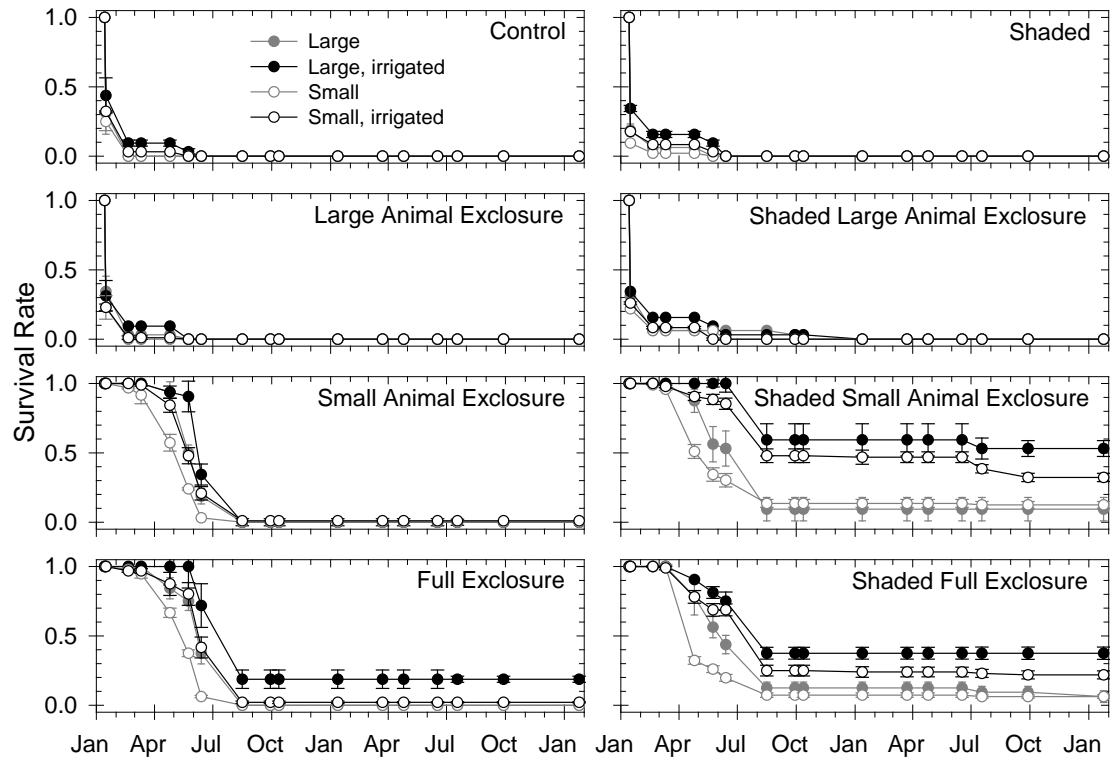


Figure 4.4. Survival rates of *Parkinsonia florida* seedlings in experimental plots from January 2012 to January 2014.

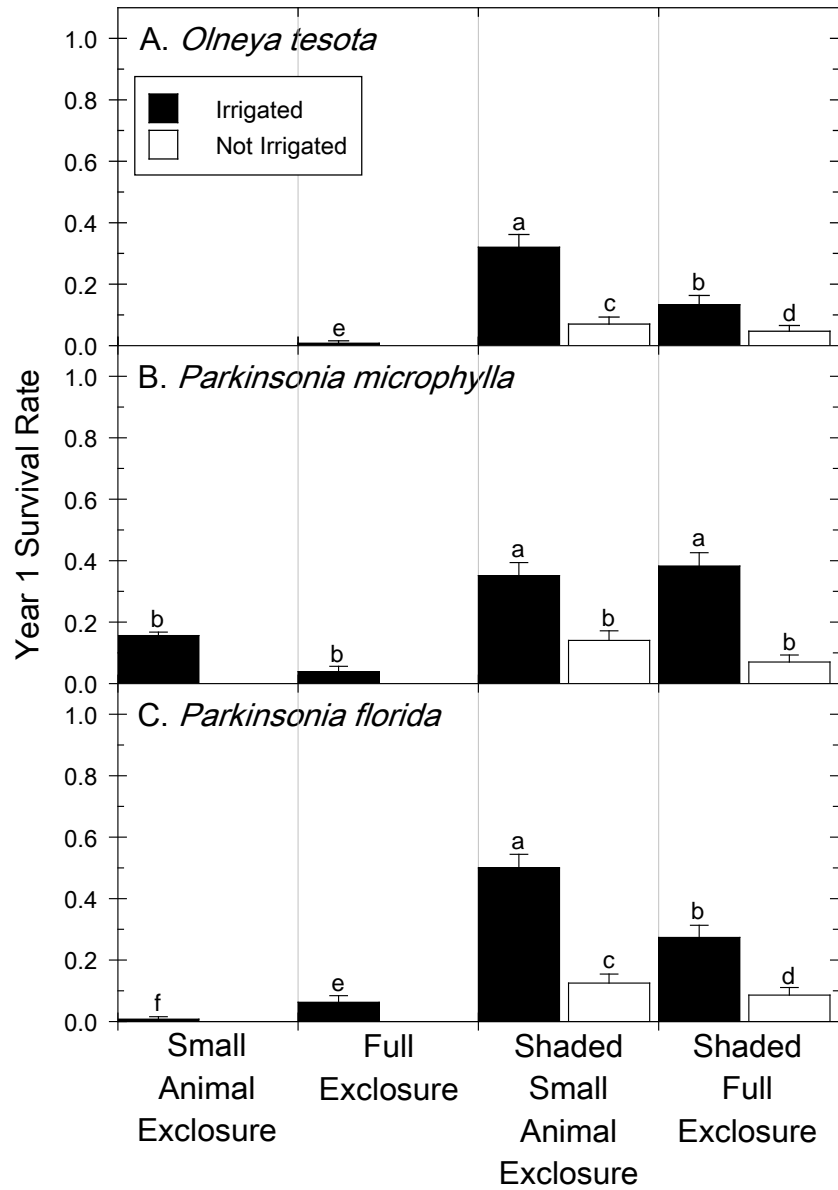


Figure 4.5. Comparison of survival rates for (A) *O. tesota*, (B) *P. microphylla* and (C) *P. florida* across treatment and irrigation levels during the first year. Values are averaged across replicates, and error bars are 1 SE. Letters indicate significant differences among least-squares means at $\alpha = 0.05$.

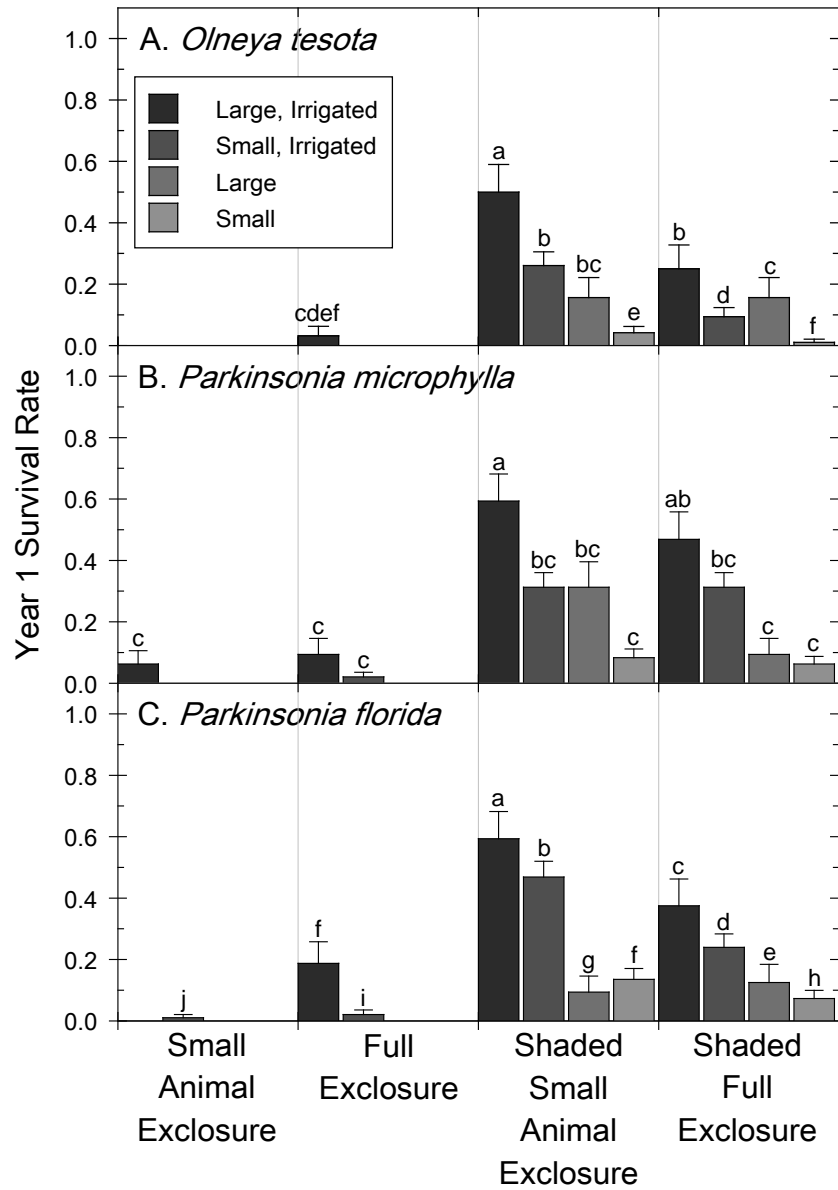


Figure 4.6. Comparison of survival rates for (A) *O. tesota*, (B) *P. microphylla* and (C) *P. florida* across experimental factors during the first year. Values are averaged across replicates, and error bars are 1 SE. Letters indicate significant differences among least-squares means at $\alpha = 0.05$.

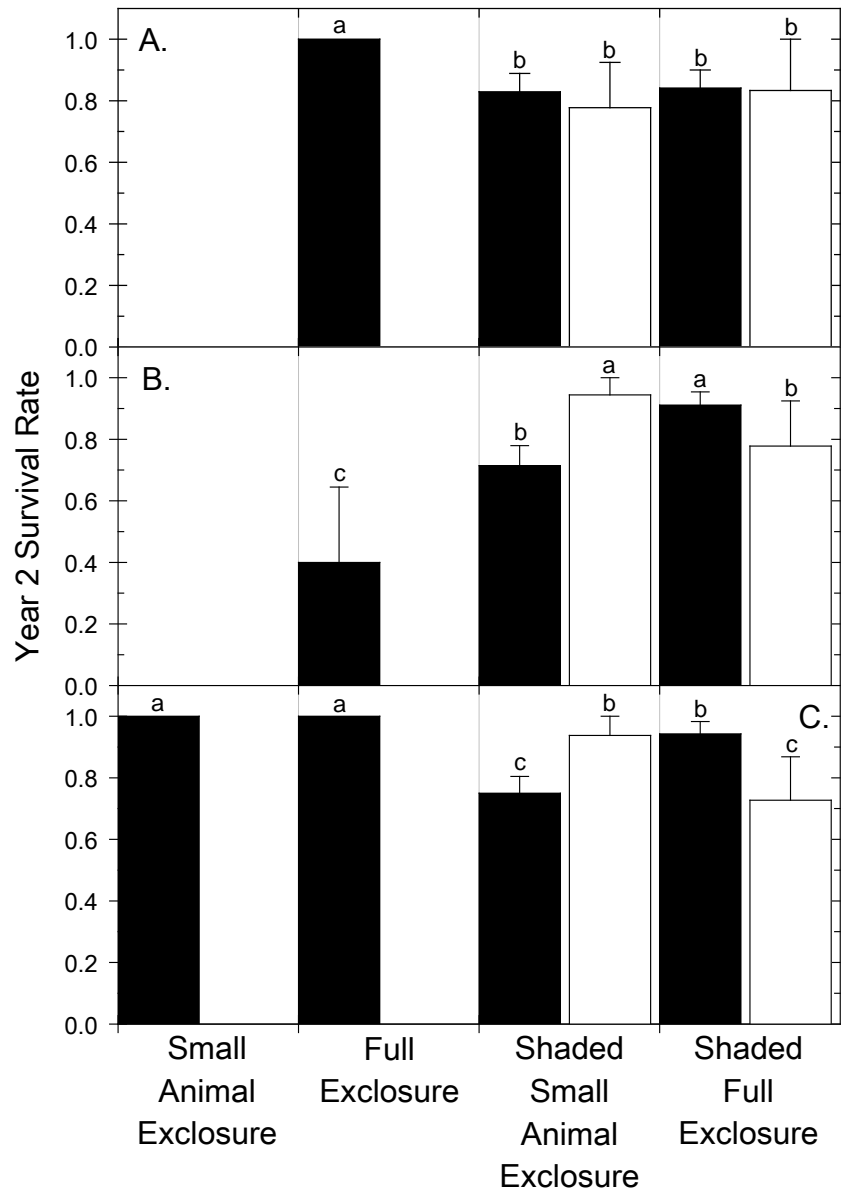


Figure 4.7. Comparison of survival rates for (A) *O. tesota*, (B) *P. microphylla* and (C) *P. florida* across treatment and irrigation levels during the second year. Values are averaged across replicates, and error bars are 1 SE. Letters indicate significant differences among least-squares means at $\alpha = 0.05$. See legend in Figure 4.5.

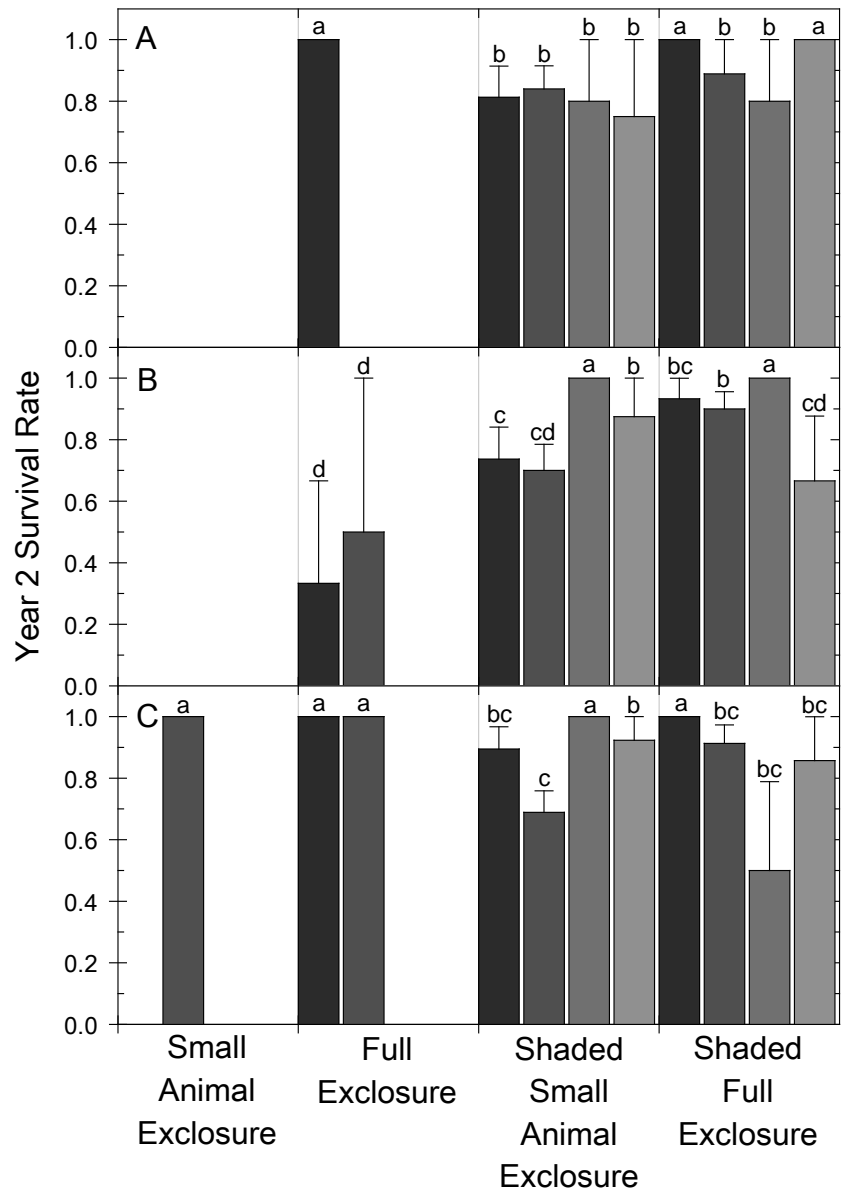


Figure 4.8. Comparison of survival rates for (A) *O. tesota*, (B) *P. microphylla* and (C) *P. florida* across experimental factors during the second year. Values are averaged across replicates, and error bars are 1 SE. Letters indicate significant differences among least-squares means at $\alpha = 0.05$. See legend in Figure 4.6.

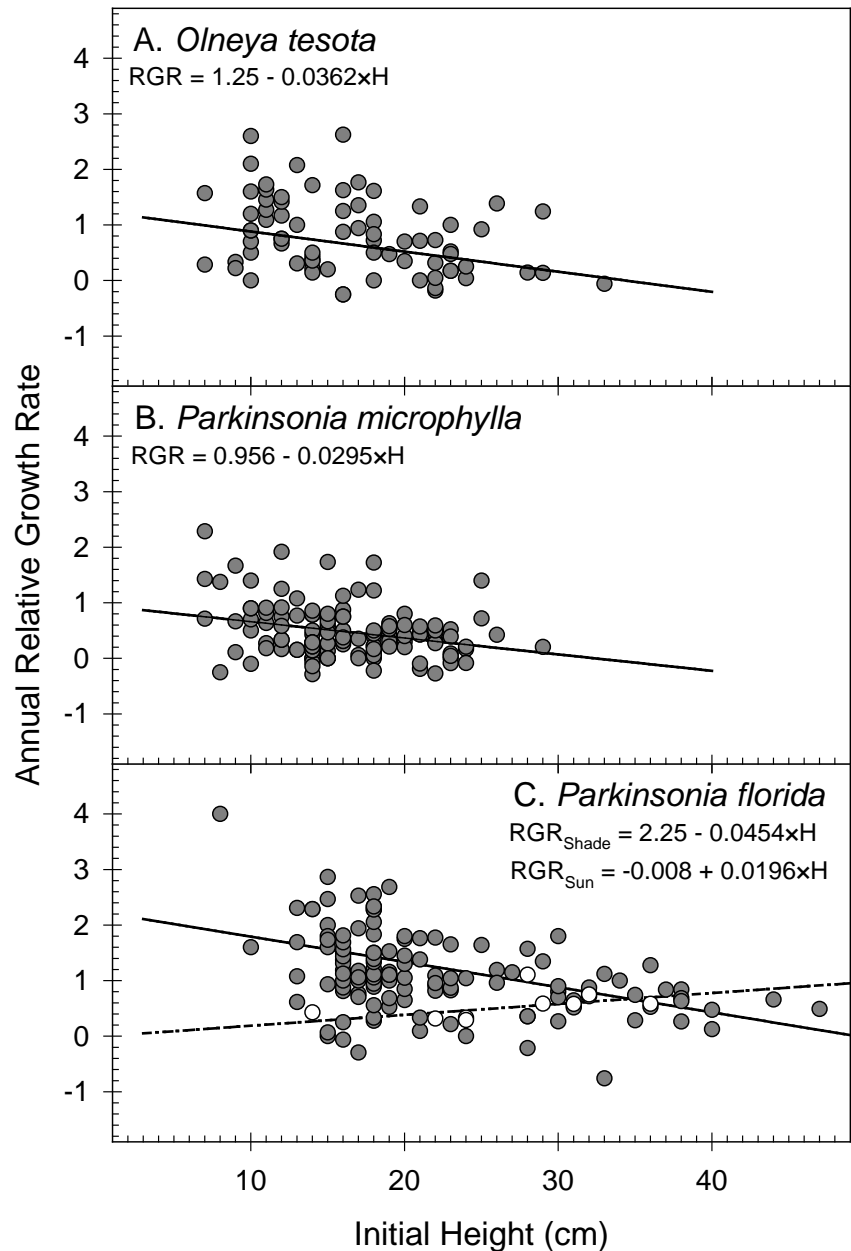


Figure 4.9. Relative growth rates of (A) *O. tesota*, (B) *P. microphylla*, and (C) *P. florida* during the first year as a function of initial height (cm). In C, filled symbols = shade, open symbols = sun.

5 Synthesis

The preceding chapters shed light on fundamental issues in dryland riparian plant ecology. Analysis of spatial patterns in riparian vegetation within the context of a hydrogeomorphic stream classification identified the physical drivers of reach-scale compositional variation, and the species and plant functional groups underlying these spatial patterns (Chapter 2). Examination of seasonal ecohydrological dynamics in riparian trees along a fluvial gradient highlighted the role of alluvial characteristics in mediating the responses of plant water relations to hydrologic variations (Chapter 3). A two-year factorial field experiment showed that herbivory outweighed abiotic stressors in limiting woody plant establishment, and clarified how annual rainfall influences the importance of facilitative mechanisms to seedling survival (Chapter 4). These findings can be used to inform management and restoration activities by clarifying the relative sensitivities of stream types to disturbance and hydrologic alteration, facilitating the identification of appropriate reference conditions, and providing a basis for sample stratification.

My results also revealed novel ecohydrological processes that contradict current ideas on how large woody plants use available water in arid ecosystems. In habitats with deep sediment profiles, all four of the dominant riparian tree species in the western Sonoran Desert relied on shallow water sources throughout much of the year, despite higher water availability in deeper sediments (Chapter 3). This contrasts with previous investigations from a broad range of habitats, which found that large woody plants rely on deep water sources, and only briefly access shallow soil water during favorable conditions (Kolb et al. 1997, Snyder and Williams 2000, Williams and Ehleringer 2000, Schwinning et al. 2002, 2003, Chimner and Cooper 2004, West et al. 2007a, Kray et al. 2012). Throughout the ephemeral stream continuum, I also showed that co-

dominant tree species did not partition water sources, even in stream types subjected to chronic water limitation (Chapter 3). These findings provide new avenues for future research, and help to refine our understanding of how plants interact with their environment. Further clarification could be gained by testing the following hypotheses: (1) Nutrient (e.g., nitrogen) uptake is maximized during seasons when shallow alluvial water sources are used. (2) Hydrologic niche partitioning among species is greatest during severe and prolonged drought periods.

Variation in riparian vegetation throughout ephemeral stream networks of the Sonoran Desert corresponded to differences in channel planform, substrate type, and lateral confinement (Chapter 2). Hydrogeomorphic stream types defined by these qualitative descriptors supported distinctive plant species and functional group assemblages. Spatial variation in plant composition within these arid watersheds was driven by abundances of the most common species and functional types in the regional flora. Vegetation differences among stream types corresponded primarily to variation in channel gradient. The importance of this physical driver reflects the direct influence of fluvial disturbance, and the indirect effects of substrate-mediated water availability, in shaping riparian ecological dynamics.

Seasonal patterns of water stress, and the sources of water that sustain riparian trees, differed among hydrogeomorphic stream types (Chapter 3). Water stress was most severe and persistent in distal portions of Sonoran Desert ephemeral stream networks, where thin alluvium limited subsurface water storage. In these stream types, water use was tightly coupled to periodic rainfall and streamflow inputs. Trees growing in downstream segments containing thick alluvium relied largely on water derived from the upper 50 cm of alluvium, but accessed deeper water sources during summer droughts. Seasonal water stress was lowest and riparian tree water use was least variable in these stream types. Across this gradient of riparian habitats, co-occurring species did not partition subsurface water sources.

Riparian tree seedling survival in these watersheds was most strongly dependent on herbivore protection provided by nurse shrubs, while the importance of facilitation through canopy shading varied with annual rainfall (Chapter 4). Herbivory by leporids killed all accessible seedlings within months of planting, regardless of shading or rainfall amounts. When protected from small herbivores, no seedlings survived beyond one year without shading under approximately median annual rainfall. In contrast, up to 6 % of seedlings receiving the same rainfall survived in shaded small animal exclosures. Survival rates were significantly higher under enhanced annual rainfall corresponding to a 5.5-year recurrence interval, and shading was not required for seedling survival. Despite significant effects on survival, seedling growth rates were not significantly affected by shade or rainfall amounts. Establishment of Sonoran Desert riparian trees is strongly dependent on herbivore protection and canopy shading provided by nurse shrubs, but the importance of shade varied with annual rainfall.

These studies highlighted critical elements of the physical environment, across spatial scales ranging from watersheds to shrub canopies, which condition vegetation responses to hydrologic fluxes in an arid ecosystem. Variation in network position and alluvial characteristics give rise to distinctive ecohydrological responses to rainfall and streamflow events. Co-varying gradients of fluvial disturbance and channel morphology, superimposed on contrasting substrate types, interact with these water stress regimes to produce spatial variation in riparian vegetation composition. At finer spatial scales, nurse shrub canopies mediate the survival response of woody plant seedlings to climatic variation and biotic disturbance.

These analyses also demonstrate that hydrogeomorphic stream classifications can provide a valuable conceptual framework for understanding spatiotemporal dynamics in dryland riparian ecosystems. The ephemeral stream classification described by Sutfin et al. (2014) characterizes segments of the fluvial continuum that correspond to differences in ecohydrological process

domains. Specific physical and biotic attributes of each stream type will likely vary across regions with differing geology, climatic patterns, biogeography, and land use. However, consistent biotic attributes of stream types within the study area, and analogous patterns reported from arid regions across the globe, indicate that this conceptual approach is broadly applicable.

5.1 Implications for a Changing Climate

Projected increases in temperatures and reduced winter precipitation are expected to result in vegetation changes throughout the southwestern United States (Notaro et al. 2012). Considerable uncertainties remain in predicting changes in precipitation derived from the North American Monsoon (Farrara and Yu 2003) and El Nino-Southern Oscillation events (Geil et al. 2013). However, significant decreases in the magnitude or frequency of rainfall, and increases in evapotranspiration rates, will amplify seasonal drought stress.

Plant communities in piedmont headwater, bedrock, and bedrock with alluvium streams are likely to experience the most immediate effects from climatic shifts. Less frequent hydrologic pulses in these stream types will cause greater reductions in plant-available water, due to limited subsurface water storage capacity (Kampf et al. *in review*). The ability to access more stable water sources in deeper alluvium can buffer riparian trees along incised alluvium and braided streams from short-term droughts (Chapter 3), but reduced near-surface water availability may cause declines in the abundances of shallow-rooted plants such as herbs, cacti, and subshrubs (Jackson et al. 1996, Schenk and Jackson 2002b). Although trees and other deep-rooted plants in these stream types could minimize drought stress by using deeper water sources, access to nutrient pools in shallow alluvium would decline. Woody plant mortality due to short but severe droughts would likely be most extensive in distal network positions. Over longer time-scales, increased aridity could result in compositional shifts throughout ephemeral stream networks.

Establishment of the dominant riparian tree species in this region is most successful during years of above-average rainfall (Chapter 4). Therefore, projected climate changes will likely result in less frequent reproduction of large woody plants. Over decadal time scales, this could lead to reduced structural complexity in riparian plant communities. Tree density would decline as mature individuals die, but are not replaced.

The effects of more frequent and intense storm events on channel morphology and riparian vegetation are expected to differ among stream types. Increased flood disturbance will probably not cause significant changes in bedrock streams, where channel boundaries are resistant to erosion, but alluvial stream segments could experience more extensive vertical and lateral adjustment to changing water and sediment fluxes (Knighton 1998). Channel widening and bank erosion may have the greatest impact on riparian vegetation along incised alluvium streams, particularly where channel confinement is high and floodplain surfaces are limited to narrow benches. Lateral channel adjustment from periodic floods is a common feature of braided streams (Graf 1981, Merritt and Wohl 2003), so lesser changes are likely in this stream type. Infrequent flood events provide deep recharge in braided and large incised alluvium streams, whereas direct precipitation typically does not infiltrate below 100 cm (Kampf et al. *in review*), so increased storm severity could benefit deep-rooted vegetation in these downstream segments.

5.2 Management Implications

Since the hydrogeomorphic stream types characterize distinctive physical and biological environments throughout stream networks (Chapter 2), they provide a mechanistic basis for sample stratification in resource assessments and mapping. Resource managers can also make inferences on ecological processes and properties, based on the qualitative features of channel confinement, planform, and boundary materials. By identifying the hydrogeomorphic channel

type of a given stream reach, managers can infer the composition of riparian vegetation and seasonal water relations of large woody plants.

Differences in ecohydrological processes and riparian vegetation among stream types suggest differing sensitivities to disturbance and land use. Bedrock with alluvium and piedmont headwater streams are likely to be the most sensitive stream types to hydrological alterations from land use and infrastructure development. Plant ecophysiological functioning in these streams are tightly coupled to streamflow pulses, where seasonal variations in water availability and plant water stress are greatest (Chapter 3). Similarly, disturbance to vegetation in piedmont headwater streams will likely have long-lasting effects, since limited water availability in these channels could impair plant establishment (Chapter 4). Ecological impacts can be minimized by considering these ecohydrological dynamics when planning the location and types of land use.

5.3 Restoration Implications

The hydrogeomorphic stream types can be used to determine reference conditions for ephemeral stream restoration. Appropriate plant community composition and density (Chapter 2), as well as channel dimensions and hydraulic geometry, can be estimated from unimpacted reaches from the same stream type. This approach will provide realistic restoration targets, enhancing the likelihood of success.

Revegetation efforts will also be facilitated by understanding the limitations to woody plant establishment. Protection from herbivores and shading are critical requirements for tree seedling survival in the western Sonoran Desert (Chapter 4). Multiple approaches could be used to provide these conditions, ranging from shaded cages and tree shelters, to phased planting plans beginning with pioneer shrubs before tree seedlings. Plantings should consist of the largest seedlings possible, since they have the highest survival rates under all conditions. Supplemental irrigation is needed to maximize transplant survival under typical climatic conditions, but

logistical constraints and additional costs may limit the feasibility of this technique at remote or extensive sites. Revegetation projects during infrequent wet years are likely to be most effective.

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7.1 Designation of Plant Functional Groups

Table 7.1. Plant species and *a priori* plant functional groups. EGTR = evergreen tree; PSTR = photosynthetic stem tree; WDTR = winter deciduous tree; COCA = columnar cactus; EGSH = evergreen shrub; DDSH = drought deciduous shrub; PSSH = photosynthetic stem shrub; WDSH = winter deciduous shrub; CASH = shrubby cactus; EGSS = evergreen subshrub; DDSS = drought deciduous subshrub; PSSS = photosynthetic stem subshrub; WDSS = winter deciduous subshrub; CASS = low cactus; VINE = vine; HERB = herbaceous; GRAS = grass; PARA = epiphytic parasite. 1 = Baldwin et al. 2002; 2 = Chiang and Landrum 2009; 3 = Christie et al. 2006; 4 = Christy et al. 2003; 5 = Flora of North America Editorial Committee 1993+; 6 = Fryxell 1993; 7 = Kearny and Peebles 1960; 8 = Levin 1995; 9 = Mason 1999; 10 = Rhodes et al. 2011; 11 = Shreve and Wiggins 1964; 12 = Sundell 1994; 13 = Turner et al. 1995.

Species	Growth Form	Sources
<i>Acalypha californica</i> Benth.	DDSH	1,7,8,11
<i>Acacia constricta</i> Benth.	WDSH	7,11,13
<i>Acacia greggii</i> A. Gray	WDSH	1,7,11,13
<i>Adenophyllum porophylloides</i> (A. Gray) Strother	DDSS	1,5,11
<i>Ambrosia ambrosioides</i> (Cav.) W.W. Payne	EGSS	5,7,11,13
<i>Ambrosia deltoidea</i> (Torr.) W.W. Payne	DDSS	5,7,11,13
<i>Ambrosia dumosa</i> (A. Gray) Payne	DDSS	1,5,7,11,13
<i>Ambrosia salsola</i> (Torrey & A. Gray) Strother & B.G. Baldwin	DDSH	5,7,11,13
<i>Argythamnia lanceolata</i> (Müll. Arg.) Pax & K. Hoffmann	DDSS	1,11
<i>Aristida purpurea</i> Nutt.	GRAS	1,11
<i>Argythamnia serrata</i> (Torr.) Müll. Arg.	DDSS	1,7,11
<i>Ayenia microphylla</i> A. Gray	WDSS	11
<i>Bahiopsis parishii</i> (Greene) E.E. Schilling & Panero	DDSH	1,5,7,11,13
<i>Baccharis sarothroides</i> A. Gray	PSSH	1,5,7,11
<i>Bebbia juncea</i> var. <i>aspera</i> Greene	DDSH	1,5,11
<i>Brickellia coulteri</i> A. Gray	DDSS	7,11
<i>Carlowrightia arizonica</i> A. Gray	PSSS	1,5,7,11
<i>Calliandra eriophylla</i> Benth	WDSH	7,11,13
<i>Carnegiea gigantea</i> (Engelm.) Britton & Rose	COCA	1,5,11,13
<i>Celtis pallida</i> Torr.	EGSH	7,11,13
<i>Chilopsis linearis</i> (Cav.) Sweet	WDTR	1,7,11,13
<i>Colubrina californica</i> I.M. Johnston	WDSH	1,3,7,11,13
<i>Condalia globosa</i> var. <i>pubescens</i> I.M. Johnston	EGTR	7,11
<i>Cottisia gracilis</i> (A. Gray) W.R. Anderson	VINE	7,11
<i>Commicarpus scandens</i> (L.) Standl.	DDSS	7,11
<i>Cylindropuntia acanthocarpa</i> var. <i>coloradensis</i> (L.D. Benson) D.J.	CASH	5,11
Pinkava		
<i>Cylindropuntia ramosissima</i> (Engelm.) F.M. Knuth	CASH	1,5,7,11,13

<i>Daucus pusillus</i> Michx.	HERB	1
<i>Echinocactus polycephalus</i> Engelm. & J.M. Bigelow	CASS	1,5,11,13
<i>Encelia farinosa</i> A. Gray ex Torrey	DDSS	7,11,13
<i>Encelia frutescens</i> (A. Gray) A. Gray	DDSS	5,13
<i>Ephedra aspera</i> Engelm. ex S. Watson	PSSH	1,5,7,11,13
<i>Eriogonum inflatum</i> Torrey & Fremont	HERB	1,5,7,11
<i>Euphorbia polycarpa</i> var. <i>polycarpa</i>	HERB	1,5,7,11
<i>Fagonia laevis</i> Standley	DDSS	7,11
<i>Fagonia pachyacantha</i> Rydberg	DDSS	7,11
<i>Ferocactus cylindraceus</i> (Engelm.) Orcutt	CASH	1,5,11,13
<i>Fouquieria splendens</i> (Engelm.)	DDSH	1,7,9,11,13
<i>Heteropogon contortus</i> (L.) P. Beauvois ex Roem. & Schult.	GRAS	1,11
<i>Hibiscus denudatus</i> Bentham	DDSS	1,6,7,11
<i>Hilaria rigida</i> (Thurb.) Benth. ex Scribn.	GRAS	1,11,13
<i>Horsfordia newberryi</i> (S. Watson) A. Gray	EGSH	6,13
<i>Hyptis emoryi</i> Torrey	EGSH	1,4,7,11,13
<i>Justicia californica</i> (Bentham) D.N. Gibson	PSSH	1,5,7,11,13
<i>Krameria erecta</i> Willd. ex Schult.	PSSH	1,7,9,11
<i>Krameria grayi</i> Rose & Painter	PSSH	1,7,9,11
<i>Larrea tridentata</i> (Sesse & Moc. Ex DC.) Coville	EGSH	1,7,11,13
<i>Lycium andersonii</i> A. Gray	DDSH	1,2,7,11
<i>Lycium berlandieri</i> Dunal	DDSH	2,7,11
<i>Lycium fremontii</i> A. Gray	DDSH	1,2,7,11
<i>Lycium macrodon</i> A. Gray	DDSH	2,7,11
<i>Lycium parishii</i> A. Gray	DDSH	1,2,7,11
<i>Lycium torreyi</i> A. Gray	DDSH	1,2,7,11
<i>Mammillaria dioica</i> K. Brandegee	CASS	1,5,11
<i>Menodora scabra</i> A. Gray	DDSS	1,7,11
<i>Mirabilis laevis</i> var. <i>villosa</i> (Kellogg) Spellenberg	DDSS	1,5,7,11
<i>Muhlenbergia microsperma</i> (DC.) Kunth	GRAS	1,11
<i>Muhlenbergia porteri</i> Scribn. ex Beal	GRAS	1,11
<i>Olneya tesota</i> A. Gray	EGTR	1,7,11,13
<i>Opuntia basilaris</i> Englem. & J.M. Bigelow	CASS	11,13
<i>Opuntia echinocarpa</i> (Engelm. & Bigelow) F.M. Knuth	CASH	1,5,11
<i>Opuntia leptocaulis</i> (DC.) Knuth	CASH	5,11,13
<i>Parkinsonia florida</i> (Benth. ex A. Gray) S. Watson	PSTR	1,7,11,13
<i>Parkinsonia microphylla</i> (Torrey) Rose & I.M. Johnston	PSTR	1,7,11,13
<i>Peniocereus greggii</i> (Engelm.) Britton & Rose	CASS	11
<i>Penstemon parryi</i> (A. Gray) A. Gray	HERB	7,11
<i>Peucephyllum schottii</i> A. Gray	EGSH	1,5,7,11,13
<i>Phoradendron californicum</i> Nuttall	PARA	1,7,11,12
<i>Pleurocoronis pluriseta</i> (A. Gray) R.M. King & H.E. Robinson	DDSS	1,11
<i>Porophyllum gracile</i> Bentham	PSSS	1,5,7,11
<i>Prosopis velutina</i> Wooton	WDTR	7,11,13
<i>Psoralea spinosa</i> (A. Gray) Barneby	PSTR	1,7,10,11,13
<i>Sarcostemma cynanchoides</i> ssp <i>Hartwegii</i> (Vail) R. Holm	VINE	7,11,12

<i>Salazariia mexicana</i> Torrey	DDSS	7,11
<i>Sebastiania bilocularis</i> S. Watson	EGTR	7,11
<i>Senna covesii</i> (A. Gray) H.S. Irwin & Barneby	HERB	7,11
<i>Simmondsia chinensis</i> (Link) C.K. Schneider	EGSH	1,7,11,13
<i>Sphaeralcea ambigua</i> A. Gray	HERB	1,7,11
<i>Stephanomeria pauciflora</i> (Torr.) A. Nelson	DDSS	1,5,7,11
<i>Tetracoccus fasciculatus</i> var. <i>hallii</i> (Brandege) Dressler	DDSH	1,7,11
<i>Tiquilia canescens</i> (A. DC.) A.T. Richardson	EGSS	1,7,11
<i>Trixis californica</i> Kellogg	DDSH	1,7,11,13
<i>Tridens muticus</i> (Torr.) Nash	GRAS	1,11
<i>Xanthisma spinulosum</i> var. <i>gooddingii</i> (A. Nelson) D.R. Morgan & R.L. Hartman	DDSS	1,5,7,11
<i>Ziziphus obtusifolia</i> var. <i>canescens</i> (A. Gray) M.C. Johnston	PSSH	1,3,5,7,11,13
