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Structure and Function of Ephemeral Streams in the Arid and Semiarid Southwest: Implications for Conservation and Management

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14. ABSTRACT

This project's goal was to improve understanding of the hydroclimatic drivers of biotic communities and ecosystem processes in ephemeral stream channels as a basis for projecting response to regional climate change. Data were collected on stream hydrology, litter decomposition, nutrients, vegetation, seed banks, and ground-dwelling soil arthropods. Relationships between rainfall and stream flow permanence varied by stream flow type. Duration of flow and precipitation were decoupled for intermittent and semiperennial streams because of contributions from groundwater discharge and the vadose zone. Decomposition and nutrient release were tightly coupled to stream flow for the narrow band along the stream channel, but not for the associated riparian zone. Along the continuum from ephemeral to semiperennial stream flow, trade-offs were apparent between riparian plant biomass (high at wetter sites) and plant species diversity (high at dry sites with sparse canopy). Ground dwelling arthropods were strongly influenced by flow permanence, with effects being seasonally dynamic. The results demonstrate the need to conserve a variety of stream flow types to meet the sometimes mutually exclusive goals of high ecosystem productivity and high species richness. The many small, unnamed ephemeral streams in the piedmont of the Huachuca Mountains and Barry Goldwater Range have high conservation value.

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List of Acronyms

AI= Aridity index
AIC= Akaike information criterion
ANOVA= Analysis of variance
AWP= Annual water presence
ASF= Annual surface flow presence
C=Carbon
Ch= Channel
CPI= Cohort production interval
EC= Electrical conductivity
g= gram
LC= Lower canyon
MAP_{30}= 30-year mean annual precipitation
MAT= Mean annual temperature
mg= milligram
N= Nitrogen
P= Phosphorus
PD= Piedmont
R= Riparian
SOM= Soil organic matter
U= Upland
UC= Upper canyon
USGS= United States Geological Survey

Keywords

Arid and semiarid, climate change, decomposition, ephemeral stream, ground-dwelling arthropods, hydrology, infiltration, nutrient cycling, riparian vegetation, species diversity.

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Abstract

Objectives. The goal of this project was to improve understanding of the hydroclimatic drivers of biotic communities and ecosystem processes in ephemeral stream channels of southwestern United States as a basis for projecting response to the changing regional climate. Guiding questions were: (1) How do catchment attributes, precipitation, and position in the stream network predict duration of stream flow? (2) How do community structure and function vary: (i) across a climatic aridity gradient; (ii) among streams that differ in stream flow duration and presence of shallow groundwater; (iii) among channel, riparian, and upland positions; and (iv) between wet and dry seasons?

Technical Approach. A space-for-time substitution approach was followed in which changes across spatial water gradients are considered representative of anticipated changes in time under the climate change scenario of increased aridity. Sixteen stream sites were selected that spanned aridity zones (arid, semiarid, semihumid), stream flow permanence (ephemeral to perennial), and location within the stream network (piedmont, canyon, or alluvial basin). Electrical resistance sensors and USGS stream gauge data were used to quantify stream flow duration and stream water presence, and flow data and stream channel sediment data were used to estimate saturated hydraulic conductivity and potential annual infiltration. Groundwater monitoring wells were installed at streams in different landscape settings. Seasonal and annual variability in community composition and ecosystem processes were characterized via biannual sampling from 2010 to 2012. Data were collected on vegetation volume, above-ground herbaceous biomass, ground cover, and alpha species diversity. Soil seed banks were assessed with the seedling emergence method. Soil nutrient dynamics and release, among other standard soil physical and chemical characterizations, were assessed by measuring exchangeable nitrogen extracts and resins. Using grey oak (*Quercus grisea)* and Arizona sycamore (*Platanus wrightii)* litterbags, decomposition rates were assessed over an 18-month period. For arthropods, pitfall traps were set during dry and wet seasons in channel, riparian and upland locations in canyon and piedmont reaches to measure spatio-temporal variation in alpha- and beta-diversity. Monthly collections of arthropods were used to measure secondary production.

Results. Annual stream flow duration of the 16 stream sites ranged from widely, attributable to variation in precipitation, temperature, and stream density in the catchment. Five flow regimes were defined based on flow and water duration: dry-ephemeral, wet-ephemeral, dry intermittent, wet intermittent, and semiperennial. Relationships between magnitude and temporal distribution of rainfall and stream flow permanenance varied by stream flow type. Duration of flow and precipitation were decoupled for intermittent and semiperennial streams because of contributions from groundwater discharge and the vadose zone. By contrast, stream flow at ephemeral sites responded rapidly to rainfall and overland flow. Infiltration rate (except where flow was perennial) was directly related to duration of stream flow.

Riparian vegetation was influenced by stream flow duration and water table presence, seasonal rain and flood pulses, and direct effects of aridity. As aridity increased among the ephemeral stream sites, the riparian zone had increasingly less vegetation volume, fewer plant species, and greater relative abundance of woody (versus herbaceous) vegetation. Further, the riparian vegetation and the matrix vegetation became increasingly dissimilar. Deep-stored flood water, and direct precipitation, maintained the combination of trees and herbaceous plants, respectively, at ephemeral streams. Within the semihumid Huachuca Mountains, seasonal fluvial disturbance from the strong monsoonal floods increased evenness of the herbaceous vegetation. Of note, introduced Lehmann's lovegrass (*Eragrostis lehmanniana)* was dominant only in the uplands and not in the riparian zone of the Huachuca Mountain ephemeral streams.

Along the continuum from ephemeral to semiperennial stream flow, trade-offs were apparent between riparian forest biomass and plant species diversity. Woody plant biomass provides the main structure in riparian communities, and was linked with a shallow water table and high stream flow duration. Herbaceous plants provide most of the species diversity, and their response was decoupled from that of trees: herbaceous cover and richness *decreased* with stream flow duration (owing to light limitation) and, at sites with sparse tree cover, seasonally pulsed with monsoon rains and floods (and to a lesser extent with winter precipitation). Because herbaceous species were numerous, the net effect was a

decline in total plant species richness at the wetter sites. The numbers of species in soil seed banks showed an interaction between site elevation and aridity. For ephemeral streams, seed banks had increasingly more species as aridity decreased (and precipitation increased), similar to patterns shown by terrestrial vegetation. Soil seed bank species numbers in riparian zones of intermittent streams showed a reverse pattern, given that few herbaceous species were present in the densely canopied streams of the high elevation semihumid sampling areas.

Decomposition and nutrient release were tightly coupled to stream flow and water presence only for the narrow band immediately associated with the stream channel. Leaf decomposition rates were higher in channels than in riparian zones, and for the channel position, were higher in wet-intermittent and semiperennial sites than in those with less frequent flow. Cumulative days of soil-water presence emerged as a significant explanatory variable for rate of decomposition. Surprisingly, rate of decomposition did not differ between the riparian zone and adjacent upland, perhaps owing to regulation by precipitation. Nitrate availability and release were higher in the riparian and upland positions compared to channel positions and, in the channel position only, were highest at ephemeral sites.

The production and community composition of ground dwelling arthropods were strongly influenced by flow permanence, with effects being seasonally dynamic. Median secondary production was positively related to annual stream flow presence and was consistently high in the wetter stream sites (i.e., most canyon sites). Peak secondary production, however, was highest in the ephemeral streams (including piedmont settings) but was highly transitory, pulsing during the one to two month period following monsoon rainfall. Alpha-diversity and beta diversity (total turnover across the channel-upland transition) were related to annual water presence but varied by season (positive and asymptotic in dry season, negative in monsoon).

Benefits. This project's results show the need to conserve and protect a variety of stream flow types, in a variety of locations, to meet the multiple (and sometimes mutually exclusive) goals of maintaining high ecosystem productivity and high species richness. They also show that individually and collectively, the many small, unnamed ephemeral streams in the piedmont of the Huachuca Mountains and Barry Goldwater Range have high conservation value. Maintaining many small ephemeral washes across the landscape will help to maintain regional diversity and help to buffer upland taxa from periodic drought.

Understanding the ways, and rates, in which different water sources influence the structure and function of temporary streams will help managers interpret and anticipate ecosystem changes arising from regional climate shifts. Riparian zones are ecotones between terrestrial and aquatic zones, and are influenced by processes associated with each type of ecosystem. For ephemeral streams, structure and function is strongly regulated by terrestrial processes (e.g., precipitation) and many elements of the vegetation will shift rapidly in response to precipitation changes owing to their capacity to regenerate from soil seed banks. Structure and function of semiperennial streams, in contrast, are strongly regulated by aquatic processes (e.g., surface and subsurface water flows). Such sites will be slow to respond, given their dominance by long-lived riparian trees, but also will be buffered from rapid hydrologic change owing to the slower movement of riparian water sources through the hydroclimatic system.

One anticipated consequences of climate change is more intense storms, hence increased scour of vegetation. The soil seed bank results have implications for management actions that focus on restoration of plant communities following disruption from events such as scouring floods, given that donor soils can be an effective restoration tool for restoring small-seeded, herbaceous plant species to depauperate sites.

Finally, the results highlight the need to document, map, name, and protect the many ephemeral channels and associated riparian zones on the piedmont of the mountains in semiarid and semihumid areas of the Arizona Sky Islands (including the Huachuca Mountains). These stream ecosystems are narrow and easily overlooked on drainage maps and in the field, given their similarity in vegetation structure to adjacent uplands. Despite this apparent structural similarity, they contribute disproportionately to ecosystem processes including decomposition of organic matter and to ecosystem structure by supporting diverse communities of plants and arthropods.

Chapter 1: Objectives

Our primary objective was to address the need for additional information on the structure and function of ephemeral streams on Department of Defense lands in dryland regions, as these streams cover larger area but remain poorly understood. A related goal was to speculate as to how these systems would change in response to predicted increases in aridity and storm intensification associated with regional climate change. Goals, by sub-group, were:

Stream hydrology

- Determine to what extent frequency of stream flow in temporary streams in arid and semi-arid regions varies with climate and landscape characteristics
- Classify streams based on their flow permanence
- Quantify rates of potential annual infiltration of ephemeral and intermittent streams in arid and semi-arid regions

Climate and vegetation

- Determine how ephemeral stream vegetation will change in biomass, life form, species richness, composition, and annual variability in richness as aridity increases
- Determine how the degree of similarity between riparian and upland plant communities will change with increasing aridity
- Identify plant species that are restricted to, or more abundant in, ephemeral streams than in the matrix vegetation (e.g., surrounding uplands)

Stream flow and riparian vegetation

- Determine how plant species richness and plant biomass change spatially and seasonally along gradients of stream flow permanence, depth to water table, and drainage basin size
- Determine if patterns of overstory (woody) and understory (herbaceous) vegetation vary in tandem along hydrological gradients
- Identify controls on seasonal and annual variation of plant species diversity
- Identify site conditions producing greatest levels of plant species richness and biomass

Aridity, stream flow regime, and riparian soil seed banks

- Determine whether patterns of variation of soil seed bank communities along an aridity/elevation gradient differ between ephemeral and perennial streams
- Determine if soil seed bank communities are more similar between riparian and upland zones in arid versus less arid climates
- Determine if riparian soil seed banks have utility as an ecosystem restoration tool for a range of stream types

Stream flow regime and ground-dwelling arthropods

-Determine how patterns of α- and β-diversity of ground-dwelling arthropods change spatially and seasonally along gradients of stream flow permanence
- Quantify the relationship between stream flow permanence and the biomass and productivity of ground-dwelling terrestrial macroinvertebrates
- Determine the extent of spatio-temporal variation in biomass and secondary production within and across sites

Nutrient and litter cycling

- Determine rates of litter decomposition among ephemeral, intermittent and perennial streams in Arizona and channel, riparian and upland positions associated with these streams.
-Evaluate the consequence of differences in stream flow permanence and seasonality for nutrient release and cycling.

Chapter 2: Background

Ephemeral to intermittent stream flow is the dominant flow regime in dryland regions and is likely to increase in distribution under a changing climate (Seager et al. 2010; Larned et al. 2010; Doll and Schmied 2012). In southwestern USA (Arizona, New Mexico, Nevada, Utah, Colorado and California), for example, over 80 percent of streams flow only in response to rainfall and/or shortly thereafter (USGS 2006; Levick et al 2008). These temporary streams (*sensu* Larned et al. 2010) provide many critical watershed and ecosystem functions yet remain poorly understood and characterized. Increasingly, however, attention is being paid to the processes that sustain stream flow (Reynolds at al. 2015), to the cycling of carbon and nitrogen under varying stream flow conditions, and to the linkages between stream hydrology and riparian vegetation, insect life and bird life in dryland regions (Brand et al. 2008; Stromberg et al. 2009; Katz et al. 2012; McCluney and Sabo 2012).

The hydrology and biota of riparian ecosystems are changing in response to climate shifts, with effects varying by region and by stream type (Palmer et al. 2008). In western USA, regional warming is causing snow-melt dominated rivers to have earlier flood peaks, increased winter flows, and reduced summer flows (Barnett et al. 2008; Rood et al. 2008). For rivers sustained by rainfall runoff and regional groundwater inflow, regional warming is causing evaporation rates to increase and stream recharge rates to decrease, and thus producing declines in stream base flows and water tables (Serrat-Capdevila et al. 2007; Ajami et al. 2012). As aridity increases in the American Southwest (Seager et al. 2007) there likely will be increases in the extent of river segments with ephemeral flow and decreases in those with perennial flow, as well as increases in flood intensity. These changes have implications for changes in structure and function of riparian biota (Stromberg et al. 2010) (Fig. 2.1). Given projections of transitions from perennial to intermittent flow, and intermittent to ephemeral flow under a changing climate (Seager et al. 2013), understanding linkages between the abiotic and biotic components of ecosystems are a critical starting point for predicting the trajectory of changes in ecosystem functions and associated services.

Stream Hydrology

Stream flow is predominantly temporary in water limited such as the Western United States (Meinzer 1923; Newman et al. 2006). These brief stream flow episodes have a profound effect on ecohydrological processes (Blasch et al. 2010; Jaeger and Olden 2012) and groundwater recharge (Constantz 1982; Blasch et al. 2006; Callegary et al. 2007; Cataldo et al. 2010). Despite the importance of temporary surface waters to biological processes and water resources, fundamental traits such as the frequency and temporal distribution of stream flow remains poorly quantified for most dryland streams.

Stream flow in the arid and semi-arid Southwest occurs in response to spatially heterogeneous convective summer precipitation (The North American Monsoon), protracted and widespread winter precipitation, dissipating tropical storms, snowmelt and groundwater discharge (Goodrich et al. 2004; Baillie et al. 2007). Stream channels in this region are areas of focused infiltration and subsequent recharge (Coes and Pool 2007) resulting in significant stream flow losses (Goodrich et al. 2004). Evapotranspirative fluxes can alter water redistribution (Leenhouts et al. 2006; Scott et al. 2008). As a result of the coupling between precipitation patterns, channel infiltration losses, and high evapotranspirative fluxes, stream flow regimes can be temporally variable and have a high degree of intermittency in these water limited regions.

Stream flow patterns in water limited systems are influenced by differences in partitioning of precipitation within catchment drainage networks (Leenhouts et al. 2006; Biederman et al. 2014). Hydrologic conceptual models developed in the arid and semi-arid Southwest indicate that stream flow may transition from perennial in mountain headwater streams to intermittent in the mountain fronts and alluvial basins owing to stream channel infiltration losses (Tillman et al. 2011). Hydrologic discontinuities result in more pronounced stream flow intermittency at lower elevations (Blasch et al. 2002; Jaeger and Olden 2012). In addition, geochemical studies show differential partitioning of winter and summer precipitation to infiltration and subsequent recharge (Eastoe et al. 2004; Baillie et al. 2007; Ajami et al. 2011). For example, Wahi et al. (2008) note that in the Huachuca Mountains of southern Arizona, high elevations springs are comprised of a greater fraction of winter precipitation than lower elevation shallow riparian waters, which are comprised of a greater fraction of summer rainfall.

Mountain-system recharge, or recharge that occurs due to percolation along rock fractures and faults (mountain block) in the mountain front, is considered to be the main groundwater recharge mechanism in semi-arid systems (Wahi et al. 2008). In these systems, water losses to infiltration along intermittent stream reaches, exclusive of mountain-connected streams, may account for 12 to 19 percent of recharge in some basins (Coes and Pool 2007). At a localized scale, intermittent stream recharge can contribute as much 85 percent to shallow riparian groundwater during the summer rainfall season (Baillie et al. 2007). However, stream channel recharge estimates in intermittent systems can be constrained by the scarcity of stream flow and stream water presence measurements. An extensive body of literature has addressed intermittent stream infiltration and recharge in arid and semi-arid systems using geochemical studies, water balance approaches, in-situ infiltrometers, and thermal monitoring and modeling approaches (Besbes et al. 1978; Heath 1983; Sorman and Abdulrazzak 1993; Constantz et al. 2003; Dowman et al. 2003; Goodrich et al. 2004; Coes and Pool 2005; Blasch et al. 2006; Callegary et al. 2007; Cataldo et al. 2010). However, the temporal dynamics of intermittent stream flow, a major control on potential infiltration, remain to be explicitly quantified.

Riparian Vegetation

Although many parts of the world are becoming warmer and wetter, several arid and semiarid regions are becoming warmer and drier (Seager et al. 2007; Vicente et al. 2012). Analyses of long-term data sets from the American Southwest have revealed upward elevational range shifts for many plant taxa (Brusca et al. 2013), documented drought-related declines in desert shrub abundance (Bowers 2005), and identified the season (i.e., winter vs. summer) in which precipitation deficits will cause the greatest mortality (McAuliffe and Hamerlynck 2010; Munson et al. 2013). Analyses of vegetation patterns along spatial aridity gradients reveal decreases in above and below ground biomass, declines in species richness, and shifts in plant growth form (Schultze et al. 1996; Munson et al. 2013; Ulrich et al. 2014), changes that presumably will occur through time.

The networks of streams that drain arid and semiarid uplands also will be altered as aridity increases. Riparian vegetation of these streams will be affected by direct changes in temperature and precipitation, and by the indirect effects of these factors on stream flows (Perry et al. 2012; Garssen et al. 2014). Many ephemeral streams support drought-adapted shrubs and small trees referred to as xeroriparian scrub (Johnson et al. 1984; Nilsen et al. 1984; Leitner 1987; Atchley et al. 1999; de Soyza et al. 2004; Hardy et al. 2004). If the vegetation has high compositional overlap with surrounding desert vegetation, it may respond in similar fashion to upland vegetation in response to increased aridity (i.e., show a terrestrial type response).

However, the response of ephemeral stream riparian vegetation to climate change remains poorly understood.

Throughout the world, freshwater ecosystems are undergoing loss of species owing in part to alteration of stream flows (Arthington et al. 2010). Maintaining high biodiversity, inclusive of species richness, is a common goal for resource managers (Angermeier and Karr 1994). In dryland regions, species richness can be limited by low resources, such as reduced stream flow, although relationships between productivity and richness are complex (Huston 2014). As streams change from perennial to intermittent, riparian vegetation will transition from tall, broad-leaf riparian forests to shorter-statured and smaller-leaved shrubs, and from herbaceous perennials to annual species (Stromberg et al. 2010; Seager et al. 2013). Plant species richness initially will increase as flow becomes intermittent, and then decline to lowest levels as flow becomes ephemeral, consistent with the intermediate productivity hypothesis (Stromberg et al. 2009; Katz et al. 2012; Huston 2014). Although case studies in the American Southwest have indicated that plant species richness peaks at streams with intermittent flow (versus perennial or ephemeral flow), more studies are needed to determine the robustness of this hypothesis.

To gain a comprehensive understanding of vegetation response to changing environmental conditions, it is critical to understand how different plant growth form responds to changes in stream flow regimes. In semiarid uplands, tall woody plants utilize deep stored rain water and perennial grasses utilize near-surface rain water, according to the "two-layer pulse reserve" hypothesis (Walker 1971; Noi-Meyer 1983; but see Ogle and Reynolds 2004 and Reynolds et al. 2004). Riparian vegetation also is vertically stratified, with distinct canopy layers. Many riparian zones have a tall canopy of deep-rooted phreatophytes that have year-round access to a shallow water table, a mid-height shrub layers, and an herbaceous layer composed largely of shallow-rooted responders to rains and floods (Scott et al. 2003; Bagstad et al. 2005; Stromberg et al. 2013). These different structural layers have different functional roles (for example, tall trees can provide habitat for insect-gleaning birds whereas grasses and forbs sustain seed-eating birds) and can be temporally decoupled with respect to the factors that regulate plant growth (Sagers and Lyon 1997; Lyons and Sagers 1998; Snyder et al. 2002; Salinas and Casas 2007).

Studies in dryland regions have documented a decoupled response of the trees and herbaceous species to environmental factors, with the former typically responding to water table conditions and the latter to light, rain and flood pulses, or soil texture. In a dry to subhumid montane region of Spain, for example, riparian zone tree species richness was positively related to stream discharge, whereas herbaceous species richness was related to riverbed sediment grain size (Bruno et al. 2014). In dry, saline river basins of Mediterranean Spain, woody richness and cover increased with stream flow permanence, or hydroperiod, whereas herbaceous richness and cover either did not vary with hydroperiod or showed a tendency to *increase* at the drier sites (Salinas and Casas 2007). In a sand-bed basin stream of semiarid southern Arizona, woody species richness increased with stream flow permanence (a factor strongly correlated with depth to water table), whereas herbaceous response varied with different factors in wet and dry years (Lite et al. 2005). Clearly, additional studies are needed to disentangle the many factors that influence riparian plant species richness and composition.

Riparian Soil Seed Banks

Plants have various reproductive strategies to persist in environments that have temporally varying resources (Chesson et al. 2004). Plants that have a long life span and disperse their seeds yearly, including shrubs and trees, are characterized as endurers. Many others,

including annual plants and short-lived perennials, are storers that retain diaspores in the environment via a “bank”. A soil seed bank is made up of the viable seeds in the soil and leaf litter and is a collection of ungerminated seeds that have the potential to replace adults as they die (Leck et al. 1989).

The deserts of the American Southwest have distinctive seasonal rainfall, and their rivers have distinctive seasonal stream flow patterns (Sheppard et al 2002). Seasonality of flows is known to affect many attributes of riparian plant communities (Greet et al. 2014), but the extent to which flow presence interacts with temperature to regulate riparian seed germination is poorly known (Wolden et al. 1994; Kehr et al. 2014). Germination ecology is well understood for many riparian trees, with some being vernally adapted and others affiliated with warm summer conditions (Cox et al. 1993; Young and Clements 2003; Stelle et al. 2006). Few studies, however, have addressed the factors that trigger germination of the many annual and herbaceous perennial plants present in desert riparian ecosystems.

In the deserts of the Southwest, there are distinctive suites of seed-banking annual plants. Some are adapted to germinate during winter rains (cool-season plants), some germinate during summer rains (warm-season plants), and others are season-indeterminate (Went 1949; Freas and Kemp 1983). If riparian zones of ephemeral streams of desert regions have high overlap with the surrounding desert, one would expect a high degree of similarity in seasonal germination patterns for both zones (with both influenced by terrestrial processes). The seed banks of riparian zones of perennial desert streams, in contrast, consist of a mix of facultative riparian species and obligate riparian plants (Richter and Stromberg 2005; Stromberg and Boudell 2008; Stromberg and Boudell 2013). Given the presence of year-round moisture, plant germination patterns may be decoupled from seasonal rain patterns.

The hydroclimate in the American West is changing. The region is becoming warmer, the intensity of El Niño- associated winter storms is increasing, and the timing of stream flows is changing (Garfin and Lenart 2007; Rood et al. 2008; Dominguez et al. 2012). These changes will influence the vegetation of desert rivers in part by influencing germination of seed stored in the soil seed banks.

Arthropod Diversity and Stream Flow Regimes

Ecologists and conservation biologists have long been interested in riparian areas due to the perception that riparian zones are biodiversity hotspots (Naiman et al. 1993). More recent research has suggested that this generalization is not always accurate, and in fact upland zones may harbor more species than riparian zones in some cases (Burnham 2002; Sabo et al. 2005; Stromberg 2007; Suazo-Ortuño et al. 2010; Soykan et al. 2012). As a result, comparisons of the number of species in riparian and upland zones (α-diversity) and the turnover in species between habitats (β-diversity) have been of great interests to ecologists and conservation biologists (Sabo et al. 2005). Although no clear pattern of α-diversity between riparian and upland zones exists, species turnover between these two habitats is extremely high such that riparian zones support unique species that are not found in the surrounding uplands (Sabo et al. 2005; Sabo & Soykan 2006; Soykan et al. 2012). However, these relationships have primarily been assessed in perennial streams. Intermittent and ephemeral streams comprise the majority of stream channels in a given landscape, and they often harbor different riparian species than comparable perennial reaches (Stromberg et al. 2009; McCluney & Sabo 2012). The rarity of flows in ephemeral channels may make them more similar to the surrounding uplands, but on the other hand these seasonal pulses of water and increased proximity to the water table may have important effects on their riparian zones.

Seasonal diversity patterns noted by some authors (e.g., Stromberg 2007; Suazo-Ortuño et al. 2010) may be related to seasonal precipitation patterns which influence stream flow regimes. Variation in flow regime can cause both seasonal and spatial patterns in the diversity of a number of riparian taxa (e.g., Brand et al. 2008; Stromberg et al. 2009; McCluney & Sabo 2012), but in some cases has no effect on diversity (e.g., Hinojosa-Huerta et al. 2013; Corti & Datry 2014). These effects are complicated because the response of one group of organisms is likely to depend on the response of others (e.g., Brand et al. 2011; Hinojosa-Huerta et al. 2013). Further, functional groups within a single taxon (e.g., birds) may respond differentially to differences in flow regime; riparian obligates may avoid riparian areas adjacent to dry streams whereas other species may colonize such a habitat (Brand et al., 2011). As a result, variation in flow regime may be responsible for causing spatial variation in riparian-upland diversity gradients, but other factors may confound this relationship.

Secondary Production of Terrestrial Macroinvertebrates and Stream Flows

Arid lands of the Southwestern United States are characterized by low precipitation and high evapotranspiration and thus water is an important limiting resource (Noy-Meir 1973). Empirical work from deserts suggests that water may be more important than energy in driving trophic interactions and that animals in dry conditions make foraging decisions based on water needs rather than energy needs (McCluney and Sabo 2009). In arid and semiarid regions, streams are a valuable source of water that support a wide range of fauna that vary from surface water-dependent to ground-water dependent consumers (Bonada et al. 2007; Tsai et al. 2007; Shaw and Cooper 2008).

Despite their abundance and ecological importance, little is known about the relationship between non-perennial streams and the riparian biota that depend on them. For example, there is a need for better understanding of how the seasonal variability of stream flow in montane Southwestern ecosystems affects the production of invertebrate biomass in stream channels and the adjacent riparian areas (Datry et al. 2014). Studying the effects of stream flow on primary consumers and their predators will provide a link between flow permanence and higher trophic levels in the riparian environment (Smith et al. 2006).

Nutrient Cycling and Decomposition

Dryland regions encompass over 40 percent of the terrestrial land surface (Millenium Ecosystem Assessment 2005) and are likely to increase in distribution under a changing climate (Seager et al. 2010; Larned et al. 2010; Doll and Schmied 2012) and with increasing human appropriation (Postel et al. 1996; Alley et al. 2002). Despite their hydrologic importance in surface and subsurface water storage and exchange (Lane 1983; Renard et al. 1993; Goodrich et al. 1997; Goodrich et al. 2004), connectivity and continuity (Jaeger and Olden 2012; Jaeger et al. 2014) and ground-water recharge and discharge (Scanlon and Goldsmith 1997; Scanlon et al. 1999 & 2003; Scott et al. 2000; Walvoord et al. 2002a & 2002b; Heilweil et al. 2004), key ecological functions in ephemeral and intermittent stream remain poorly understood and characterized (Datry et al. 2014; Larned et al. 2010).

In particular, little is known about how changes in the frequency and duration of stream flow or water presence associated with ephemeral and intermittent streams will influence organic matter and nutrient dynamics and their controls. Moreover, little is known about how organic matter processing differs across areas physically associated with the ephemeral to intermittent stream channels such as the floodplain or riparian zones and uplands (Langhans et al. 2008). Given projections of transitions in duration of stream flow (Seager et al. 2013), understanding

how key carbon and nitrogen processes are likely to change with temporary stream flow and associated position in the landscape will be critical to predict the trajectory of ecosystem functions and services associated with these streams and surrounding environments.

Decomposition of terrestrially derived organic matter or litterfall is often the main source of energy (carbon) to headwater streams (Tank et al. 2010) and also the primary pathway for nutrients to return to soil. It is also considered a key indicator of stream integrity and ecosystem functioning (Bruns et al. 1991; Young et al. 2008). Several studies have focused on the impacts of droughts or flood duration on decomposition in perennial streams (Anderson et al. 2006; Sangiorgio et al. 2006; Langhans and Tockner 2006; Tank et al. 2010). The few studies in intermittent streams have focused on short-term (<40 day) decomposition dynamics and on processes occurring during the aquatic phase, such as microbial film establishment (Schade and Fisher 1997; Daltry et al. 2011; Dieter et al. 2011). In perennial streams, the primary controls on decomposition are considered to be the chemical and physical properties of the organic matter (litter quality), the detritivores present (e.g., invertebrates and fungi), and stream temperature and nutrient concentration (Webster and Benfield 1986; Tank et al. 2010). As a stream transitions from a perennial to intermittent and even ephemeral flow regime, an ecologically significant terrestrial phase in the stream channel and surrounding environment will likely start to exert influence. Abiotic processes such as frequency and duration of stream flow and drying and wetting cycles, as well as factors important in arid region uplands such as soil movement and UV radiation, may become more important in controlling rates decomposition (Austin and Vivanco 2006, Throop and Archer 2007, Barnes et al. 2012, Barnes et al. 2015). Thus, the relative importance of abiotic and biotic controls on decomposition may tip back and forth with changes in the terrestrial and aquatic phase of the stream flow regime. A shift towards ephemeral stream flow may ultimately push these systems beyond a threshold such that the terrestrial state and controls dominate.

For all of the processes discussed above, there is a need to scale up from the site level to the landscape level. Riparian and aquatic field biologists capture a high level of detail with their measurements and observations, and there is a need to scale-up from observations made at reach-scales to the catchment-scale (Thorp 2014).

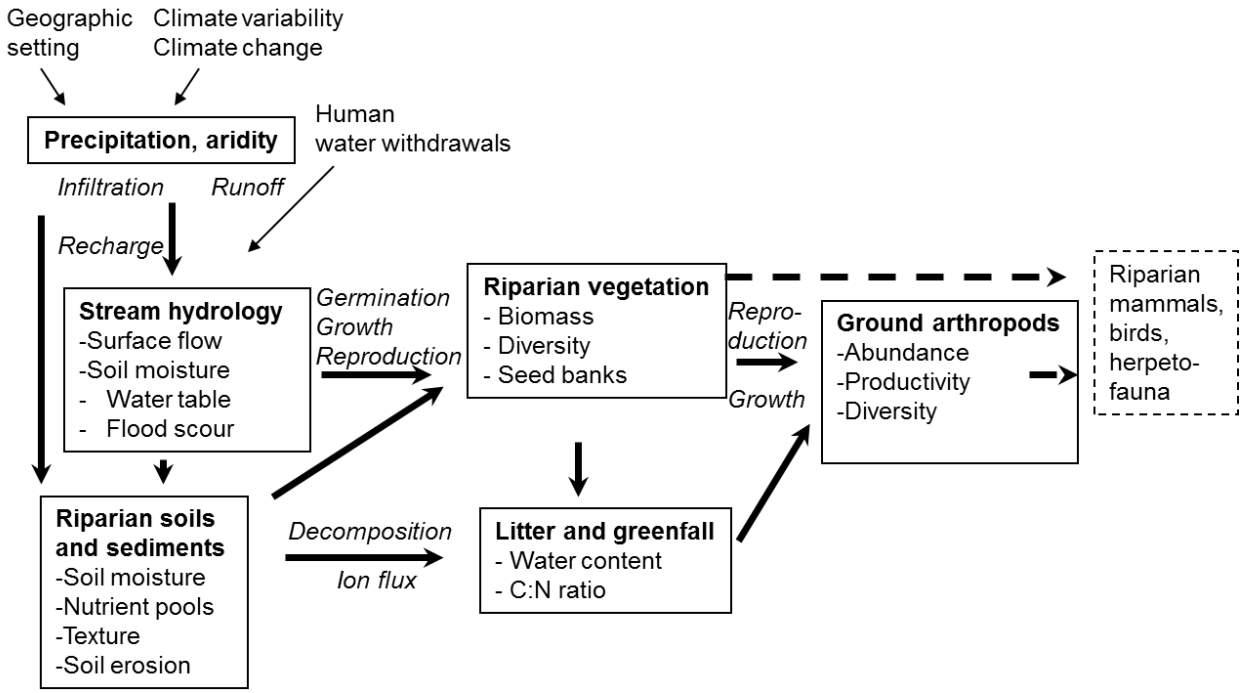

Fig. 2.1. Conceptual model of processes influencing riparian biota of temporary streams.

Chapter 3: Materials and Methods

Study Area and Study Sites

In the American Southwest, temporary streams vary regionally among areas with arid to subhumid climates, winter-dominant versus summer-dominant precipitation, and topography and watershed size (Warren and Anderson 1985; Gutierrez-Jurado et al. 2013). We selected 15 temporarily wet stream channels in southern Arizona that span three aridity zones and a range of geomorphic conditions (Fig. 3.1, Table 3.1).We calculated aridity using the de Martonne Aridity Index (mean annual precipitation in mm divided by mean annual temperature in ^{o}C plus a constant of 10) (Quan et al. 2013). In this system, a value of less than five is arid, five to 10 is semiarid, 10 to 20 is semihumid, 20 to 30 is humid, and greater than 30 is perhumid. Precipitation across the region is bimodal. Summertime convective rainfall (the North American Monsoon) is intense, of short duration, spatially heterogeneous and lasts from mid-late June to mid-late September. A second precipitation period is observed primarily between December and March with rainfall of lower intensity and longer duration arising from widespread storm systems.

The streams are located in largely undisturbed military facilities, long term ecological research areas, and a nature preserve (Table 3.1). At each study stream we selected a monitoring reach 200 m in length. The catchment upstream of each monitoring reach was delineated and characterized using ArcMap 10.2 (ESRI, Redlands, CA). The arid study washes, Black Gap (BGA) and Sauceda Wash (SWA), are located within the Barry M. Goldwater Air Force Range near Gila Bend, Arizona in the Lower Gila River Basin on semi-consolidated alluvial basin fans at 324 and 258 m in elevation, respectively. Both have catchments primarily composed of dacite and sand. The catchment upstream of the BGA reach is 10.2 km^2 and ranges in elevation from 324 to 676. The 30 year mean annual precipitation (MAP_{30}) at these sites ranges between 160 mm at the lower elevations and 250 mm at the higher elevations (https://climatedataguide.ucar.edu/climate-data/prism-high-resolution-spatial-climate-data-united-states-maxmin-temp-dewpoint). Mean annual temperature (MAT) is 23°C and can range between 5°C to 43°C (US Climate Data; http://www.ncdc.noaa.gov/).

Two semiarid study streams are located on the Santa Rita Experimental Range near Sahuarita, Arizona in the Santa Cruz River Basin (SSA and SRA). These are center-of-basin braided unconsolidated sandy channels 947 and 952 m in elevation. The catchment upstream of SSA is 1.7 km^2 and ranges in elevation from 947 to 1105 m, whereas the catchment upstream of SRA is 18 km^2 and ranges in elevation from 952 to 1748 m. The MAP_{30} ranges between 350 mm at the lower elevations and 570 mm at the higher elevations (PRISM, 2013); MAT is 22°C and can range between 6°C and 38°C.

Nine sites are located on the Huachuca Mountains near Sierra Vista, Arizona within the San Pedro River Basin. The Huachuca Mountains are within the Madrean Archipelago of the EPA Ecoregion Level III classification. This region is referred to as the Sky Islands because of the many water-catching mountain “islands” that are separated by desert and grassland “seas”. This ecoregion has high floristic diversity owing to the convergence of multiple floristic provinces. The Huachuca Mountains, in particular, are noteworthy for supporting many plant species (Bowers and McLaughlin 1996) although woody species in the region are not unusually abundant (Poulos et al. 2007). The Huachuca Mountains rise 2800 m above sea level (Bogan et al. 2013) and the higher altitudes of the mountain range support oak and pine forests, whereas lower altitudes support grasslands and desert mesquite scrub (Poulos et al. 2007). The seasonality of precipitation in the Huachucas is highly bimodal, with a peak between July and

September during the summer Monsoon and another peak between November and April during the winter wet season. The average rainfall across the region is 350 mm but with considerable spatiotemporal variation (Ballie et. al 2007; Bogan et al. 2013).

Six of the Huachuca sites were distributed among three canyon streams that have spatial variation in surface flow over their length. Huachuca and Garden Canyon are on Fort Huachuca, managed by the U.S. Department of Defense, and Ramsey Canyon is in a Nature Conservancy Preserve. Half of the sites were in lower canyon positions and half were farther upstream. The remaining three sites were along streams on the piedmont that appeared to be disconnected from the mountain canyon systems. Two of the piedmont streams were on Fort Huachuca; the other was on Coronado National Forest land.

The lowest elevation Huachuca sites (HP, GP, RP) are piedmont semi-consolidated alluvial channels at 1453-1533 m in elevation and have MAP_{30} ranging from 430 mm to 580 mm. The HP, GP and RP catchments are the smallest (1.3, 0.5 and 0.3 km^2, respectively), and have stream channel densities similar to those of the alluvial basin sites with values ranging between 2.4 and 6.3 km km^{-2}. The three lower canyon sites (HL, GL, RL) range between 1539 and 1592 m in elevation and are incised streams with non-cohesive alluvial banks; MAP_{30} ranges between 520 to 650 mm. Finally, the three upper canyon sites (HU, GU, RU) are located at 1582 to 1726 m in elevation and are on cohesive bedrock with moderate alluvium present. These sites have MAP_{30} ranging from 590 to 750 mm.

Precipitation and Stream Flow

We obtained monthly precipitation from the nearest tipping bucket gauge available to each monitoring reach. For sites in the Barry M. Goldwater Air force range we used precipitation data from the Maricopa Alert System Gauge #6923 at Sauceda Wash (http://alert.fcd.maricopa.gov/alert/Flow/6923.htm). For sites in the Santa Rita Experimental Range we used data from long term research station monitoring tipping bucket rain gauges (http://ag.arizona.edu/SRER/data.html). For sites in the Huachuca Mountains we used National Weather Service data processed and provided by Lainie Levick and Russ Scott from the USDA-ARS-SWRC in Tucson, AZ (personal communication).

At each reach, we established three cross-sectional transects 100 m apart and characterized the channel geometry, including channel slope using GPS and differential surveying. Survey data were processed using winXPRO (Hardy et al. 2005). We installed electrical resistance sensors (TidbiT v2 UTBI-001 data logger, Onset Corporation, Bourne, MA) at the thalweg of each cross-sectional transect to identify surface water presence frequency and duration, with the exception of the high elevation Ramsey Canyon site (RU), which is classified as a sensitive area. The electrical resistance sensors were temperature sensors modified as outlined in Blasch et al. (2002), with two electrical leads exposed; we followed the method outlined by Jaeger and Olden (2012) to identify the onset and cessation of runoff. In brief, the onset of runoff is marked by the sudden and rapid increase in the relative electrical conductivity (EC) signal to a less negative or a positive number, whereas the termination of stream flow is also marked by a similarly sudden shift in the EC signal back to a more negative signal (Fig. 3.2). In this study, EC = -94 indicates dry conditions. The sensors logged an EC signal every 10 minutes. We quantified the percent of stream flow at each monitoring transect (stream $flow_{transect}$) as follows:

$$\text{stream flow}_{transect} = \sum_0^t \frac{n_{streamflow}}{n_{total}} \times 100$$

(1) where $n_{stream\ flow}$ is the number of "stream flow" signals, or instances of sudden and clear shift in EC to a more positive number indicative of stream flow as illustrated in Fig. 3.2 over a period of time t, and n_{total} is the total number of EC observations made during that same time period. The site % stream flow was estimated by averaging the % stream flow$_{transect}$ for each stream reach.

We were able to quantify the duration of surface water presence as moist soil or ponded water because the EC signal for runoff is distinct from that of a moist soil and soil-drying conditions (Blasch et al. 2002; Jaeger and Olden 2012). In contrast to the stream flow presence signal, the surface water presence signal has a distinct inflection point that marks a shift from a steep EC signal recession to a less steep EC signal recession (Fig. 3.2). We quantified the % surface water presence at each transect (% water presence$_{transect}$) as:

$$\text{water presence}_{transect} = \sum_0^t \frac{n_{water_presence}}{n_{total}} \times 100$$

(2) where $n_{water_presence}$ is the number of "surface water presence" signals, or instances of sudden and clear shift in EC from stream flow to a water ponding or soil drying signal. Because it is difficult to distinguish EC signals indicative of water ponding from soil moisture presence, here we define all EC signals indicative of water presence, including stream flow, as "water presence". We were interested in identifying maximum length of time that water might be present in the stream either as ponded water, shallow soil water, or stream flow available for biological activity, therefore we used the maximum % water presence$_{transect}$ observed at each monitoring reach as the reach % water presence.

To complement our data set, we coupled our monitoring data to USGS data (http://waterdata.usgs.gov) from three discharge (Q) gauges- #09471310, #09470800 and #09470750 located in Upper Huachuca Canyon, Upper Garden Canyon, and Upper Ramsey Canyon, respectively. The gauges are near the upper canyon reaches (HU, GU and RU) and their catchments are similar in elevation, size, and stream channel density. We treated data from USGS gauges in a similar manner where if the instantaneous discharge (Q, liters per second) > threshold, then signal = "stream flow". Because stream gauge data can be noisy at low Q, we used stage-discharge curves generated using the published USGS data http://waterdata.usgs.gov) to determine "noise" threshold where Q < 0.3 liters per second = "no flow". Here we assumed that surface water presence was at minimum the same as stream flow presence for all USGS gauges. Finally, we estimated the ratio of percent annual water presence to percent annual stream flow (AWP:ASF).

Statistical analyses were performed using JMP 10 (Cary, NC; SAS Institute Inc.). We used non-standardized Wards Clustering Analyses (Tan et al. 2006; Sall et al. 2012) on percent annual stream flow and percent annual water presence to identify statistically distinct ($p < 0.05$) groups of sites with similar stream flow and water presence responses or regimes. Clusters with a Euclidian vector length greater than 0.93 were retained for further analyses. We used Wilcoxon non-parametric comparison of means and linear regression models (Zar 1999) to identify differences in surface water presence, infiltration rates, and infiltration volumes of each stream type, and to identify differences in relationships between percent stream flow and precipitation during the monitoring period and between seasons. We define seasons as: Spring (April 1 to June 30), Summer (July 1 to September 30), Fall (October 1 to December 31), and Winter (January 1 to March 31).

Infiltration

We collected triplicate channel sediment samples from 0 to 10 cm depth to determine bulk density and substrate texture at each monitoring transect. We used the pipette method for particle size analyses to determine percent sand, silt, and clay (Day 1965) and soil texture of the channel sediments; and a modified cavity method to estimate bulk density in g cc^{-1} (Grossman and Reinsch 2002) using an eight cm cavity diameter. The bulk density samples were sieved to remove particles greater than two mm, and were not treated to remove organic carbon or carbonates. We used bulk density and soil texture to estimate the saturated hydraulic conductivity (K_{sat}) of the bed sediment at each monitoring transect using Rosetta pedotransfer functions (Schaap 1999). We estimated the infiltration depth, *I*, over time t as follows:

$$I = K_{sat} * (1\text{-}rvf) * t_{sf}$$

(3) Where (*1-rvf*) is the volume of the soil sample, including the rock and void volume normalized to 1, minus the rock volume fraction; and t_{sf} is the duration of stream flow estimated using the EC sensors over a period of time t. We estimated the total catchment potential infiltration ($I_{catchment}$) by multiplying the infiltration depth by the total catchment stream channel length and the channel width. We repeated this process for every monitoring transect so that for each catchment we had 3 distinct estimates of $I_{catchment}$. Our infiltration estimates assume that every stream flow event the entire stream channel contributed to infiltration and that the stream geometry remained constant during the study period. We estimated the fraction of the catchment that is comprised of stream channels and that can contribute to infiltration ($fCA_{streams}$) by diving the product of the total catchment stream channel length and channel width by the catchment area. We repeated this process for every monitoring transect so that for each catchment we had 3 distinct estimates of $fCA_{streams}$. Finally, we estimated the ratio of $I_{catchment}$ to total precipitation ($I_{catchment}$:P) over the observation period.

Scaling-Up

To scale up our results to the landscape level for the Huachuca Mountains study area, we compared our data on stream flow duration (as measured using resistance sensors at 200 m long river field sites) to data from Levick et al. (2015) who simulated stream flow permanence using the AGWA/SWAT (Automated Geospatial Watershed Assessment Tool/Soil and Water Assessment Tool) for mapped streams in Fort Huachuca as a whole. We used linear regression to determine the similarity of our two approaches for estimating stream flow permanence. Given the high correspondence between the two methods, we generated a map of the modeled stream flow using seven categories based on the number of days per year the stream is flowing and overlaid our study sites on this landscape-scale map.

Depth to Water Table

We installed monitoring wells of 10 m depth at one of the three piedmont sites (near Garden Canyon) and at one of the lower canyon sites (Lower Huachuca). The wells were installed by Tanner Well Service, Sierra Vista, Arizona, and were made of 2-inch steel casing with the bottom three meters perforated by saw cut. Fort Huachuca granted clearance for the monitoring wells, and each was registered with the state of Arizona. Each well was instrumented with Levelogger Edge pressure and temperature sensors (Solinst Canada, Georgetown, ON,

Canada) that recorded water depth data every 15 minutes. We used a sounder to calibrate the pressure transducers, and used Solinst's Levelogger Software 4.0 (Solinst Canada, Georgetown, ON, Canada) to download and process the pressure transducer data and generate depth to groundwater data. Depth to ground water at the piedmont site was greater than 12 meters and at the Lower Huachuca site was at approximately five meters. We used the well data to divide sites into those with a shallow water table (<8 m) and those with a deeper water table (>8 m). We refer to the former as phreatic sites and to the latter as non-phreatic sites. We assumed that sites in similar hydreogeomorphic settings (e.g., piedmont sites, canyon sites) had similar water table conditions.

Riparian Vegetation, Aridity, and Stream Flow

A site consisted of a stream/riparian segment 200 m in length and of variable width (15 to 58 m among sites, inclusive of stream width). At each site, the lateral boundaries of the riparian zone were determined based on visual cues from the vegetation (e.g., the outer limit of riparian tree canopy or increased size of desert shrubs). An upland zone of comparable length and width was established, with a buffer of at least 15 meters between the designated riparian zone and upland zone.

Field data collection was initiated in May of 2010 and completed in September of 2012. As an index of total plant biomass, we measured vegetation volume using the vertical line intercept method: using a telescoping pole, we determined the number (and type) of vegetation intercepts at decimeter intervals, at 10 random points per zone. We then calculated total vegetation volume and the component comprised of woody vegetation. We measured canopy cover using a densiometer at eight random points per zone. We measured above-ground biomass of herbaceous vegetation by destructively harvesting plant material from 15, 0.4m^2 plots per zone and then determining dry weight in ovens at Arizona State University. Ground cover of vascular plants, by species, was measured in 1x1-meter quadrats (10 per zone) using Daubenmire cover classes. Each 1x1 meter plot was embedded within in a 2x5 meter (10m^2) plot within which incidence data was collected for all plant species. Plots were sampled twice per year to capture seasonal variation. Sampling during multiple years allowed for inter- and intra-annual contrasts and a more complete characterization of the flora. However, we undoubtedly 'missed' some annuals that stay dormant in soil seed banks until the onset of particular rainfall and temperature conditions (Went 1949). Vascular plants were identified to species, when possible, using Kearney and Peebles (1960), the Vascular Plants of Arizona Project (http://nhc.asu.edu/vpherbarium/vpap.html), and other regional references. Voucher specimens were deposited in the herbarium at Arizona State University.

To examine how riparian vegetation of the seven ephemeral streams varies with aridity, and to project future changes, we used the well-tested approach of a space-for-time substitution study (Wang et al. 2014). For these seven streams, we used Pearson correlation analysis (in SYSTAT Version13) to determine if vegetation volume and species richness (and the woody and herbaceous fractions thereof) increased with Aridity Index, for riparian and upland positions. To determine similarity in species composition between riparian and adjacent zones, we calculated Sørensen similarity coefficients. As a measure of temporal variability in species richness, we calculated coefficients of variation (standard deviation/mean) using data from four sampling seasons.

To examine how riparian vegetation varies with stream hydrology, we focused on streams within the Huachuca study area. We used general linear models to identify hydrologic factors associated with the following dependent variables: total species richness, species richness within five life-form categories (trees, shrubs, suffrutescents, herbaceous perennials, and

annuals), vegetation volume, canopy cover, herbaceous cover, and herbaceous biomass. For richness and herbaceous abundance we calculated seasonal averages and cumulative values through time. Independent variables in each model were percent annual surface flow presence, drainage area above the study site, and a dichotomous variable for shallow ground water (one=absent, two=present). Models were assessed based on their AIC scores. We used paired t-tests to compare species richness and herbaceous cover and biomass between seasons within a year and between years within seasons. This study reports only on alpha diversity. Future analysis will examine beta diversity and landscape diversity (Poulos and Camp 2010) as well as species composition and functional types (Merigliano 2005; Engelhardt et al. 2012).

Riparian Soil Seed Banks

To understand how increases in aridity and changes in storm seasonality will effect rivers and their biota, we collected seeds from river sites that spanned gradients in climate and hydrogeology and examined their germination response to temperature in a controlled environment (Fukami and Wardle 2005; Stromberg et al. 2010). We expanded upon the 15 study streams to include a greater number of streams in central and southern Arizona, Study sites range in elevation from 566 m to 1797 m and included areas with arid, semiarid, and semihumid climates. Seven of the sites are located on ephemeral streams. The remaining fourteen sites are located along spatially intermittent streams that have perennial, intermittent, and ephemeral reaches. Stream flow permanence at the sites was determined either from prior studies that used monthly site visits to assess flow presence/absence (Katz et al. 2012) or from electrical resistance sensors placed in the stream channel.

To study soil seed banks, seeds can be extracted from the soil and counted (seedling extraction method) or the soil can be placed in a growth chamber or greenhouse to allow the seeds to germinate (seedling emergence method) (Leck et al. 1989; Baskin and Baskin 2001; Price et al. 2010). We used the latter method. Soil seed bank samples were collected in January and February of 2012. At each study site, eight samples of soil were collected at random locations from the riparian zone and from the upland zone. (Soil was not collected from the upland of six of the sites). Each sample consisted of multiple subsamples. Using a standard bulb corer, we collected cores from the top 5 cm of soil within a 0.5 m^2 area until the container had 700 ml of compressed soil. We included the small litter and duff layer in the sample so to capture of species with transient and persistent seeds (Walck et al. 2005), but removed debris larger than 13.2 mm on site using a soil sieve. The soil samples were stored in a cold room at Arizona State University until two environmental growth chambers were available.

To assess whether riparian and upland soil seed banks contain warm-temperature and cool-temperature guilds, each soil sample was divided into two, with one half assigned to a warm temperature treatment and the other to a cold temperature treatment. During sample preparation approximately one cm (200 ml) of soil from each sample was layered on top of a three cm (500 ml) layer of autoclaved base soil (sandy loam) in small flats. The total number of samples was 576 (21 sites x two topographic positions x two temperature treatments x eight replicates; minus the six unsampled upland sites). The samples were placed in the growth chambers in January, 2013. After a seven-day dry-down period the samples were fully saturated for three days and then allowed to dry until damp. Samples were then watered as necessary to maintain moist soils and ensure that water was not limiting.

Temperature within each growth chamber was programmed to change at six-hour time steps within each 24-hour cycle, with daytime maxima and minima of 35ºC and 25ºC (warm treatment) and 20ºC and 10 ºC (cold treatment). Day-length was programed to simulate the

conditions expected for the time of year associated with the temperature bands. The seed bank samples were grown for twelve weeks. While in the growth chambers, individuals were harvested/collected as they became identifiable to species. After the twelve-weeks, the remainder of the samples were transferred to greenhouses and grown until the plants were mature enough to identify to species or, in some cases, to genus. We are waiting on species identification of some of the specimens thus we report data on morphospecies. It is possible that some species remained undetected in our sampling (Gremer and Venable 2014).

We analyzed the data with general linear models, separately for uplands, ephemeral streams, and intermittent to perennial streams. The number of species emerging from each seed bank collection site was the dependent variable, and temperature treatment (one=cold, two=warm) and natural-log transformed elevation (continuous variable) or Aridity Index were independent variables. We also analyzed data to determine whether the percentage of species that emerged under the cool-season treatment varied with site elevation and site type.

Ground Dwelling Arthropods- Diversity

The arthropod study was conducted in the Huachuca Mountains in the Madrean Sky Islands of southeastern Arizona. We sampled ground-dwelling riparian arthropods in and near Garden, Huachuca, and Ramsey canyons. We focus on diversity gradients of ground-dwelling arthropods because their communities are known to vary along gradients of surface water permanence and their generally limited dispersal capabilities allows for finer partitioning between channel margin, riparian, and upland communities (Hughes 2011; Ober et al. 2011; Steward et al. 2011; McCluney and Sabo 2012). In each canyon, we sampled two sites with non-perennial flow and one additional site with ephemeral flow near the base of each canyon. We measured percent leaf litter cover and percent canopy cover over the stream channel in June and September of 2010 to characterize the biotic environment. We established three parallel transects measuring 100 m each at each site: one along the stream channel margin (channel transect), one five meters away from the channel margin (riparian transect), and one 25 m away from the channel margin (upland transect). At each sampling event, we set one pitfall trap (9.5 cm diameter) filled with propylene glycol every 20 m along each transect for a total of five traps per transect. Pilot data suggested this design sufficiently captured the ground-dwelling taxa present in the riparian zone. Pitfall trapping was conducted in June and September of 2011 and 2012. These periods correspond to the period before and after summer monsoon rains, respectively, in the study region. Traps were left open for three nights before collection. All invertebrates collected were removed and preserved in 95 percent ethanol for later identification.

In the laboratory all ground-dwelling invertebrates were identified to morphospecies. Each morphospecies was then assigned to the lowest taxonomic level possible with the help of expert taxonomists. We defined ground-dwelling invertebrates specifically as those which we felt the pitfall traps reliably sampled. Pitfall traps have been shown to provide good estimates of community composition when only cursorial forms are analyzed (Uetz and Unzicker 1976). Additionally, the catch of a pitfall trap is highly dependent on the size of cup and preservative used (Work et al. 2002; Santos et al. 2007). Our standardized methods across all sites allow us to compare differences in community composition between all study reaches. A number of other taxa including various members of Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and other orders were excluded because they primarily live on vegetation or other habitats and thus sampling was not likely representative of their true presence and abundance. We are preparing voucher specimens of each morphospecies to deposit in the Frank Hasbrouck Insect Collection at Arizona State University.

From these data we calculated the Shannon-Wiener diversity index, Pielou's evenness, and rarefied species richness using the v*egan* package in the statistical software R (Oksanen et al. 2014; R Core Team 2014). We then calculated β-diversity and partitioned it into turnover and richness components (Podani and Schmera 2011; Legendre 2014). We calculated β-diversity between channel and riparian transects, between riparian and upland transects, and between channel and upland transects at each site. For the calculation of each index we combined the total species numbers from all traps per individual transect. We then tested whether α-diversity varied among transects and whether α- and β-diversity varied with season, year, and stream flow permanence using linear mixed-effects repeated measures models with maximum likelihood parameter estimation using the *nlme* package in R (Pinheiro et al. 2015).

Ground Dwelling Arthropods- Productivity

In each of the transects sampled for arthropod diversity, we selected five $1m^2$ plots (with a random number generator) to sample for secondary production. The same selected plot was sampled at each transect every month. We sampled arthropods using a quadrat sampler made of $1m^2$ PVC pipe frame with memory foam attached to the bottom to minimize arthropod escape from sample plots. Upon arriving at each plot, we set the PVC frame and then collected all arthropods using a variety of methods including hand collections, sweep nets, a gasoline-powered bug vacuum, and sifting through leaf litter with a bucket sifter when leaf litter was present. We also searched under rocks for remaining invertebrates, but in doing so, did not dig below the soil surface. We placed the samples on ice in the field until they were transported to lab freezers. We later thawed samples and measured and identified all macroinvertebrates to the family level, and for key taxa, to the genus or species level. Orders included in the total biomass calculations are Araneae, Blattodea, Coleoptera, Collembola, Diptera, Geophilomorpha, Hemiptera, Hymenoptera, Isopoda, Lepidoptera, Lithobiomorpha, Microcoryphia, Opiliones, Orthoptera, Phasmatodea, Pseudoscorpion, Pseudoscorpiones, Scolopendramorpha, Scorpiones, and Spirobolida.

We used mass-length relationships (Sabo et. al 2002) to estimate the dry mass of each invertebrate collected. To compare values, we used the mean monthly biomass (biomass is defined here as g/m^2). We calculated the mean monthly biomass for the isopod *Armadillidium vulgare*, the field cricket *Gryllus sp. nov.*, and for all macroinvertebrates collected. This population of crickets represents a species that is currently undescribed but was not discovered by our research group (D. Weissman personal communication). Without sampling underground and in wood, we could not collect larvae for many abundant riparian species such as ants and beetles, thus we chose abundant species with completely above-ground life cycles as focal taxa for our calculations of secondary production. This approach has clear limitations since most of the dominant taxa in piedmont sites are ants and beetles with belowground life stages. Hence, we also analyzed patterns of monthly changes in biomass as an index of "community production." This method likely underestimates secondary production for the entire assemblage as it does not account for all state changes in a life table (i.e., mortality or predation on uncounted individuals).

To calculate secondary production for *Gryllus* and *A. vulgare*, we chose the non-cohort size-frequency method (Benke and Huryn 2006). The size-frequency method is akin to static life table analysis in that it assumes that the mortality curve generated by a mean size frequency distribution represents an "average cohort" of the macroinvertebrate population. This method was chosen over the cohort-based increment-summation method (Mothiversen and Dall 2006) because it proved too difficult to differentiate between cohorts with overlapping generations. Using a size-frequency method we multiply the change in density (ΔN, individuals/m^2) between

size categories (mass-based categories as in Mothiversen and Dall 2006) by the mean weight ($\bar{W}$) between the two categories. This value is then multiplied by the total number of size categories, which are an estimate of the number of cohorts in the population.

$$Interval\ Production = (\#size\ classes)(\bar{W}\Delta \mathrm{N}) \qquad \text{Eq. 1}$$

If the population has a development time much different than one year, a cohort production interval (CPI) correction factor must be used (Benke and Huryn 2006). The CPI is the amount of time required for a macroinvertebrate to grow from larvae to full size. If the CPI is measured in days, the correction factor will be equal to 365/CPI. If months are used, then the correction factor will be equal to 12/CPI. The CPIs used for *Armadillidium vulgare* and *Gryllus sp.* were 12 and three months respectively. Although there were no published CPI values for these species, we believe these values are appropriate based on published life history information and personal observations from previous studies (Holland 2014). Although often ignored, the number of size classes and number of samples per CPI can affect the accuracy of the calculated production. In this study, we created size classes by using biomass intervals of one mg. We did not include empty size classes in our calculations. Community production was analyzed with respect to variation in stream flow permanence and position within a site.

Nutrient Dynamics and Litter Decomposition

To characterize soil physio-chemical properties, soils and sediments associated with the upland, riparian and channel positions of each sites were collected from zero to five cm depth (n=117 total). Soils in the lab were passed through a two mm sieve. Soil bulk density (g cm^{-3}) was calculated using a modified version of the excavation method (Grossman and Reinsch 2002), and fine and coarse fractions were determined from bulk density sampling. Soil texture (percentages of sand, silt, and clay) was determined using the modified pipette method for particle size analyses (Gee and Bauder 1986). Water holding capacity was determined following Dane et al. (2002). Soil pH was determined on a 2:1 water to soil with probe calibrated using pH 10.01, 7.00, and 4.01 buffer solutions (Thomas 1996). Percent soil organic matter was estimated from mass lost on ignition of organic matter at 450°C for eight hours relative to initial sample dried at 105°C. Percent soil carbon and nitrogen were determined on a Fisons NA-1500 elemental analyzer (Fison Instruments, Milan, Italy) at Idaho State University.

We deployed litterbags in upland, riparian, and channel positions to evaluate the role of subsidy of water and nutrients on decomposition. We deployed grey oak (*Quercus grisea*) and a smaller set of Arizona sycamore (*Platanus wrightii*) litterbags (sourced from the wettest sites) at three replicate reach transects at 13 sites in Arizona over an 18-month period. Senesced greay oak and sycamore leaves were collected in October 2010 at upper Ramsey Canyon. Litter was collected in plastic bags, brought to the lab, and dried at 40°C prior to packing to obtain a constant water weight. Nylon mesh litterbags (10 cm × 15 cm, 1 mm nylon mesh) were packed with four g dried leaf material. Every 35th bag was packed and then transferred to a pre-dried envelope for wet-dry correction and initial chemical analysis. Initial carbon (C) and nitrogen (N) contents were determined using the elemental analyzer, after drying samples at 55°C. On 10 January 2010, nine randomly selected litterbags were placed in upland, riparian, and channel positions at each of the three transects at all sites (for oak, 81 per site, 1100 total). Only one replicate per site for sycamore was deployed due to limited litter material (nine per site, 288 total). Litterbags were collected at time zero, one day, seven days, two weeks, four weeks, three months, six months, one year, and 1.5 years. Following collection from the field, litter was

cleaned to remove residual soil, dried at 55˚C for 12 to 24 hours, and then weighed. Litter samples were ground to a fine powder (pass through no. 40 sieve) and stored in vials. Ash free dry mass was determined on 1.0 g of homogenized subsample by combusting it at 450˚C for four hours and reweighing the mass after combustion. A subsample of the ground litter was analyzed for C and N content by packing 6.0 mg of ground litter into tin capsules and analyzing it on the elemental analyzer.

We measured soil and sediment nutrient dynamics and related these to seasonal variability in water availability associated with stream flow and water presence. Soil and sediments were collected from upland, riparian and channel positions during winter/spring (January-March), pre-monsoon (May-June) and post-monsoon (August-September) seasons, periods that maximized thermal and hydrologic contrasts, from June/September 2010 to June 2012. Specifically, surface soils from 0 to 5 cm depth were collected with a core sampler along the three transects at the associated positions, stored in plastic bags and returned to the laboratory where they were subsampled for soil gravimetric moisture content, nutrient pools, and nutrient process rates. In the lab, soils were sieved to < 2-mm, and one 25 g soil subsample was dried at 105ºC to determine gravimetric soil moisture. A 10 g subsample was extracted with 50 ml of 2N potassium chloride (KCl) to determine exchangeable mineral N pools. Another subsample was incubated under aerobic conditions for seven days in the dark to determine actual rates of net mineralization and nitrification (Hart et al. 1994). Cycling and release of nutrients with the initiation of the monsoon was simulated by wetting one set of pre-monsoon soils to 60% water holding capacity (WHC), incubating these soils for seven days at this 60% WHC, and then analyzing soil extracts for ammonium (NH_4^+) and nitrate (NO_3^-) on a SmartChem discrete autospectrophotometer at Idaho State University.

To assess nutrient availability and release associated with decomposition of materials, we used exchange resin bags, which have been shown to be a useful integrator of chemical flux over time (Binkley and Matson 1983). Resin bags were deployed in upland, riparian and channel positions during winter/spring, pre-monsoon, monsoon (August-September), and post-monsoon seasons. We deployed two sets of exchange resin bags, one for cations (Dowex 50W-8X; H^+form) and one for anions (Dowex 1-8X; $C1^-$ form). One cation and one anion exchange resin bag were placed in the soil at a depth of three to five cm at each location (234 resin bags per collection). Bags were retrieved at the end of each seasonal period, and new bags deployed in similar positions. In the lab, resin bags were washed free of soil using 18.2 mOhm distilled water. The resins were then placed in centrifuge tubes for extraction in 2 mol/L sodium chloride (NaCl) (40 ml) for six hours on low-medium orbital shaking speed. This solution was analyzed for NH_4^+ and NO_3^- on the discrete autospectrophotometer.

Statistical analyses were performed in JMP 11 (SAS, Carey, NJ) following a nested ANOVA design. Sites were classified into flow regimes with landscape position as nested variable. Repeated measures ANOVA were performed for decomposition and nutrient dynamics by flow regime treatment and nested position. Multiple linear regression models were performed on calculated decay constants, calculated as natural log transformation mass after 18 months of deployment divided by the initial mass. Transformations were performed to meet assumptions of normality and homoscedascity. Santa Rita sites (SS and SR) and Garden Canyon Piedmont (GP) were included in in initial decomposition analyses and reporting. These sites were then dropped analyses due to confounding issues of asynchronous deployment of litter bags due to permitting (Santa Rita sites) as well as trampling/disturbance of litterbags by cattle (Santa Rita sites). A fire at the Garden Canyon piedmont (GP) site burned the litter bags in month six of deployment and precluded comparison across sites.

Table 3.1. Catchment characteristics of study sites.

	Site name (ID)	Elevation (min, max)[1]	Mean annual precip. (mm)	Mean annual temp. (°C)	Area (km^2)	Stream density (km/km^2)	Lat, long. (dec. deg. N, W)	Parent material Type	%
	Barry M. Goldwater Air Force Range								
Alluvial Basin	Black Gap (BGA)	324, 676	97	22.3	10.2	5.72	32.711123, 112.831066	dacite sand	82 18
Alluvial Basin	Sauceda (SWA)	258, 1114	97	21.6	326	2.38	32.878405, 112.752874	dacite sand	78 22
	Santa Rita Experimental Range								
Alluvial Basin	Small Santa Rita (SSA)	947, 1105	227	19.0	1.7	5.06	31.885414, 110.88042	sand	100
Alluvial Basin	Large Santa Rita (SRA)	952, 1748	227	18.1	18	6.28	31.880545, 110.883672	sand granite	55 45
	Huachuca Mountains								
Piedmont	Pied. Huachuca (HP)	1453, 1564	293	16.7	1.3	4.00	31.540278, 110.334113	sand granite	95 5
Piedmont	Pied. Garden (GP)	1494, 1556	335	16.6	0.5	5.12	31.506705, 110.316744	sand granite	64 36
Piedmont	Pied. Ramsey (RP)	1533, 1762	397	16.3	0.3	4.99	31.468538, 110.294548	granite	100
Lower Canyon	Lower Huachuca (HL)	1592, 2533	308	13.6	17	1.30	31.537735, 110.377248	sandstone conglomerate granite limestone	31 30 22 17
Lower Canyon	Lower Garden (GL)	1539, 2630	409	13.6	30	1.22	31.485624, 110.327657	sandstone limestone granite conglomerate	52 29 18 1
Lower Canyon	Lower Ramsey (RL)	1573, 2798	443	12.8	13	1.24	31.459062, 110.295734	sandstone granodiorite granite rhyolite	48 28 18 6
Upper Canyon	Upper Huachuca (HU)	1646, 2533	276	13.2	15	1.37	31.526465, 110.382684	sandstone conglomerate limestone granite	34 33 20 13
Upper Canyon	Upper Garden (GU)	1582, 2630	416	13.1	23	1.12	31.478043, 110.342776	sandstone limestone granite conglomerate	61 37 1 1
Upper Canyon	Upper Ramsey (RU)	1726, 2798	456	11.9	9.8	1.28	31.445808, 110.313850	sandstone granodiorite rhyolite granite	53 38 8 1
Upper Canyon	HU @ USGS 09471310	1708, 2533	276	13.2	10.6	1.09	31.518056, 110.387222		
Upper Canyon	GU @ USGS 09470800	1618, 2630	416	13.1	22	1.20	31.472778, 110.305833		
Upper Canyon	RU @ USGS 09470750	1726, 2798	456	11.9	9.8	1.37	31.446667, 110.305833		

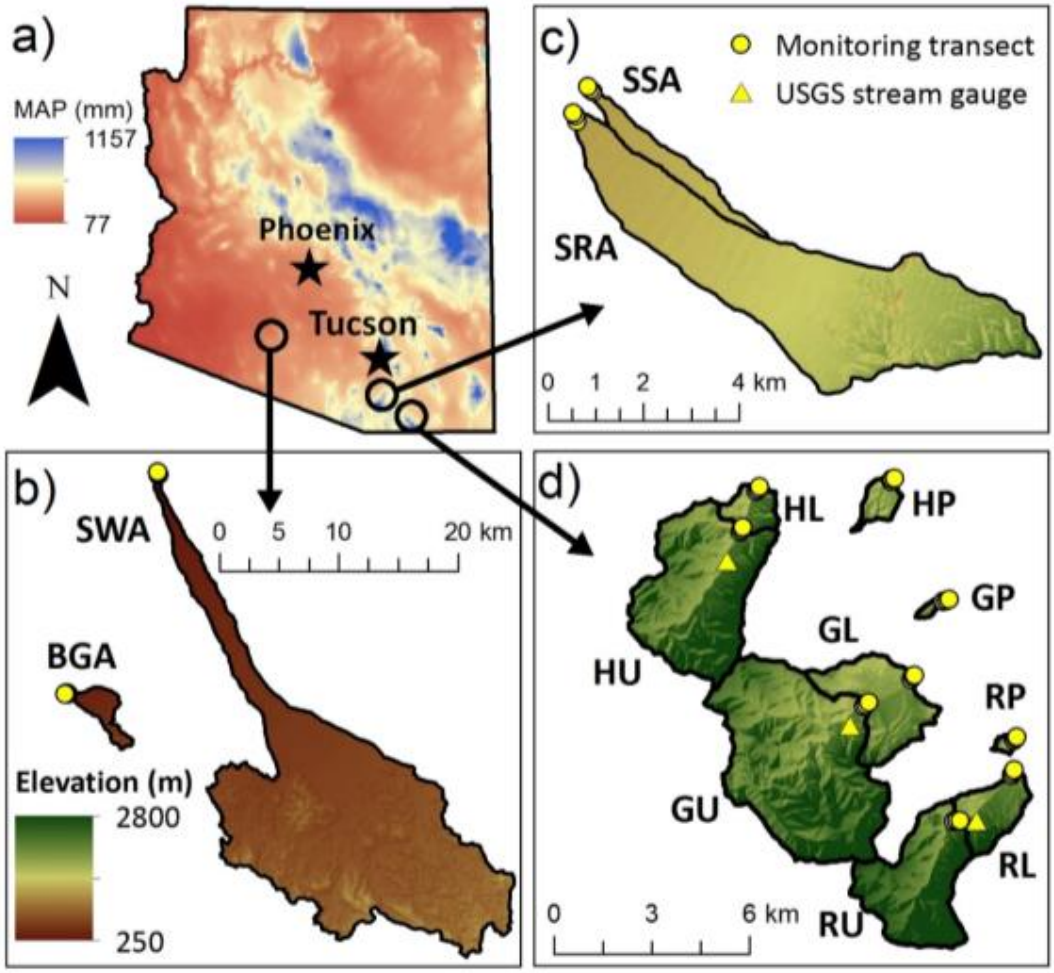

Fig. 3.1. Study sites in southern Arizona. Sites are located at b) the Barry Goldwater Range (SWA, BGA); c) the Santa Rita experimental range (SRA, SSA); and d) in the Huachuca Mountains at Huachuca Canyon (HU, HL, HP), Garden Canyon (GU, GL, GP), and Ramsey Canyon (RU, RL, and RP).

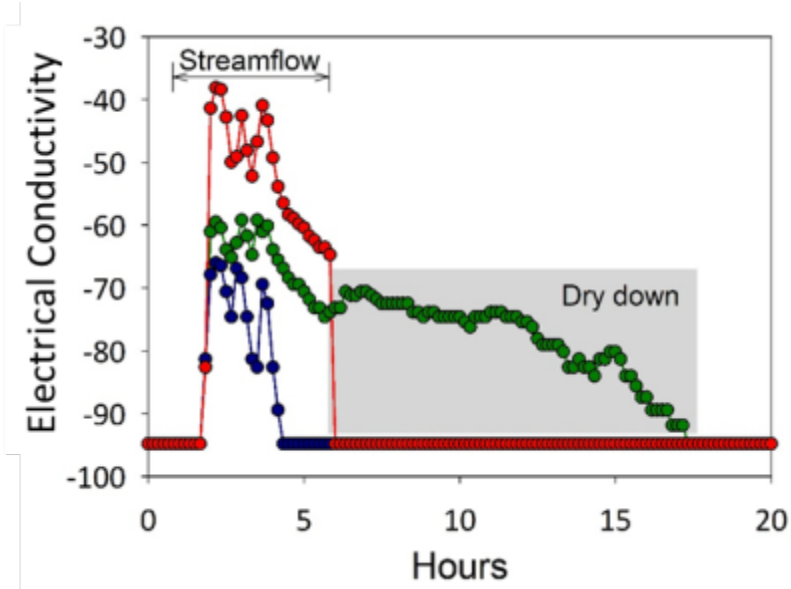

Fig. 3.2. Typical electrical conductivity profile for a runoff event at a monitoring reach. Each data set (red, green, blue) represents a different sensor at a single reach. The onset of runoff is marked by a rapid increase in EC. The cessation of stream flow can be identified by either EC returning to -94, the baseline reading, or by an inflection in the rate of change in EC to a less steep slope, indicative of soil drying conditions.

Chapter 4:
Flow Regimes and Infiltration Potential of Streams in Southwestern USA

Q1: What Factors Influence Stream Flow of Temporary Streams?

Annual stream flow and stream water presence were variable across sites but predictable based on climatic factors and stream channel density. Annual stream flow presence ranged among sites from 0.6 percent (two days) to 82 percent (301 days). Surface water presence ranged from three percent (10 days) to 82 percent (Table 4.1). Both stream flow and surface water presence increased significantly ($p<0.05$) and exponentially with mean annual precipitation and decreased significantly and exponentially with mean annual temperature ($r^2= 0.38$ and 0.53, respectively) and stream channel density (Fig. 4.1; Table 4.2). These results are consistent with findings in other dryland regions that point to a coupling between rainfall magnitude, evaporation, evapotranspiration, and stream channel infiltration losses as mechanisms resulting in intermittent stream flow (Goodrich et al. 1997; Maurer 2006; Izbicki 2007).

Five stream flow and water presence regimes were identified with clustering analyses: 1) dry ephemeral, 2) wet ephemeral, 3) dry intermittent, 4) wet intermittent, and 5) semi-perennial (Fig. 4.2). All alluvial basin and piedmont sites classified as ephemeral, one lower canyon classified as wet ephemeral, and the remaining lower and upper canyon sites classified as dry-intermittent, wet-intermittent and semi-perennial. Annual stream flow in the dry ephemeral and wet ephemeral clusters ranged from 0.6 to 2.0% and 1.1 to 3.4%, respectively, and was significantly lower ($p < 0.05$) than the intermittent and semi-perennial groups where annual stream flow ranged from 16% to 82% (Table 4.3, Fig. 4.3). Annual water presence at the dry-ephemeral cluster ranged from 2.6 to 17.9% and was significantly lower than in all other clusters; it was highest at the wet-intermittent and semi-perennial clusters, where it ranged from 47 to > 82% (Table 4.3, Fig. 4.3).

Collectively our results indicate that landscape variables have a large effect on annual stream flow and water presence regimes. If climate was the main driving mechanism controlling annual flow regimes, then all of the monitoring sites would classify according to a precipitation, temperature or aridity gradient, a pattern not supported by our data. For example, piedmont sites HP and GP received more rainfall during the monitoring period than did the alluvial SWA and SRA, however, all classified in the dry-ephemeral cluster (Fig. 4.2).

Q2: Which Stream Flow Types are most Responsive to Precipitation?

Percent annual stream flow and water presence varied positively and significantly with precipitation at ephemeral sites (Table 4.2) indicating a strong coupling with climate. The most responsive sites to rainfall were the dry-ephemeral and wet-ephemeral sites, where rainfall could account for up to 47% of stream flow and 60% of water presence. In contrast, at the dry-intermittent sites, annual precipitation explained only up to 11% of the stream flow and water presence variance. No correlations between annual precipitation and flow regime were observed at the wet-intermittent and semi-perennial sites. The absence of correlations with annual precipitation at the at the wet-intermittent and semi-perennial sites indicates that flow regimes are subsided by groundwater or vadose zone discharge, a mechanism observed in this and other dryland regions (Izbicki 2007; Levick et al. 2008; Wahi et al. 2008).

The annual water presence to stream flow ratio (AWP:ASF) varied between 1.0 and 33.6 (Table 4.3). The AWP:ASF ratio at the ephemeral sites ranged from 4.6 to 33.6 and was significantly higher than ratios at all other clusters where they ranged from 1.1 to 3.3 (Fig. 4.5).

The large ratios observed at the dry-ephemeral (mean = 9.3, SD = 4.3) and wet-ephemeral (mean = 23.0, SD = 11.8) sites indicate that water as soil moisture and/or ponds is present over four times longer than stream flow which has significant implications for biological processes at these dry sites. Biological and biogeochemical processes in dryland systems are primarily water limited (Austin et al. 2004; Belnap et al. 2005) and the water available as soil moisture and ponds can therefore offset water demands during non-stream flow periods and extend the period of time for biologically mediated processes to occur. Indeed, studies show that biogeochemical processes such as respiration and organic matter mineralization can continue under low matric potentials (Carbone et al. 2008), and their duration and magnitude vary with, and depend on, moisture availability (Belnap et al. 2005). Therefore, at the drier sites we expect biological activity to continue for an extended period of time following stream flow. The mechanism behind this pattern, whether related to hydraulic redistribution of deep water to shallow stream sediments (Hultine et al. 2004; Naumburg et al. 2005), or to soil traits, remains to be determined.

The mean annual precipitation during our study period ranged from 97 to 456 mm across sites. Across all sites, at a regional scale, precipitation varied significantly and positively with elevation ($r^2 = 0.74$); however, we did not observe a significant correlation between precipitation and elevation at the Huachuca Mountain sites (piedmont, upper and lower canyon) where rainfall ranged from 276 to 457 mm. At the Huachuca Canyon sites (HP, HL and HU), we observed lower than expected precipitation given their elevation and mean annual temperature. Comparison of our monitoring record with MAP_{30} (PRISM, 2013) indicates that these sites consistently receive less rainfall than the adjacent southeastern canyon and piedmont sites. In the mountainous Western US, spatial heterogeneity and topography can largely control localized precipitation patterns whereas at the regional scale, summertime monsoonal rainfall decreases in a northward direction (Mock 1996; Adams and Comrie 1997; Wilson and Guan 2004). Therefore it is likely that the physical location of Huachuca Canyon coupled with storm rainout result in significantly lower mean annual precipitation than at the Garden and Ramsey Canyon sites.

Q3: Do Temporal Dynamics of Flow Permanence Vary among Stream Types?

Although rainfall had a clear bimodal distribution, this was not the case for stream flow and water presence across flow regimes. The relationship between the temporal distribution of precipitation and stream flow and water presence differed by flow regime (Fig. 4.4, Fig. 4.5). Percent monthly stream flow at the dry-ephemeral sites varied positively and significantly with precipitation during the summer only; percent monthly flow at the wet-ephemeral sites varied with precipitation during summer and fall (Table 4.4). Similarly, percent monthly water presence varied positively and significantly with precipitation at the dry-ephemeral sites during the fall and summer, and only during the spring at the wet-ephemeral sites. The spring months were the driest, and similar to findings for Santa Catalina Mountains in semiarid southern Arizona (Ajami et al. 2011), this period also had the statistically lowest stream flow and water presence across sites and flow regimes (Table 4.1). We expected stream flow and water presence to be of longer duration during the summer (July, August and September) and fall (October, November and December), when precipitation was statistically highest, averaging 220 and 64 mm, respectively, and accounting for 68% and 21% of annual rainfall. Surprisingly, stream flow presence and water presence were statistically highest during these periods only at the dry-ephemeral and wet-ephemeral sites (Table 4.3). Although not explicitly addressed in this study, a coupling between the characteristics of seasonal precipitation, stream flow generation mechanisms and channel infiltration losses likely results in these temporal flow regime patterns (Blasch et al. 2004).

Winter rainfall in the region is of low intensity and long duration allowing for significant infiltration and transmission losses, and stream flow occurs in response to saturation excess overall flow and local subsurface flows after rainfall (Levick et al. 2008; Ajami et al. 2011). In contrast, summertime precipitation is of high intensity and short duration, resulting in infiltration, excess overland flow and rapid stream flow generation following episodic rainfall (Goodrich et al. 1997; Levick et al. 2008). These processes explain the positive responses to rainfall during the summer. Finally, a variable not explicitly addressed here that warrants further study is that of antecedent moisture conditions, which can significantly alter stream flow responses in water limited regions (Blasch et al. 2004; Vivoni et al. 2009; Hawkins and Ellis 2010).

We did not observe any seasonal responses to precipitation in the dry and wet-intermittent flow regimes. The seasonal flow regime patterns observed at the canyon sites in the dry-intermittent, wet-intermittent and semi-perennial flow regimes point towards geologic and subsurface connectivity controls on stream flow. Despite the larger magnitude of summer time rainfall, stream flow presence and water presence at the dry-intermittent sites did not significantly vary between the summer, fall and winter; at the wet-intermittent sites the highest stream flow and water presence occurred during the winter (Table 4.3). In contrast, stream flow and water presence at the semi-perennial sites were greatest during the fall and winter and varied significantly and inversely with precipitation during the summer and spring (Table 4.3). Within the context of generalized mountain block hydrology conceptual models and geochemical evidence of studies in the region (Eastoe et al. 2004; Wilson and Guan 2004; Wahi et al. 2008; Ajami et al. 2011), it is likely that the stream flow and water presence observed at these canyon sites is sourced from discharge and subsurface flow of water stored within the fractured bedrock matrix. Finally, the flow regimes patterns at these canyon sites appear to be buffered in the short term from varying climate, suggesting that biological riparian and stream channel processes relying on soil moisture might be more resilient to climate change and potential shifts in the regional timing of precipitation.

Q4: What are Rates of Saturated Hydraulic conductivity (K_{sat}) and Potential Infiltration ($I_{catchment}$)?

The K_{sat} estimates were high and wide ranging, from a reach average of 235 cm day^{-1} to 961 cm day^{-1}; potential infiltration depths ($I_{catchment}$) varied between < 1 and 941 m per year (Table 4.4). Annual $I_{catchment}$ estimates assume that infiltration occurs every time stream flow is present, therefore it is not surprising that annual $I_{catchment}$ was significantly higher at the wet-intermittent and semi-perennial sites, which have the greatest stream flow, than at the ephemeral sites (Fig. 4.6), which have the lowest stream flow. The fraction of the catchment that can contribute to channel infiltration is statistically greatest at the dry-ephemeral flow regime (up to 5.0%). Higher stream channel densities alluvial and piedmont sites when compared to mountainous canyons are expected and might contribute to spatial discontinuities in stream flow due to increases in upstream channel infiltration losses and divergent surface flow paths (Levick et al. 2008).

The potential annual infiltration to precipitation ratios ($I_{catchment}$:P) indicate a coupling between climate and flow regime only in the driest sites. The $I_{catchment}$:P ratios, assuming that only 50% of the stream substrate contributes to infiltration, ranged from 0.1 to 8.7; whereas the ratio varied from 0.2 to 14.8 assuming that the entire stream channel contributes to infiltration (Table 4.4). The $I_{catchment}$:P ratio was significantly lower at the two ephemeral and ephemeral site types (0.1 to 2.9), and was highest at the wet-intermittent and semi-perennial sites (3.6 to 17.3,

Fig. 4.6). Our infiltration depth estimates assume only a vertical flux, no lower boundary condition and that whole channel contributes to infiltration; however, in reality it is difficult to know exactly the fraction of the channel substrate that contributes to infiltration. Despite the uncertainty, low $I_{catchment}:P$ ratios (I:P < 1.5), particularly under the assumption that only 30 – 50% of the channel contributes to infiltration, support the idea that stream flow is primarily generated by rainfall at the ephemeral sites. High ratios at the canyon sites provide further evidence of subsurface connectivity resulting in groundwater discharge and vadose zone water contribution consistent with mountain system recharge and stream flow generation mechanisms described in generalized conceptual models (Wilson and Guan 2004; Wahi et al. 2008; Ajami et al. 2011) .

Q5: Scaling-up

Results of linear regression showed a high correspondence between our field-based approach for determining stream flow permanence and the modelling approach taken by the Levick team for the Huachuca Mountains (Fig. 4.7). Given the high correspondence between the two methods, we generated a landscape-scale map of the modeled stream flow using seven categories based on the number of days per year the stream is flowing; we then overlaid our study sites on this map (Fig. 4.8). This map (Fig. 4.8) indicates that our field sampling in the Huachuca Mountains captured most, but not all, of the hydrological stream types present at Fort Huachuca. Notably, our sampling did not capture the many hyper ephemeral sites distal from the mountains. Notably, too, the dry-ephemeral channels on piedmont were too small to be captured by the Levick model and thus could be overlooked by hydrological models.

Table 4.1. Percent annual stream flow and water presence at each study reach.

	Site	Annual Stream Flow (%)	Annual Water Presence (%)
		Barry M. Goldwater Air Force Range	
Alluvial Basin	BGA	0.6	2.6
	SWA	1.1	17.9
		Santa Rita Experimental Range	
	SSA	1.1	36.3
	SRA	2.0	17.7
		Huachuca Mountains	
Piedmont	HP	1.9	17.9
	GP	2.0	15.0
	RP	1.3	32.3
Lower Canyon	HL	33.6	47.4
	GL	23.2	37.1
	RL	3.4	35.4
Upper Canyon	HU	16.0	27.7
	GU	50.6	57.2
	HU_USGS	30.2	30.2
	GU_USGS	82.4	82.4
	RU_USGS	79.0	79.0

Table 4.2. Coefficients of determination (r^2) for significant ($p<0.05$) regressions of percent stream flow and water presence versus precipitation. "-" indicates a non-significant regression; (-) indicates a negative correlation.

	Annual	**Fall**	**Winter**	**Spring**	**Summer**
Stream flow					
Dry ephemeral	0.31	-	-	-	0.50
Wet ephemeral	0.47	0.40	-	-	0.31
Dry intermittent	0.06	-	-	-	-
Wet intermittent	-	-	-	-	-
Semi-perennial	-	-	-	0.40 (-)	0.45 (-)
Dry ephemeral	0.47	0.38	-	-	0.42
Wet ephemeral	0.33	-	-	0.60	-
Dry intermittent	0.11	-	-	-	-
Wet intermittent	-	-	-	-	-
Semi-perennial	-	-	-	0.40 (-)	0.45 (-)

Table 4.3. Annual and seasonal stream flow and percent water presence, by stream type. Values are mean (and SD).Means sharing a superscripted letter across seasons are not significantly different.

	Annual	Fall	Winter	Spring	Summer
Stream flow presence					
Dry ephemeral	1.5 (0.6)	**2.0 (1.8)** ^{A}	0.6 (0.6) ^{B}	0.4 (0.5) ^{B}	**3.1 (2.3)** ^{A}
Wet ephemeral	1.9 (1.3)	**2.3 (2.4)** ^{AB}	1.2 (1.4) ^{BC}	0.5 (0.5) ^{C}	**3.8 (2.1)** ^{A}
Dry intermittent	23.1 (7.1)	**28.2 (20)** ^{A}	**24.5 (19.7)** ^{A}	0.6 (0.6) ^{B}	**39.3 (24.9)** ^{A}
Wet intermittent	42.1 (12.1)	43.5 (21.9) ^{B}	**73.6 (18.6)** ^{A}	7.9 (10.6) ^{C}	43.4 (33) ^{B}
Semi-perennial	80.7 (2.3)	**100 (0)** ^{A}	**100 (0)** ^{A}	48.8 (44.7) ^{B}	74 (31.7) ^{AB}
Water presence					
Dry ephemeral	14.2 (6.6)	**21.1 (19.4)** ^{A}	3.7 (3.5) ^{B}	1.7 (2.7) ^{B}	**30.4 (20.4)** ^{A}
Wet ephemeral	34.7 (2.0)	38.6 (24.5) ^{B}	24.3 (25.1) ^{B}	3.2 (3.0) ^{C}	**72.8 (14.9)** ^{A}
Dry intermittent	31.7 (4.9)	**41.2 (26)** ^{A}	**35.3 (25.9)** ^{A}	0.7 (0.7) ^{B}	**49.6 (31.2)** ^{A}
Wet intermittent	52.3 (6.9)	51.4 (26.4) ^{B}	**84.2 (16.6)** ^{A}	12.5 (14.8) ^{C}	61 (31.1) ^{AB}
Semi-perennial	80.7 (2.3)	**100 (0)** ^{A}	**100 (0)** ^{A}	48.8 (44.7) ^{B}	74 (31.7) ^{AB}

Table 4.4. Stream substrate characteristics and potential infiltration at each study reach. The potential annual infiltration (**K_{sat}**) assumes that the entire streambed contributes to infiltration. We report two infiltration to precipitation ratios (I:P): the first assumes that only half (0.5) of the streambed contributes to infiltration and the second assumes that the entire streambed contributes to infiltration. Standard deviations are reported in parentheses.

	Site	Sand, silt, clay (%)	Bulk Density (g cc^{-1})	K_{sat} (cm day^{-1})	Potential annual infiltration (m)	I:P 0.5; 1.0
			Barry M. Goldwater Air Force Range			
Alluvial Basin	BGA	94, 5, 2	2.4 (0.5)	354 (334)	1 (<1)	0.3 (0.3); 0.6 (0.6)
Alluvial Basin	SWA	97, 2 1	2.1 (0.7)	709 (316)	12 (4)	1.1 (0.5); 2.3 (1)
			Santa Rita Experimental Range			
Alluvial Basin	SSA	97, 1, 2	2.1 (0.3)	303 (198)	11 (7)	0.2 (0.1); 0.3 (0.2)
Alluvial Basin	SRA	96, 2, 2	1.7 (0.1)	601 (113)	29 (4)	1.5 (0.3); 2.9 (0.7)
			Huachuca Mountains			
Piedmont	HP	86, 7, 7	1.4 (0.3)	492 (585)	5 (5)	0.1 (0.1); 0.1 (0.1)
Piedmont	GP	91, 6, 3	1.7 (0.3)	407 (509)	5 (2)	0.1 (0.1); 0.2 (0.2)
Piedmont	RP	96, 2, 1	1.4 (0.2)	961 (115)	29 (6)	0.3 (0.2); 0.6 (0.3)
Lower Canyon	HL	95, 3, 2	1.3 (0.1)	870 (124)	514 (46)	8.7 (0.2); 17.3 (0.3)
Lower Canyon	GL	94, 5, 2	1.5 (0.1)	648 (98)	313 (109)	2.6 (0.6); 5.2 (1.2)
Lower Canyon	RL	84, 14, 2	1.4 (0.4)	333 (310)	23 (26)	0.1 (0.1); 0.2 (0.3)
Lower Canyon	HU	93, 5, 2	1.4 (0.3)	622 (204)	164 (97)	2.5 (1.1); 4.9 (2.2)
Upper Canyon	GU	90, 7, 3	1.5 (0.6)	491 (216)	578 (233)	4.4 (0.8); 8.8 (1.6)
Upper Canyon	HU_USGS	90, 7, 3	1.5 (0.6)	622 (204)	311 (183)	6.7 (3); 13.4 (6.1)
Upper Canyon	GU_USGS	94, 4, 2	1.9 (<0.1)	491 (216)	941 (379)	7.4 (1.4); 14.8 (2.8)
Upper Canyon	RU_USGS	93, 5, 2	1.4 (0.3)	235 (17)	679 (48)	3.6 (1.1); 7.2 (2.3)

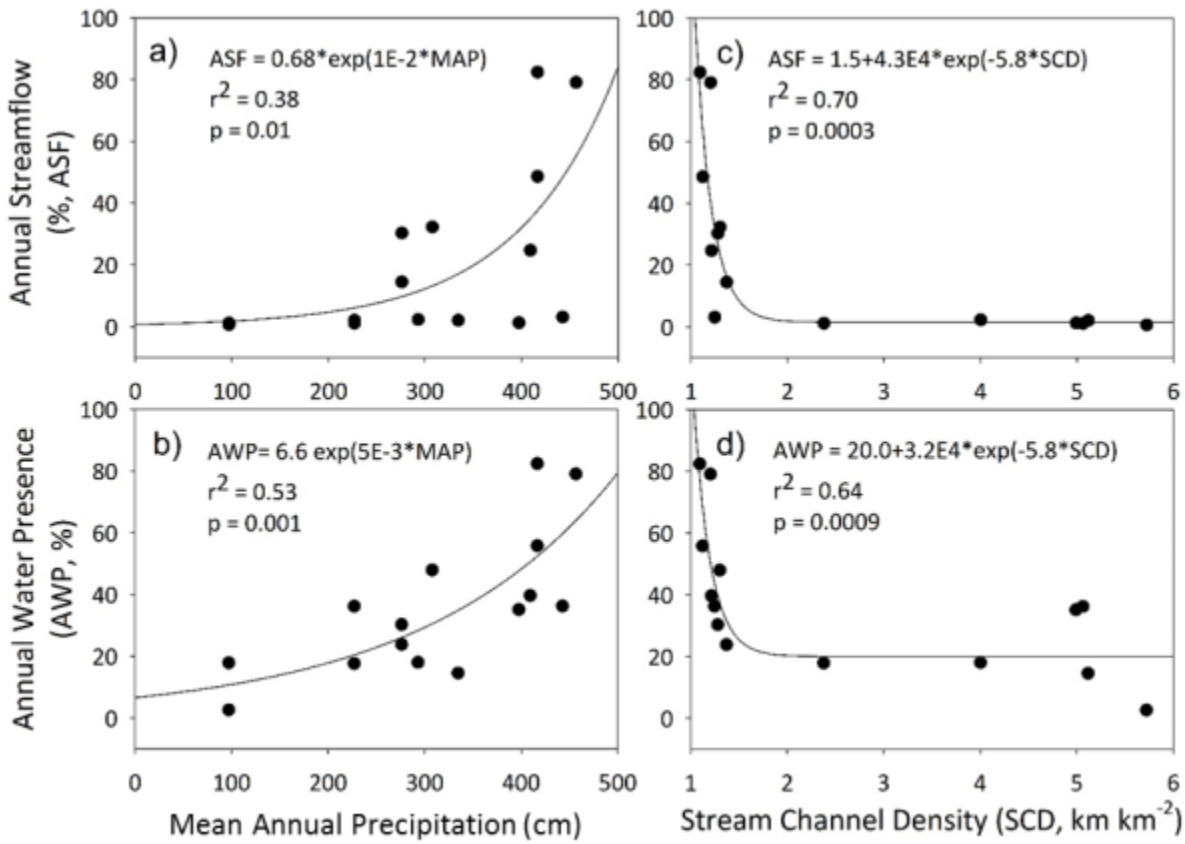

Fig. 4.1. Percent annual stream flow and percent annual water presence versus mean annual precipitation (a and b) and versus stream channel density (c and d). All regressions were signficant ($p < 0.05$).

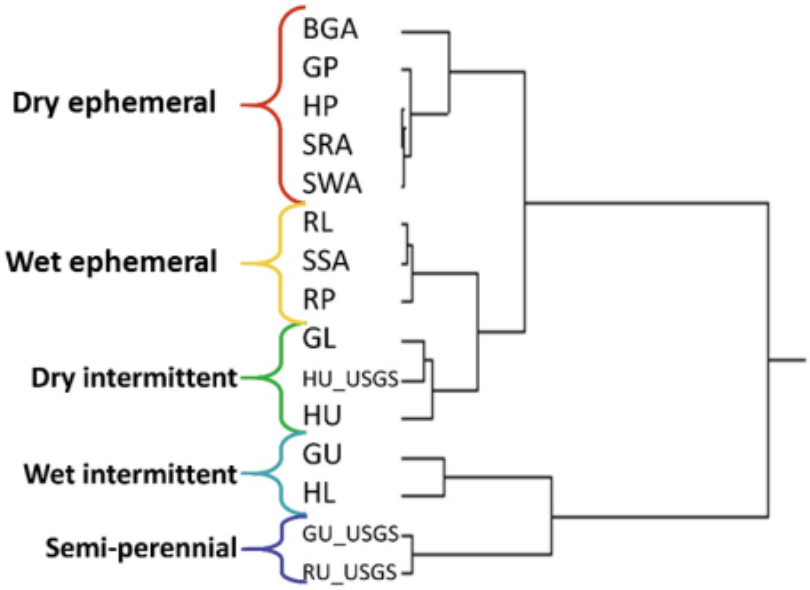

Fig. 4.2. Clustering analysis dendrogram of temporary streams based on percent annual stream flow presence and percent annual water presence. We identified 5 distinct stream flow categories.

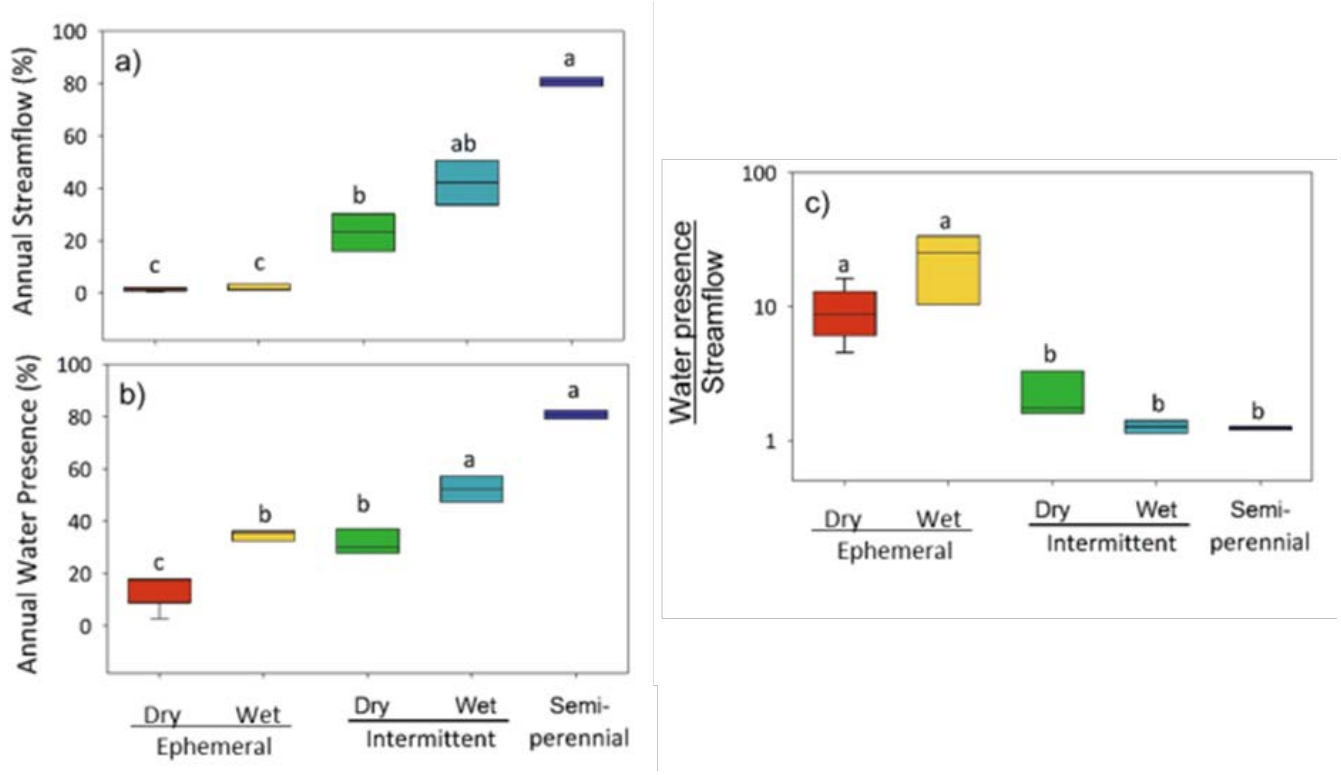

Fig. 4.3. Box plots of percent annual stream flow, percent annual water presence, and ratio of water presence to stream flow, by stream flow regime. Box plots sharing a lower case letter are not ($p>0.05$) significantly different.

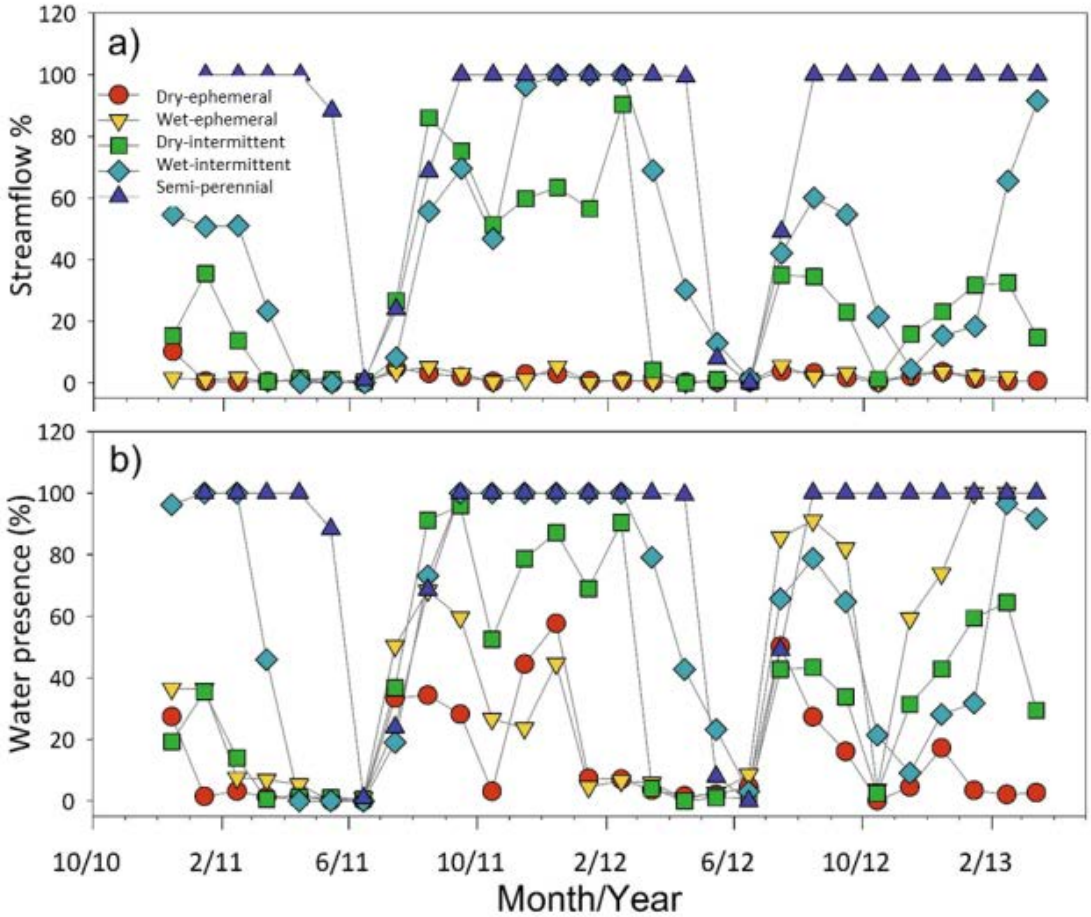

Fig. 4.4. Mean monthly percent stream flow and water presence through time, by stream flow type. Calendar year 2011 had greater percent stream flow and water presence than calendar year 2012, perhaps owing to wet antecedent conditions (i.e., above average precipitation in 2010).

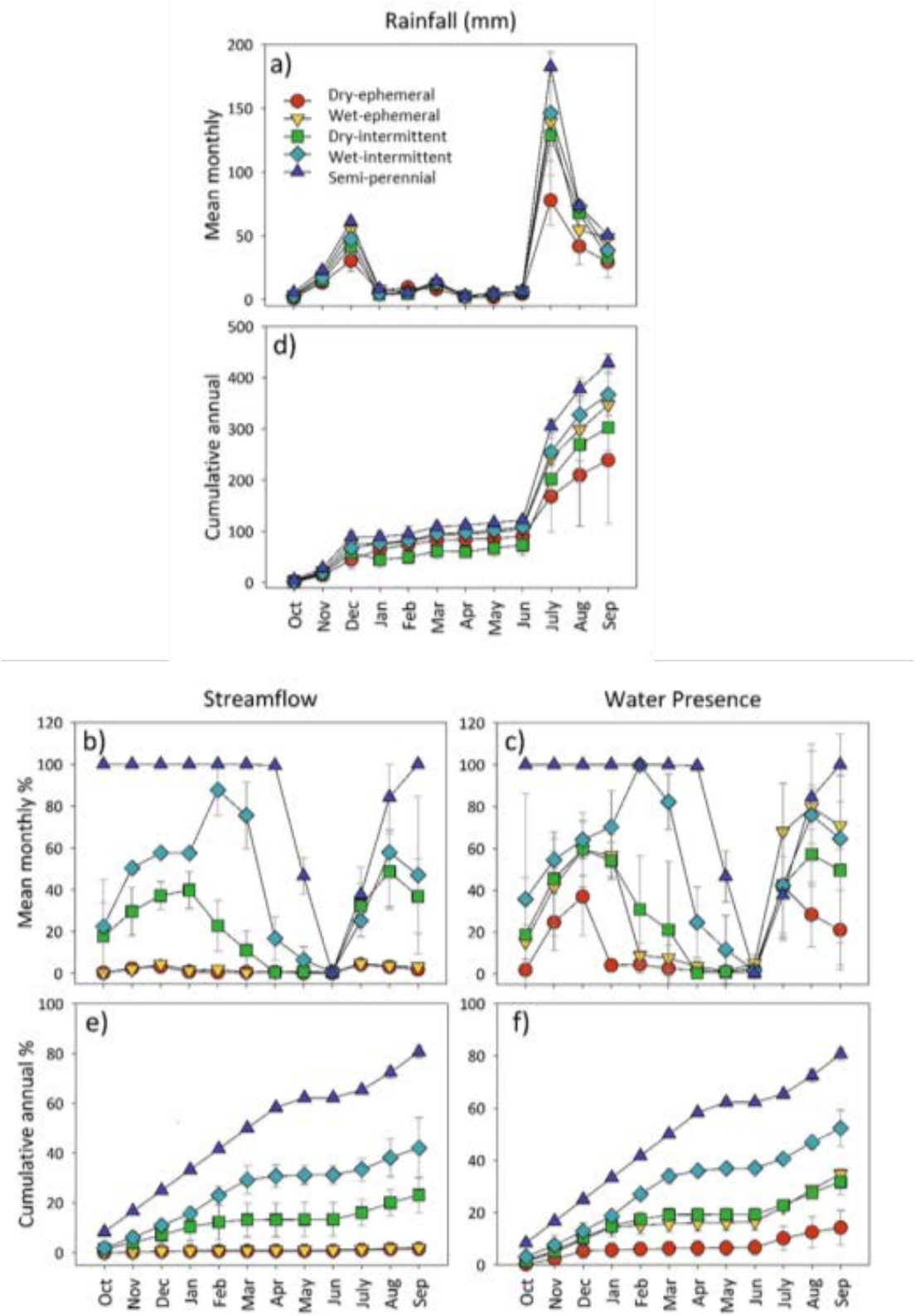

Fig. 4.5. Mean monthly and cumulative annual values for rainfall, percent stream flow, and percent water presence for each stream type. Bars are standard deviation.

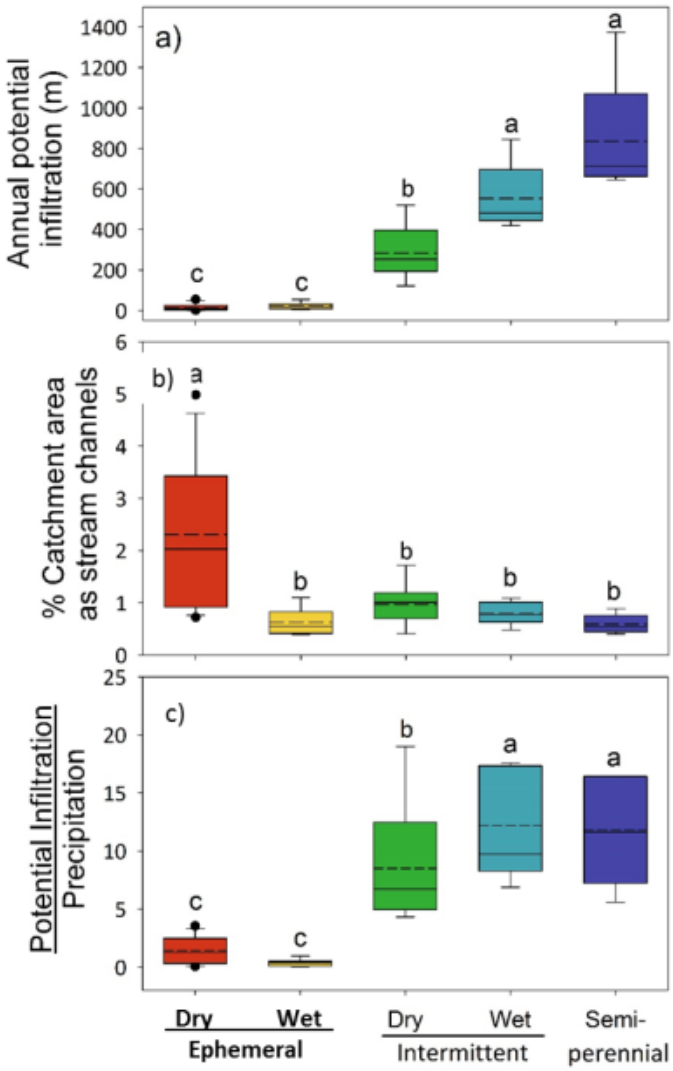

Fig. 4.6. Box plots of annual infiltration depth, percent of catchment that is comprised of stream channels, and ratio of total annual potential infiltration to precipitation, by stream flow type. Dashed lines denote means, solid lines denote medians. Box plots with distinct small case letters have significantly ($p < 0.05$) different means.

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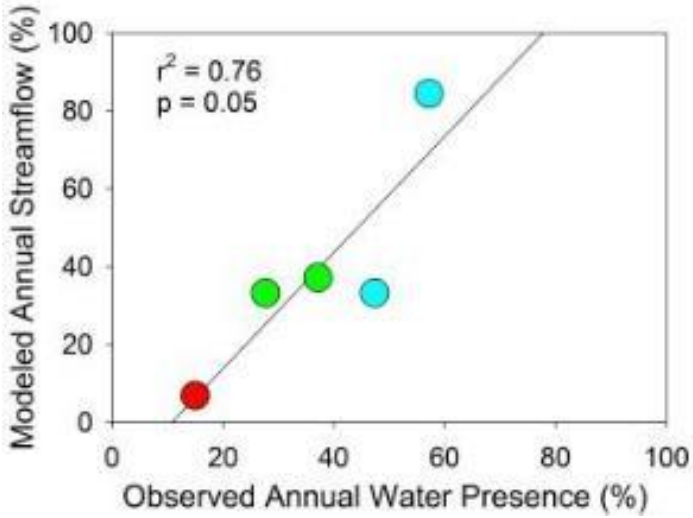

Fig. 4.7. Correspondence between annual stream flow presence as predicted by models and as measured in the field.

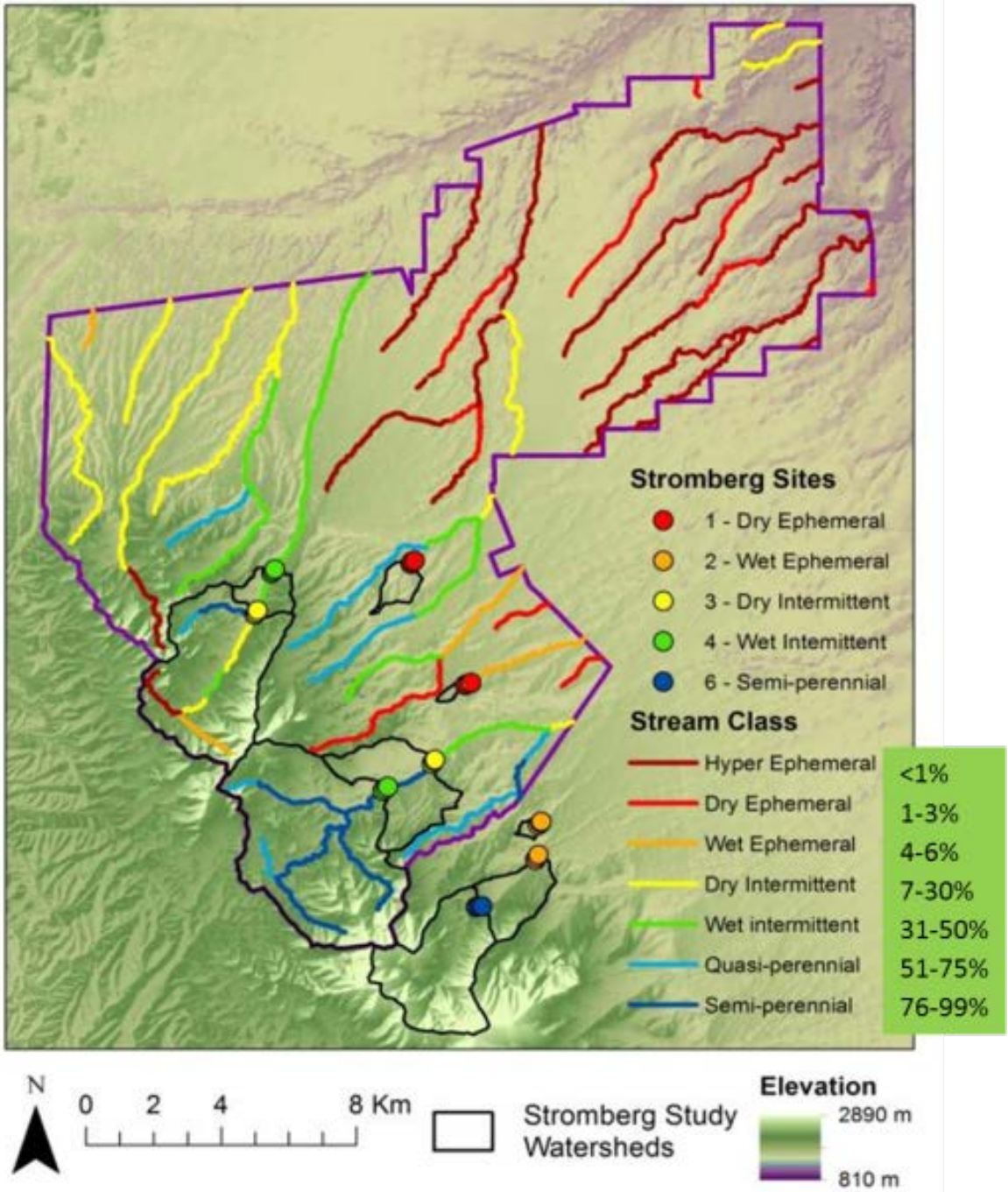

Fig. 4.8. Modeled stream flow of mapped streams within Fort Huachuca. Stromberg study sites are shown as circles, and black lines show catchments. Stream class indicates the percent of time a stream has surface flow.

Discussion

Here we quantify stream flow and stream water presence in streams exhibiting temporary flow across a wide climate gradient. We show a coupling of landscape characteristics and the magnitude and timing of rainfall in controlling flow regimes at a regional scale. At this scale, stream channel density is a better predictor of stream flow and water presence than rainfall alone. Based on the percent of time stream flow and water presence occurred at our sites we identified five distinct flow regimes: 1) dry-ephemeral, 2) wet-ephemeral, 3) dry intermittent, 4) wet intermittent and 5) semi-perennial. We show that water availability as soil moisture and/or surface ponds can be 4 to 33 times greater than the duration of stream flow at the driest sites, which has important implications for biogeochemical processes. We document variable responses to the magnitude and temporal distribution of rainfall among flow regime groups, with the most responsive sites to precipitation being those classified as ephemeral. These sites exhibit a bimodal stream flow and water presence distribution similar to that of the regional precipitation, with the highest stream flow and water presence occurring during the summer and fall months. In contrast, flow regimes in the dry-intermittent, wet intermittent and semi-perennial flow classes did not significantly vary with or increase with seasonal rainfall, and were highest at the wet-intermittent and semi-perennial sites in the winter months. The seasonal responses to rainfall, potential infiltration estimates and the ratio of potential infiltration to rainfall indicate that stream flow at the driest sites likely occurs in response to rainfall and overland flow, whereas groundwater discharge and vadose zone contributions may enhance stream flow at the wetter sites. This study highlights the high degree of variability in stream flow regimes at the regional scale across a climate gradient. Our data suggests that on a short temporal scale, and with respect to water presence, wetter sites might be overall better buffered against shifts in the timing and distribution of precipitation in response to climate change. However, additional studies should aim to identify how land cover characteristics and antecedent moisture alter flow regimes, particularly in the drier sites, where stream flow is highly sensitive to rainfall.

Chapter 5: Variation in Ephemeral Stream Vegetation Along an Aridity Gradient

Q1: How does Ephemeral Stream Vegetation Vary along an Aridity Gradient?

As aridity increased (Table 5.1), riparian-zone vegetation volume decreased (Fig. 5.1). Values averaged 0.48 m^3/m^2 at semihumid Huachuca and 0.27 m^3/m^2 at arid Goldwater. The proportional distribution of vegetation volume among woody and herbaceous types also differed with aridity, owing to different trends among the vegetation types: herbaceous vegetation volume in the riparian zone increased as sites became more humid, whereas woody vegetation volume remained constant along the aridity gradient (Fig. 5.2). Average maximum vegetation height, surprisingly, was greatest at the arid site.

Vascular plant species and family richness varied along the aridity gradient (Fig. 5.3). At arid Goldwater, the greatest seasonal species richness was only 33±9 (March, 2012) compared to 71±2 at semihumid Huachuca (September, 2011); values at semiarid Santa Rita were intermediate. Through time (four seasons), an average of 48 plant species was sampled in the riparian/channel zone at Goldwater compared to 104 at Huachuca; respective values for the combined tally of two streams per site were 65 species (in 19 families) and 147 species (in 35 families). Species richness was more temporally variable at the arid sites (mean coefficient of variation of 0.56±0.01 at Goldwater and 0.46±0.03 at Huachuca).

The distribution of species among growth forms and life forms differed among aridity zones. Eighty-four percent of the species sampled in the riparian/channel zone of the arid site were annuals, with the remainder being small trees, shrubs, or stem succulents (Table 5.2). Semihumid Huachuca, in contrast, was vegetated primarily by herbaceous perennials (51% of species) with annuals comprising only 33%. The proportion of woody species in the flora was greater at the arid sites (Fig. 5.2).

Q2: Does Riparian Vegetation Become more Distinct from Matrix Vegetation as Aridity Increases?

As aridity increased, riparian vegetation became more distinct from the matrix vegetation in several ways. First, although vegetation volume was greater in the riparian zone than uplands at all sites, the between-zone difference was greatest where it was arid (delta of 0.5 m^3/m^2 at Goldwater and 0.2 m^3/m^2 at Huachuca (Fig. 5.2). Second, more species were present in the riparian/channel zone than uplands, but the greatest inter-zonal difference occurred where it was arid. There were 58% more species (and 36% more families) in the riparian/channel zone than surrounding piedmont at Goldwater (four season, two stream totals) but only 28% more species and 13% more families for the respective comparisons at Huachuca (Fig. 5.3)

. Temporal variability in plant species richness was greater between zones at the arid sites. At arid Goldwater, seasonal variability in species richness was considerably higher in the uplands (coefficient of variation of 0.70±0.01) than in the riparian zone (0.56±0.01). In contrast, the coefficients of variation were nearly identical among zones at semihumid Huachuca (0.57±0.03 upland, 0.54±0.02 riparian).

Compositional similarity between the riparian and upland zones was greatest at the semihumid sites (Fig. 5.4). At semihumid Huachuca, many of the same herbaceous species were present in the upland and riparian zones even during the dry season, thereby increasing inter-zonal similarity. During the driest sampling season at arid Goldwater, in contrast, no herbaceous species were detected in either zone: upland vegetation consisted largely of the shrub creosote

bush (*Larrea tridentata),* whereas the riparian zone supported several small legume trees and various shrubs and stem succulents.

Focusing just on herbaceous ground cover, there was a pronounced difference in evenness between riparian and upland zones only at the semihumid site (Table 5.3; Fig. 5.5). In the riparian zone of the near-Huachuca stream, five species shared dominance during the summer wet season- the native annuals Arizona signalgrass (*Urochloa arizonica),* Mexican panicgrass *(Panicum hirticaule),* tapertip cupgrass (*Eriochloa acuminata),* and fragrant flatsedge (*Cyperus odoratus),* and the introduced perennial Lehmann's lovegrass (*Eragostis lehmanniana).* In the uplands, in contrast, *E. lehmanniana* was a clear dominant. In the riparian zone of the near-Garden stream, the dominants were *P. hirticaule, E. lehmannniana*, and the rhizomatous forb Cuman ragweed (*Ambrosia psilostachya)*; *E. lehmanniana* was a clear dominant in the uplands, with the perennial forb Jewels of Opar (*Talinum paniculatum)* also abundant. For the ephemeral stream near Ramsey Canyon, the introduced perennial giant spear grass (*Trachypogon spicatus)* was the clear dominant in the uplands whereas in the riparian zone *T. spicatus* shared dominance with *E. lehhmanniana,* and the annuals *P. hirticaule,* erect spiderling (*Boerhavia erecta),* and white girdlepod *(Mitracarpus breviflorus).*

Q3: Which Plant Species and Families are more Abundant along Ephemeral Streams?

At each study area, several species were sampled exclusively in the riparian zone (Fig 5.6, Fig. 5.7, Appendix 2 and 3). At Goldwater, sixteen percent of species (11 of 70), including the woody taxa burrobrush (*Ambrosia salsola),* water jacket (*Lycium andersonii),* ironwood *Olneya tesota,* blue palo verde *(Parkinsonis florida),* and velvet mesquite (*Prosopis juliflora* var. *velutina*), and several annuals *w*ere sampled exclusively in the riparian/channel zone. Only one species was sampled more frequently in the uplands. At Huachuca, eleven percent (24 of 211) of species sampled at three sites were exclusive to the riparian/channel zone, with most of these being annuals or herbaceous perennials. No species were exclusive to the upland zone. (Infrequent species were excluded from these calculations). Rutter's fasle goldenaster *(Heterotheca rutteri),* a rare taxon and a species of concern, was sampled in the upland and riparian zone of the near-Ramsey ephemeral stream.

At the arid sites, the family structure was similar between zones with one notable exception. Common families in the riparian/channel at arid Goldwater were Boraginaceae (11 species), Fabaceae (10 species), Asteraceae (nine species), Brassicaceae (six species), and Onagraceae (five species). In the uplands, Fabaceae were much less frequent (one species), but Asteraceae (10 species) and Boraginaceae (nine species) remained common. Family structure was similar between zones at Fort Huachuca: Common families in the riparian/channel zone were Poaceae (28 species), Asteraceae (25 species), Fabaceae (15 species), Euphorbiaceae (ten species), and Amaranthaceae (nine species). Common families in the uplands were Poaceae (23 species), Asteraceae (21 species), Fabaceae (12 species), Convolulaceae (seven species), and Euphorbiaceae (six species).

Table 5.1. Attributes of seven ephemeral study streams. Black Gap Wash and Sauceda Wash are in the Barry Goldwater Range, Small and Large Santa Rita are in the Santa Rita Experimental Range, and the remaining three are in the Huachuca Mountains.

Site name	Elevation (m)	Mean precip. (mm)	Mean temp. (°C)	Aridity Index	Catchment area (km^2)	Surface flow (% of time)	Latitude, longitude (decimal degrees) (N, W)
Black Gap Wash	324	97	22.3	3.0	10	0.6	32.711123, 112.831066
Sauceda Wash	258	97	21.6	3.1	326	1.1	32.878405, 112.752874
Small Santa Rita	947	227	19.0	7.8	2	1.1	31.885414, 110.88042
Large Santa Rita	952	227	18.1	8.1	18	2.0	31.880545, 110.883672
Piedmont- Huachuca	1453	293	16.7	11.0	1.3	1.9	31.540278, 110.334113
Piedmont- Garden	1494	335	16.6	12.6	0.5	2.0	31.506705, 110.316744
Piedmont- Ramsey	1533	397	16.3	15.1	0.3	1.3	31.468538, 110.294548

Table 5.2. Percent distribution of plant species by growth form. Data based on two streams and four sampling times per aridity zone.

	Arid (Goldwater)		Semihumid (Huachuca)	
	Rip./Chan	Upland	Rip./Chan.	Upland
Annuals (%)	53 (84%)	39 (95%)	49 (33%)	31 (27%)
Herbaceous perennials (%)	0 (0%)	0 (0%)	71 (51%)	66 (58%)
Vines (woody or herbaceous) (%)	0 (0%)	0 (0%)	9 (6%)	9 (8%)
Stem or leaf succulents (%)	1 (2%)	0 (0%)	4 (3%)	0 (0%)
Shrubs (%)	4 (6%)	2 (5%)	12 (6%)	6 (5%)
Trees (%)	5 (8%)	0 (0%)	2 (1%)	1 (1%)
Unknown	2 (3%)	0 (0%)	0 (0%)	1 (1%)
Sum	63 (100%)	41 (100)	147 (100%)	114 (100%)

Table 5.3. Diversity measures, by sampling season and sampling zone, for herbaceous ground cover of ephemeral streams. Values are means and standard error of two sites per aridity zone (BG= Barry Goldwater; HU= Huachuca). Ten, 1x1 m^2 plots were sampled in riparian (rip.) and upland (upl.) zones.

	Shannon Diversity Index		Evenness (Simpson's E)		Species Richness	
	Rip.	Upl.	Rip.	Upl.	Rip.	Upl.
BG- April 2010	2.5(0.2)	1.8(0.4)	4.9(1.5)	4.4(2.0)	19(3)	16(6)
BG- Sept. 2010	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0(0)	0(0)
BG- March 2011	1.6(0.1)	1.1(0.5)	4.4(0.5)	3.2(1.2)	6(1)	4(2)
BG- Sept. 2011	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0(0)	0(0)
BG- March 2012	2.1(0.0)	1.9(0.1)	6.3(0.5)	5.4(0.0)	15(2)	12(3)
BG- Sept. 2012	0.0(0.0)	0.5(0.5)	0.5(0.5)	1.7(0.7)	1(1)	2(1)
HU-June 2010	1.5 (0.4)	1.6(0.1)	1.5(0.4)	1.6(0.1)	21(4)	18(2)
HU-May 2011	0.6 (0.3)	0.6(0.2)	0.2(0.0)	0.3(0.1)	8(3)	8(1)
HU-Sept. 2011	2.8(0.1)	2.4(0.2)	11.1(1.7)	5.5(1.7)	40(1)	39(2)
HU- Sept. 2012	2.6(0.4)	1.6(0.2)	8.4(3.7)	2.5(0.4)	43(12)	28(5)

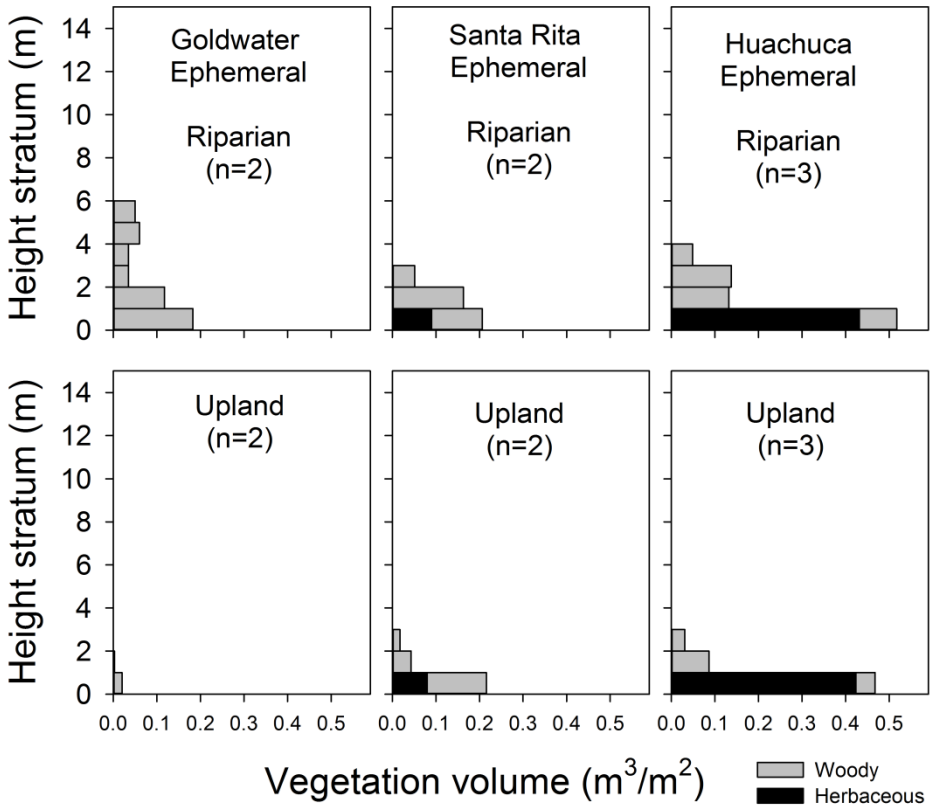

Fig. 5.1. Vegetation volume, by height strata, for ephemeral stream riparian zones and adjacent uplands. Aridity of the stream location increases from left to right.

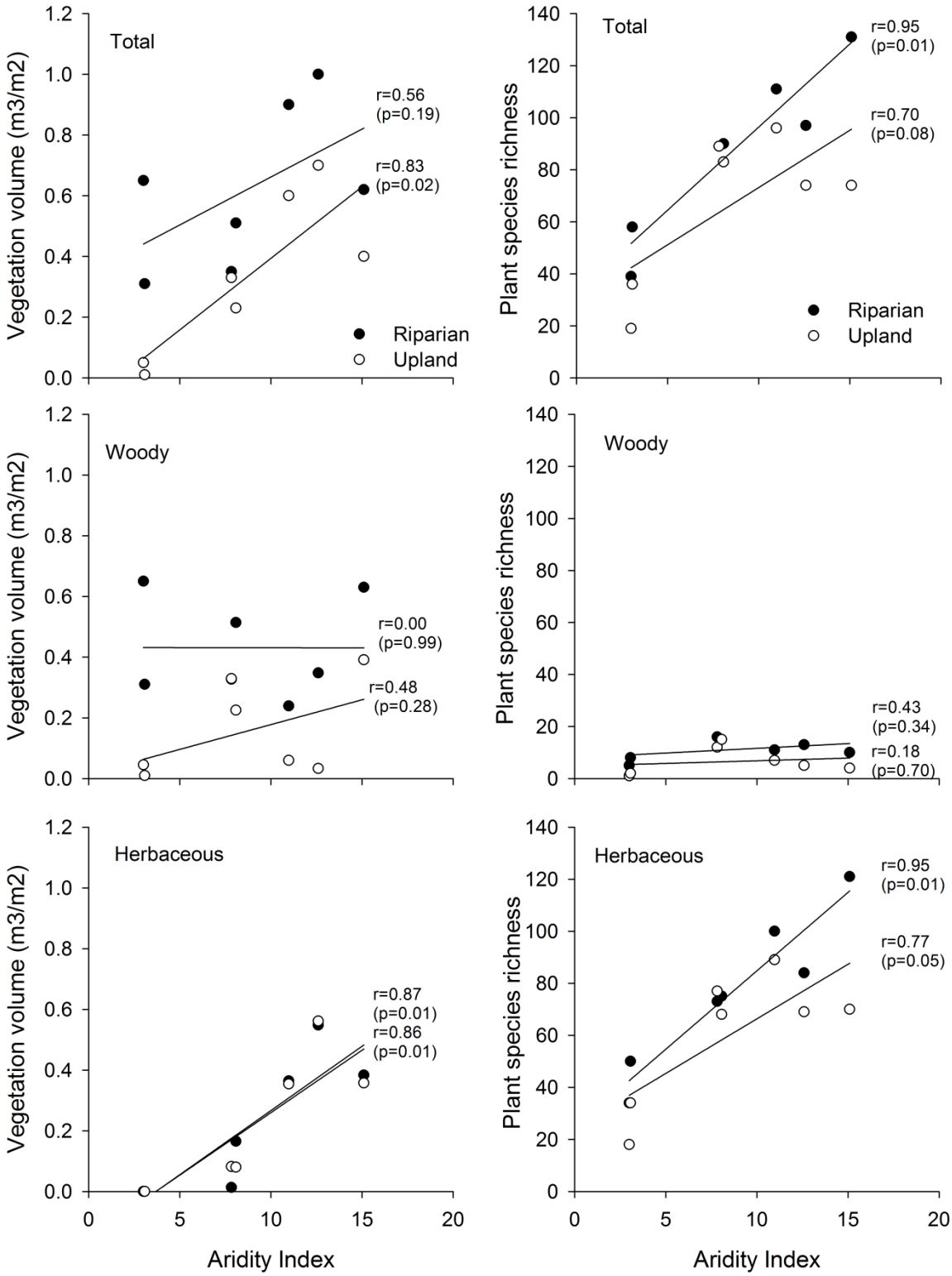

Fig. 5.2. Vegetation volume and plant species richness in relation to Aridity Index. Values are shown for riparian zones of seven ephemeral streams and adjacent uplands. Species richness is a four-season total. Also shown are Pearson correlation coefficients ("r" values).

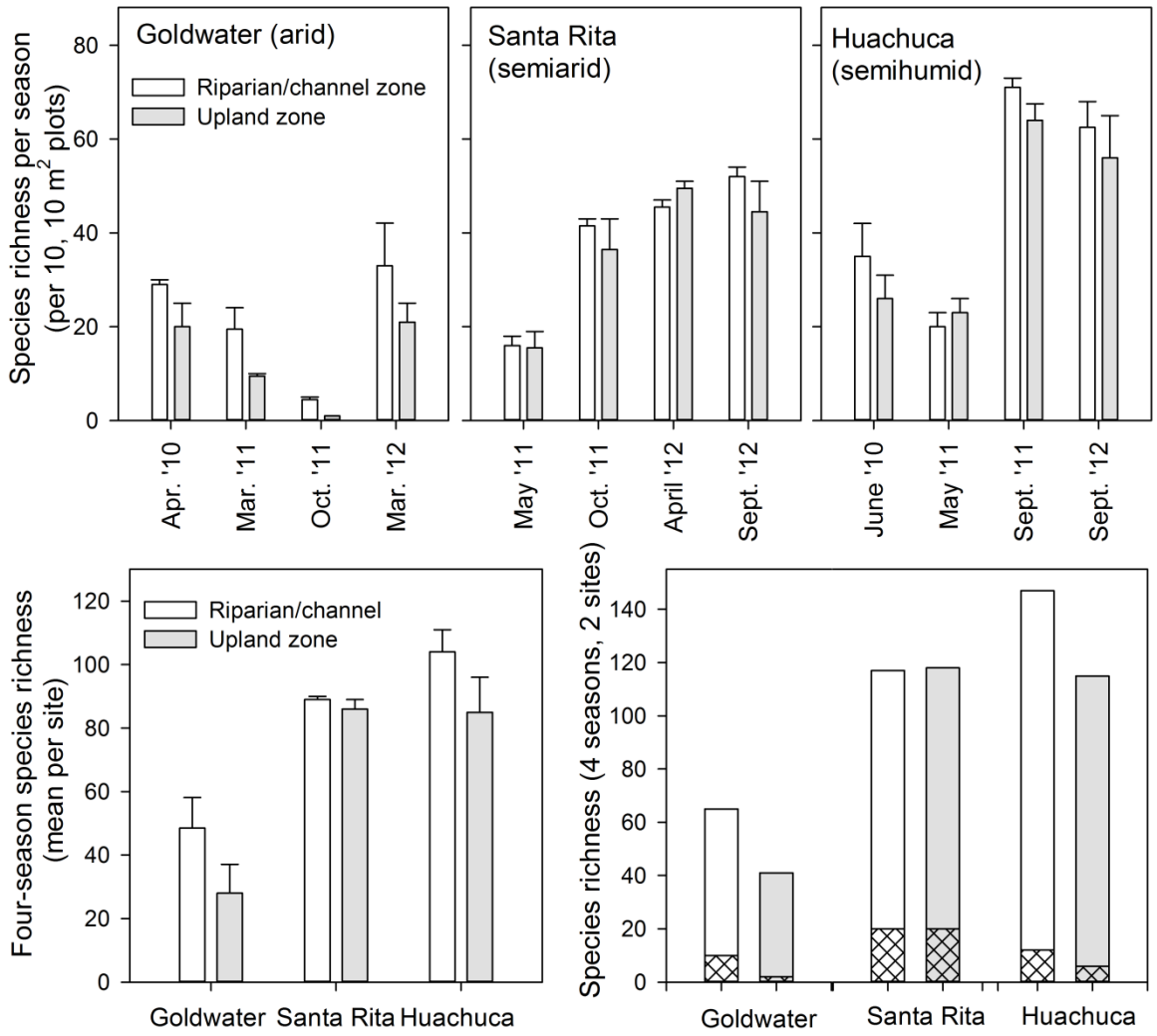

Fig. 5.3. Plant species richness comparison among aridity zones. Top panel: Mean plant species richness, by season and sampling zone, for two ephemeral streams per aridity zone (10, 10-m^2 plots sampled per zone per season). Bottom left: Mean cumulative plant species richness per site across four seasons. Bottom right: Total richness across sites (hatch marks indicate woody taxa).

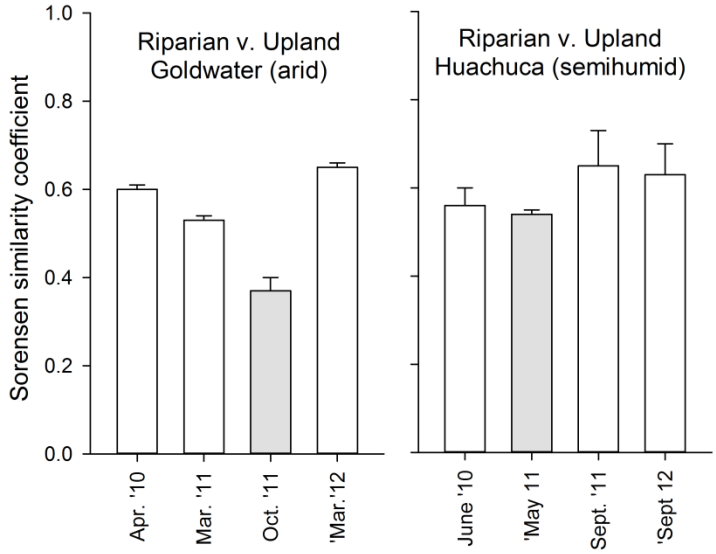

Fig. 5.4. Sørensen similarity coefficients between riparian/channel and upland zones. Values are means (with standard error bar) of ten, $10m^2$ plots per zone and per season. The coefficient ranges from zero (no similarity) to one (complete similarity). Gray fill indicates the driest sampling time per region.

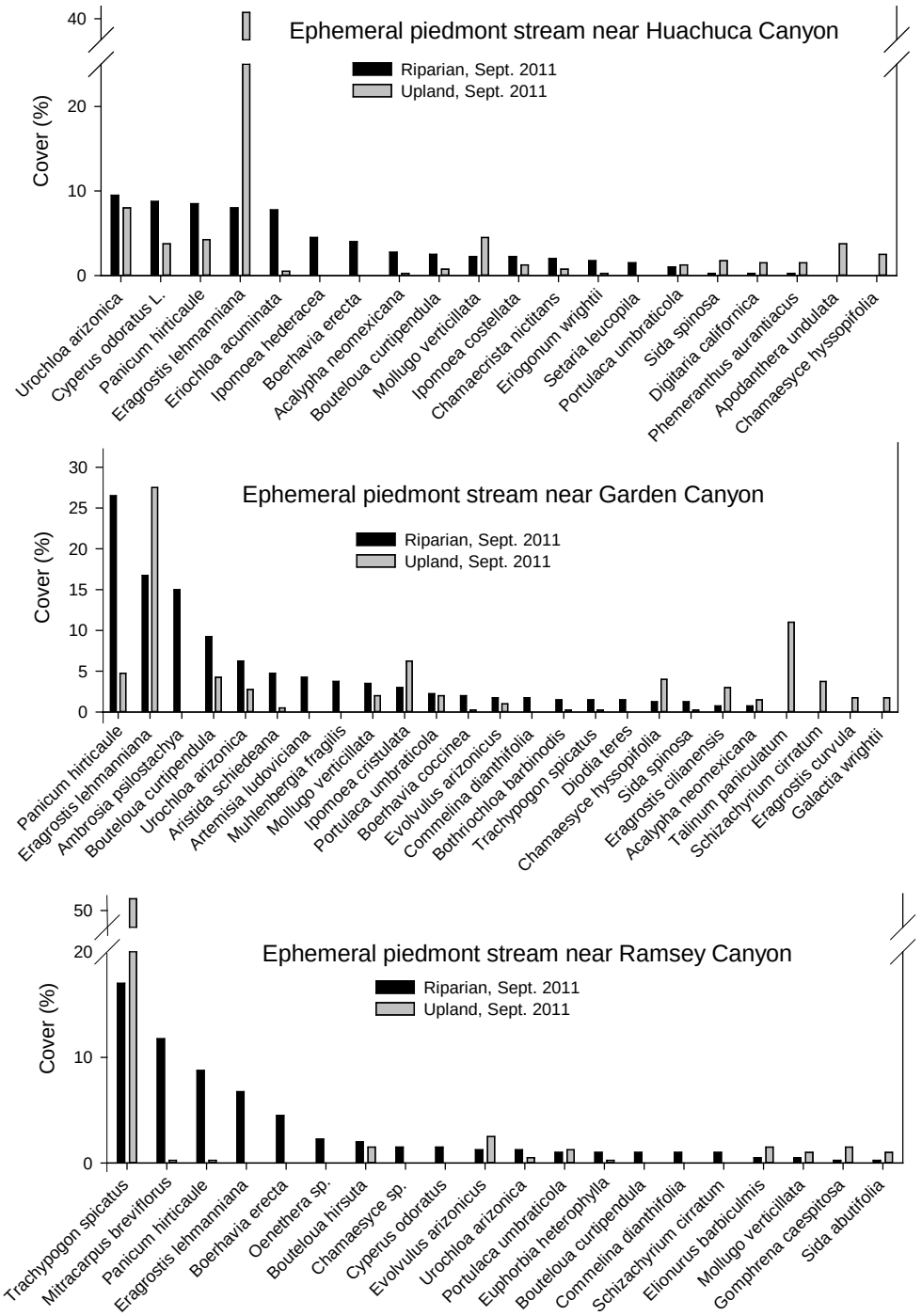

Fig. 5.5. Ground cover of herbaceous plant cover within the riparian zone and adjacent upland of three ephemeral streams in the Huachuca Mountains. Data were collected during September of 2011. Species are listed in descending order from most to least abundant within the riparian zone. Plants with less than one percent cover are not shown.

Fig. 5.6. Examples of plant species more frequent in the upland zone (A) and the riparian zone (B) of Goldwater sites, and in the upland zone (C) and riparian zone (D) of Huachuca sites. Photographs from SEINet.

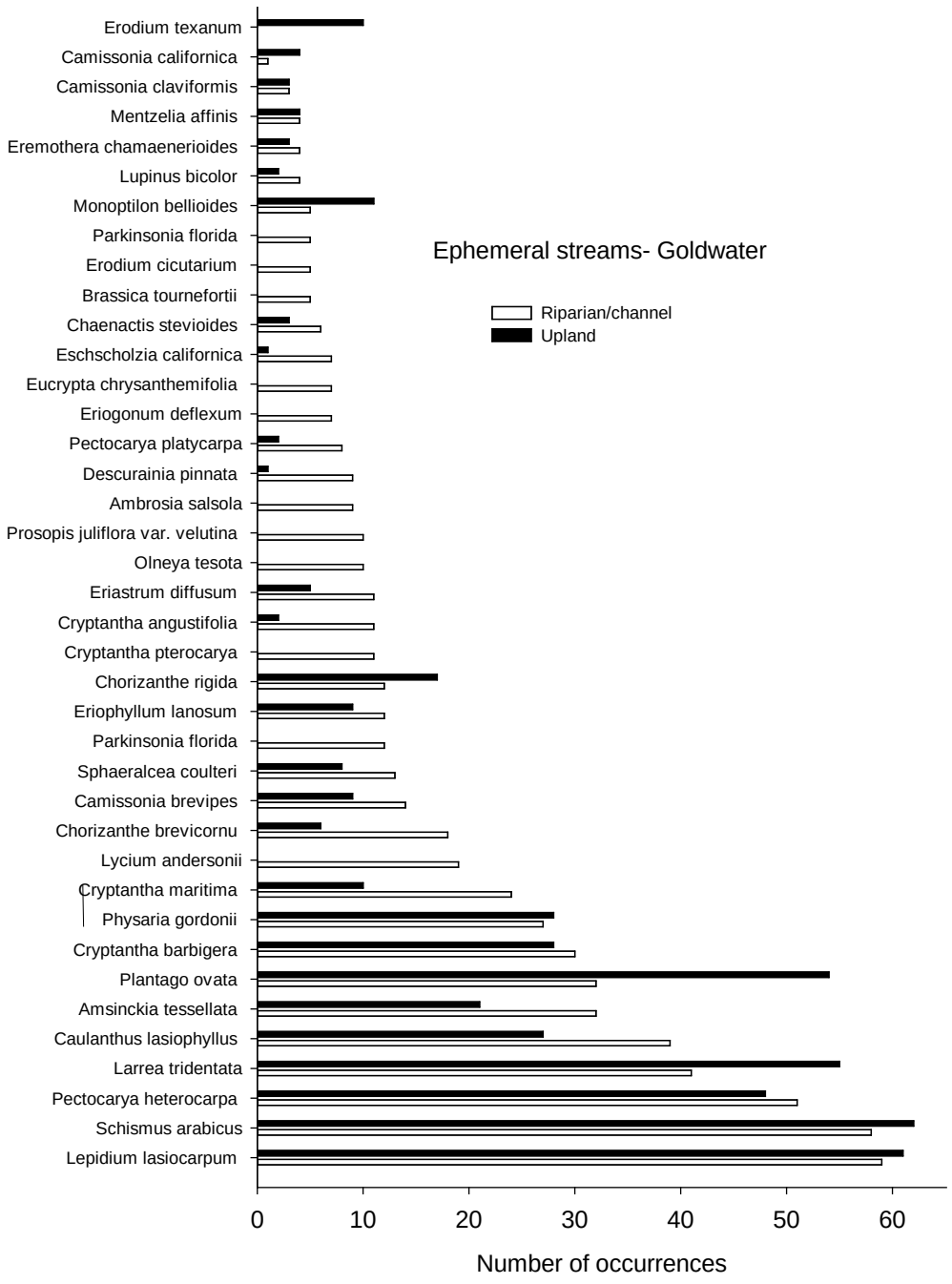

Fig. 5.7. Number of occurrences of plants sampled in riparian and upland zones of arid Goldwater. Maximum possible occurrence per species is 80 (two sites x four times x 10 plots). Plants with less than five occurrences are excluded from the figure.

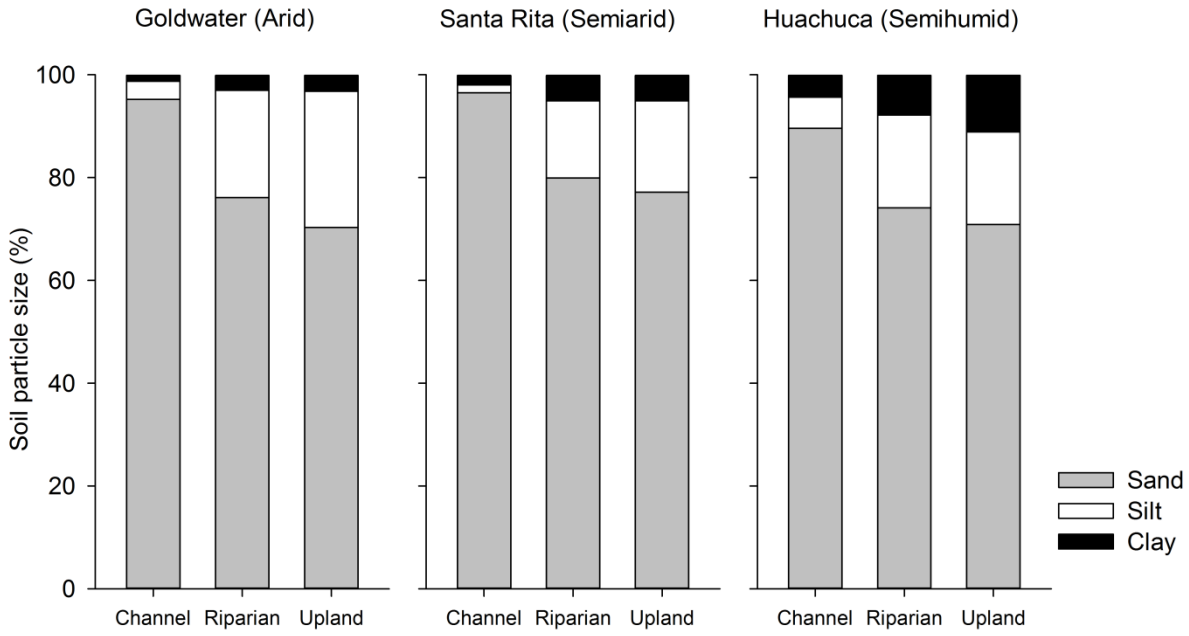

Fig. 5.8. Percentages of sand, silt and clay in three topographic positions of three study areas.

Discussion

This study examined attributes of ephemeral stream plant communities along a spatial climatic aridity gradient. By keeping surface flow constant, we provide a broad look at differences attributable to direct effects of aridity. We conclude that the following changes will occur through time as climatic aridity increases in the American Southwest. As aridity increases, the riparian zone of ephemeral streams will have increasingly less vegetation volume, greater proportional abundance of woody (versus herbaceous) vegetation, fewer plant species, a higher percentage of annual species in the flora, and greater variance between years in species richness. If urbanization encroaches on the ephemeral streams, these changes either will be exacerbated by the increased temperatures that accompany the urbanization or be mitigated by increased urban runoff (Martin et al. 2012; Hutmacher et al. 2014).

Ephemeral washes, despite having only infrequent stream flow, are 'hot spots' of productivity and diversity in the arid and semiarid American Southwest. They had greater vegetation volume and supported more plant species than the surrounding desert or semidesert uplands, with these differences greatest at the most arid sites. Burquez et al. (2010) similarly reported a large (four-fold) difference in above-ground-biomass between a Sonoran Desert arroyo (ephemeral stream) and the plains (uplands). At the semiarid and semihumid sites, in contrast, the abundant summer rains minimized the differences between the riparian and upland zone (with both zones supporting savannahs). Based on this and other findings we conclude that the vegetation in the uplands and riparian zone will become increasingly dissimilar as the climate became more arid.

Upland and riparian zones differ fundamentally in their water sources. Whereas plants in the uplands typically are pluviophytes that rely solely on seasonal infiltration of rain into soils, the riparian vegetation of ephemeral streams has an additional water source- infrequent floods that wet the floodplain soils, sustain short-term stream flows, and induce development of a shallow perched water table (Atchley et al. 1999; Rassam et al. 2006). The seasonal differences in volumetric soil water content between the ephemeral stream margin and the matrix vegetation can be small, but the additional water reduces plant water stress and allow for persistence of shrubs and small trees (Virginia et al. 1992; Smith et al. 1995; Free et al. 2013). This supplemental water source is critical for sustaining the small xerophytic legume trees (*Prosopis, Olneya, Parkinsonia*) that provide the major biomass structure of the arid region washes (Johnson et al. 1984). Woody vegetation presumably is relying on deep-stored 'riparian' water sources whereas herbaceous vegetation is relying on direct precipitation, leading us to conclude that the direct effects of regional increases in aridity will be more pronounced for herbaceous vegetation than for woody vegetation.

Precipitation is highly temporally variable in arid regions (Sponseller et al. 2012). Plant diversity and ground cover are sparse for much of the year at arid sites, punctuated by bursts of activity following rain and runoff events. Low amounts of precipitation, as well as high coefficient of variation in mean annual precipitation, favors annual plants (Comstock and Ehleringer 1992). Short-lived annual plants, sometimes referred to as ephemerals, predominated in the riparian and upland zones of the arid site after rains. Their seasonal pulses of abundance are consistent with the "storage effect" concept wherein short-lived plants emerge from the soil only in response to adequate amounts and timing of rainfall (Facelli et al. 2007). Factors contributing to the greater diversity of annuals in the riparian zone versus upland may include wetter soils, differences in soil particle size (Fig. 5.8), and reduced evaporative stress arising from the transpiration of the legume trees. Further, it is feasible that there are differences in bet-

hedging strategies between upland and riparian populations, wherein the latter germinate more frequently and thus have greater detection rate in any given season (Gremer et al. 2014).

Composition of the matrix plant community influences the plant species present in desert washes (Levi and Fehmi 2014) and the converse is presumably true, as well. In our study system we observed high overlap in species composition between desert washes and uplands, with the degree of similarity increasing at sites with higher rainfall and thus with the percentage of rain-dependent species. High overlap is typical for small desert washes (Leitner 1987; Bloss and Brotherson 1979; Warren and Anderson 1985). That said, the ephemeral streams did sustain several plant species not found in the uplands, as well as larger populations of species that were infrequent in adjacent uplands. Ephemeral streams, with their supplemental moisture from winter or summer flood pulses and unique species, thus increase regional diversity (Sabo et al. 2005). They also may function as reservoirs for regional diversity by maintaining populations of plants that are declining in the uplands because of seasonal or long-term drought (Gitlin et al. 2006; McAuliffe and Hamerlynck 2010). For example, *Bouteloua curtipendula* is one perennial grass species that is expected to decline in cover in the American Southwest in response to decreasing summer precipitation (Munson et. al 2013). The role of ephemeral streams as diversity reservoirs for drought-sensitive regional species may become increasingly important as climatic aridity intensifies.

Diversity of ephemeral streams is influenced by moisture and by fluvial disturbance. Periodic scour and sediment transport during floods create opportunities for species turnover and suppress dominance by any single species. This was particularly evident in the semihumid setting, where the summer monsoon rains produce large seasonal runoff events (Sheppard et al. 2002). In this setting, the riparian zone of the ephemeral streams had greater evenness of species compared to the uplands. If storms intensify in the region, this pattern will become more pronounced. Of note, introduced Lehmann's lovegrass, a species of concern to many managers, was dominant in the uplands of the Huachuca Mountain piedmont zone. This grass was widely seeded onto overgrazed rangelands in the mid 1900s and is currently viewed by some as an over-abundant nuisance species. Its populations over recent decades have fluctuated but in many semidesert uplands it remains as the dominant species (Morris et al. 2013). The many small washes that flow through the semidesert grasslands serve to fragment the upland grass patches and allow other species to coexist in higher numbers with Lehmann's lovegrass. The ephemeral streams of the Huachuca Mountains support populations of several other "native" species of grass including E. intermedia.

Individually and collectively, the many small, unnamed washes in the mountain piedmonts and alluvial basins of the American Southwest, which can be readily overlooked in the landscape, have high conservation value owing to their high productivity and diversity compared to the matrix vegetation. Over large spatial scales, Warren and Anderson (1985) reported greater richness of species in desert washes versus uplands, attributed to greater variability at the landscape scale in the factors that influence diversity (Shaw and Cooper 2008). At the smaller spatial scales of our study we also detected more plant species in the riparian zone. Ephemeral washes and adjacent lands do not always differ in diversity, however. Leitner (1987) found similar numbers of species in the upland canyon slopes and the riparian zones of ephemeral streams in Punto Cirio, Mexico. The rocky slopes, with water stored in fractured bedrock, can be wetter and more species-rich than the upland piedmonts and alluvial basins examined in our study.

Inferring temporal changes from spatial patterns must be done with caution. For example, $C0_2$ fertilization may offset projected declines in grass cover resulting from aridity increase

(Notaro et al. 2012). Further, historic legacies of land use, including livestock grazing, and disequilibria notions must be taken into account in predictions of change. In the Sonoran Desert (inclusive of ephemeral streams), perennial grasses may have been a larger component of the vegetation prior to the intensive period of unregulated cattle grazing that occurred during the early 1900s. Some studies in the Sonoran Desert indicate that grasses are increasing and shrubs are declining, suggesting that the ecosystem is rebounding from past landscape use and soil changes (Bagchi et al. 2012). Our conclusions also are tempered by the fact that significant change in ecosystems, such as shifts in growth form or species dominance, can be a result of extreme weather events such as major floods or drought rather than of cumulative stresses (Weltzin and McPherson 2000).

Chapter 6: Plant Diversity and Biomass Along a Stream Flow Gradient

Q1: Does Plant Species Richness Increase with Stream Flow Permanence and Groundwater Availability?

Riparian-zone plant species richness (five-season total) ranged among sites in the Huachuca Mountains from a high of 137 (ephemeral piedmont stream near Ramsey Canyon) to a low of 55 (Ramsey Canyon, upper canyon). As indicated by general linear models, richness was significantly related to shallow water table presence (fewer species at phreatic sites) and drainage basin size (more species in larger basins) (Table 6.1).

Distinct plant growth forms differed in their response to the hydrological variables (Table 6.1, Fig. 6.1). Twenty-one of 366 species sampled across three seasons were trees, and tree species richness was positively related to both surface and subsurface hydrology. The presence of shallow ground water explained most of the variability, with the percentage of time that surface flow was present also contributing to the model. Where a shallow water table was present, the number of tree species present ranged among sites from six to 10 including Arizona madrone (*Arbutus arizonica),* Arizona walnut *(Juglans major),* Alligator juniper *(Juniperus deppeana),* Arizona sycamore *(Platanus wrightii),* gray oak *(Quercus grisea),* and silverleaf oak (*Quercus hypoleucoides*); where not present, numbers ranged from one to two (Emory oak, *Quercus emoryi; P. velutina*). Considering only obligate riparian trees (such as Arizona ash, *Fraxinus velutina; J. major;* and *P. wrightii*), a similar positive relationship with stream flow was evident.

Herbaceous species comprised two-thirds of the taxa with 132 annuals and 134 herbaceous perennials. Given the abundance of herbaceous species in the flora, they heavily weighted patterns for total species richness, which showed a negative relationship with stream flow (with the slope of the relation between site species richness being steepest in September, 2011, the wettest of the seasons analyzed; Fig. 6.2). Herbaceous species, annuals in particular, also increased in abundance at non-phreatic sites and at sites draining larger watersheds. Another 27 species were suffrutescent plants or subshrubs (e.g., fairyduster, *Calliandra eriophylla;* wooly senna, *Senna hirsuta*) and 28 were shrub species including false indigobush, (*Amorpha fruticosa),* four species of *Baccharis,* Wilcox's barberry *(Berberis wilcoxii), Wright's silktassel (*Garrya wrightii*),* sacahuista *(Nolina microcarpa),* fragrant sumac *(Rhus aromatica),* and poison ivy *(Toxicodendron radicans*). Shrub species showed no pattern with stream hydrology. Suffrutescent plants shared a pattern with the annuals in having greater species numbers at non-phreatic sites.

Q2: Does Vegetation Abundance Increase with Stream Flow Permanence and Groundwater Availability?

Canopy cover ranged widely among sites, from 14±10% to 92±4% (mean ± SE), as did vegetation volume (<1 m^3/m^2 to >4 m^3/m^2). Both variables were significantly related to the presence of shallow water table at a site, with marked differences between the six phreatic sites and the three non-phreatic sites (Table 6.2, Fig. 6.3). Stream flow duration contributed to the model for canopy cover, with the relation being positive. Herbaceous cover and herbaceous biomass, as averaged across seasons, also were significantly related to presence of shallow water table at a site. For these variables, in contrast, values were greater at sites without shallow water tables.

Q3: How Seasonally Variable is Herbaceous Riparian Vegetation?

Precipitation and stream flow varied among years and seasons of the study. Of the three study years, 2010 was the wettest (Fig. 6.4). 2010 was an El-Nino year, with above average winter precipitation region wide. The years 2011 and 2012, in contrast, experienced La Nina conditions, with below average winter precipitation. Summer monsoon rains and stream flows were abundant in all three years, although temporal patterns varied among canyons (Fig. 6.5).

Species richness of annuals and herbaceous perennials in particular showed high seasonal and annual variability, with coefficients of variation (for three seasons) ranging among sites from 0.46 to 0.68. The main source of this variability was the late summer monsoon pulse. During 2011, for example, mean species number per site increased from 33±2 in May to 75±5 in September ($t=10.7$, $p<0.01$, $df=8$; paired t-test). Percent herbaceous cover also increased significantly from May to September (27±6 to 60+9, $t=5.4$, $p<0.01$, $df=8$), as did herbaceous biomass (4±1 g/m2 to 8±2 g/m^{2,}, $t=2.0$, $p=0.08$, $df=8$).

Also in response to the summer monsoon pulse, the total number of species sampled across all sites in 2011 increased from 124 in May to 229 in September 2011. (Annuals increased in number from 20 to 82, herbaceous perennials from 60 to 96, and suffrutescents from 11 to 18). Among the many species stimulated by the late summer rains and floods, and sampled only during late summer, were Torrey's craglily (*Echeandia flavescens),* pineywoods geranium (*Geranium caespitosum),* fringeleaf lobelia (*Lobelia fenestralis),* red hoarypea (*Tephrosia tenella)* and several species each of *Bidens, Cyperus, Desmodium,* and *Ipomoea***.** The site with the greatest number of species at any point in time was the ephemeral piedmont stream near Ramsey Canyon, with 104 species in September 2011.

Variability in winter precipitation also contributed to variability in plant cover and richness. More plant species were detected following the unusually wet winter of 2010 (163 in May/June) than during dry 2011 (124 species in May/June). Mean (± SE) site-level plant species richness was 38±3 in May/June of 2010 and 33±2 in May/June of 2011 ($t=1.8$, $p=0.10$, $df=8$; paired t-test). There were few annuals during this season and their numbers did not differ between years (4±1 versus 3±1, $t=1.1$, $p=0.29$, $df=8$), nor did numbers of herbaceous perennials (20±2 in 2010 versus 17±1 in 2011; $t=1.4$, $p=0.18$ $df=8$). Among the species detected in May/June of 2010 but not of 2011 were trailing fleabane (*Erigeron flagellaris),* interior rush *(Juncus interior),* seep monkeyflower *(Mimulus guttatus),* narrowleaf four o-clock *(Mirabilis linearis),* and Hopi tea greenthread (*Thelesperma megapotamicum).*

Q4: Does Woody Plant Abundance influence the Herbaceous Understory?

Herbaceous plants showed a strong negative response to woody plant abundance. Herbaceous cover and biomass, as averaged across seasons, decreased at shadier sites (Table 6.5, Fig. 6.6). Species richness of annuals and of herbaceous perennials (seasonal average) decreased as woody vegetation volume increased.

The strength of the relationships between understory and overstory vegetation varied seasonally, with richness and cover of herbaceous vegetation varying most sharply with overstory cover in wet seasons. Of note, during the monsoon season, herbaceous species richness increased steeply as woody abundance decreased among sites ($r^2=0.75$, Sept. 2010, $r^2=0.59$, Sept. 2011). Herbaceous cover also decreased significantly with woody plant abundance during the monsoon season ($r^2=0.64$, Sept 2010, and $r^2=0.59$, Sept 2011).

May/June herbaceous species richness varied significantly among sites with woody plant abundance only when winter precipitation was abundant ($r^2=0.72$, $p<0.01$. $df=8$; June 2010); no pattern was evident in dry years (Fig. 6.7). Herbaceous cover was sparse in early summer of both

years (24±4 in 2010 and 27±6 in 2011), but still declined among sites as woody plant abundance increased (2010 r^2=0.35, p=0.09; 2011, r^2=0.44, p<0.01, df=8).

Q5: Does Species Richness Vary Among Canyons?

Ramsey Canyon had lower plant diversity than Garden Canyon, when comparing sites with similar hydrological conditions (Fig. 6.8). This is consistent with a prior study showing Ramsey Canyon to have lower plant diversity and a more incised stream channel than Garden Canyon (Richter and Stromberg 2005). Huachuca Canyon also had fewer species than at Garden Canyon. This pattern may be attributable to the lower-than-expected precipitation levels in Huachuca Canyon (Chapter 4).

Table 6.1. General linear models depicting relationships between riparian zone plant species richness and physical variables (drainage basin size, water table presence/absence, and stream flow duration). Dependent variables are average (Avg.) and cumulative (Cum.) richness for three seasons (June 2010, May 2011, Sept. 2011) based on species totals in 15, 10m^2 plots (df=8). NS= Not significant.

Dependent variable		Independent variables	P-value	AIC	model r^2
Tree species richness	Avg.	P/A water table (+)	<0.01	28	0.93
		Stream flow permanence (+)	0.09		
	Cum.	P/A water table (+)	<0.01	32	0.91
		Stream flow permanence (+)	0.09		
Shrub species richness	Avg.		NS		
	Cum.		NS		
Suffrutescents	Avg.		NS		
	Cum.	P/A water table (-)	0.01	46	0.60
Herb. perennials	Avg.	P/A water table (-)	0.01	46	0.67
		Drainage basin size (+)	0.03		
	Cum.		NS		
Annual species	Avg.	P/A water table (-)	<0.01	54	0.78
		Drainage basin size (+)	0.06		
	Cum.	P/A water table (-)	<0.01	69	0.83
		Drainage basin size (+)	0.02		
All plant species	Avg.	Water table (-)	<0.01	55	0.89
		Drainage basin size (+)	<0.01		
	Cum.	P/A water table (-)	<0.01	76	0.75
		Drainage basin size (+)	0.02		

Table 6. 2. General linear models depicting relationships between vegetation abundance and physical variables (drainage basin size, water table presence/absence, and stream flow duration) (df=8).

Dependent variable	Independent variables	p-value	AIC	model r^2
Canopy cover	P/A water table (+)	<0.01	65	0.96
	Stream flow presence (+)	0.09		
Vegetation volume	P/A water table (+)	<0.01	25	0.73
Herbaceous cover*	P/A water table (-)	0.01	11	0.62
Herbaceous biomass*	P/A water table (-)	<0.01	48	0.77

* Seasonal averages

Table 6.3. General linear models depicting relationships between understory and overstory vegetation (df=8).

Dependent variable	Independent variables	p-value	AIC	model r^2
Annual species richness	Vegetation volume (-)	<0.01	53	0.78
Herbaceous perennial richness	Vegetation volume (-)	0.03	47	0.53
Herbaceous cover	Canopy cover (-)	<0.01	68	0.87
Herbaceous biomass	Canopy cover (-)	<0.01	48	0.78

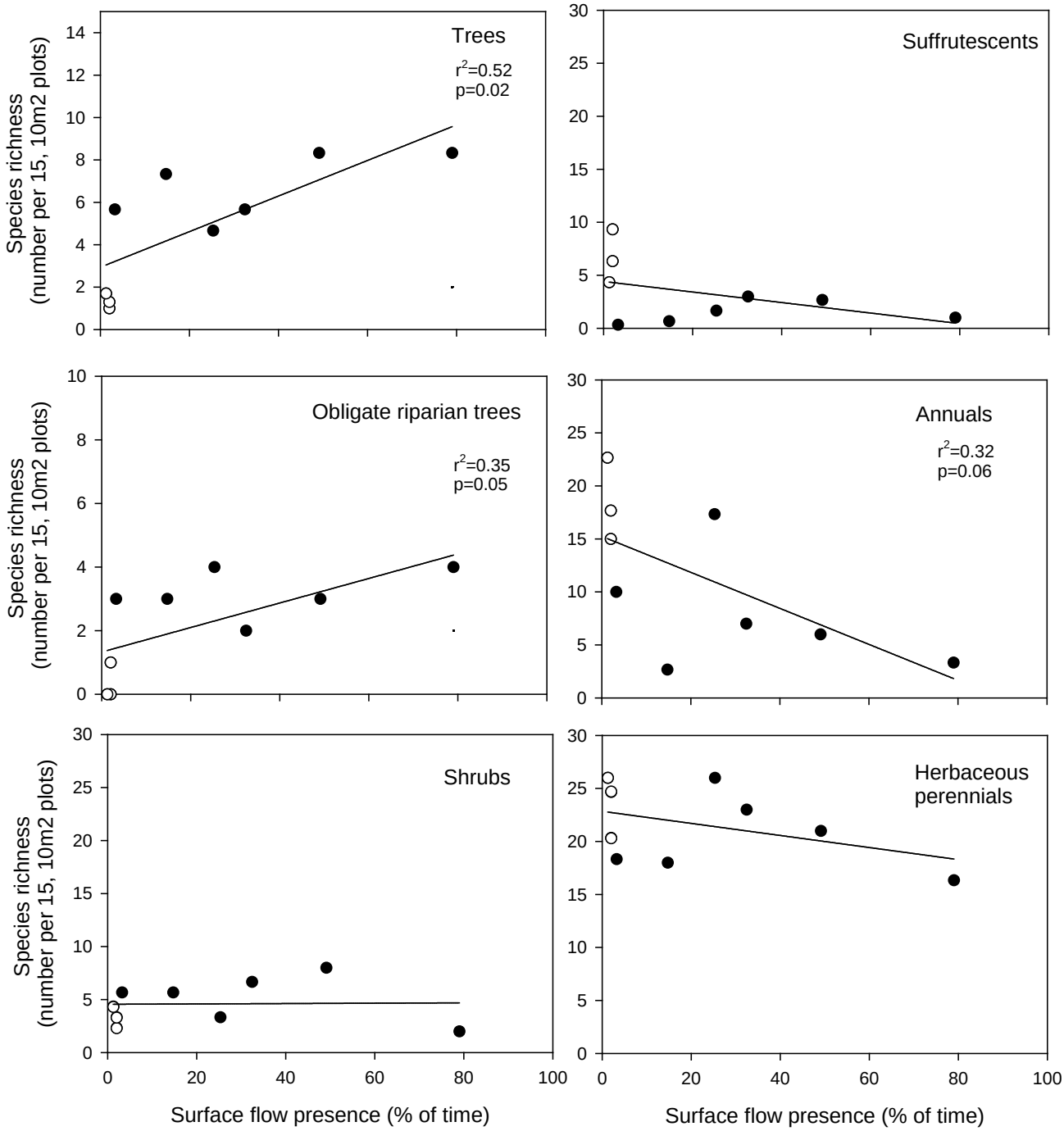

Fig. 6.1. Number of plant species, by growth form, at sites in the Huachuca Mountains in relation to stream flow duration and water table presence. Unfilled circles indicate sites at which the water table is below plant rooting depth. Species richness values are averages of three sampling seasons

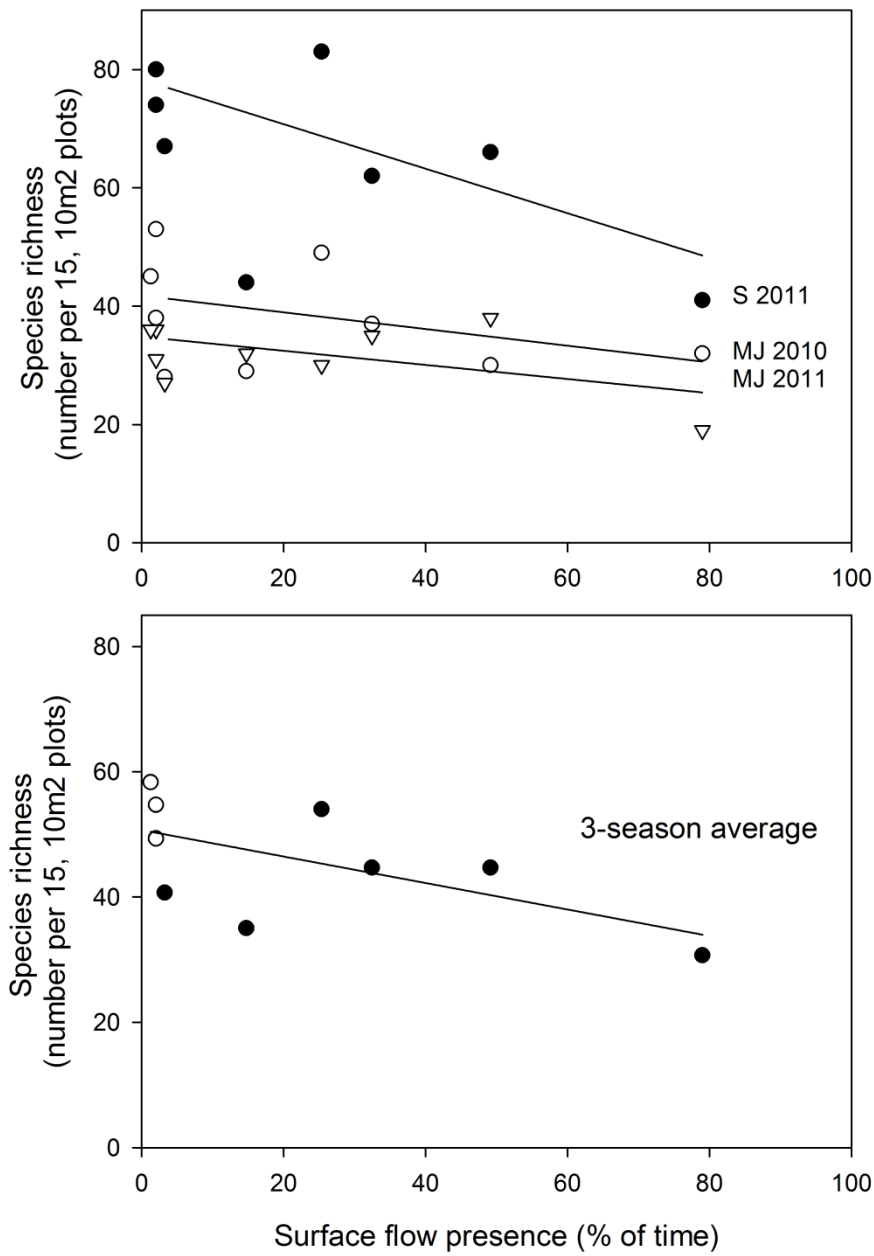

Fig. 6.2. Number of plant species per site in relation to percent of time the stream was flowing. Each symbol represents a riparian study site in the Huachuca Mountains. The bottom panel shows averages of three seasons and the top panel shows three individual sampling seasons (S= September 2011; MJ 2010= May/June of 2010; MJ 2011= May/June of 2011).

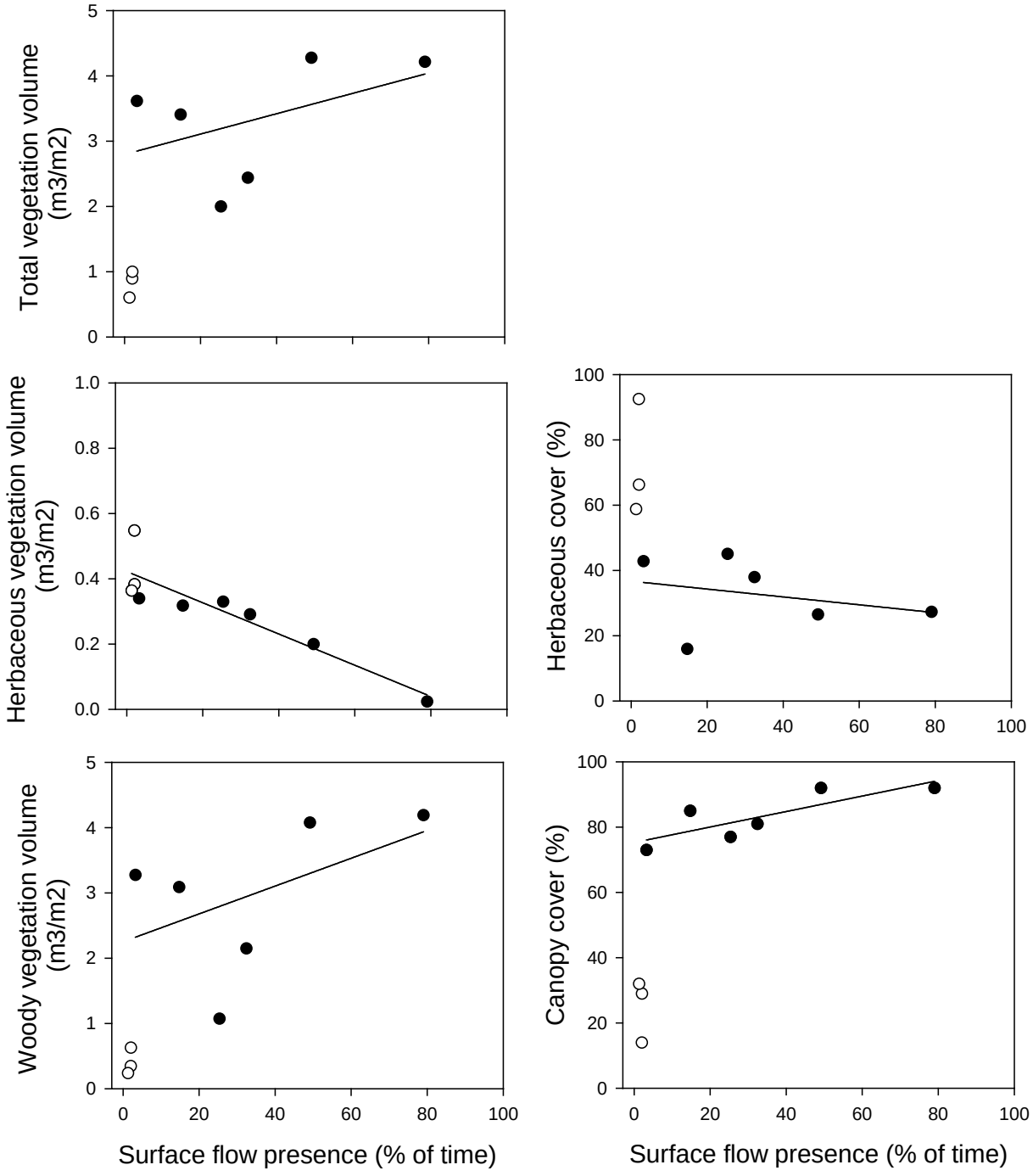

Fig. 6.3. Vegetation abundance in the riparian zone in relation to stream surface flow duration, for sites in the Huachuca Mountains. Open symbols indicate sites without a shallow water table. Herbaceous cover is a seasonal average.

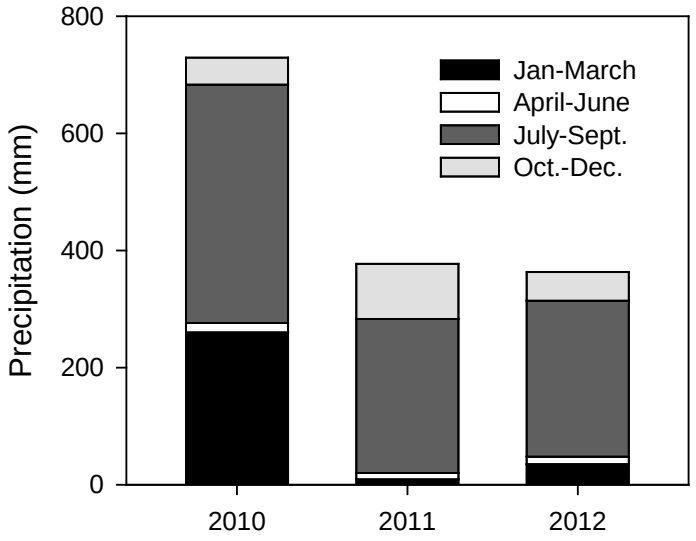

Fig. 6.4. Precipitation during three study years at Huachuca Mountains.

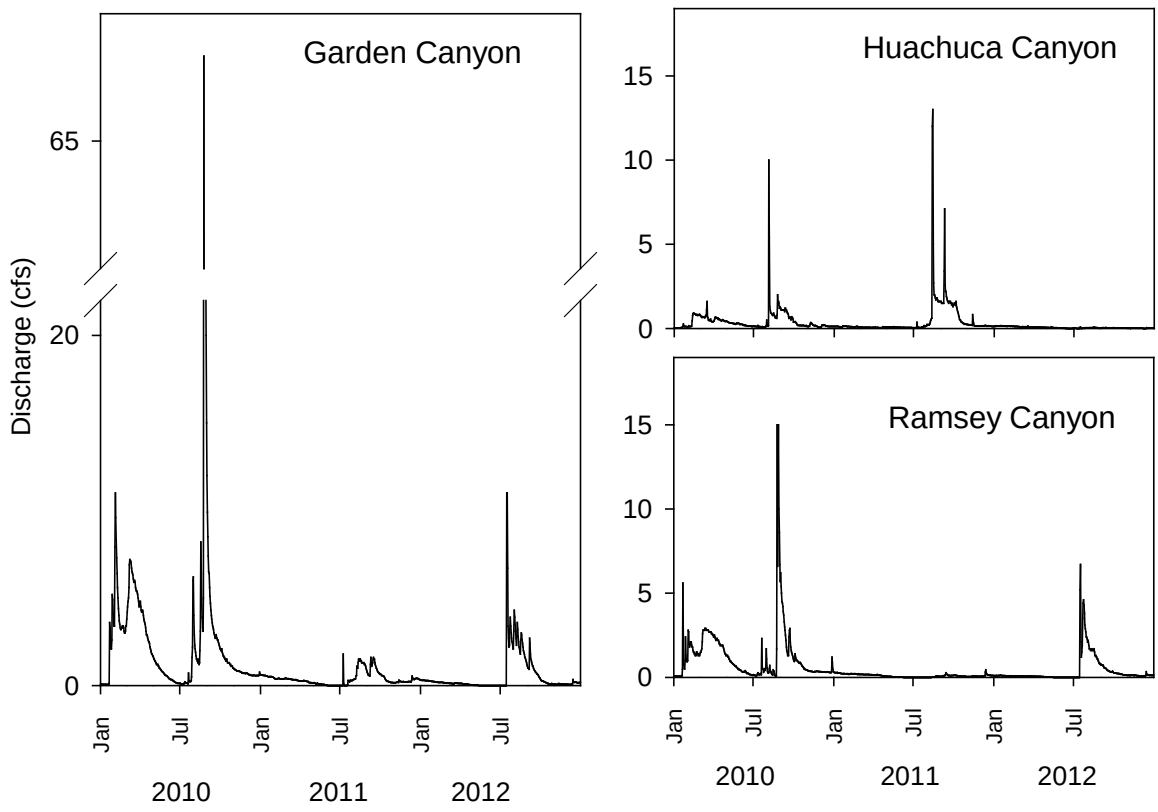

Fig. 6.5. Mean daily discharge for USGS stations near Huachuca Mountain study sites. The gauges are 09470800 (Garden Canyon- Fort Huachuca), 09471340 (Huachuca Canyon- Fort Huachuca), and 09470750 (Ramsey Canyon near Sierra Vista) (http://waterdata.usgs.gov/nwis/rt).

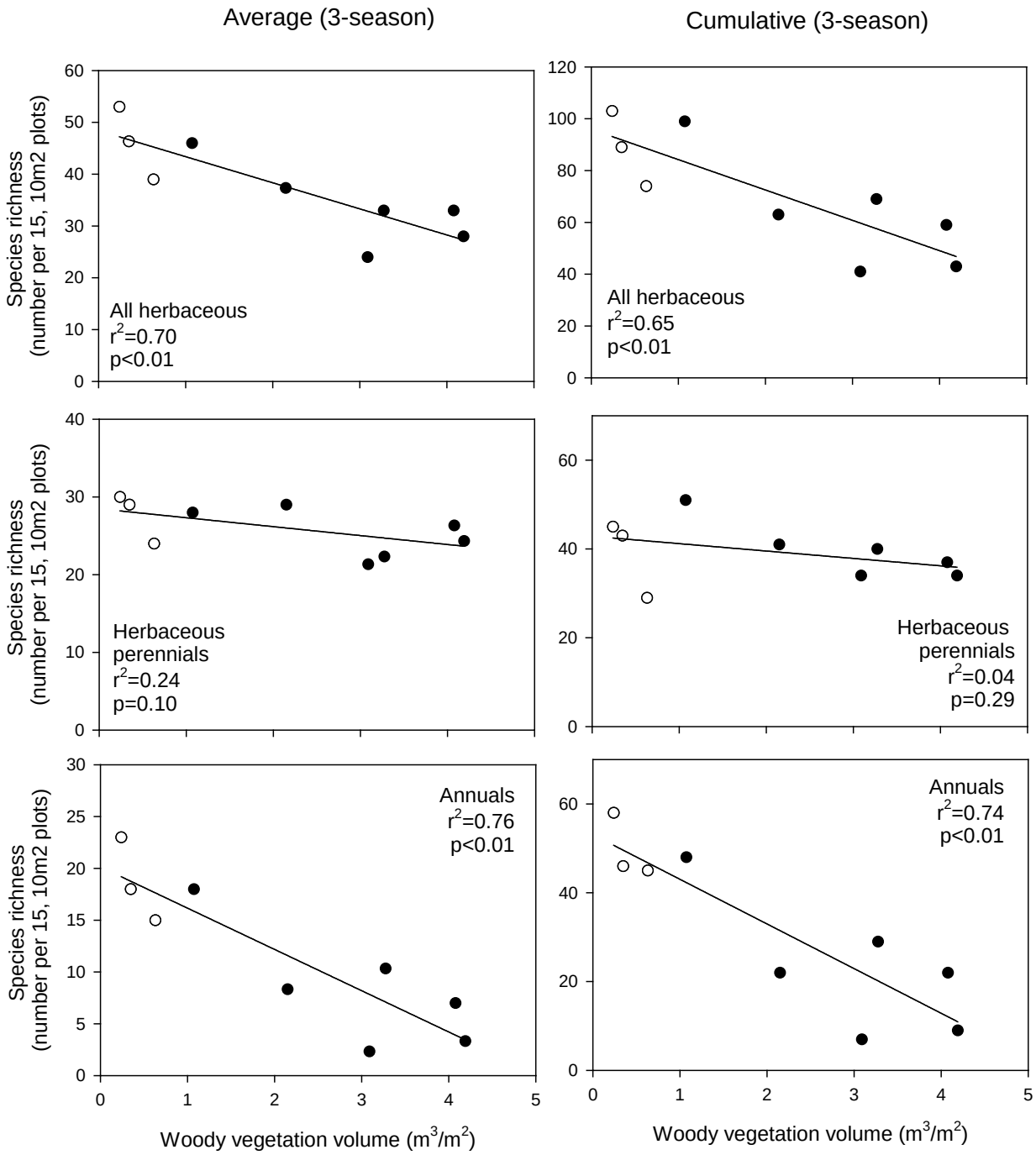

Fig. 6.6. Plant species richness in relation to vegetation volume at nine riparian sites in the Huachuca Mountains. For the linear regressions, df=8. Unfilled circles indicate piedmont sites, at which water tables are below plant root depth.

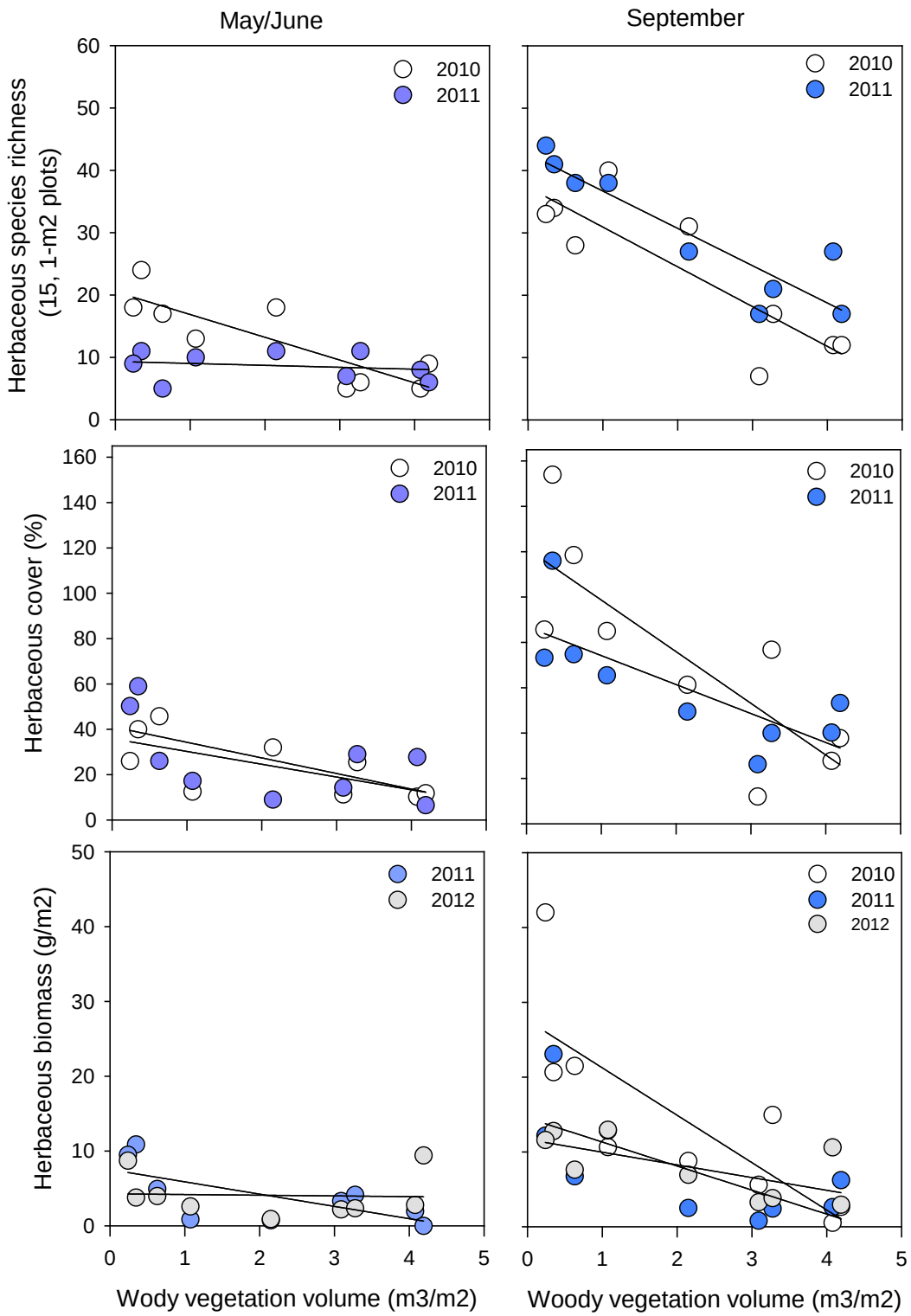

Fig. 6.7. Herbaceous species richness, cover, and above-ground biomass in relation to woody vegetation volume, for riparian sites in the Huachuca Mountains. Data are shown for the pre-monsoon and monsoon season of three study years.

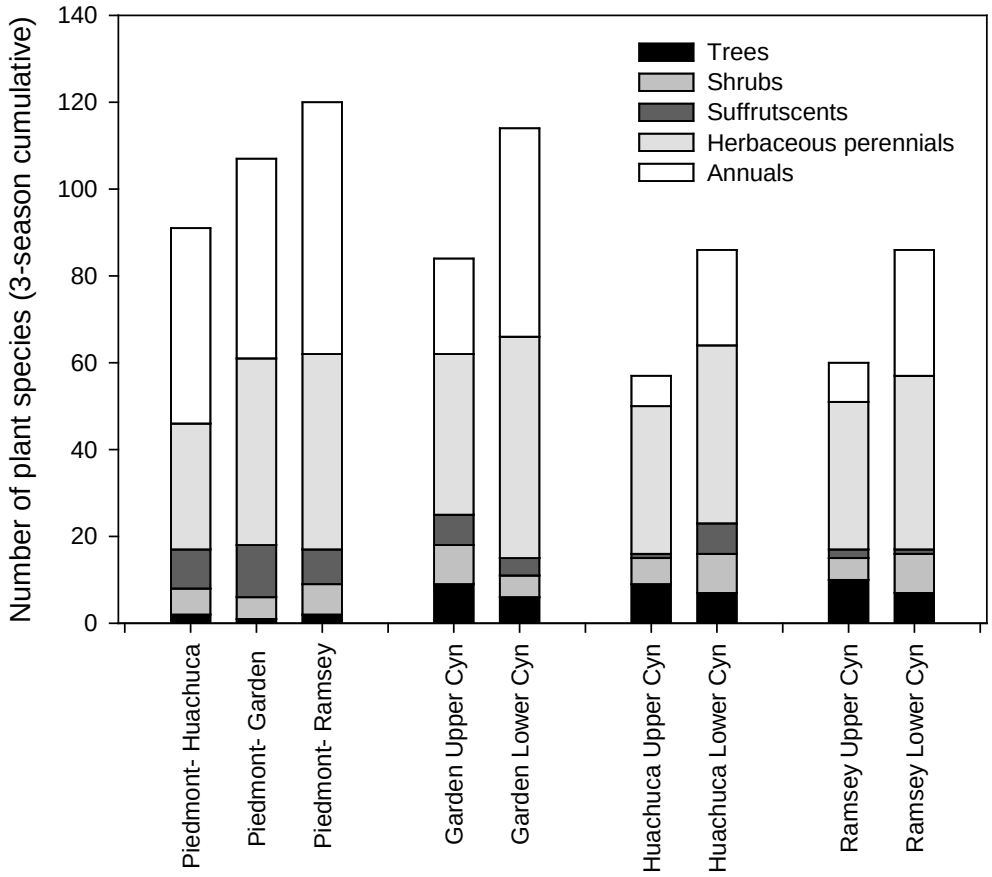

Fig. 6.8. Plant species richness of Huachuca riparian sites grouped by stream position and canyon.

Discussion

Stream surface water, subsurface water, flood water, and precipitation all are strong regulators of riparian vegetation in the semihumid environment of the Huachuca Mountains, with the importance of each water source varying among plants with different growth form. The patterns in our riparian study system are reminiscent of the "pulse-reserve" species-coexistence model described for upland desert systems. In this model, there is a dichotomous response between shallow rooted plants that respond rapidly to rain pulses and the more deeply rooted and longer lived plants that respond to deeper reserves of soil moisture from prolonged rains (Nano and Pavey 2013). In the riparian context, the annuals and many of the herbaceous perennials are pulse species responding to seasonal wetting of soils by rain and floods. Most of the trees and some of the shrubs are reserve species drawing from the shallow water table. The year-round presence of water in the stream aquifer (Kolb et al. 2007) is necessary to maintain the tall, productive riparian trees such as *P. wrightii* (Stromberg 2001a and 2001b) as well as a high density of deep-rooted facultative riparian trees such as Quercus spp. (Danzer et al. 2001).

Along the spatial riparian water gradients, there were trade-offs between forest biomass (sustained by more permanent water sources) and plant species diversity (with herbaceous plants sustained by seasonal rain and flood pulses). Plant biomass increased along the stream water availability gradient, with highest values at the wettest sites sampled (>50% flow permanence and shallow water table). Woody plants comprised the greatest fraction of our biomass indicator (vegetation volume) and their patterns heavily weighted the overall biomass response. In this semihumid region, forest biomass was limited by availability of water (Noy-Meir 1973).

In contrast to patterns for biomass, plant species richness *decreased* along the riparian water gradient. In some riparian ecosystems, species diversity is highest at sites with groundwater discharge (Jansson et al. 2007). In our study area, diversity of trees (including obligate riparian ones) was positively related to riparian water sources but, as in many other areas, woody species were far less diverse than herbaceous taxa (Williams et al. 1999; Stromberg et al. 2009c; Viers et al. 2012). Herbaceous species were co-limited by light and seasonal rains and floods, and their response heavily weighted that of the total species response, producing a negative relationship between species diversity and stream water availability. A decrease in plant species richness at wetter stream sites is somewhat counterintuitive, but is consistent with the Intermediate Productivity Hypothesis (Huston 2014). Studies in arid and semiarid regions of the American Southwest show that plant species richness peaks at streams with intermittent flow (versus perennial or ephemeral flow) (Stromberg et al. 2009a; Katz et al. 2012). In the semihumid setting of the Huachuca Mountains, plant species richness peaked at stream sites with ephemeral flow (with the greatest number at piedmont streams with ephemeral flow and sparse canopy cover).

Our results indicate that the responses of riparian overstory and understory plants to regional climate changes will be decoupled. As increasing aridity causes a decrease in the spatial extent of perennial and semi-perennial stream reaches (Seager, et al.2013), there will be a decrease in extent of densely-canopied riparian forests and a replacement of such by riparian areas with low woody biomass but high alpha plant species richness. Whether or not such a decline in forest density would affect individual herbaceous plant species remains to be investigated. Herbaceous species range from helophytes (high sunlight plants) to shade-tolerant plants, and light gaps in dense riparian canopy are critical for persistence of some understory herbaceous species (Oshima et al. 1997). Further research is needed to determine which, if any, Huachuca Mountain riparian species are associated with dense shade.

Influence of canopy trees on herbaceous understory can range from positive to neutral or negative depending on environmental context and functional traits of the particular tree species (Menges 1986; Schade et al. 2003; Xiong et al. 2003; Sponseller and Fisher 2006; Bottollier-Curtet et al. 2012). Aridity is a key contextual factor. Trees reduce understory light and produce deep litter which impedes germination of many species (Frost and McDougald 1989; Xiong and Nilsson 1999) but also ameliorate evaporative stress, of importance in hot, arid environments. (Lite et al. 2005). For the semihumid Huachuca streams, canopy cover had a depressing effect on understory diversity in wet seasons but a neutral effect in dry seasons. Patterns in the Huachucas are similar to those in other subhumid to humid contexts in which forest thinning increases richness of understory plants (Carr and Krueger 2011; Burton et al. 2013). Such responses can produce management trade-offs between forest biomass and species diversity.

The Huachuca Mountains are in a climatic region dominated by late summer precipitation, and the effect of summer rains and floods on pulsing of annual species and herbaceous perennials in the riparian zone was quite strong. Late-summer pulses of diversity and productivity also are evident for other streams in this region (Bagstad et al. 2005). Winter precipitation is much less abundant than summer precipitation in the Huachuca Mountains, but our timing was fortuitous in that we captured one wet, El-Nino year. The late summer monsoons and winter frontal storms both contributing to seasonal increases in species richness. The plant response (cover, biomass, and richness) to the winter moisture pulse was appreciably smaller than that to the summer moisture pulse, and to smaller than the response to winter precipitation seen on lower elevation rivers (Stromberg et al. 2009b). Cool temperatures (and infrequent winter rains) appear to preclude development of a diverse spring annual flora in the Huachuca Mountains.

Historic land use influences present day plant species richness and composition. Of the three canyons studied, Garden Canyon had the greater number of plant species, even when controlling for site water availability. Historic land use influences plant species richness, and the three study canyons have different land use histories. Ramsey Canyon, although presently a nature preserve, has had the greatest use by people, having been the site of a small town over a century ago. This long-term use likely contribued to reduced species numbers. Whole canyon inventories of other streams in the Huachuca Mountains would be useful to determine the extent to which certain canyons support unique species (Zimmerman et al. 1999).

Chapter 7: Riparian and Upland Soil Seed Banks Along an Aridity Gradient

Q1: Do Numbers of Species Emerging from Soil Seed Banks Vary with Site Elevation and Aridity?

Upland zones and riparian zones of ephemeral streams showed similar positive relationships between seed bank species richness and site elevation and aridity. For upland sites, the numbers of species emerging from soil seed banks increased significantly with elevation ($t=4.67$, $p<0.001$, $df=28,1$) and with Aridity Index (i.e., as sites became less arid) ($t=4.77$, $p<0.001$, $df=28,1$) (Fig. 7.1). Upland sites ranged in vegetation type from Sonoran desertscrub to oak-pine woodland, and in Aridity index from 3 (arid) to 20 (semihumid) (Table 7.1). For ephemeral riparian sites, general linear models similarly indicated that the number of species emerging from soil seed banks increased significantly with site elevation ($t=3.45$, $p=0.003$; $df=18,1$) and Aridity Index ($t=2.47$, $p=0.02$; $df=18,1$). Ephemeral riparian sites ranged in vegetation type from small legume trees (*Parkinsonia, Olneya*) to scattered broad leaf trees (*P. wrightii*) and in Aridity index from 3 to 19

For intermittent to perennial riparian sites, in contrast, the number of species emerging *decreased* as site elevation increased ($t=-2.61$; $p=0.02$; $df=20,1$) and as Aridity Index increased ($t=-2.43$; $p=0.03$; $df=20,1$) (Fig. 7.1). Riparian vegetation of these streams ranged from cottonwood/willow *(Populus/Salix*) forests and woodlands to mixed broadleaf forests.

Q2: Does the Percentage of Cool-Season versus Warm-Season Species in Soil Seed Banks Vary with Site Elevation?

The percentage of species emerging under the cool-season treatment increased with site elevation as indicated by analysis of variance ($F=7.3$, $p=0.01$, $df=32,1,2$) (Fig. 7.2). There was a small effect of site type ($F=1.8$, $p=0.17$), with upland sites tending to have a higher percentage of species emerging during the cool-season compared to the riparian sites.

Table 7.1. Description of study areas for riparian seed bank study. Flow status codes are P (perennial), I (intermittent), and E (ephemeral). "P" is annual precipitation. T" is average annual temperature, "AI" is Aridity Index, and "SP" is summer precipitation (as a percentage of annual).

Loca-tion	Site code	Elev ation (m)	Flow	Vegetation-Riparian	Vegetation- Upland	P (mm)	T (°C)	AI	SP (%)
Ramsey Canyon	RC PER	1797	P	Mixed broadleaf	Oak woodland with conifer	449	14.9	18.0	64
	RU	1755	I	Mixed broadleaf	Oak woodland with conifer	456	11.9	20.8	
	RL	1596	E	Mixed broadleaf	Oak woodland with conifer	443	12.8	19.4	
	RP	1536	E	Savanna	Grassland with juniper, mesquite	397	16.3	15.1	
Huachuca Canyon	HU	1658	I	Mixed broadleaf	Oak woodland with conifer	276	13.2	11.9	64
	HL	1616	I	Mixed broadleaf	Oak woodland with conifer	308	13.6	13.1	
	HP	1455	E	Savanna	Mesquite savanna	293	16.7	11.0	
Garden Canyon	GC PER	1631	P	Mixed broadleaf	Oak woodland with conifer	425	13.0	18.5	64
	GU	1593	I	Mixed broadleaf	Oak woodland with conifer	416	13.1	18.0	
	GL	1545	I	Mixed broadleaf	Grassland with oak	409	13.6	17.3	
	GP	1505	E	Mesquite savanna	Mesquite savanna	335	16.6	12.6	
Santa Rita Experimental Range	SRL	958	E	Mesquite savanna	Mesquite savanna	227	18.1	8.1	59
	SRS	956	E	Mesquite savanna	Mesquite savanna	227	19.0	7.8	
Barry Goldwater	SW	265	E	Legume trees	Creosote, cactus	97	21.6	3.1	50
	BG	324	E	Legume trees	Creosote, cactus	97	22.3	3.0	
Hassayampa River Preserve	HR PER	595	I	Willow/cottonwood, forest		280	18.7	9.8	45
	HR INT	566	I	Willow-cottonwood forest		270	19	9.3	
	HR EPH	558	E	Mesquite, burrobrush		260	19.4	8.8	
Cienega Creek	CC PER	1027	I	Willow/cottonwood, forest	Mesquite and shrubs	394	17.8	14.2	64
	CC INT	1050	I	Willow-cottonwood forest	Mesquite and shrubs	394	17.8	14.2	
	CC EPH	1089	**E**	Willow/cottonwood, forest	Mesquite and shrubs	394	17.8	14.2	

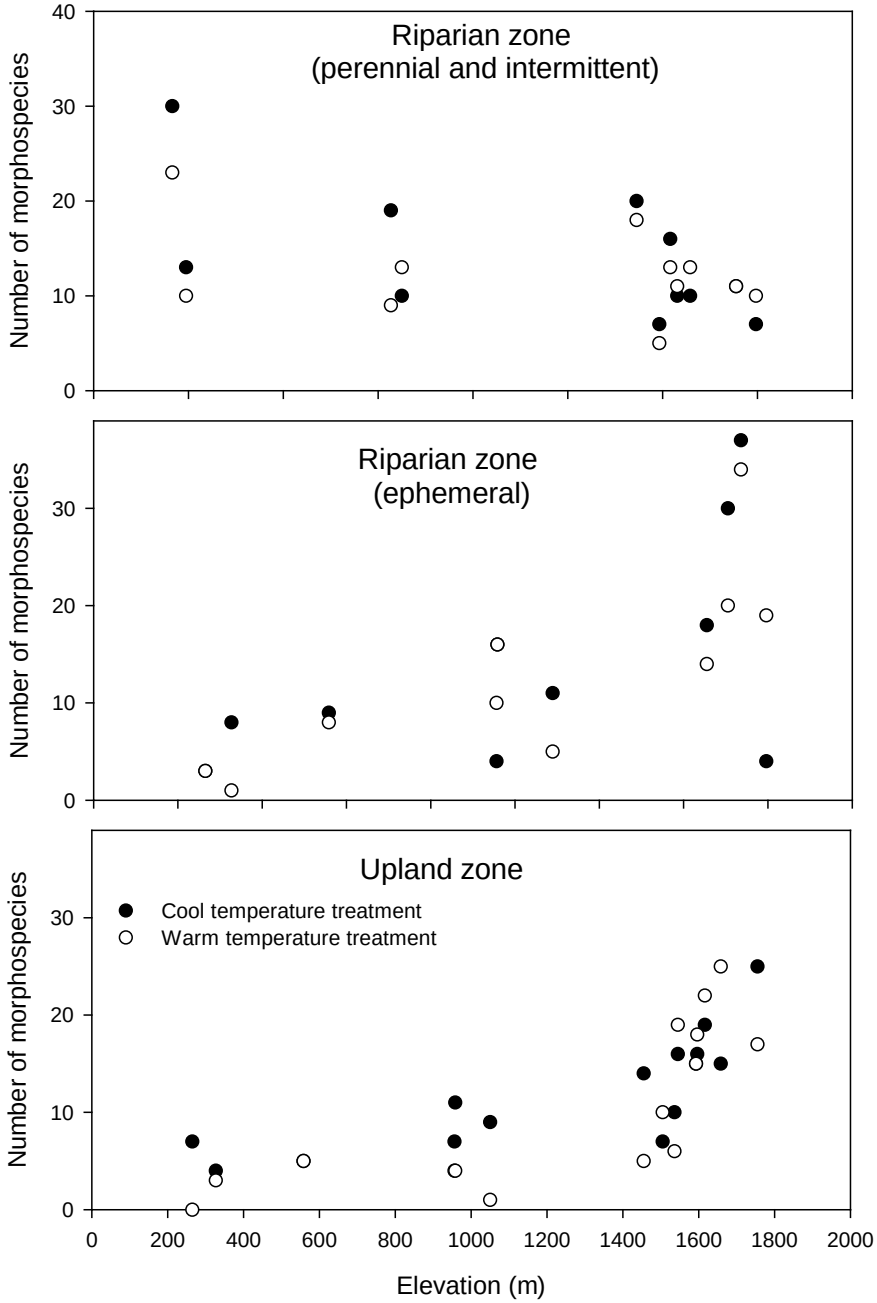

Fig. 7.1. Number of plant species emerging from soil seed banks in relation to site elevation. Filled symbols indicate the cool temperature treatment and open symbols indicate the warm treatment. Each symbol represents a study site. The top, middle, and bottom figures respectively portray intermittent to perennial riparian zones, ephemeral riparian zones, and upland zones.

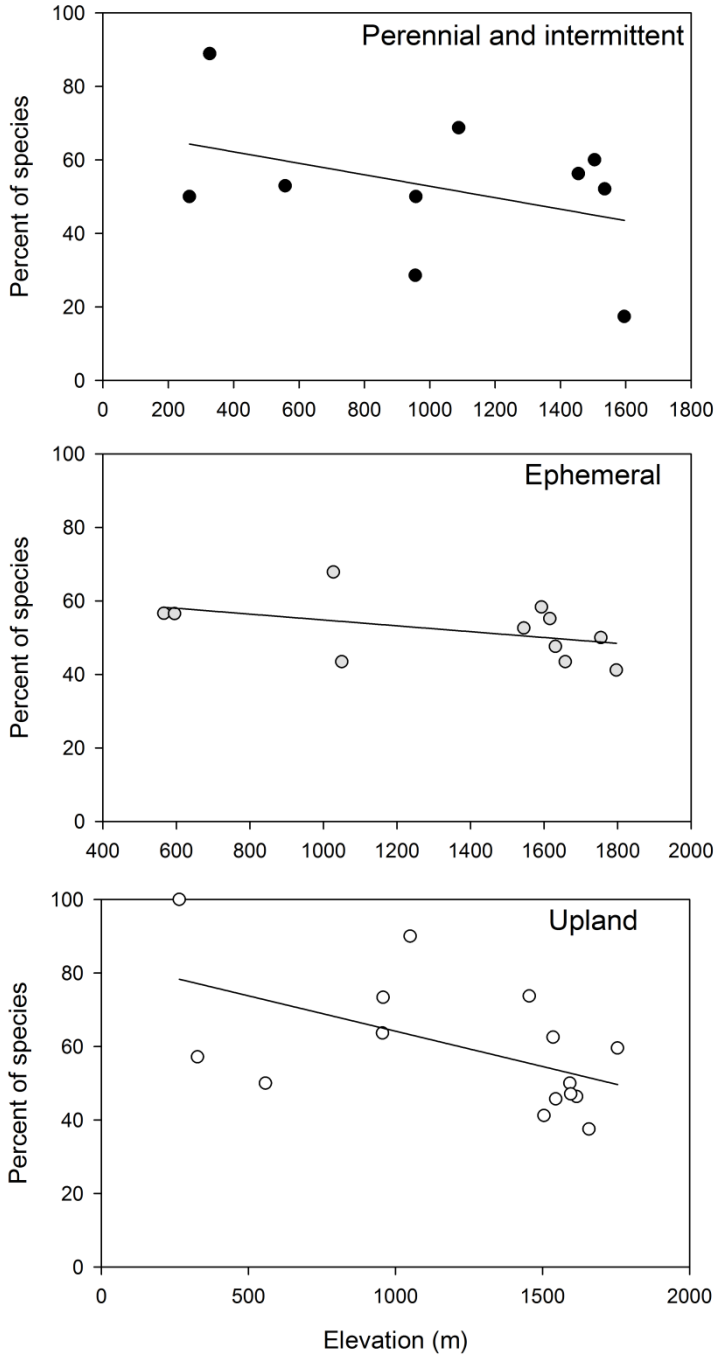

Fig. 7.2. Site elevation versus the percentage of seed-bank species emerging during the cool-season treatment, for ephemeral riparian, non-ephemeral riparian, and upland sites.

Discussion

Elevation-related patterns of change in numbers of seed-banking plant species differed markedly by stream type. Soil seed bank species numbers in riparian zones of ephemeral streams (and of upland deserts) increased with site elevation, thus precipitation. Seed bank species numbers in riparian zones of intermittent to perennial streams, in contrast, *decrease* with elevation. From this we conclude that the seed-banking species of each stream type, which consist primarily of herbaceous species, are limited by different factors. Riparian zones of ephemeral streams, similar to upland deserts, are water-limited and influenced by terrestrial processes. Riparian zones of intermittent to perennial streams, in contrast, become light-limited at high elevations, with few herbaceous species in the understory and seed bank. The pattern we observed in this soil seed bank study is consistent with our companion study which shows that herbaceous species richness is sparse at high elevation perennial riparian sites with dense canopy cover of riparian trees (Chapter 6).

Rapidity of response to environmental change will vary with the importance of the soil seed bank in the plant community and thus with stream type. Differences in reliance on soil seed banks have implications for the rate of community response to environmental change. Systems with high percentages of seed-banking species, such as low-elevation perennial streams and high-elevation ephemeral streams, should respond rapidly to environmental change owing to the short live span that typifies many seed-banking species. Further, soil seed banks can be viewed as a type of resilience to environmental change given that they contain seeds derived from many types of plant associations and from many generational cohorts that have experienced different selective pressures (Templeton and Levin 1979; Aikio et al. 2002; Boudell and Stromberg 2008a; Casanova 2015).

A diverse soil seed bank can assist with ecosystem restoration efforts. Results of this study have implications for management actions that focus on restoration of plant communities. Donor soils (with stored seeds) can be an effective tool for restoring plant species to degraded sites or to created sites (Richter and Stromberg 2005). Our findings indicate that donor soils would be an important component of restoration plans for a variety of hydrological stream types (and upland zones), given that seed-banking species were found in all types studied.

Chapter 8: Arthropod Diversity Gradients Along Temporary Stream Channels

Q1: Does Alpha Diversity of Ground-dwelling Arthropods Vary with Flow Permanence and Landscape Position?

We collected 36,005 invertebrates over two years of pitfall trapping in the Huachuca Mountain streams and associated riparian zone and uplands. Of these, we identified 394 morphospecies of ground-dwelling arthropods. Annual water presence (a measure of stream flow permanence above and below ground) was a good predictor of $\alpha-$ level diversity metrics for terrestrial arthropods, but the effect varied seasonally and between years in some cases. Specifically, α-diversity increased with water permanence during the dry season but decreased with increasing water permanence during the monsoon season (Fig. 8.1). We found no effect of distance from the stream channel for any measure of α-diversity suggesting that lateral gradients in richness, diversity and evenness were negligible as suggested by Sabo et al. (2005).

Q2: How do Summer Monsoon Flows Influence Diversity of Ground-dwelling Arthropods?

There was a significant interaction between % Annual Water Presence (AWP) and season (Monsoon *versus* Dry) in predicting the diversity (Shannon-Wiener Index; $F=10.57$, $df=1,81$, $p<0.01$; Table 8.1), rarefied species richness ($F=12.42$, $df=1,81$, $p<0.01$; Table 8.1) and the distribution of abundances (Pielou's evenness, $F = 5.04$; $df = 1,81$, $p<0.05$). Evenness varied seasonally and annually and the effect of AWP further varied across seasons and years (significant three way interaction). The high temporal variation of evenness is not surprising given the pulsed nature of secondary production of arthropods (see Chapter 9).

Q3: Does Beta Diversity of Ground-dwelling Arthropods Vary with Flow Permanence?

In contrast to negligible differences in α-diversity along the channel-upland gradient, β-diversity was strong and seasonally and annually sensitive to hydrology. Turnover between transects was generally high and comprised the majority of β-diversity in most cases. Species turnover contributed to over 50 percent of β-diversity in 97 percent of comparisons between channel margin and upland transects, 94 percent of comparisons between channel margin and riparian transects, and 83 percent of comparisons between riparian and upland transects. However, of all models predicting total β-diversity, total turnover diversity, and the percentage of β-diversity comprised of turnover, only total β-diversity metrics were significantly related to the predictor variables (Table 8.2).

Total β-diversity between channel and riparian sites was significantly predicted by the season * year interaction ($F=9.14$, $df=1,21$, $p=0.01$) and β-diversity between channel and upland sites was significantly predicted by the water permanence (APW) * season * year interaction ($F=4.52$, $df=1,21$, $p=0.05$; Fig. 8.3). Hence, differences between arthropod faunas along the channel-upland gradient are stronger than differences in numbers (richness) and relative abundance (evenness) of species; these β -diversity gradients were well predicted by hydrology but the magnitude and direction of the correlation between hydrology and β-diversity was seasonally and annually variable.

Table 8.1. Predictors of α-diversity measured by the Shannon-Wiener Index and rarefied species richness. Significance of predictors was determined using linear mixed-effects models fitted with maximum likelihood parameter estimation.

Variable	**df**	**F**	**p**
Shannon-Wiener Index (Diversity)			
Annual Water Presence %	**1, 27**	**4.21**	**0.05**
Transect	2, 27	0.05	0.95
Season	1, 81	0.01	0.93
Year	1, 81	0.01	0.92
Annual Water Presence % * Transect	2, 27	0.72	0.49
Annual Water Presence % * Season	**1, 81**	**10.57**	**<0.01**
Annual Water Presence % * Year	1, 81	1.24	0.27
Transect * Season	2, 81	0.96	0.39
Transect * Year	2, 81	0.01	0.99
Season * Year	1, 81	1.14	0.29
Rarefied Species Richness			
Annual Water Presence %	1, 27	2.61	0.12
Transect	2, 27	0.01	0.99
Season	1, 81	0.06	0.81
Year	1, 81	0.10	0.75
Annual Water Presence % * Transect	2, 27	0.95	0.40
Annual Water Presence % * Season	**1, 81**	**12.42**	**<0.01**
Annual Water Presence % * Year	1, 81	0.18	0.67
Transect * Season	2, 81	1.22	0.30
Transect * Year	2, 81	0.03	0.97
Season * Year	1, 81	0.44	0.51
Pielou's evenness			
Annual Water Presence %	1, 27	0.45	0.51
Transect	2, 27	0.05	0.95
Season	**1, 81**	**7.66**	**0.01**
Year	**1, 81**	**4.52**	**0.04**
Annual Water Presence % * Transect	2, 27	0.31	0.74
Annual Water Presence % * Season	**1, 81**	**5.04**	**0.03**
Annual Water Presence % * Year	1, 81	1.62	0.21
Transect * Season	2, 81	1.10	0.34
Transect * Year	2, 81	0.16	0.85
Season * Year	**1, 81**	**11.74**	**0.00**

Table 8.2. Predictors of β-diversity measured by dissimilarity (Sorensen's β), and the additive turnover and nestedness components of dissimilarity between channel and upland. Significance of predictors was determined using linear mixed-effects models fitted with maximum likelihood parameter estimation.

Variable	**df**	**F**	**p**
Dissimilarity			
Annual Water Presence %	1, 21	2.56	0.15
Season	1, 7	0.59	0.45
Year	1, 21	1.89	0.18
Annual Water Presence % * Season	1, 21	0.15	0.70
Annual Water Presence % * Year	1, 21	0.69	0.41
Season * Year	**1, 21**	**8.56**	**<0.01**
Annual Water Presence % * Season*year	**1, 21**	**4.52**	**<0.05**
Turnover			
Annual Water Presence %	1, 21	0.45	0.52
Season	1, 7	1.32	0.26
Year	1, 21	0.20	0.66
Annual Water Presence % * Season	1, 21	0.25	0.62
Annual Water Presence % * Year	1, 21	0.24	0.63
Season * Year	1, 21	0.13	0.72
Annual Water Presence % * Season*year	1, 21	0.22	0.64
Nestedness			
Annual Water Presence %	1, 21	0.05	0.82
Season	1, 7	1.67	0.21
Year	1, 21	0.01	0.90
Annual Water Presence % * Season	1, 21	0.34	0.57
Annual Water Presence % * Year	1, 21	0.55	0.47
Season * Year	1, 21	0.59	0.45
Annual Water Presence % * Season*year	1, 21	1.44	0.24

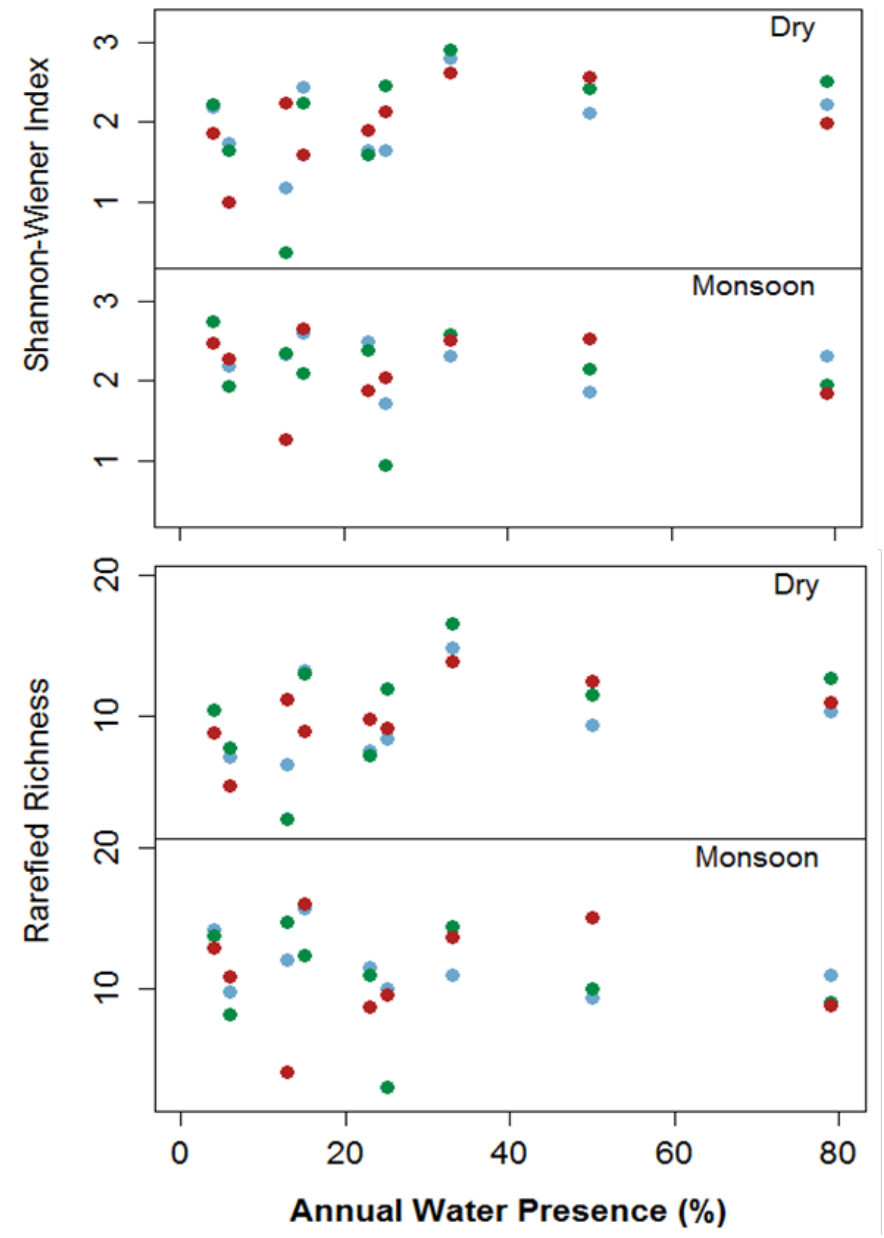

Fig. 8.1. Shannon-Wiener diversity index and rarefied morphospecies richness (n=30) of ground-dwelling arthropod communities versus annual water presence from the dry and monsoon seasons of 2011. Blue symbols represent channel margin, green symbols represent riparian, and red symbols represent upland. Results for 2012 (not shown) are similar to 2011.

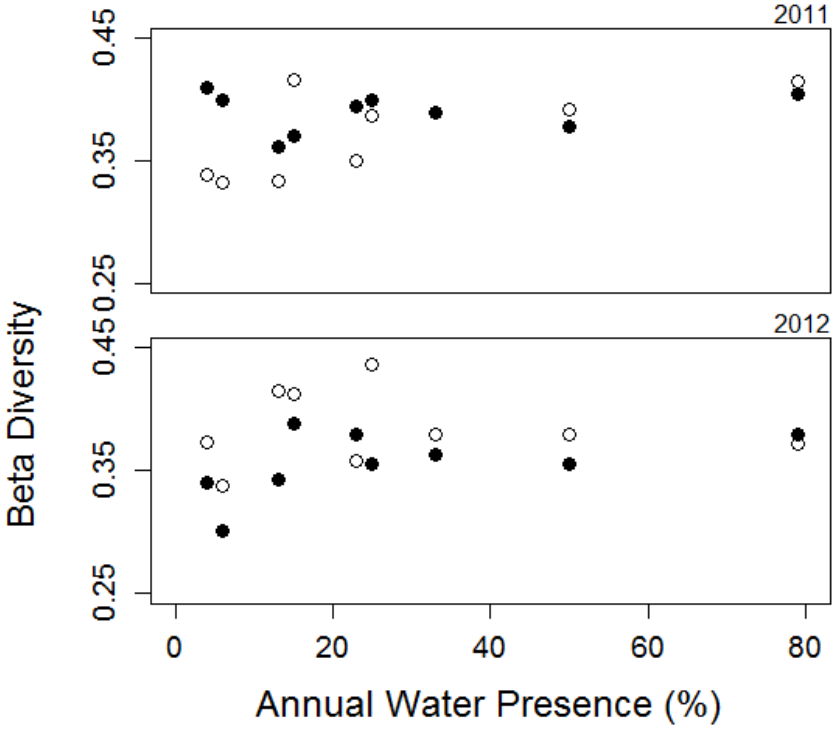

Fig. **8.2**. Community dissimilarity (β-diversity) of ground-dwelling arthropods between channel margins and uplands in the dry and monsoon seasons (June and September, respectively) of 2011 and 2012 versus annual stream water presence at each site. Closed symbols represent dry season samples, open symbols represent monsoon season samples.

Discussion

Our findings indicate stream flow permanence and seasonality cause high variation in diversity patterns of riparian arthropods. We found strong differences in both the diversity and community composition among sites and seasons. Annual flow presence is a good predictor of arthropod biodiversity, but it varies seasonally. Flow appears to be positively (though non-linearly) related to a-diversity in the dry season but perhaps negatively related to a-diversity during Monsoon. This may have to do with contrasting effects of water as a limiting resource in the dry season and as a physical disturbance flood disturbance during the Monsoon. As a result, diversity may be higher in wetter reaches in particularly dry years, whereas wet years will see higher diversity at more ephemeral reaches. It is thus important to maintain riparian habitat across the flow permanence spectrum to maintain a high regional diversity pool across years and seasons.

There were no significant effects of lateral position (along the channel-upland gradient) on alpha-richness and no interactions between lateral position and any other variable. This is consistent with observations in Sabo et al. (2005) that riparian zones harbor different not more species. Patterns of dissimilarity between channel and upland sites were strong (mirroring Sabo et al. 2005) but highly variable among sites, seasons, and years. We believe this temporal variation in the effect of water presence on beta diversity is related to variable effects of flood disturbance and water-resource effects in near channel versus upland habitats across reaches with different hydrology as underscored by the significant AWP*season*year interaction.

Chapter 9: Secondary Production of Terrestrial Macroinvertebrates Along a Gradient of Stream Flow Permanence

Q1: Does Terrestrial Macroinvertebrate Community Production vary with Flow Permanence and Landscape Position?

Terrestrial macroinvertebrate community production along the channel varied non-linearly with stream flow permanence (Fig. 9.1). Above stream flow permanence values of 20%, there was a positive linear relationship between stream flow permanence and median monthly biomass. Streams with low levels of flow permanence (less than 10%) had higher levels of peak monthly biomass.

Q2: Does the Extent of Temporal Variation in Biomass vary Among Stream Types?

Temporal variation in total biomass was most pronounced at the ephemeral, piedmont sites (Fig. 9.2). The driest streams (less than 10 percent annual stream flow permanence) had the greatest variability in median monthly biomass. In contrast, streams with higher levels of flow permanence (greater than 10%) had much less variation in median monthly biomass.

At the ephemeral stream sites there were large increases in biomass in all sampling zones (channel, riparian, and upland) from July through September coinciding with the monsoon season. The largest peak occurred in the channel zone (suggesting influence of flood water), but this surge in biomass extended to the upland positions as well (indicating that it was precipitation-driven). Prior to the monsoon season (February to July), there was low biomass at the ephemeral piedmont sites (average of 0.84 mg/m^2). By contrast, the wetter canyon sites supported a modest but relatively consistent amount of biomass throughout the year. The biomass increases which did occur in September at the canyon sites were far less than those at the piedmont sites and were most evident in the channel position.

Q3: How Does Biomass of Key Taxa Vary with Flow Permanence and Landscape Position?

The common pillbug *(Armadillidium vulgare)* was found in relatively high abundance along the channels of the upper canyon streams where water availability was relatively constant (Fig. 9.3, Table 9.1). This species had lower abundance along the channels of the lower canyon streams. It was present in very low abundance or virtually absent at all other locations, including the piedmont channels. .

The field cricket *(Gryllus sp. nov)* was abundant at all canyon stream sites except LC-C (Fig. 9.3, Table 9.1). It was most abundant at the upper canyon riparian sites, where it maintained an annual biomass density of 1.47 mg/m^2. In terms of landscape position, throughout the year, it was most abundant in the riparian zones of the canyon streams (Fig. 9.2: UC-R and LC-R). This is most likely due to the presence of leaf litter from the riparian trees present at these sites (Stromberg 2001). By contrast, *Gryllus sp. nov* was not found at any piedmont site . These results indicate that like *A. vulgare*, *Gryllus sp. nov* preferred sites with higher and consistent levels of water availability.

Gryllus sp. nov. and *A, vulgare* are detritivores that play important roles in energy and nutrient flow in Southwestern riparian environments by processing energy from leaf litter and dead animals (Smith et al., 2006; Sabo et al. 2005). Crickets play an especially important role in transferring energy and nutrients from riparian vegetation to higher consumer species through the consumption of leaf litter. *Armadillidium vulgare*, like *Gryllus sp. nov*., was also only present in high abundance along the canyon streams. However, *A. vulgare* was most prevalent in the channel positions of the streams, instead of the riparian zones. A common cause of death for the

gilled isopod *A. vulgare* is desiccation, and studies have found positive correlations between moisture and isopod abundance (Smith et. al 2006). This species is poorly adapted to the transient stream flow which characterizes ephemeral streams.

Table 9.1. Biomass **s**ummary table**.** UC and LC are Upper Canyon and Lower Canyon respectively, PD is Piedmont. C is channel (zero meters from stream), R is Riparian (five meters from stream), and U is upland (25+ meters from stream). The cohort production interval is 12 months for *A. vulgare* and three months for *Gryllus sp. nov*. Dash (-) indicates negative production value due to small sample size.

Site	All species	*A. vulgare*	*Gryllus sp.*	All Species	All Species	*A. vulgare*	*Gryllus sp.*
	----------Average Biomass--------- ($mg*m^{-2}*yr^{-1}$)			Coefficient Variation-Biomass	Greatest Monthly Biomass Increase (mg/m^2)	Secondary Production ($mg*m^{-2}*yr^{-1}$)	
UC-C	126	1.69	0.64	153	49 (Aug-Sep)	39.71	-
UC-R	95	0.08	1.47	102	21(Mar-Apr)	1.27	19.61
UC-U	98	0.00	0.56	120	24 (Jun-Jul)	-	-
LC-C	79	0.25	0.01	95	10 (Oct-Nov)	-	-
LC-R	56	0.02	0.48	101	11 (Jun-Jul)	-	-
LC-U	61	0.07	0.17	99	9 (Jun-Jul)	-	-
PD-C	277	0.00	0.00	192	132 (Aug-Sep)	-	-
PD-R	167	0.03	0.00	186	71 (Aug-Sep)	-	-
PD-U	123	0.00	0.00	212	74 (Aug-Sep)	-	-

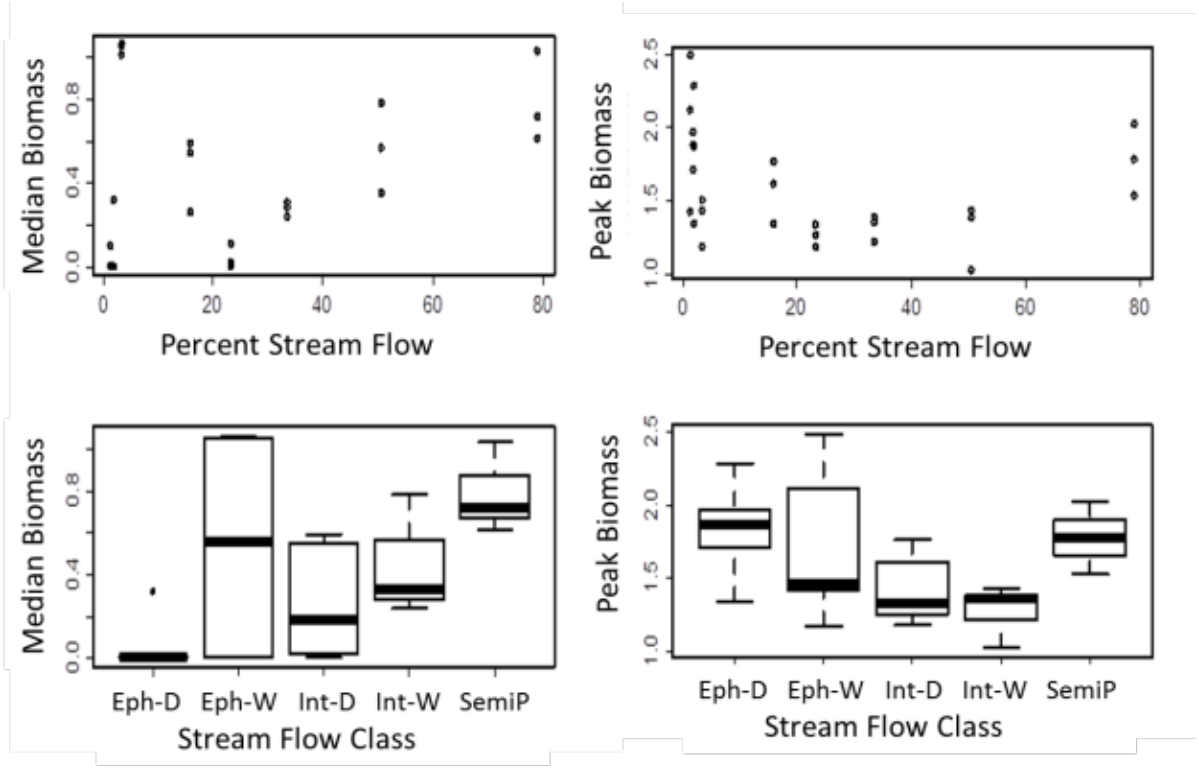

Fig. 9.1. Median monthly biomass levels, peak monthly biomass levels, and annual biomass as related to stream flow permanence. Stream flow permanence represents the amount of time flow was observed in the channel (i.e., 10 percent means stream flow was present 36.5 days per year). The streams were also placed into five different categories based on similarity in stream flow using a clustering analysis.

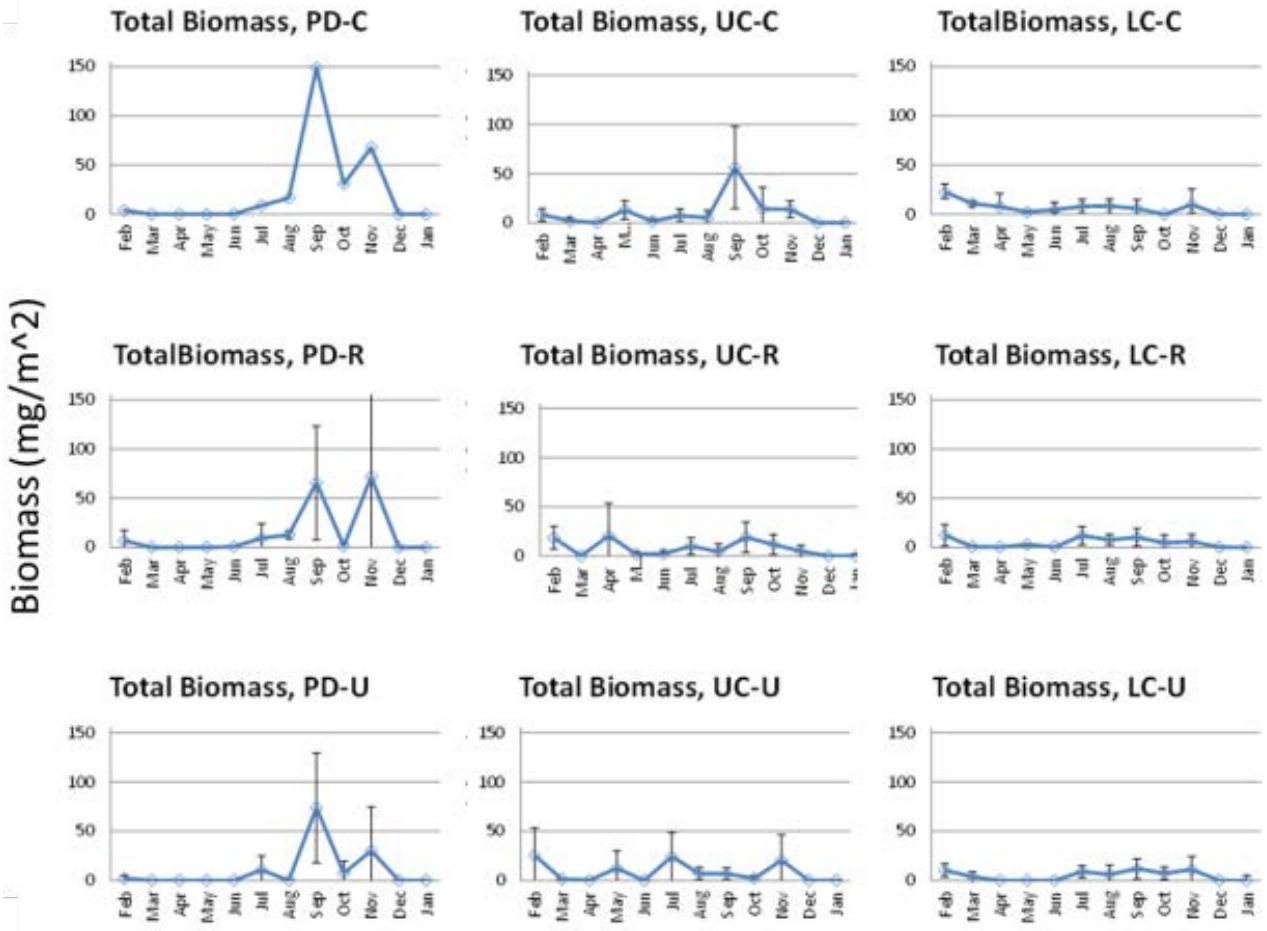

Fig. 9.2. Monthly biomass trends for all macroinvertebrates collected during one year of sampling. The values for each month are averages from sites sampled at or near Huachuca Canyon, Garden Canyon, and Ramsey Canyon. PD is Piedmont, UC and LC are Upper Canyon and Lower Canyon respectively, C is channel (zero meters from stream), R is Riparian (five meters from stream), and U is upland (25+ meters from stream).

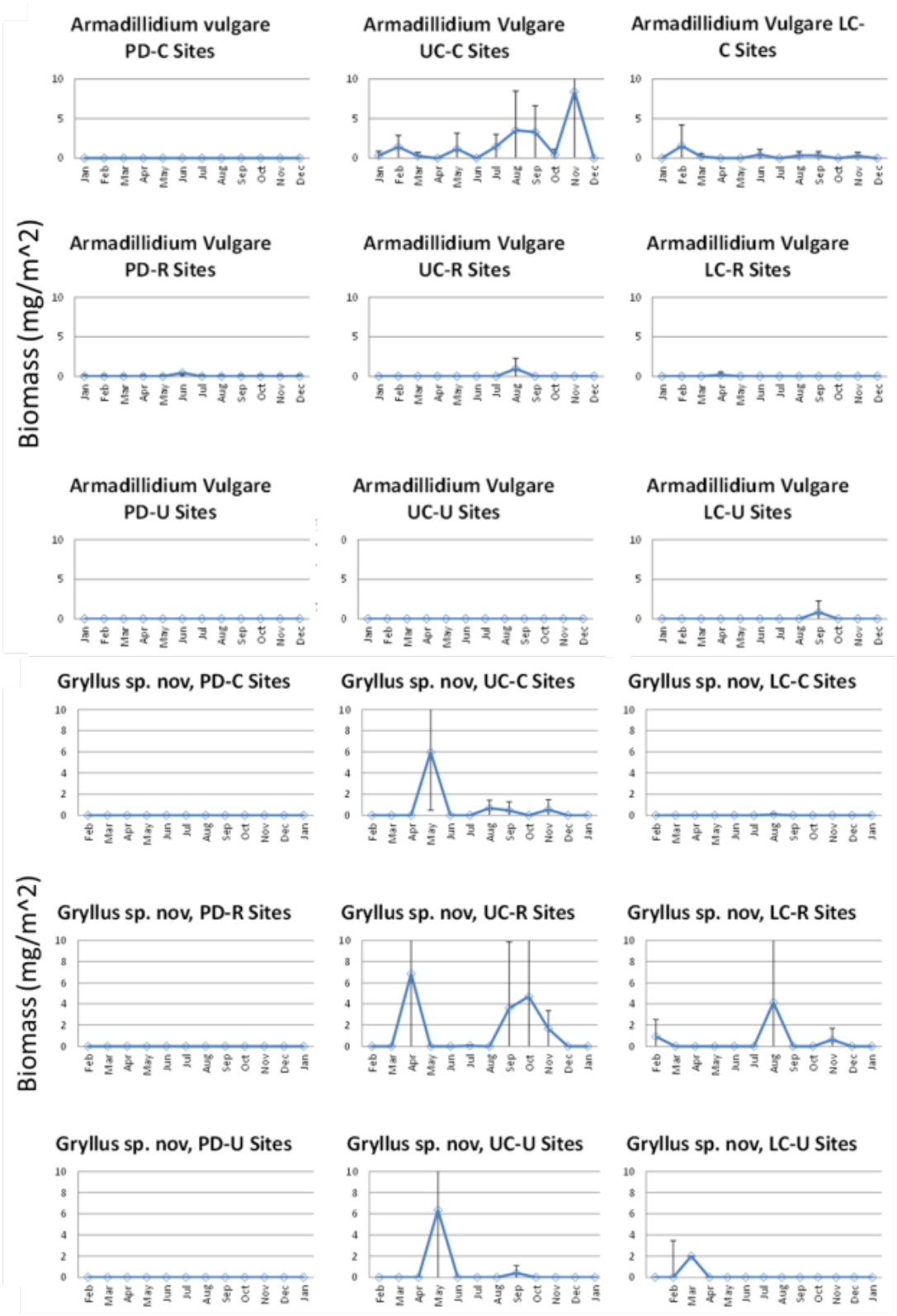

Fig. 9.3. Monthly biomass trends for all *A. vulgare* and all *Gryllus sp. nov*. collected during one year of sampling. Values are averages from sites sampled at or near Huachuca Canyon, Garden Canyon, and Ramsey Canyon (see Fig. 9.2).

Discussion

Hydroclimate and hydrology determine the temporal dynamics of terrestrial biomass and secondary production of ground-dwelling arthropods in dryland ecosystems. Peak production in total monthly biomass was observed during the monsoon. More consistent levels of biomass were found in streams with at least intermittent flow. Finally, the monsoon peak in biomass was strongest for piedmont streams and muted for canyon sites with at least intermittent flow.

Stream flow permanence leads to consistent secondary production of ground-dwelling arthropods throughout the year, presumably by allowing for development of dense forest canopy and associated litter fall, whereas seasonality in rainfall conveys exceptional but episodic secondary production at sites with ephemeral flow. Relatively permanent levels of stream flow are necessary to maintain a stable population of terrestrial macroinvertebrates in dryland riparian ecosystems. This was especially true for *Gryllus* and *A. vulgare*, which are important detritivores, and which may serve as useful monitoring organisms for detecting changes in channel and riparian conditions, respectively. The apparent paucity of detritivores at piedmont sites may be partially responsible for slower rates of leaf decomposition at those locations (see Chapter 10).

The response of riparian ground-dwelling arthropods to rainfall seasonality diminishes in magnitude with stream flow permanence. Each piedmont stream type's peak biomass average in the month of September was larger than any monthly biomass value in any of the canyon stream sites. This pattern extended to the uplands, indicating that it was precipitation-driven. Although ephemeral streams may have highly variable median monthly biomasses and have very low productivity throughout most of the year, these streams are capable of supporting more terrestrial biomass than semi-perennial streams following the typical monsoon precipitation events.

Secondary production was difficult to measure for all but a few common taxa. However, our results comparing stream flow permanence directly to community-level biomass suggest that stream flow permanence could be used to predict secondary production trends and estimate monthly biomass in dryland riparian ecosystems. Ultimately, differences in secondary production of arthropods could affect higher consumers that feed on these resources including a number of reptile, amphibian, and bird species including the threatened Chiricahua leopard frog and Mexican garter snake.

Chapter 10: Controls of Temporary Stream Flow and Water Presence on Rates of Litter Decomposition and Nutrient Release in Dryland Ecosystems

Q1: What Regulates Litter Decomposition in Temporary Streams and Associated Riparian Zones?

Litter mass decreased with time across all sites, with landscape position exerting a stronger influence than litter type on rates of decomposition within and across sites (Fig. 10.1). Oak litter in upland and riparian positions had greater than 50 percent of mass remaining as ash free dry mass at the end of the 18th month deployment. Mass loss was greater in the channels, with less than 20% remaining after 18 months, and with values differing significantly across sites and flow regimes. Indeed, these differences among flow regime emerged as early as four weeks after deployment (RMANOVA: time; F: 171.19, $p<0.01$; time*site; F: 97.04, $p<0.01$; time*[position] site; F: 104.07, $p<0.01$). A single exponential decay model fit the data well (r^2 from 0.75 to 0.99). Analysis of variance (ANOVA) tests and post-hoc Tukey tests conducted for decay rates (k) showed that rates of decomposition in channels were significantly higher in semi-perennial and dry-intermittent and wet-intermittent channels compared to other flow regimes (F 35.1, $p<0.01$).

Mass loss of sycamore followed similar patterns to oak, though there was an observed gain in mass initially at most sites in the riparian and wetter sites in the upland positions (Fig. 10.1), likely owing to the higher carbon to nitrogen (C:N) ratio in sycamore litter (85.7 ± 9.4) compared to oak litter (32.2 ± 0.55) (C:N F 95.126, $p<0.0001$). Decay rates for sycamore leaves ranged from 0.001-0.003 d-1, with a mean of 0.0017 d^{-1}, and did not differ significantly from oak decay rates. Loss of sycamore litterbags in channel over the course of the 18-month period precluded statistical tests for differences in decay rates across flow regime and are minimally discussed hereafter.

Oak litter nitrogen dynamics varied substantially with position. There were net gains of N mass in upland and riparian positions but net losses of N mass in the channel position (Fig. 10.2). Specifically, percent N mass in litter *increased* as much as 20 to 40 percent from the initial value of 1.5 ± 0.04 % N in the riparian and upland positions, respectively, especially at the wetter sites, indicating immobilization of N from the surrounding environment. In the channels, percent N mass decreased at all stream types, especially the semi-perennial and wet-intermittent types. Oak litter in upland and riparian position lost proportionally less N than total mass, yielding slopes of less than one (0.45 for upland and 0.74 for riparian). In contrast, in the channel, total N loss was proportional to total mass, with a slope of 1.03 (r^2=0.34), indicating that physical fragmentation was the main factor causing loss of N and mass in this position (Throop and Archer 2007). At the end of the 18-month deployment, the percent N mass remaining was significantly lower in the channel compared to upland and riparian positions (F 3.7, $p=0.02$).

Regression analyses conducted to elucidate controls on decomposition rates ($k_{18\text{-month}}$) showed that cumulative water presence (i.e., stream flow days), landscape position, and its interaction term (cumulative water presence x position) explained 56 percent of the variation in the decomposition decay constants (k) across sites (Table 10.1). (Over the 18-month litter deployment period, cumulative stream flow days varied dramatically among sites from <1 to 434; Fig. 10.3). Percent cumulative stream flow and percent cumulative water presence were highly correlated (r=0.97) but cumulative water presence, the cumulative percentage of the year that the channel was wetted, was a slightly better predictor of decomposition rates. The percent of N remaining in the litter mass explained additional variation in rates of decomposition and was a better explanatory variable than C:N ratio. Soil C and N, soil C:N, soil nutrients

(ammonium and nitrate), and cumulative precipitation did not have significant effects in the model.

Q2: How do Soil Physio-chemical Characteristics Differ with Flow Regime and Landscape Position?

In-situ gravimetric soil moisture was lower in dry- and wet-ephemeral stream channel positions relative to riparian and upland positions, mostly likely owing to low organic matter and coarse texture (Fig 10.4., Table 10.2, Table 10.3). Soil moisture was higher and more variable in the wet-intermittent and semi-perennial channels relative to uplands and riparian zones, owing to subsidy of water in the channel as well as higher organic matter content.

Soil moisture dynamics varied considerably across years; 2010 was a relatively wet period and moisture dynamics did not differ substantially among positions following the monsoon season. In contrast, 2011 was a relatively dry year and soil moisture was clearly elevated under semi-perennial relative to ephemeral stream flow conditions. Notable increases in soil moisture were observed during and after the monsoon season during this year.

Soil physio-chemical characteristics varied with flow regimes and positions (Tables 10.2 and 10.3). Soil bulk density (<2 mm fraction) was significantly higher in the channels of the dry-ephemeral washes (1.99±0.15 g/cm^3) compared to other flow regimes. Average sand content was high across sites, ranging from 70 to 94 percent, whereas silt and clay made up a smaller and more variable percentage. Soil pH varied from 6.89 to 8.56 across sites.

Percent soil organic matter (SOM) was significantly lower in channels than in other positions, and tended to be similar in riparian and upland positions. Across sites, SOM was lowest in the dry-ephemeral channels (0.6 percent) and highest in the semi-perennial channels (three percent). Percent soil carbon (C) followed similar patterns. Soil percent nitrogen (N) was very low in most of the channel positions (0.03-0.07%) except in the semi-perennial channels, where %N was a high as 0.37%. Consequently, the C:N in channel sediments was highest in the dry-intermittent and wet-intermittent flow sites (41 to 47) and low at the flow regime extremes (range of 7 to11 for ephemeral and perennial flow conditions).

Upland and riparian C:N ratios were lower than 20 at all sites except the dry- and wet-intermittent sites. Relatively low C:N in channel sediments and upland and riparian positions (<20) suggests that these sites will have high rates of net N mineralization and associated release of nutrients. Observed higher C:N (>20-25) in upland sites at the dry and wet intermittent sites lead to expectation of possible immobilization by microbes due to limited availability of N relative to carbon.

In contrast to our expectations that increased hydrologic variability in the ephemeral stream channel would lead to elevated nutrient release and more rapid processing than surrounding uplands, we found the opposite pattern. Of note, soil exchangeable ammonium (NH_4^+) concentrations were high in all channel positions and generally higher in upland and riparian position of the wet-intermittent to semi-perennial stream sites (Fig. 10.4). The wet year resulted in higher exchangeable NH_4^+ whereas drier years, especially after monsoon, reduced NH_4^+ concentrations under wet-intermittent and semi-perennial stream conditions.

Soil exchangeable (NO_3^-) concentrations were surprisingly elevated under dry-ephemeral stream conditions, particularly in the riparian zone during the wet year (2010). Similar to NH_4^+, soil exchangeable NO_3^- was generally higher in the riparian and upland positions than the channel positions. Rates of net mineralization varied substantially with dry and wet years and were significantly elevated following the monsoon in the wet years across most sites. This pattern was particularly pronounced in the semi-perennial stream sites. In-situ net rates of

mineralization and nitrification were generally higher in the upland and riparian positions compared to channel positions. The ratio of net nitrification to net mineralization approached 1 across all sites and position with a few exceptions suggesting that most of the available ammonium that was mineralized was also nitrified to nitrate.

Q3: How does Nutrient Availability Differ among Streams and Landscape Position?

Nutrient availability and potential loss as measured by accumulation of nutrients on cation and anion exchange resin bags for two month time periods varied significantly with flow regime, position, and time (Fig. 10.5). Repeated measures ANOVA for the four collections showed that ammonium varied significantly with time, flow regime, and position (Position: F 6.88, df=10, p=0.0004, Flow regime: F 3.89, d 4, p=0.02, Time: F 6.56, df 3, p=0.005). Post-hoc Tukey tests showed that ammonium in the channel position was significant lower at semi-perennial flow streams compared to drier flow regimes prior to the monsoon (F 94.02, df=4, p<0.01) and to lesser extent after the monsoon. This reduced availability of ammonium was likely biologically significant for stream biota and organic matter release.

Resin nitrate in the channel position was lower under semi-perennial flow conditions compared to dry ephemeral conditions, but was more variable than ammonium. Repeated measures ANOVA did not detect statistically significant differences among flow regime and positions over time, but the differences were likely biologically significant in that concentrations of nitrate in the semi-perennial systems were two to three orders of magnitude lower in the semi-perennial compared to the dry-ephemeral washes during and after the monsoon. The lower values in the semi-perennial stream flow likely can be explained by the more frequent presence of flowing water which exported nutrients; in the ephemeral channels, nutrients accumulate between monsoon runoff events.

Q4: What are the Potential Net Mineralization and Nitrification Rates in Soils?

Laboratory wetting of pre-monsoon soils to assess the potential rates of release and process rates showed that potential rates of net mineralization and nitrification were two to five times higher than in-situ net rates measured under pre-monsoon moisture conditions. These patterns were particularly pronounced in the riparian and upland positions (Fig. 10.6). Potential mineralization and nitrification did not vary substantially with position in the dry- to wet-ephemeral sites but did vary with position under intermittent and semi-perennial stream conditions. Specifically, in the channel of the wetter streams, low to negative rates of potential net mineralization and nitrification were observed indicative of immobilization of N from the surrounding environment. This pattern is consistent with higher soil C:N ratios and possible N-limitation to mineralization rates. These findings are also consistent with biogeochemical theory that holds that the threshold for mineralization of N is typically below a C:N of 20-25 because more N is available relative to C for microbial uptake and utilization. Above this ratio, N is limiting to mineralization and needs to be taken up from the surrounding soil environment. Highest rates of potential mineralization were observed in the upland semi-perennial sites consistent with observed in-situ rates of net mineralization following wet up in 2011.

Table 10.1. Multiple regression model showed strong effect of water presence and interaction with position on litter decomposition rates (r^2= 56, r^2_{adj}=0.51, Whole model, F ratio 11.15, p<0.0001).

Effect test	F Ratio	P>F
Cumulative water presence (days)	27.1	<0.0001
Position	9.73	0.0003
Cumulative water presence (days) * position	5.06	0.0097
% N remaining	3.8	0.05

Table 10.2. Soil characteristics for sites in different flow categories. Study sites within each flow category are indicated in parentheses. Values reported are means (±SE; n=3) and significant differences indicated by lower case letter. Lower case letters indicate significant differences between sites with nested position within sites.

Flow regime	Position	Soil Bulk Density	% Sand	% Silt	% Clay	Soil pH
Dry-Ephemeral (BG, SW, HP)	Channel	2.00 ± 0.16^{a}	93.10 ± 1.3^{a}	4.5 ± 0.7^{d}	2.4 ± 0.7^{c}	8.20 ± 0.12^{a}
	Riparian	1.27 ± 0.05^{b}	75.4 ± 2.8^{cd}	19.8 ± 2.4^{ab}	4.8 ± 1.0^{abc}	7.64 ± 0.20^{ab}
	Upland	1.24 ± 0.06^{b}	70.5 ± 1.9^{d}	23.3 ± 1.8^{a}	6.2 ± 1.2^{abc}	7.42 ± 0.25^{ab}
Wet-Ephemeral (RL, RP)	Channel	1.40 ± 0.12^{b}	90.3 ± 5.0^{abc}	8.1 ± 5.1^{bcd}	1.6 ± 0.2^{bc}	7.27 ± 0.37^{ab}
	Riparian	1.02 ± 0.08^{b}	76.6 ± 2.9^{bcd}	17.6 ± 1.7^{abc}	5.8 ± 1.2^{abc}	6.89 ± 0.39^{b}
	Upland	1.16 ± 0.10^{b}	76.7 ± 2.5^{bcd}	18.1 ± 2.1^{abc}	5.2 ± 0.6^{abc}	6.94 ± 0.31^{b}
Dry-Intermittent (GL, HU)	Channel	1.48 ± 0.08^{ab}	93.4 ± 1.4^{ab}	5.0 ± 0.3^{cd}	1.7 ± 0.2^{abc}	8.43 ± 0.10^{a}
	Riparian	1.03 ± 0.07^{b}	66.7 ± 6.5^{d}	25.6 ± 5.3^{a}	7.8 ± 1.2^{ab}	7.83 ± 0.16^{ab}
	Upland	1.16 ± 0.09^{b}	68.2 ± 6.0^{d}	23.8 ± 4.5^{a}	8.0 ± 1.7^{a}	7.68 ± 0.28^{ab}
Wet-intermittent (HL, GU)	Channel	1.27 ± 0.20^{b}	90.2 ± 1.9^{abc}	7.1 ± 1.5^{bcd}	2.8 ± 0.5^{abc}	8.56 ± 0.11^{a}
	Riparian	0.97 ± 0.10^{b}	70.5 ± 3.2^{d}	22.3 ± 2.7^{ab}	7.2 ± 0.9^{abc}	7.94 ± 0.13^{ab}
	Upland	0.98 ± 0.12^{b}	73.1 ± 4.9^{cd}	19.8 ± 3.5^{abc}	7.1 ± 1.5^{abc}	7.49 ± 0.32^{ab}
Semi-perennial RU	Channel	1.2 ± 0.2^{b}	88.4 ± 6.0^{abcd}	9.3 ± 5.8^{abcd}	2.3 ± 0.3^{abc}	8.02 ± 0.09^{ab}
	Riparian	0.86 ± 0.10^{b}	66.1 ± 4.8^{d}	25.2 ± 4.1^{ab}	8.7 ± 0.7^{abc}	7.38 ± 0.23^{ab}
	Upland	1.08 ± 0.24^{b}	73.5 ± 2.1^{abcd}	19.9 ± 2.2^{abcd}	6.6 ± 0.2^{abc}	7.28 ± 0.26^{ab}

Table 10.3. Additional soil characteristics for sites in different flow categories. Study sites within each flow category are indicated in parentheses. Values reported are means (±SE; n=3). Lower case letters indicate significant differences between sites with nested position within sites.

Flow regime	Position	Water holding capacity	Soil organic matter	Soil C (%)	Soil N (%)	Soil C/N
Dry-ephemeral	Channel	20.5 ± 1.0^{d}	0.6 ± 0.1^{c}	0.34 ± 0.12^{e}	0.04 ± 0.01^{c}	7.0 ± 1.31
(BG, SW, HP)	Riparian	26.6 ± 1.5^{cd}	1.3 ± 0.2^{bc}	0.91 ± 0.07^{de}	0.08 ± 0.01^{c}	10.7 ± 0.5
	Upland	29.4 ± 2.0^{bcd}	1.2 ± 0.2^{bc}	1.04 ± 0.26^{de}	0.09 ± 0.01^{c}	11.0 ± 0.7
Wet-ephemeral	Channel	30.3 ± 5.3^{bcd}	2.0 ± 0.8^{bc}	1.19 ± 0.49^{de}	0.07 ± 0.02^{bc}	13.4 ± 5.7
(RL, RP)	Riparian	45.9 ± 11.1^{abc}	4.8 ± 1.6^{bc}	3.13 ± 2.04^{bcde}	0.22 ± 0.07^{bc}	14.1 ± 1.4
	Upland	39.7 ± 8.5^{abcd}	5.5 ± 3.3^{bc}	4.19 ± 3.28^{bcde}	0.25 ± 0.11^{bc}	14.2 ± 1.8
Dry-intermittent	Channel	23.8 ± 1.3^{cd}	1.4 ± 0.5^{bc}	1.23 ± 0.70^{cde}	0.03 ± 0.00^{c}	34.7 ± 16.8
(GL, HU)	Riparian	44.3 ± 5.0^{abc}	7.4 ± 1.8^{bc}	5.22 ± 0.37^{abcd}	0.25 ± 0.08^{bc}	27.1 ± 5.6
	Upland	42.5 ± 5.3^{abc}	7.6 ± 1.5^{bc}	5.77 ± 0.48^{abc}	0.32 ± 0.07^{ab}	18.3 ± 3.4
Wet-intermittent	Channel	30.9 ± 4.0^{bcd}	1.2 ± 0.3^{bc}	1.88 ± 1.07^{cde}	0.04 ± 0.01^{c}	47.6 ± 18.1
(HL, GU)	Riparian	48.0 ± 5.7^{ab}	9.0 ± 2.9^{b}	8.12 ± 2.21^{ab}	0.32 ± 0.10^{ab}	23.6 ± 0.2
	Upland	58.0 ± 6.5^{a}	20.1 ± 5.9^{a}	10.17 ± 2.14^{a}	0.52 ± 0.05^{a}	19.1 ± 2.9
Semi-perennial	Channel	36.3 ± 2.2^{abcd}	3.0 ± 2.0^{bc}	6.29 ± 1.68^{abcd}	0.37 ± 0.12^{ab}	17.9 ± 5.0
RU	Riparian	61.5 ± 2.1^{a}	9.0 ± 2.9^{abc}	2.22 ± 1.91^{bcde}	0.11 ± 0.08^{bc}	13.21 ± 4.0
	Upland	52.2 ± 9.1^{abc}	10.5 ± 1.1^{abc}	5.80 ± 2.29^{abcde}	0.37 ± 0.14^{ab}	15.73 ± 4.0

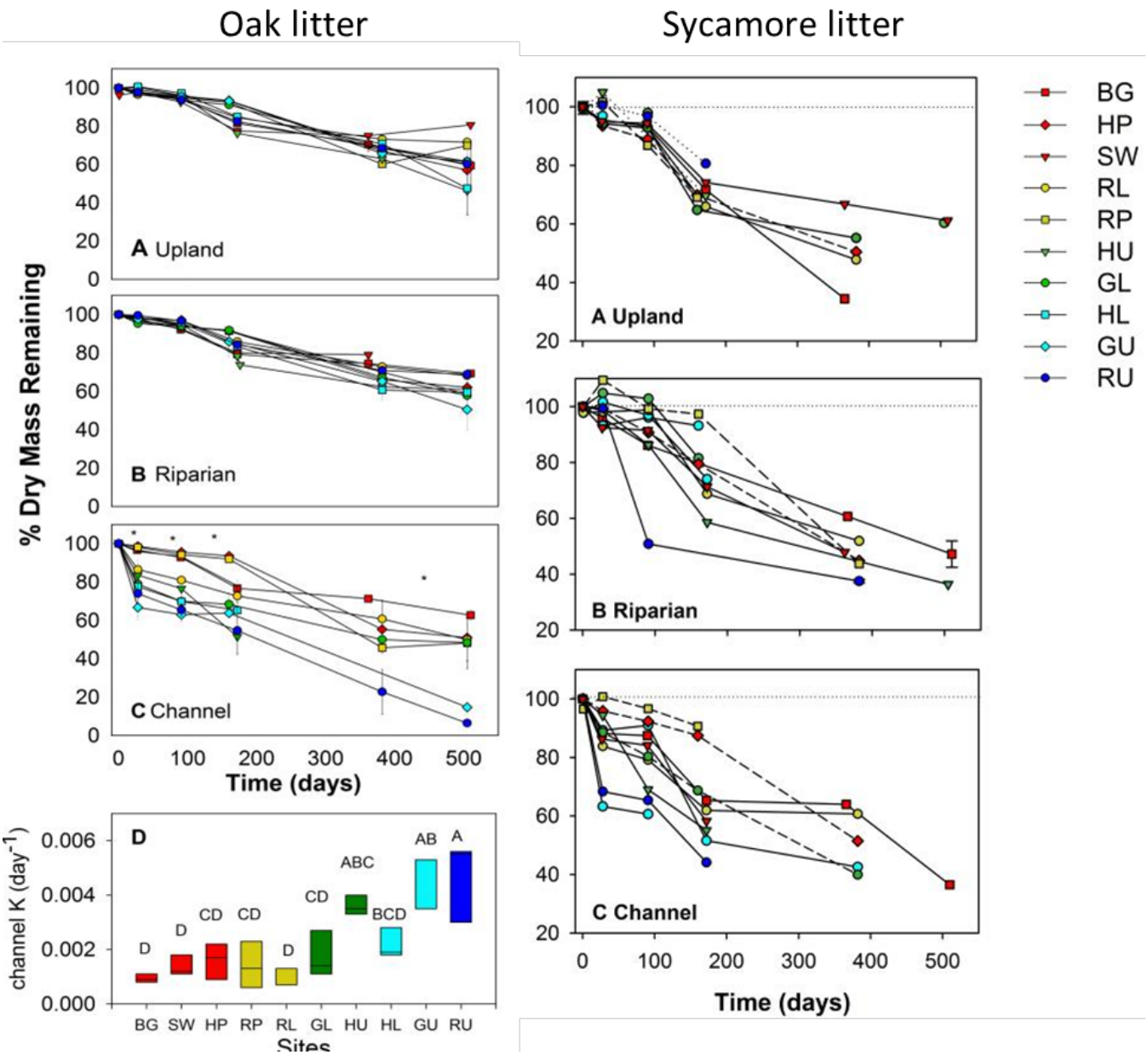

Fig. 10.1. Oak and sycamore leaf mass decomposition through time for three positions at each of 10 sites. Values are percent of initial litter mass, with mas expressed in ash free dry mass. Color codes indicate flow regime classification: Dry Ephemeral (red), Wet Ephemeral (yellow), Dry Intermittent (green), Wet Intermittent (aqua), and Semi-perennial (blue). Asterisks indicate significant differences among sites at different times. Panel D indicated decomposition decay rates in the channel position of the study sites. Different letters indicate significant differences in decay rate among sites for oak ($p<0.05$).

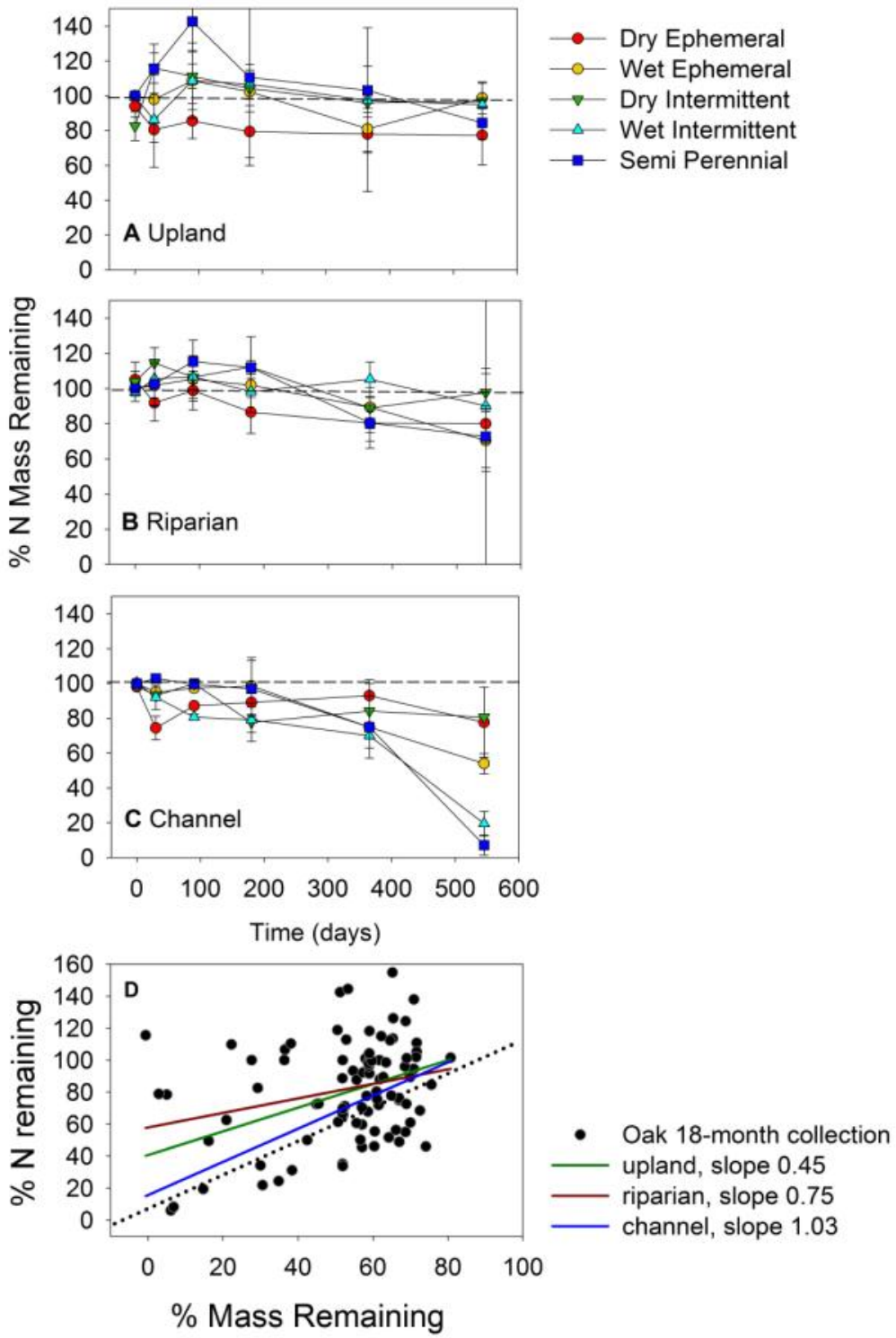

Fig. 10. 2. Percent nitrogen (N) mass remaining from initial litter over time (day since deployment) by flow regime and position (channel, riparian, upland). Color codes indicate flow regime classification: Dry Ephemeral (red), Wet Ephemeral (yellow), Dry Intermittent (green), Wet Intermittent (aqua), and Semi-perennial (blue). Panel D shows the relationship between

percent N remaining and percent mass remaining, and indicates that upland and riparian locations showed net gain whereas N loss in channel positions was proportional to mass loss.

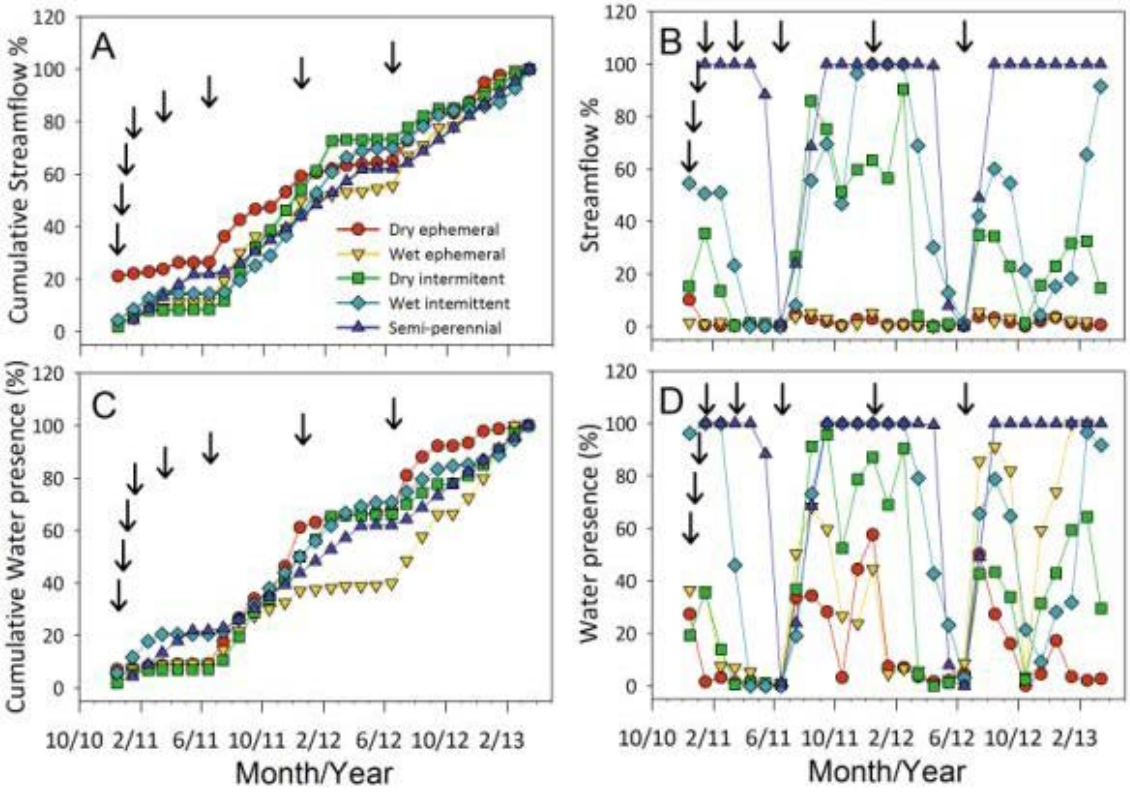

Fig 10.3. Cumulative stream flow and stream water presence, and percent monthly stream flow and stream water presence at dry-ephemeral (BG, SW, HP, GP, SR), wet-ephemeral (RP, RL, SS), dry-intermittent (HU, GL, HU_USGS), wet-intermittent (HL, GU), and semi-perennial (RU, GU_USGS) locations. Arrows indicate time of litterbag collections.

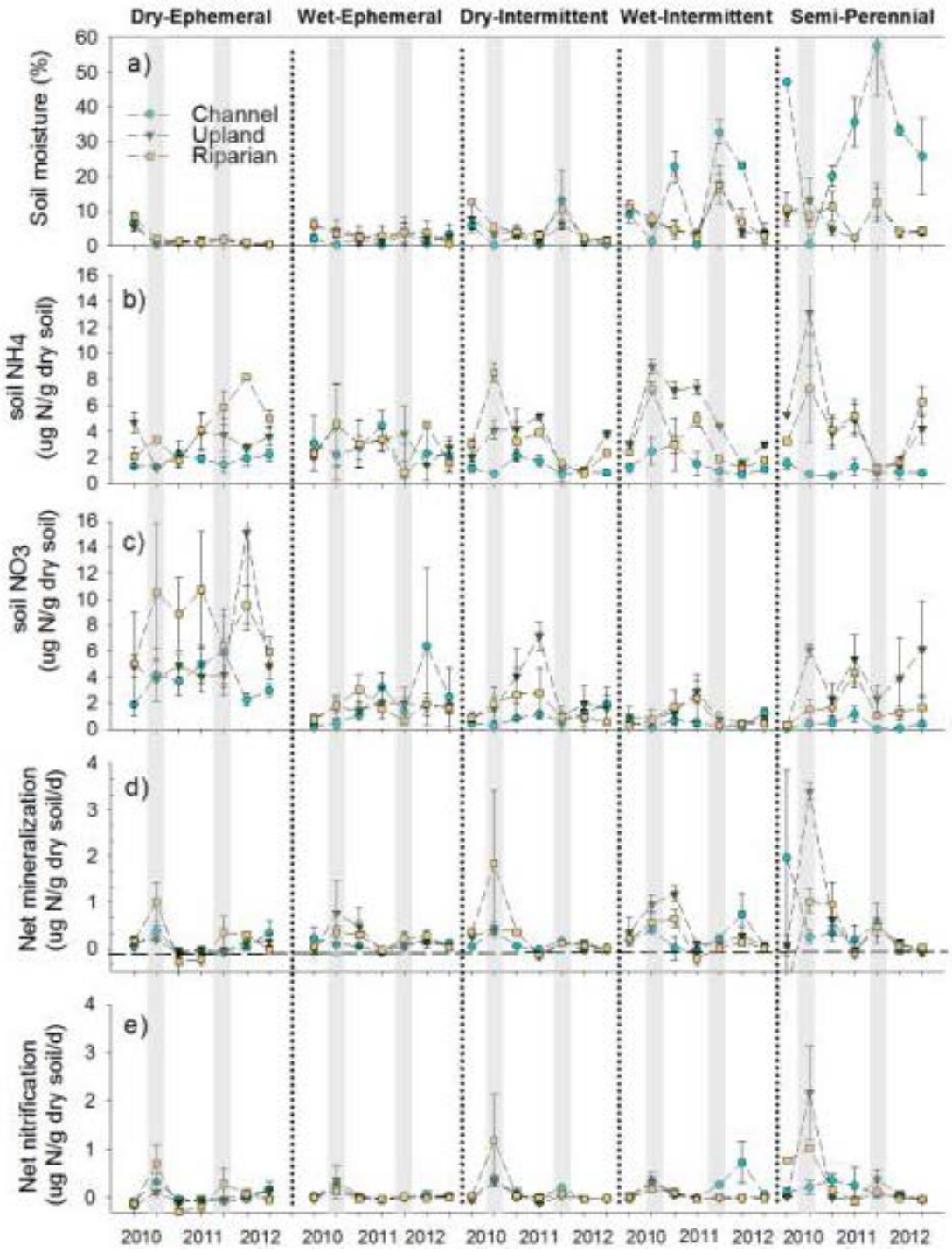

Fig. 10.4. In-situ temporal dynamics of gravimetric soil moisture, soil exchangeable ammonium and nitrate, and rates of net mineralization and nitrification by landscape position and flow regime. Gray shading within flow regime classes indicates post-monsoon response.

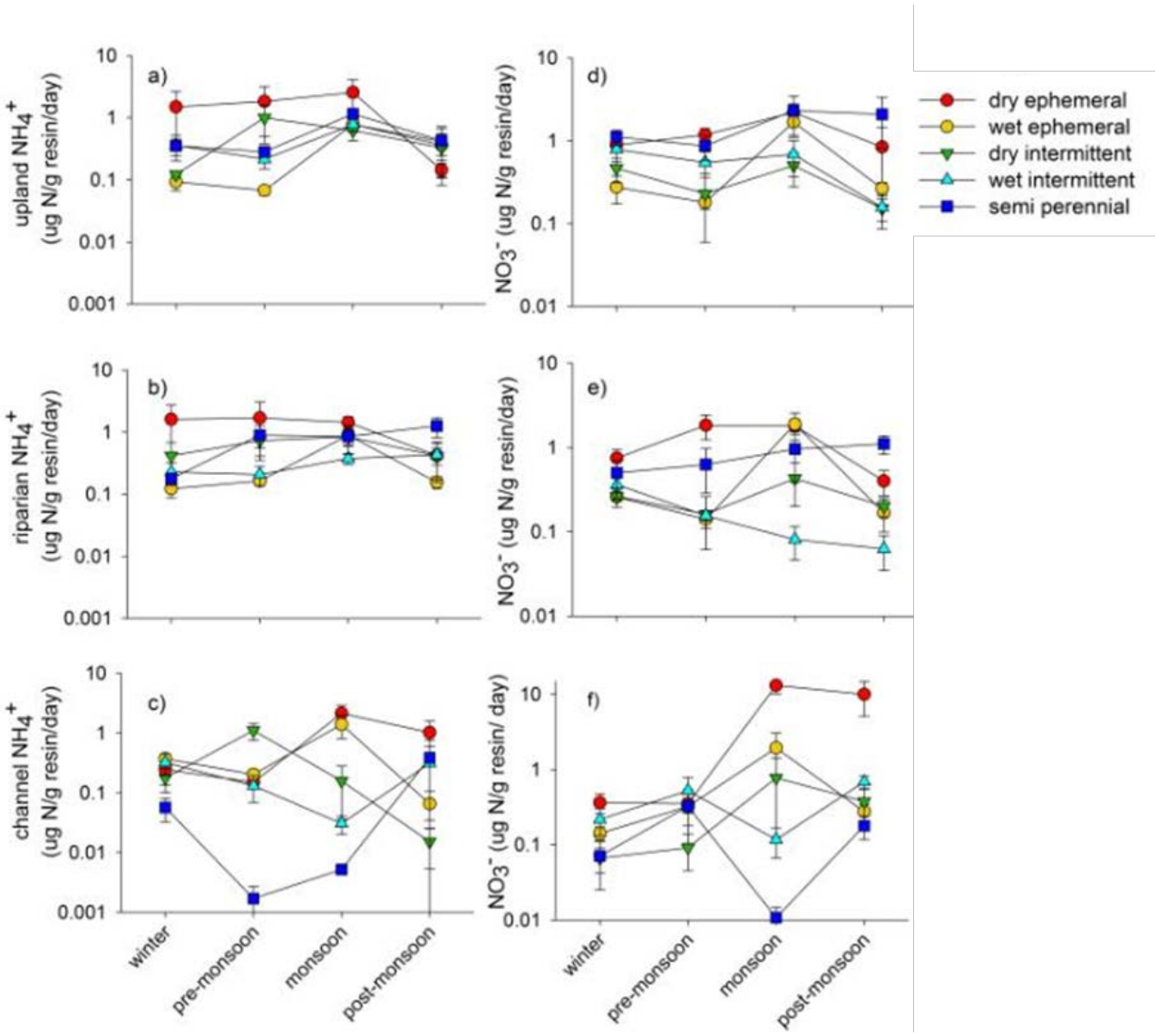

Fig 10. 5. Ammonium and nitrate availability and release, as measured by anion and cation exchange resins, by landscape position, flow regime, and season. Season are winter (January-March), pre-monsoon (March-June), monsoon (July-September), and post-monsoon (September-January). Nutrient availability was highest in the dry ephemeral channels during and post-monsoon whereas it was low in channels under the semi-perennial conditions.

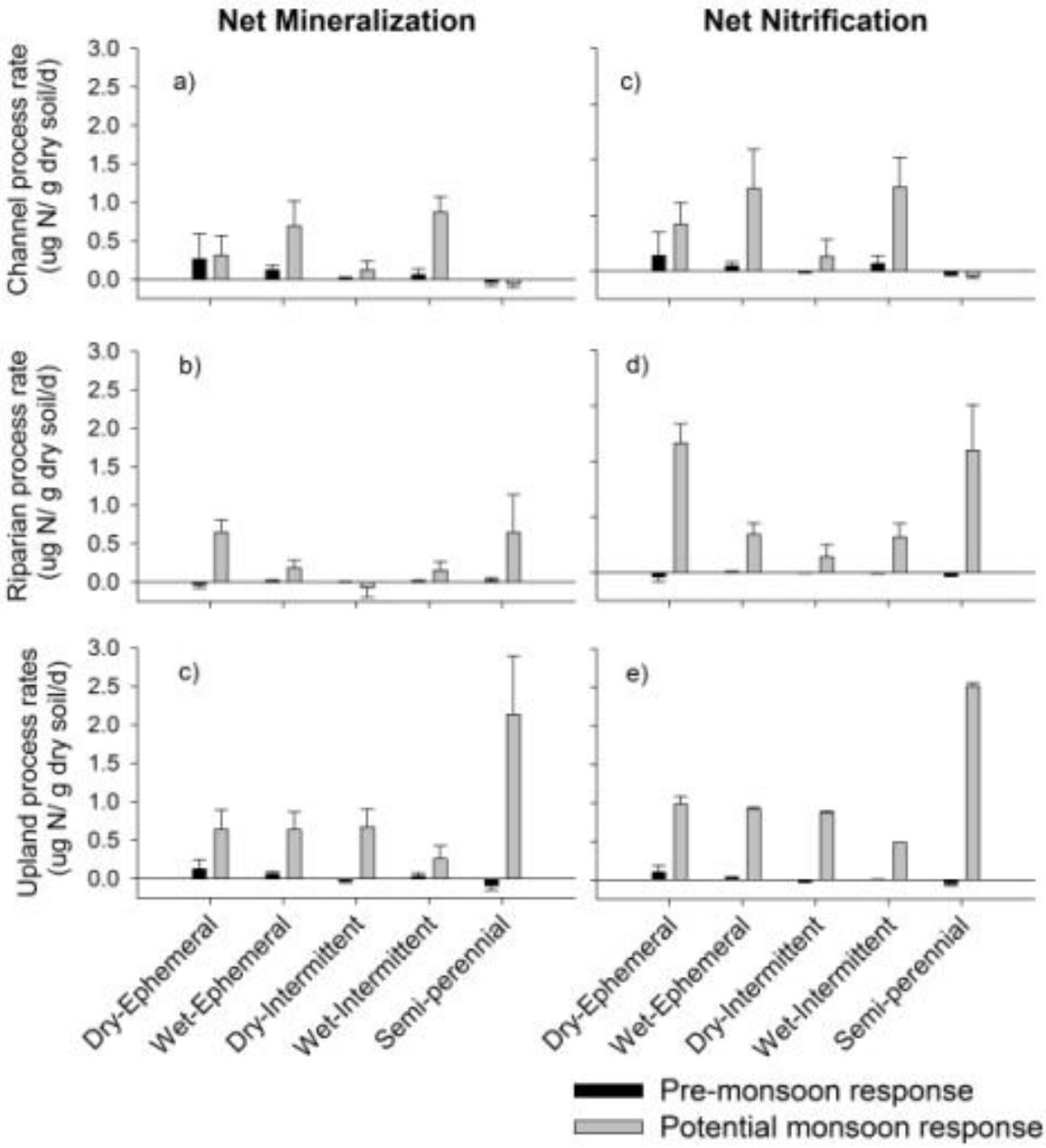

Fig. 10.6. Effects of laboratory wetting of pre-monsoon soils on net mineralization and net nitrification. Sites were grouped according to flow regime.

Discussion

To our knowledge, this is the first study to examine the influence of different temporary stream flow conditions, especially ephemeral stream flow and water presence, on rates of decomposition and the role of landscape position in controlling these processes. Higher decomposition rates observed in the semi-perennial and wet-intermittent channels than in the wet-ephemeral and dry-ephemeral channels were consistent with expectations that mass loss would be higher under a more permanent flow regime. Rates of decomposition decreased by a factor of three to six with the transition from semi-perennial to intermittent and ephemeral flow regimes. Channels showed N loss in proportion to mass loss indicating that physical fragmentation was the main factor contributing to break down of litter. Cumulative days of soil-water presence emerged as a significant explanatory variable explaining rates of decomposition, indicating that this factor merits further investigation and consideration.

The few decomposition studies conducted in intermittent or drought-influenced streams have shown decreases in rates of decomposition under drier conditions (Sangiorgio et al. 2006; Langhans and Tockner 2006; Anderson et al. 2006). In Mediterranean stream channels experiencing drought conditions, Sangiorgio et al. (2006) observed lower rates of leaf decay in dry compared to wet sites (0.003 compared to 0.006 d^{-1}), with rates comparable to this study (range: 0.001 to 0.006 d^{-1}). The one study focused on short-term (40 day) decomposition rates of different litter in the aquatic phase of an intermittent desert stream in Arizona showed faster rates of decomposition (0.017-0.005 d^{-1}) compared to this study. The lowest rates of decomposition were observed in sycamore leaves (0.005 d^{-1}) relative to ash, cottonwood, and willow leaves. Decay rates for sycamore leaves in our study were lower and did not differ significantly from oak decay rates after 18 months. These differences may indicate that short-term decomposition studies in temporary streams, particularly intermittent and ephemeral streams, may overestimate organic matter dynamics and decay rates if only conducted during the aquatic phase.

To our knowledge, the role of landscape position and inundation on rates of decomposition has only been evaluated in perennial streams. Faster rates of leaf decay have been observed in channels compared to flood plain positions, similar to our findings, but these effects have often only emerged after 12 to 18 months (Langhans and Tockner 2006; Langhans et al. 2008; Gurtz and Tate 1988; Anderson et al. 2006). In our study, differences in decomposition emerged among position as early as four weeks after deployment, perhaps owing to differences in controls on decomposition in dryland compared to more humid environments.

Rates of tree leaf litter decomposition were significantly higher in channels than in riparian and upland positions. Our findings that differences in rates of leaf decay were only associated with the channel positions, not the upland and riparian positions, despite the wide range of precipitation across sites, support the idea that the subsidy of water in the channel was the main factor decomposition. If climate factors were driving these differences, higher rates of decomposition would have been observed in the riparian and upland positions at the higher elevation, less arid sites. Decreases in annual cumulative daily stream flow and water presence below wet-intermittent flow conditions (<40%) lead to declines in organic matter dynamics suggesting that the aquatic portion of dryland systems may be more sensitive to changes in climate and possible sentinels of changes to come in the future.

Our results showing little difference in decomposition rates across sites in the uplands contrast with many upland studies showing climate and litter quality as main factors controlling decomposition rates (Aerts 1997; Couteaux et al. 1995; Hobbie 1992). A growing number of studies are pointing to the importance of abiotic factors in controlling rates of decomposition in

the terrestrial (Whitford 2002; Austin and Vivanco 2006; Austin et al. 2009; Throop and Archer 2007; Barnes et al. 2015) and aquatic portion of dryland environments (Schaefer et al. 1985; Hamadi et al. 2000; Anderson et al 2006). The lack of difference in decomposition rates in the riparian and upland position despite differences in climate suggests that the terrestrial portions of these environments are relatively insensitive to declines in precipitation and increases in temperature.

Litter quality such as percent N and C:N did not emerge as a major factor explaining rates of decomposition. Rather, differences in litter N dynamics helped to explain differences in leaf decay rates. Indeed, the lack of difference in total mass loss among upland and riparian sites may be explained by net gains of N being immobilized from the surrounding environment. In channels, as the duration of stream flow decreased from intermittent to ephemeral flow, the importance of the terrestrial phase increased and N loss decreased such that N loss in ephemeral channels was similar to that in the upland and riparian positions.

Lignin was not evaluated in this study owing to the fact that studies have indicated that lignin is not likely associated with inhibiting effects in desert environments (Hobbie and Vitousek 2000; Aber and Melillo 2001). Other abiotic factors such as physical abrasion, soil coverage/sediment burial (Barnes et al 2012; Fritz et al. 2006) and UV degradation (Austin et al; Troop et al), as well as biotic factors such as invertebrates (Anderson et al. 2006) and microbial communities associated with the litter (Kaiser et al. 2014) may need further consideration to be able to explain the remaining variation in decomposition rates observed, particularly in the uplands. Our study did not address the role of invertebrates in controlling rates of decomposition and warrants further study.

The role of invertebrates and microbial films/consortium in driving decomposition was beyond the scope of this study and merits further consideration as these processes have been shown to be important in driving decomposition in both the aquatic (Langhans et al. 2008) and terrestrial (Barnes et al. 2011) portions of landscapes. It may be as Kaiser et al. (2014) posits that decomposers overcome stoichiometric imbalances between litter and biomass through adjustments of the relative turnover rates of C- and N-rich pools, driven by a microbial community response to resource stoichiometry. Other factors such as sediment burial has also been found to slow decomposition rates in intermittent coastal plain streams (Fritz et al. 2006) as well as in upland dryland environments (Barnes et al. 2012; Barnes et al. 2015) and may help to explain further variation in decomposition rates as many litterbags were often covered/coated in sediment in the channels following the monsoon season.

Similar to decomposition rates, pronounced differences in nutrient dynamics were observed in the channels across flow regime. In contrast to our expectations that increased hydrologic variability in the ephemeral stream channel would lead to elevated nutrient release and more rapid processing than surrounding uplands, especially during the monsoon season, we found high nutrient release and availability but low process rates under dry-ephemeral conditions that appeared to reflect soil substrate stoichiometry, the amount and ratio of available carbon and nitrogen, primarily, and then moisture availability. Soil nitrogen and carbon contents were extremely low across all positions under dry-ephemeral flow conditions; N was <0.05% and C:N ratio were less than 11 at these sites suggesting that both carbon and nitrogen were limiting in this environment. When water was available, any available carbon was utilized for energy and organic matter mineralized and nutrients released as a by-product. Indeed, nutrients accumulated between runoff events under dry- to wet-intermittent flow conditions. At sites with dry- to wet-intermittent flow conditions, higher C to N contents appeared to result in low to negative rates of net mineralization and nitrification indicating immobilization of N and likely N limitation.

Finally, under semi-perennial conditions, sediment carbon and nutrient increased but N availability and process rates remained low indicating that other factors such as aeration may be limiting loss of carbon and process rates in the channel when the system is in the aquatic phase.

Collectively, findings from this study indicate that decomposition and nutrient release in the channel are tightly coupled to stream flow and water presence, and these processes will likely shift as streams move from semi-perennial to intermittent and ephemeral (Fig 10). We posit that transitions from semi-perennial to wet-intermittent streams will likely tip these systems into a significant terrestrial state or phase but these transitions are likely reversible as the aquatic phase is still significant. In contrast, transitions to more temporary streams (<40% stream flow) will likely result in rapid declines in organic matter processing as well as gradual declines in soil/sediment stores of carbon and nutrients that serve as pivotal ecosystem properties (Fig 10.7) with important implications for stream food web dynamics and nutrient dynamics. This transition to a dominant terrestrial phase in temporary streams may not be reversible owing to declines in stores of soil organic matter and nutrients that are slow to accumulate/recover. Consequently, changes in stream flow permanence associated with climate change may tip the relative importance of controls on decomposition and nutrient dynamics towards terrestrial compared to aquatic ones (Fig. 10.8).

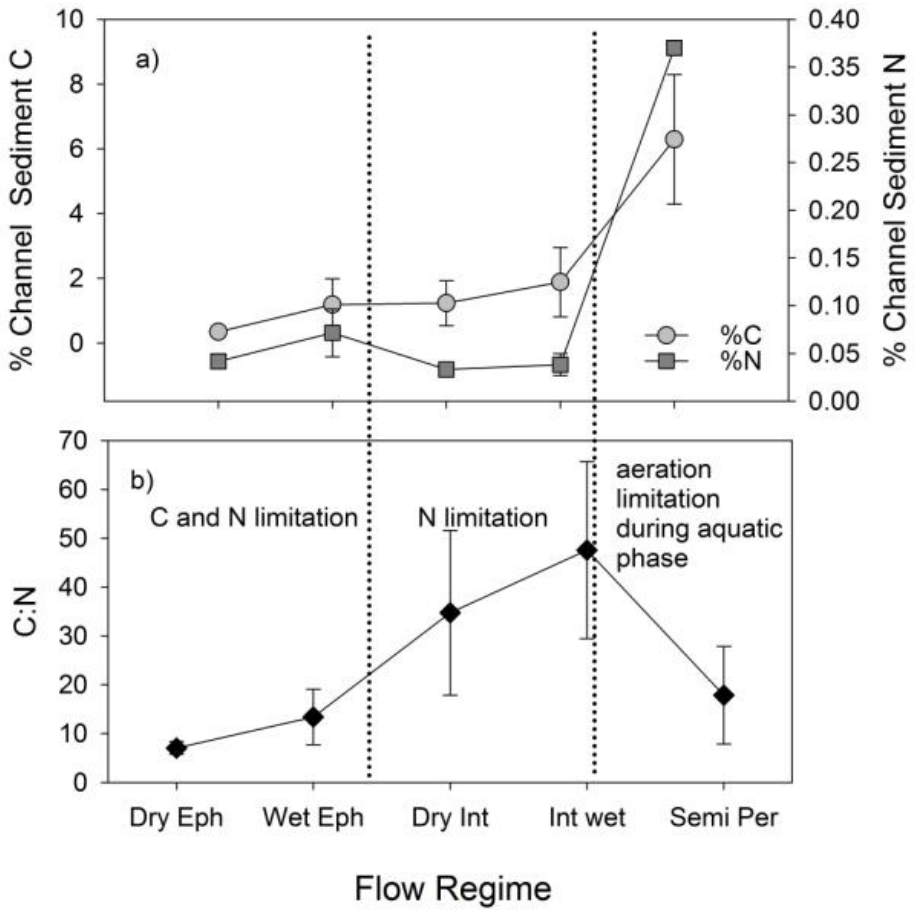

Fig. 10. 7. Stream channel carbon and nitrogen increase non-linearly with flow regime, and soil C:N peaks under intermediate flow conditions. Carbon and N limitation are hypothesized to shift with ephemeral to intermittent to semi-perennial conditions.

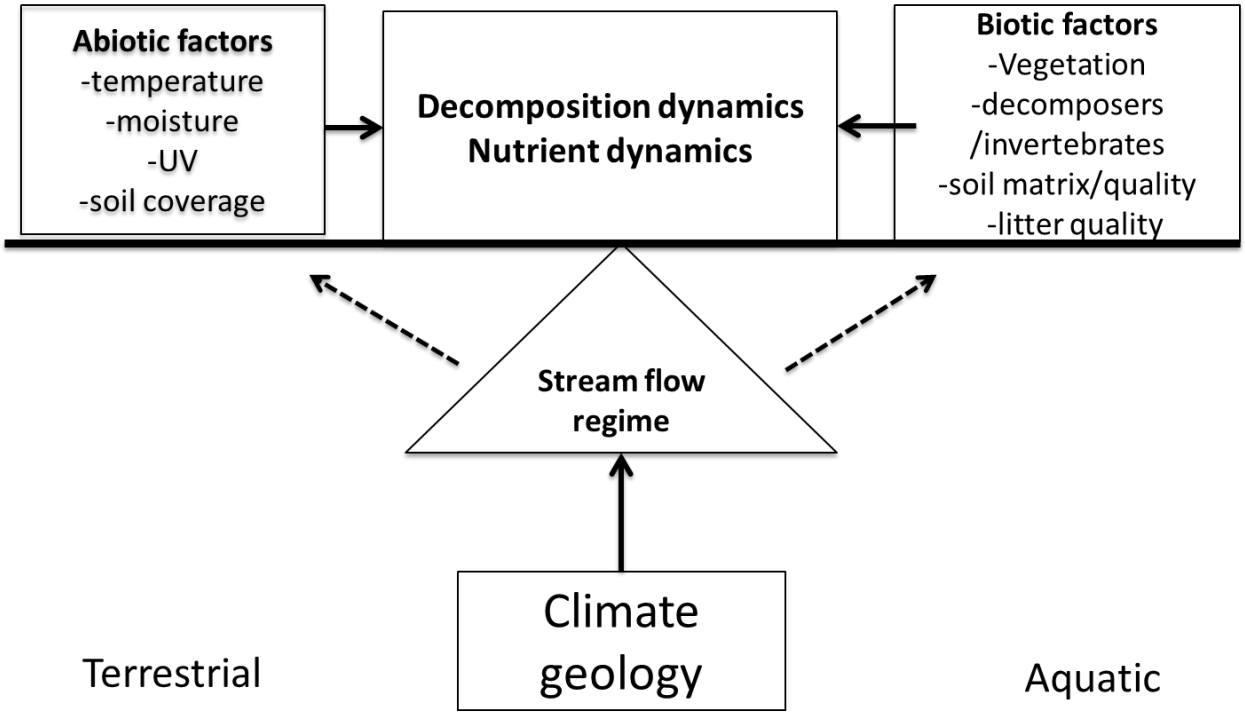

Fig 10. 8. Changes in stream flow permanence associated with exogenous factors such as climate change will tip the relative importance of controls on decomposition and nutrient release towards terrestrial phase controls compared to aquatic (teeter totter model).

Chapter 11: Conclusions and Implications for Future Research/Implementation

Advances to Stream and Riparian Ecology

Our results advance stream ecology by demonstrating that stream flow presence responds to local weather and climate to the greatest degree in areas with no connection to mountain groundwater systems, leading to the conclusion that ephemeral streams will be highly susceptible to climate change. We provide the first demonstration to our knowledge that stream drying, especially transitions from wet intermittent to ephemeral stream flow, has significant consequences for organic matter decomposition rates and nutrient release and important implications for food web dynamics and stream metabolism. We provide a comprehensive summary of how vegetation of ephemeral streams will change in response to increases in aridity, independent of changes in stream flow; demonstrate decoupling of woody and herbaceous components with respect to controlling water source; and quantify tradeoffs between riparian biomass and species diversity along the continuum from ephemeral to perennial stream flow. We advance stream and riparian ecology by addressing the degree to which various stream types are influenced by 'terrestrial' vs. 'aquatic' processes.

Hydrology of Temporary Desert Streams

Based on observational data of stream flow presence and absence we delineated five classes of temporary streams with distinct flow regimes: 1) dry-ephemeral, 2) wet-ephemeral, 3) dry intermittent, 4) wet intermittent and 5) semi-perennial. *Within this classification scheme geomorphic factors interacted with climate to predict stream flow and water presence*. The particular geomorphic factor that was important was stream channel density (total length of all streams in a drainage basin divided by the total area of the drainage basin) indicating that this mappable property is a useful approach for identifying drainages that will have more versus less frequent flow. Importantly, the best predictions came when combining stream channel density with rainfall timing and magnitude rather than rainfall alone.

Standing water was present in the channel for a significantly longer time than was flowing water. Channels remained wet longer than observed stream flow duration. This longer duration has implications for maintaining biogeochemical processing and plant growth for longer periods than stream flow occurrence alone would indicate.

The more ephemeral a site was, the more responsive to rainfall characteristics it was (and thus more regulated by terrestrial processes). Semiperennial sites had a prolonged period of streamflow extending through the winter with the sites drying in the lead up to the summer monsoon season. Streams with ephemeral flow had bimodal stream flow, with water presence distribution similar to that of the regional precipitation; the most prolonged stream flow occurred during late summer and fall.

Whereas the driest locations flow in direct response to runoff events, wetter sites are in part controlled by geologic factors. Ephemeral sites directly reflected the regions hydroclimatology whereas surface water in sites with longer flow duration were sustained by others factors including drainage and geologic characteristics of their contributing catchments. These contributions from geologic factors likely include soil drainage in the vadose zone and deeper geologic controls from the underlying rock formations in the catchment.

Wetter sites appear to be more buffered against short term climate variability than drier sites. Ephemeral sites are more susceptible to climate variability whereas more perennial sites

may represent wet refugia from climate variability and change. Ephemeral sites respond directly to weather events, and variability in climate would have a direct impact on ephemeral streams. Near-perennial sites are less susceptible to climate variability as they receive streamflow from longer term hydrologic groundwater storages. On a short temporal scale, and with respect to water presence, wetter sites will be better buffered against shifts in climate-change related to timing and distribution of precipitation. These results mirrors those on stream temperatures in other regions which have shown that higher baseflow streams are subject to less impact from climate variability and change.

Take-home messages: Precipitation and catchment characteristics control water presence and flow permanence. Water can be present without measurable streamflow in subsurface channel soils and this condition can have important ramifications for extended periods of nutrient cycling, herbaceous plant growth and arthropod productivity and richness. Both water presence and flow permanence are important characteristics differentiating our five categories of temporary streams. Wetter sites (intermittent to perennial) sites appear to be more buffered against short-term climate variability than drier (ephemeral) sites.

Vegetation of Ephemeral Streams- Response to Aridity

Riparian vegetation of ephemeral streams differs in biomass, life-form, species richness, and species composition along a spatial aridity gradient. As aridity increased among sites, the riparian zone of ephemeral streams had increasingly less vegetation volume, greater relative abundance of woody (versus herbaceous) vegetation, fewer plant species, a higher percentage of annual species in the flora, and greater variance between years in species richness. Low amounts of precipitation, as well as high coefficient of variation in mean annual precipitation, favors annual plants. As precipitation thresholds for sustaining tall grasses were met, growth form changed from xeroriparian scrub with seasonal annuals (arid sites) to mesquite savannah (semiarid and semihumid sites). We conclude that a similar suite of changes will occur through time as aridity increases in the American Southwest. Future studies should examine ephemeral streams along independent temperature and precipitation gradients, to tease apart the climatic components that contribute to aridity.

Ephemeral streams are influenced by terrestrial processes (precipitation) and by aquatic processes (flood water and fluvial disturbance).Flood disturbance serves to increase evenness of plant species in the community. The physical disturbances caused by floods, including periodic scour and sediment transport, suppress dominance of any single species. This was particularly evident in the semihumid setting, wherein the large monsoonal floods caused the riparian zones of the ephemeral streams to have greater evenness of species compared to uplands. Of note, introduced Lehmann's lovegrass, a species of concern to some managers, was dominant only in the uplands and not in the riparian zone of the Huachuca Mountain ephemeral piedmont streams. The many small ephemeral streams that flow through semi-desert grasslands fragment the dominant grass patches of the uplands and allow other grasses and forbs to coexists in higher numbers with Lehmann's lovegrass. These effects of flooding on the ephemeral stream riparian vegetation will become more pronounced if storm patterns intensify under climatic change.

Ephemeral washes, despite infrequent stream flow, are 'hot spots' of diversity in the arid to semihumid American Southwest and sustain many regional plant species not found in uplands. The riparian/channel zone of ephemeral streams sustained more plant species than occurred in the surrounding desert or semidesert uplands. This pattern is a result of the influence of multiple water sources. Direct precipitation stimulates germination of cool season and warm season

annuals. Iinfrequent floods wet the floodplain, sustain short-term stream flows, and (potentially) induce development of a shallow perched water table. These supplemental riparian water sources are critical for sustaining the small legume trees (*Prosopis, Olneya, Parkinsonia*) and other woody plants that provide the biomass structure of the arid region washes.

Ephemeral streams may function as reservoirs or sources for species that are declining in the uplands. In the semiarid and semihumid settings, there was high overlap in plant composition between the riparian zone and uplands. The riparian zone sustained populations of many herbaceous species that were infrequent in adjacent uplands including at least one rare plant taxon, *Heterotheca rutteri*. Future studies should ask whether the riparian zones of ephemeral stream serve as reservoirs (sources of seed) that augment populations of upland species during drought conditions.

Take-home messages: Riparian zones of ephemeral washes in the arid to semihumid Arnerican Southwest sustain high plant diversity, support many plant species that are absent to sparse in the uplands, and have greater biomass (of woody vegetation in particular) compared to upland desert and semidesert vegetation. These differences result from the interplay of multiple water sources- precipitation (a terrestrial source) and flood flows (an aquatic source)- as well as from the species-evening effect of fluvial disturbance. Applying results as a space-for-time substitution, there will be declines in vegetation volume and plant species richness in the riparian zone of ephemeral streams as aridity increases, with the herbaceous vegetation effected to a greater degree (in comparison to woody vegetaiton). Further, the riparian zone will become more floristically and structurally distinct from the upland zones with increasing aridity. Finally, the dominant growth form will transition from mesquite savannah (under semiarid and semihumid conditions) to xeroriparian scrub with seasonal pulses of annual plants (arid conditions).

Riparian Vegetation Response to Stream Permanence

Woody plant (and total) biomass increased along a stream flow permanence gradient, with highest values at the wettest sites sampled (>50% flow permanence and shallow water table). Woody plants comprised the greatest fraction of our biomass indicator (vegetation volume) and their patterns heavily weighted the overall biomass response. Herbaceous biomass decreased as woody biomass increased.

Diversity patterns of tree species and herbaceous species were decoupled, resulting in a pattern in which total plant species richness decreased *along the stream water availability gradient.* Tree species richness was tightly coupled with presence of a shallow water table and stream flow permanence, and increased from ephemeral to semiperennial sites. The herbaceous understory was limited by light and water, with greatest richness at sites with sparse canopy such as ephemeral washes on piedmont. These differing responses among plant growth forms led to the counterintuitive finding of total species richness declining at the wetter sites in the Huachuca Mountains. In this system, as in many, others, herbaceous taxa comprise the majority of species and their response heavily weighted the total species response.

The decrease in plant species richness at wetter stream sites is somewhat counterintuitive, but is consistent with the *Intermediate Productivity Hypothesis* (Huston 2014). Prior studies in arid and semiarid regions of the American Southwest show plant species richness to peak at streams with intermittent (versus ephemeral or perennial) flow. In the Huachuca Mountains, owing to the more humid climate, species richness peaks at stream sites with ephemeral flow.

Stream surface water, subsurface water, and flood and rain water all regulate riparian vegetation in dryland regions with each differentially affecting guilds of riparian plants. The patterns in the riparian zone of our dryland study system are reminiscent of the "pulse-reserve" species-coexistence model described for upland desert systems. In this model, there is a dichotomous response between shallow rooted plants that respond rapidly to rain pulses and the more deeply rooted and longer lived plants that respond to deeper reserves of soil moisture from prolonged rains. In the riparian context, the annuals and many of the herbaceous perennials are 'pulse' species responding to rain and flood pulses that wet surface soils (with additional research needed to tease apart the flood and rain species). Most of the trees and some of the shrubs are 'reserve' species drawing from the shallow water table. The year-round presence of water in the surface stream or more typically from the stream aquifer is necessary to maintain the tall, productive riparian trees such as *Platanus wrighti* as well as a high density of deep-rooted facultative riparian trees such as *Quercus* spp.

The responses of overstory and understory plants to regional climate changes will be decoupled, given that different plant guilds are limited by different environmental factors (trees by stream hydrology and herbaceous species by light and by seasonal rains). As climate change causes a decrease in the spatial extent of densely-canopied riparian forests, there will be an increase in the spatial extent of riparian areas that have low biomass but high alpha- richness of plant species. Further research is needed to more precisely determine whether any Huachuca Mountain species are obligately associated with dense shade.

Riparian plant species in the Huachuca Mountain show high seasonal variability in cover and richness, with the late summer monsoons and winter frontal storms both contributing to increased species richness. The Huachuca Mountains are in a climatic region dominated by late summer precipitation, and the effect of summer rains and floods on pulsing of annual species and herbaceous perennials in the riparian zone was strong (particularly at drier, sparse canopy sites). Winter precipitation is less abundant than summer precipitation in the Huachuca Mountains, but our timing was fortuitous in capturing one wet, El-Nino year. The understory plant response to the winter moisture pulse was small, however; cool spring temperatures and infrequent winter rains may preclude development of a diverse spring annual flora in the Huachuca Mountains.

Trade-offs exist in riparian zones between forest biomass (regulated by surface water and groundwater) and plant species diversity (regulated by seasonal rain and flood pulses). Influence of canopy trees on herbaceous understory can range from positive to neutral or negative depending on environmental context and functional traits of the particular tree. Aridity is a key contextual factor. Trees reduce understory light and produce deep litter which impedes germination of many species but also ameliorate evaporative stress, of importance in hot arid environments. For the semihumid Huachuca streams, canopy cover had a depressing effect on understory diversity in wet seasons and a neutral effect in dry seasons. Patterns in the Huachuca Mountains are similar to those in other subhumid to humid contexts in which forest thinning increases richness of understory plants. Such responses can produce management trade-offs between forest biomass and species diversity.

Historic land use influences present day plant species richness. The Huachuca Mountains have very high plant species richness, but richness varies spatially. Of the three canyons studied in the Huachuca Mountains (Ramsey, Garden, and Huachuca), Garden Canyon had the greater number of plant species, even when controlling for site water availability, owing in part to land use history and in part to canyon topography. Whole canyon inventories of streams in the Huachuca Mountains would be useful to determine the extent to which individual canyons support unique species.

Take-home messages: Understanding how plant species diversity and productivity vary along moisture gradients is critical to predicting environmental change**.** Tree species richness and abundance increased with greater water permanence, but annuals and herbaceous species declined, resulting in overall declines in plant species alpha richness with decreasing surface and surface water. These patterns were variable between seasons, with the Monsoon rains and flood producing large pulses of species diversity at sites where understory was not limited by canopy cover (similar to arthropods). Ephemeral piedmont streams had highest richness and lowest biomass overall. Based on these findings we conclude that stream surface, subsurface water, and rain and flood water and light all are strong regulators of riparian vegetation in dryland regions with each differentially affecting guilds of riparian plants.

The responses of the overstory and understory plants to regional climate changes will be decoupled. As climate change causes stream drying, there will be a decrease in the spatial extent of high-biomass riparian forests but an increase in the spatial extent of areas that have high alpha plant species richness.

Soil Seed Banks

The factors that limit diversity of soil seed-banking plant species vary among streams that differ in flow permanence. Soil seed bank species numbers in riparian zones of ephemeral streams increased with site elevation and declining aridity (thus increasing precipitation), similar to patterns shown by terrestrial vegetation. Soil seed bank species numbers in riparian zones of intermittent to perennial streams, in contrast, decreased with elevation and declining aridity.

There is an interaction between aridity and stream flow regime, with ephemeral streams having more seed-banking species than intermittent and perennial streams only at high elevation (and high rainfall) sites. Riparian zones of ephemeral streams, similar to upland deserts, are water-limited and increase in seed banking species as precipitation increases. Vegetation of riparian zones of intermittent to perennial streams, in contrast, become light-limited on small semiperennial canyon streams, with fewer herbaceous species and thuse fewer seeds in the soil seed bank.

Rapidity of response and resilience to environmental change varies with the importance of the soil seed bank in the plant community and thus with stream flow regime. Differences in reliance on soil seed banks have implications for the rate of community response to environmental change. Systems with high percentages of seed-banking species, such as low-elevation perennial streams and high-elevation ephemeral streams, should respond rapidly to environmental change owing to the short live span that typifies many seed-banking species resilience. Further, soil seed banks can be viewed as a type of resilience to environmental change given that they contain seeds derived from many types of plant associations and from many generational cohorts that have experienced different selective pressures

Take-home messages: Soil seed banks are a regeneration strategy of many annual and short-lived plant species (“storers”). Aridity and the flow regime (flow permanence) exert joint control on the species richness of riparian soil seed banks. Ephemeral stream sites in wetter climates and perennial streams in drier climates have the greatest number of seed banking species (with seed numbers limited by low moisture for ephemeral streams in arid climates and by light and canopy cover for perennial streams at high elevations). These patterns have implications for the rate at which plant communities will respond to environmental change. They also have implications for

management actions that focus on restoration of plant communities, given that donor soils can be an effective restoration tool for restoring plant species to degraded sites.

Arthropod Diversity

Annual flow presence is a good predictor of arthropod biodiversity, but its effect varies seasonally and inter-annually. We found strong differences in both α-diversity and turnover (β-diversity) among sites and seasons. Annual flow presence appears to be positively (though non-linearly) related to α-diversity during the dry season and negatively related to α-diversity during Monsoon. This surprising result needs further analysis, but may emerge as a result of countervailing effects of water limitation (dry season) and physical disturbance (flooding during the Monsoon).

There were no significant effects of lateral position (along the channel-upland gradient) on α-richness and no interactions between lateral position and any other variable. This result is consistent with observations from a global meta-analysis that reported riparian zones harbor different not more species (Sabo et al. 2005).

Patterns of dissimilarity (β-diversity) between channel and upland sites were strong but were variable between years and seasons. This result is again consistent with observations from the Sabo et al. (2005) global meta-analysis. Temporal variation in the effect of water presence on β-diversity is most likely related to variation in total monsoon rainfall (water stress) versus peak discharge (flood disturbance). This conclusion is underscored by the observation that the two years of this study included one dry year (with fire) followed by a wetter year with large flood events.

Take-home messages: Annual flow permanence is a reasonable predictor of arthropod richness (α-diversity), but the direction of this relationship varies temporally. Richness is positively related to flow permanence during the dry season, but weakly, negatively related to flow permanence during the Monsoon. Hence, there may be countervailing effects of water-resource limitation during the dry season and physical removal by flood disturbance during the Monsoon. Turnover in species pools (β-diversity) was significant and varied with flow permanence and this interaction also varied seasonally and inter-annually. These results suggest that changes in the strength of the Monsoon, length of intervening dry periods and magnitude of floods will have a strong influence on spatial gradients of riparian arthropod biodiversity in the Southwest. As a result, increased climate variability could lead to high seasonal and interannual variation in riparian diversity gradients. However, these findings also highlight the fact that even ephemeral stream channels still have a "riparian effect" on diversity by harboring unique species relative to the surrounding uplands. More work is needed to understand how shifts in the hydrologic regime (timing of floods and droughts) impact the capacity of riparian zones to maintain gradients of biodiversity (β-diversity) and hence higher regional pools (γ-diversity). Given that diversity may be higher in wetter reaches in very dry years, whereas wet years will see higher diversity at more ephemeral reaches, it is important to maintain riparian habitat across the flow permanence spectrum to maintain a high regional diversity pool across years and seasons.

Arthropod Production

Hydrology determines the temporal dynamics of terrestrial biomass and secondary production of ground-dwelling arthropods in dryland ecosystems. Peak production in total monthly biomass was observed during the monsoon. More temporally consistent levels of

biomass were found in streams with at least intermittent flow. Finally, the monsoon peak in biomass was strongest for ephemeral piedmont streams and muted for canyon sites with at least intermittent flow.

Stream flow permanence leads to consistent secondary production of ground-dwelling arthropods throughout the year, whereas seasonality in rainfall conveys exceptional but episodic secondary production at sites with ephemeral flow. Relatively permanent levels of stream flow are necessary to maintain a stable population of terrestrial macroinvertebrates in dryland riparian ecosystems. Although ephemeral streams may have highly variable median monthly biomasses and low productivity throughout most of the year, these streams are capable of supporting more terrestrial biomass than semi-perennial streams following the typical monsoon precipitation events. Hence ephemeral streams may represent hot spots and hot moments of secondary production across terrestrial landscapes.

Take-home messages: Arthropods are the food base for higher-level predators in the food web like birds, bats, terrestrial carnivores, reptiles and amphibians. Water presence and flow permanence determine the temporal dynamics of the production of terrestrial arthropod biomass. Average (median) biomass is temporally consistent and highest in streams with the most permanent flow (upper canyons with extensive woody canopy cover and litter). By contrast, ephemeral rivers had highest peak biomass of arthropods but these "bursts" were episodic in response to rainfall-driven flow events. Our results comparing stream flow permanence directly to community-level biomass suggest that stream flow permanence could be used to predict secondary production trends and estimate monthly biomass in dryland riparian ecosystems. Ultimately, differences in secondary production of arthropods could affect higher consumers that feed on these resources including a number of reptile, amphibian, and bird species including the threatened Chiricahua leopard frog Lithobates chiricahuensis and Mexican gartersnake *(Thamnophis eques).*

Litter Decomposition and Nutrient Cycles

Rates of tree leaf litter decomposition were significantly higher in channels than in riparian and upland positions, and within the channel, were higher in stream types that had high soil water and stream flow presence (wet-intermittent and semiperennial types). Our findings that differences in rates of leaf decay were only associated with the channel positions, not the upland and riparian positions, despite the wide range of precipitation across flow regimes (190 to 450 mm) support the idea that the subsidy of water in the channels as stream flow and/or soil-water was the main factor driving decomposition. Decreases in annual cumulative daily stream flow and water presence below wet-intermittent flow conditions (<40%) lead to declines in organic matter dynamics..

Cumulative days of soil-water presence associated with each site and the interaction with landscape position emerged as significant explanatory variables explaining rates of decomposition. These findings indicate that soil-water presence may be a more important indicator of ephemeral and intermittent stream function than stream flow alone and merits further investigation and consideration in other studies.

Surprisingly, rates of decomposition were not significantly different among sites in the upland and riparian positions despite large differences in precipitation. The lack of difference in decomposition rates among sites in the riparian and upland zones, despite differences in precipitation and aridity, suggests that decomposition rates in the terrestrial portions of these

environments are relatively insensitive to declines in precipitation and associated increases in temperature. Future studies should examine decomposition responses along independent temperature and precipitation gradients, to tease apart the climatic components that contribute to aridity. Further, our study did not address the role of invertebrates across flow regimes in controlling rates of decomposition with the smaller mesh size bag and warrants further study.

Nitrogen availability and cycling were generally higher in the upland and riparian positions compared to channel positions, and varied seasonally. Soil exchangeable ammonium was high across sites whereas nitrate was highest in the dry-ephemeral channels compared to other stream types. Ammonium as measured by resins was significantly lower in semiperennial stream type channels compared to drier flow regimes. Similarly, nitrogen availability and release in the channel as measured by exchangeable nitrogen extracts and resins was significantly lower in the semiperennial sites compared to drier sites indicating N loss in stream systems dominated by aquatic (versus terrestrial) processes.

Collectively, our findings indicate changes in stream flow permanence associated with climate change may tip the relative importance of controls on decomposition and nutrient dynamics towards terrestrial compared to aquatic ones. Transitions from semi-perennial to wet-intermittent streams will likely tip these systems into a significant terrestrial state or phase but these transitions are likely reversible as the aquatic phase is still significant. In contrast, transitions to more temporary streams (<40% stream flow) will likely result in rapid declines in organic matter processing as well as gradual declines in soil/sediment stores of carbon and nutrients that serve as pivotal ecosystem properties with important implications for stream food web dynamics and nutrient dynamics. This transition to a dominant terrestrial phase in temporary streams is likely not reversible owing to declines in stores of soil organic matter and nutrients that are much slow to accumulate/recover.

Take-home messages: Decomposition is a critical component of biogeochemical cycling. Decomposition was highest in streams with greatest water permanence (longer hydroperiod). N-mineralization was highest in channels of the wettest sites sampled (semi-perennial). N-availability and release was highest in drier channels (ephemeral sites) and in upland and riparian locations (away from the channel). These findings indicate that decomposition and nutrient release in the channel are tightly coupled to stream flow and water presence, and will decline if streams shift from semi-perennial to intermittent and ephemeral. Changes in stream flow permanence associated with climate change will have cascading effects on rates on nutrient release via the process of decomposition.

Conservation and Management Implications

Our study underscores the need to conserve and protect a variety of stream flow regimes, in a variety of locations, to meet the multiple (and sometimes mutually exclusive) goals of maintaining high ecosystem productivity and high species richness (Table 11.1). For example, the presence of canyon streams with frequent surface flow and a shallow water table supports high biomass of riparian trees, whereas piedmont streams with ephemeral flow sustain high diversity of plant species. Sustaining wet canyon streams also allows for low but constant secondary production by ground-dwelling arthropods, whereas the drier and less shaded sites allow for a biologically important pulse of productivity and richness during the summer monsoon. Ultimately, secondary production of arthropods influences the distribution and abundance of consumers occupying higher trophic levels. These species include a number of

reptile, amphibian, and bird species including the threatened Chiricahua leopard frog and Mexican gartersnake. *Maintaining riparian habitat across the flow permanence spectrum also will maintain a high regional diversity pool across years and seasons.* For example, diversity of ground dwelling arthropods may be higher in wetter reaches in very dry years, whereas wet years will see higher diversity at more ephemeral reaches.

Our study shows that individually and collectively, the many small, unnamed ephemeral streams (washes) in the piedmont zone of the Huachuca Mountains and the Barry Goldwater Range have high conservation value. They sustain high plant and arthropod diversity, support plant species that are absent to common in the uplands, and have greater biomass (of woody vegetation in particular) than occurs in uplands. Applying results as a space-for-time substitution, there will be declines in vegetation volume, plant species richness, and relative increases in woody (versus herbaceous) vegetation in the riparian zone of ephemeral streams as aridity increases. Maintaining many small ephemeral washes across the landscape will contribute to the maintenance of regional diversity and help to buffer upland taxa from periodic drought.

Riparian and aquatic field biologists capture a high level of detail with their measurements and observations, and these reach-scale results can readily be scaled-up to the catchment-scale. We found a high correspondence between our field approach for determining stream flow permanence and the modelling approach used by the Levick team for the Huachuca Mountains, indicating that our field-based findings can be extrapolated to the catchment scale. There is one important caveat, however. A third of our study sites, all ephemeral channels on the piedmont, were too small to be captured by the Levick model and could be overlooked by hydrological models that focus on mapped streams. The collaboration between RC 1727 and RC 1726 also revealed that the hyper-ephemeral channels distal from the mountains are an abundant type of ephemeral channel thaht remain in need of detailed field study.

A first step towards protecting the many ephemeral channels and associated riparian zones on the piedmont of the mountains in semiarid and semihumid areas of the Arizona Sky Islands (including the Huachuca Mountains) is to document, map, and name them. These ephemeral stream ecosystems are narrow, linear features of the landscape that are easily overlooked on maps and in the field, given their similarity in vegetation structure to adjacent uplands. Despite this apparent structural similarity, they contribute disproportionately to processes including decomposition of organic matter and maintenance of diverse communities of plants and arthropods. Thus, one basic conservation need is fine-scale mapping and naming of the small, ephemeral channels.

Understanding the ways, and rates, in which different water sources influence the structure and function of temporary streams will help managers interpret and anticipate ecosystem changes arising from regional climate shifts. Riparian zones are ecotones between terrestrial and aquatic zones, and are influenced by processes associated with each type of ecosystem. For ephemeral streams, structure and function is strongly regulated by terrestrial processes (e.g., precipitation) and many elements of the vegetation will shift rapidly in response to precipitation changes owing to their capacity to regenerate from soil seed banks. Structure and function of semiperennial streams, in contrast, are strongly regulated by aquatic processes (e.g., surface and subsurface water flows). Such sites will be slow to respond, given their dominance by long-lived riparian trees (and the reliance of same on infrequent recruitment conditions), but also will be buffered from rapid hydrologic change owing to the slower movement of riparian water sources through the hydroclimatic system.

One of the anticipated consequences of climate change is more intense storms and floods. Given the extent to which individual canyons can be scoured by localized floods, and the well-know

role of the Huachuca Mountains in sustaining high species richness, it seems advisable to conduct whole canyon inventories ("bioblitzes") of streams in the Huachuca Mountains. Such efforts would be useful to determine, for example, the extent to which certain canyons and piedmont support unique species.

All stream types studied had diverse soil seed banks, with some types having larger seed banks than others, with implications for ecosystem restoration efforts. These results have implications for management actions that focus on restoration of plant communities following disruption from events such as scouring floods, given that donor soils can be an effective restoration tool for restoring small-seeded, herbaceous plant species to degraded sites.

Table 11.1. Summary table of attributes of five stream flow types studied within the Huachuca Mountains. Elevation of sites ranges from 1450 m to 1750 m.

	Dry-ephemeral	**Wet-ephemeral**	**Dry inter-mittent**	**Wet intermittent**	**Semiper-ennial**	**Perennial**
Landscape setting	Piedmont & lower canyon	Piedmont & lower canyon	Lower & upper canyon	Lower & upper canyon	Upper canyon	Upper canyon
Hydrology						
Stream flow (% of year)	1-3%	4-6%	7-30%	31-50%	75-95%	100%
Water table	>10 m	>10 m	<5 m	<5 m	<5 m	<5 m
Riparian vegetation						
Type	Mesquite savanna	Mesquite savanna	Sycamore forest	Sycamore forest	Sycamore forest	Sycamore forest
Biomass	Low	Low	Medium	High	High	High
Canopy cover	Low	Low	High	High	High	High
Species richness	High	High	Medium	Medium	Low	N/A
Tree richness	Low	Low	Medium	High	High	High
Annual-species richness	High	High	Medium	Low	Low	N/A
Seasonal variability	High	High	Medium	Medium	Medium	N/A
Rare species		*Heterotheca rutteri*				
Ground-dwelling arthropods						
Productivity	Low	Medium	Medium	Medium	High	N/A
Dominant groups	Formicidae, Meloidae, Tenebrionidae	Formicidae, Gryllidae, Tenebrionidae	Carabidae, Formicidae, Tenebrionidae	Gryllidae, Rhaphidophoridae, Staphylinidae	Armadillidiidae, Carabidae, Gryllidae	Armadillidiidae, Carabidae, Staphylinidae
Species richness	High	High	Medium	Medium	Low	Low
Peak biomass and seasonal variability	High	High	Medium	Medium	Low	Low
Bird species richness						
Winter resident	Low	High	High	Medium	Low	N/A
Summer resident	Medium	Medium	High	High	High	N/A
Decomposition rates						
Channel	Low	Low	Medium	Medium	High	N/A
Riparian zone	Low	Low	Low	Low	Low	N/A

Chapter 12: Literature Cited

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Appendix 1. Scientific and technical publications

Journal articles and theses

Gallo, E., T. Meixner, K.A. Lohse, and H. Nicholas H. In revision. Flow regimes and infiltration potential of streams in southwestern USA. Water Resources Research.

Lohse, K.A., E. L. Gallo, S. Schwabedissen, and T. Meixner. In review. Teetering on the edge: Changing climate and stream flow regimes alter rates of litter decomposition in dryland streams but not upland environments. Proceedings for the National Academy of Sciences.

McCartin, M.P. 2014. Secondary Production of Terrestrial Macroinvertebrates Along a Gradient of Streamflow Permanence. Barrett College Honor's Thesis, Arizona State University.

Nicholas, H.D. 2012. Estimating Surface Water Presence and Infiltration for Intermittent Streams in the Semi-arid Southwest. M.S. Thesis, University of Arizona.

Stromberg, J.C., K. McCluney, M. Dixon, and T. Meixner. 2013. Dryland riparian ecosystems in the American Southwest: sensitivity and resilience to climatic extremes. Ecosystems 16:411-415.

Stromberg, J.C. and D.M. Merritt. In review. Riparian plant functional types of intermittent and perennial rivers in the American Southwest. Freshwater Biology.

Conference presentations

Moody E.K., K.A. Wyant, and J.L Sabo. October 26, 2011. Water availability alters riparian arthropod community composition and biomass along montane intermittent streams. 11th Biennial Conference of Research on the Colorado Plateau, Flagstaff, AZ.

Moody E.K. October 27, 2011. Community composition and diversity patterns of aquatic and riparian arthropods of the Huachuca Mountains. The Nature Conservancy Ramsey Canyon Preserve, Hereford, AZ.

Nicholas. H.D, T. Meixner, and K. A. Lohse. December, 2011. Estimating infiltration rates for intermittent streams in the semiarid southwest: implications for ecosystem processes. Poster at American Geophysical Union Annual Meeting, San Francisco, CA.

Nicholas, H.D., T. Meixner, K. Lohse, J. Stromberg, J. Sabo, E. Moody, D. Setaro. October 29, 2011**.** Estimating infiltration rates with temperature methods for intermittent streams in the semiarid southwest: implications for ecosystem processes on the Santa Rita Experimental Range. Poster at Research Insights in Semiarid Ecosystems 8th Annual Symposium, Tucson, AZ.

Stromberg, J.C. and G. Katz. December 9, 2011. Vegetation structure and function along ephemeral streams in the Sonoran Desert. Oral presentation at American Geophysical Union Annual Meeting, San Francisco, CA.

Appendix 2. Number of occurrences of sampled plant species in two zones of the arid Goldwater study area. (CR is the combined channel and riparian zone; U is the surrounding desert upland). Data are based on four collecting seasons and two sites. Maximum number of occurrences per zone is 80 (four seasons x two sites x 10 plots). Growth forms are A (annual). H (herbaceous perennial), S (shrub), SS (stem succulent), T (tree), and V (vine).

Species	Family	Growth form	CR	U	Delta (CR-U)
RIPARIAN EXCLUSIVE					
Lycium andersonii A. Gray	Solanaceae	S	19	0	19
Parkinsonia florida (Benth. ex A. Gray) S. Watson	Fabaceae	T	12	0	12
Cryptantha pterocarya (Torr.) Greene	Boraginaceae	A	11	0	11
Olneya tesota A. Gray	Fabaceae	T	10	0	10
Prosopis juliflora var. velutina (Woot.) Sarg.	Fabaceae	T	10	0	10
Ambrosia salsola (Torr. & A. Gray) Strother & B.G.Baldwin	Asteraceae	S	9	0	9
Eriogonum deflexum Torr.	Polygonaceae	A	7	0	7
Eucrypta chrysanthemifolia (Benth.) Greene	Boraginaceae	A	7	0	7
Brassica tournefortii Gouan	Brassicaceae	A	5	0	5
Erodium cicutarium (L.) L'Hér. ex Ait.	Geraniaceae	A	5	0	5
Parkinsonia florida (Benth. ex A. Gray) S. Wats.	Fabaceae	T	5	0	5
ABUNDANT IN BOTH ZONES					
Cryptantha maritima (Greene) Greene	Boraginaceae	A	24	10	14
Chorizanthe brevicornu Torr.	Polygonaceae	A	18	6	12
Caulanthus lasiophyllus (Hook. & Arn.) Payson	Brassicaceae	A	39	27	12
Amsinckia tessellata A. Gray	Boraginaceae	A	32	21	11
Cryptantha angustifolia (Torr.) Greene	Boraginaceae	A	11	2	9
Descurainia pinnata (Walt.) Britt.	Brassicaceae	A	9	1	8
Eschscholzia californica Cham.	Papaveraceae	A	7	1	6
Pectocarya platycarpa (Munz & Johnston) Munz & Johnston	Boraginaceae	A	8	2	6
Eriastrum diffusum (A. Gray) Mason	Polemoniaceae	A	11	5	6
Camissonia brevipes (A. Gray) Raven	Onagraceae	A	14	9	5
Sphaeralcea coulteri (S. Wats.) A. Gray	Malvaceae	A	13	8	5
Pectocarya heterocarpa (I.M. Johnst.) I.M. Johnst.	Boraginaceae	A	51	48	3
Eriophyllum lanosum (A. Gray) A. Gray	Asteraceae	A	12	9	3
Chaenactis stevioides Hook. & Arn.	Asteraceae	A	6	3	3
Cryptantha barbigera (A. Gray) Greene	Boraginaceae	A	30	28	2
Lupinus bicolor Lindl.	Fabaceae	A	4	2	2
Eremothera chamaenerioides (A. Gray) W.L. Wagner & Hoch	Onagraceae	A	4	3	1

Mentzelia affinis Greene	Loasaceae	A	4	4	0
Camissonia claviformis (Torr. & Frém.) Raven	Onagraceae	A	3	3	0
Physaria gordonii (A. Gray) O'Kane & Al-Shehbaz	Brassicaceae	A	27	28	-1
Lepidium lasiocarpum Nutt.	Brassicaceae	A	59	61	-2
Camissonia californica (Nutt. ex Torr. & A. Gray) Raven	Onagraceae	A	1	4	-3
Schismus arabicus Nees	Poaceae	A	58	62	-4
Chorizanthe rigida (Torr.) Torr. & A. Gray	Polygonaceae	A	12	17	-5
Monoptilon bellioides (A. Gray) Hall	Asteraceae	A	5	11	-6
Larrea tridentata (DC.) Coville	Zygophyllaceae	S	41	55	-14
Plantago ovata Forsk.	Plantaginaceae	A	32	54	-22
UPLAND EXCLUSIVE					
Erodium texanum A. Gray	Geraniaceae	A	0	10	-10
INFREQUENT SPECIES (<5 occurrences)					
Draba cuneifolia Nutt. ex Torr. & A. Gray	Brassicaceae	A	3	0	3
Eschscholtzia minutiflora Parish ex Greene	Papaveraceae	A	3	1	2
Gilia stellata Heller	Polemoniaceae	A	2	0	2
Lotus salsuginosus Greene	Fabaceae	A	2	0	2
Lotus strigosus var. tomentellus (Greene) Isely	Fabaceae	A	2	0	2
Lupinus sparsiflorus Benth.	Fabaceae	A	2	0	2
Pectocarya recurvata I.M. Johnston	Boraginaceae	A	2	0	2
Sonchus oleraceus L.	Asteraceae	A	2	0	2
Acacia greggii A. Gray	Fabaceae	T	1	0	1
Astragalus nuttallianus Dc.	Fabaceae	A	1	0	1
Cylindropuntia sp. (Engelm.) Kreuzinger	Cactaceae	S	1	0	1
Datura sp.	Solanaceae		1	0	1
Encelia farinosa A. Gray ex Torr.	Asteraceae	S	1	0	1
Eriogonum trichopes Torr.	Polygonaceae	A	1	0	1
Linanthus bigelovii (A. Gray) Greene	Polemoniaceae	A	1	0	1
Nemacladus glanduliferus Jepson	Campanulaceae	A	1	0	1
Oligomeris linifolia (Vahl) J.F. Macbr.	Resedaceae	A	1	0	1
Parietaria hespera Hinton	Urticaceae	A	2	1	1
Pectis sp.	Asteraceae		1	0	1
Perityle emoryi Torr.	Asteraceae	A	2	1	1
Phacelia crenulata Torr. ex S. Wats.	Boraginaceae	A	1	0	1
Phacelia distans Benth.	Boraginaceae	A	2	1	1
Monolepis nuttalliana (J.A. Schultes) Greene	Chenopodiaceae	A	1	1	0
Oenothera primiveris A. Gray	Onagraceae	A	1	1	0
Plantago patagonica Jacq.	Plantaginaceae	A	1	1	0
Vulpia octoflora (Walt.) Rydb.	Poaceae	A	1	1	0

Ambrosia dumosa (A. Gray) Payne	Asteraceae	S	0	1	-1
Camissonia chamaenerioides (A. Gray) Raven	Onagraceae	A	0	1	-1
Rafinesquia neomexicana A. Gray	Asteraceae	A	0	1	-1
Chaenactis carphoclinia A. Gray	Asteraceae	A	1	3	-2
Geraea canescens Torr. & A. Gray	Asteraceae	A	0	2	-2

Appendix 3. Number of occurrences of sampled plant species in two zones of the semihumid Huachuca study area. (CR is the combined channel and riparian zone; U is the surrounding desert upland). Data are based on four collecting seasons and three sites. Maximum number of occurrences per zone is 80 (four seasons x two sites). Growth forms are A (annual). H (herbaceous perennial), SS (stem succulent),S (shrub), T (tree), and V (vine).

Species	Family	Growth form	CR	U	Delta (CR-U)
RIPARIAN EXCLUSIVE					
Acalypha neomexicana Muell.-Arg.	Euphorbiaceae	A	43	0	43
Amaranthus palmeri S. Watson	Amaranthaceae	A	35	0	35
Acalypha ostryifolia Riddell	Euphorbiaceae	A	27	0	27
Salvia subincisa Benth.	Lamiaceae	A	27	0	27
Aristida schiedeana var. orcuttiana (Vasey) Allred & Valdés-Reyna	Poaceae	P	26	0	26
Epilobium canum (Greene) Raven	Onagraceae	P	13	0	13
Anoda cristata (L.) Schlecht.	Malvaceae	A	12	0	12
Aristida divaricata Humb. & Bonpl. ex Willd.	Poaceae	P	12	0	12
Brickellia floribunda A. Gray	Asteraceae	S	12	0	12
Quercus emoryi Torr.	Fagaceae	T	11	0	11
Heterosperma pinnatum Cav.	Asteraceae	A	10	0	10
Argemone pleiacantha Greene	Papavaraceae	P	9	0	9
Chamaesyce dioica (Kunth) Millsp.	Euphorbiaceae	A	9	0	9
Elymus elymoides (Raf.) Swezey	Poaceae	P	9	0	9
Mentzelia isolata Gentry	Loasaceae	A	9	0	9
Ambrosia psilostachya DC.	Asteraceae	P	8	0	8
Ipomoea barbatisepala A. Gray	Convolvulaceae	V	8	0	8
Cyperus dipsaceus Liebamann	Cyperaceae	P	7	0	7
Cyperus retroflexus Buckl.	Cyperaceae	P	7	0	7
Xanthocephalum gymnospermoides (A. Gray) Benth. & Hook. f.	Asteraceae	A	7	0	7
Ambrosia confertiflora Dc.	Asteraceae	P	6	0	6
Aristida adscensionis L.	Poaceae	A	6	0	6
Gomphrena nitida Rothrock	Amaranthaceae	A	6	0	6
Setaria grisebachii Fourn.	Poaceae	A	6	0	6
ABUNDANT IN BOTH HABITATS					
Boerhavia erecta L.	Nyctaginaceae	P	40	5	35
Bouteloua curtipendula (Michx.) Torr.	Asteraceae	P	64	34	30
Artemisia ludoviciana Nutt.	Asteraceae	S	32	3	29
Ipomoea cristulata Hallier f.	Convolvulaceae	V	37	13	24
Boerhavia coccinea P. Mill.	Nyctaginaceae	P	41	17	24
Prosopis juliflora var. velutina (Woot.) Sarg.	Fabaceae	T	51	28	23
Disakisperma dubium (Kunth) P. M. Peterson & N. Snow	Poaceae	P	35	13	22
Diodia teres Walt.	Rubiaceae	P	24	3	21

Bidens leptocephala Sherff	Asteraceae	A	25	4	21
Euphorbia exstipulata Engelm.	Euphorbiaceae	A	21	2	19
Ipomoea hederacea Jacq.	Convolvulaceae	V	22	3	19
Eriochloa acuminata (J. Presl) Kunth	Poaceae	A	35	16	19
Chloris virgata Sw.	Poaceae	A	22	4	18
Melampodium strigosum Stuessy	Asteraceae	P	18	1	17
Senna hirsuta (L.) Irwin & Barneby	Fabaceae	P	19	2	17
Commelina dianthifolia Delile	Commelinaceae	P	32	15	17
Euphorbia heterophylla L.	Euphorbiaceae	P	20	4	16
Eragrostis cilianensis (All.) Vign. ex Janchen	Poaceae	A	25	10	15
Heterotheca subaxillaris (Lam.) Britton & Rusby	Asteraceae	A	32	17	15
Chamaecrista nictitans (L.) Moench	Fabaceae	A	25	12	13
Eryngium heterophyllum Engelm.	Apiaceae	P	15	3	12
Mitracarpus breviflorus A. Gray	Rubiaceae	A	19	7	12
Eragrostis lehmanniana Nees	Poaceae	P	97	85	12
Chenopodium neomexicanum Standl.	Amaranthaceae	P	20	9	11
Eragrostis intermedia A.S. Hitchc.	Poaceae	P	14	4	10
Gaura coccinea Nutt. ex Pursh	Onagraceae	P	21	11	10
Setaria leucopila (Scribn. & Merr.) K. Schum.	Poaceae	P	10	1	9
Gomphrena sonorae Torr.	Amaranthaceae	P	11	3	8
Oenothera laciniata Hill	Onagraceae	P	11	4	7
Cirsium neomexicanum A. Gray	Asteraceae	P	7	1	6
Schkuhria pinnata (Lam.) Kuntze ex Thell.	Asteraceae	A	7	1	6
Schizachyrium cirratum (Hack.) Woot. & Standl.	Poaceae	P	8	2	6
Portulaca suffrutescens Engelm.	Portulacaceae	P	10	4	6
Astragalus nuttallianus Dc.	Fabaceae	P	7	2	5
Eragrostis curvula (Schrad.) Nees	Poaceae	P	8	3	5
Lotus plebeius (Brand) Barneby	Fabaceae	P	10	5	5
Panicum hirticaule J. Presl	Poaceae	A	51	46	5
Froelichia arizonica Thornb. ex Standl.	Amaranthaceae	P	5	1	4
Helianthus petiolaris Nutt.	Asteraceae	A	5	1	4
Leptochloa dubia (Kunth) Nees	Poaceae	P	5	1	4
Cyperus sphaerolepis Boeckl.	Cyperaceae	P	9	5	4
Digitaria californica (Benth.) Henr.	Poaceae	P	10	6	4
Lepidium thurberi Woot.	Brassicaceae	A	13	9	4
Ipomoea costellata Torr.	Convolvulaceae	V	15	11	4
Sida spinosa L.	Malvaceae	P	21	17	4
Schizachyrium sanguineum (Retz.) Alston var. hirtiflorum (Nees) Hatch	Poaceae	P	23	19	4
Heliomeris longifolia var. annua (M.E. Jones) Yates	Asteraceae	P	31	27	4
Pseudognaphalium canescens (DC.) Anderb.	Asteraceae	P	7	4	3
Plantago patagonica Jacq.	Plantaginaceae	A	12	9	3
Bothriochloa barbinodis (Lag.) Herter	Poaceae	P	17	14	3
Cyperus odoratus L.	Cyperaceae	P	4	2	2

Rhynchosia senna var. texana (Torr. & A. Gray) M.C. Johnston	Fabaceae	v	4	2	2
Chenopodium fremontii S. Wats.	Amaranthaceae	A	5	3	2
Kallstroemia parviflora J.B.S. Norton	Zygophyllaceae	P	5	3	2
Lycurus setosus (Nutt.) C.G. Reeder	Poaceae	P	5	3	2
Proboscidea parviflora (Woot.) Woot. & Standl.	Martyniaceae	A	5	3	2
Aristida ternipes Cav. var. ternipes	Poaceae	P	12	10	2
Elionurus barbiculmis Hack.	Poaceae	P	20	18	2
Phaseolus angustissimus A. Gray	Fabaceae	V	5	4	1
Convolvulus equitans Benth.	Commelinaceae	V	16	15	1
Bouteloua hirsuta Lag.	Asteraceae	P	19	19	0
Chamaesyce hyssopifolia (L.) Small	Euphorbiaceae	A	27	27	0
Bouteloua aristidoides (Kunth) Griseb.	Asteraceae	A	4	5	-1
Muhlenbergia fragilis Swallen	Poaceae	A	7	8	-1
Dalea albiflora A. Gray	Fabaceae	P	8	9	-1
Bouteloua gracilis (Kunth) Lag. ex Griffiths	Asteraceae	P	4	6	-2
Galactia wrightii A. Gray	Fabaceae	V	5	7	-2
Jatropha macrorhiza Benth.	Euphorbiaceae	P	2	5	-3
Phemeranthus aurantiacus (Engelm.) Kiger	Montiaceae	P	12	15	-3
Urochloa arizonica (Scribn. & Merr.) O. Morrone & F. Zuloaga	Poaceae	A	39	42	-3
Hybanthus verticillatus (Ortega) Baill.	Violaceae	P	1	5	-4
Lepidium lasiocarpum Nutt.	Brassicaceae	A	2	7	-5
Guilleminea densa (Humb. & Bonpl. ex Willd.) Moq.	Amaranthaceae	P	4	9	-5
Ipomoea tenuiloba Torr.	Convolvulaceae	V	6	11	-5
Lithospermum incisum Lehm.	Boraginaceae	P	7	12	-5
Ayenia filiformis S. Watson	Sterculiaceae	P	8	13	-5
Eriogonum wrightii Torr. ex Benth.	Polygonaceae	P	25	30	-5
Physalis subulata var. neomexicana (Rydb.) Waterfall ex Kartesz & Gandhi	Solanaceae	A	0	6	-6
Krameria erecta Willd. ex J.A. Schultes	Fabaceae	S	1	7	-6
Talinum paniculatum (Jacq.) Gaertn.	Talinaceae	P	7	13	-6
Bouteloua eriopoda (Torr.) Torr.	Asteraceae	P	1	8	-7
Chaetopappa ericoides (Torr.) G.L. Nesom	Asteraceae	P	5	12	-7
Aspicarpa hirtella Rich.	Malpighiaceae	P	0	8	-8
Mimosa aculeaticarpa var. biuncifera (Benth.) Barneby	Fabaceae	S	6	14	-8
Sida abutifolia P. Mill.	Malvaceae	P	22	31	-9
Heteropogon contortus (L.) P. Beauv. ex Roem. & Schult.	Poaceae	P	1	11	-10
Mollugo verticillata L.	Molluginaceae	A	17	27	-10
Baccharis pteronioides Dc.	Asteraceae	S	14	26	-12
Portulaca umbraticola Kunth	Portulacaceae	A	26	39	-13
Evolvulus sericeus Sw.	Convolvulaceae	P	2	17	-15
Solanum elaeagnifolium Cav.	Solanaceae	P	10	25	-15

Gomphrena caespitosa Torr.	Amaranthaceae	P	21	41	-20
Calliandra eriophylla Benth.	Fabaceae	S	2	24	-22
Trachypogon spicatus (L. f.) Kuntze	Poaceae	P	26	48	-22
Evolvulus arizonicus A. Gray	Convolvulaceae	P	27	59	-32
INFREQUENT SPECIES					
Acacia angustissima (Mill.) Kuntze	Fabaceae	S	5	0	5
Aristolochia watsonii Woot. & Standl.	Aristolochiaceae	P	5	0	5
Baccharis sarothroides A. Gray	Asteraceae	S	5	0	5
Brickellia eupatorioides (L.) Shinners var. chlorolepis (Woot. & Standl.) B.L. Turner	Asteraceae	P	5	0	5
Desmodium rosei Schub.	Fabaceae	A	5	0	5
Mimulus guttatus DC.	Scrophulariaceae	A	5	0	5
Sorghum halepense (L.) Pers.	Poaceae	P	5	0	5
Vitis arizonica Engelm.	Vitaceae	V	4	0	4
Juniperus deppeana Steud.	Cupressaceae	T	4	1	3
Kallstroemia grandiflora Torr. ex A. Gray	Zygophyllaceae	A	4	1	3
Pectis prostrata Cav.	Asteraceae	A	4	1	3
Acalypha phleoides Cav.	Euphorbiaceae	P	3	0	3
Carminatia tenuiflora Dc.	Asteraceae	A	3	0	3
Cenchrus spinifex Cav.	Poaceae	P	3	0	3
Cuphea wrightii A. Gray	Lythraceae	A	3	0	3
Digitaria sanguinalis (L.) Scop.	Poaceae	A	3	0	3
Lithospermum cobrense Greene	Boraginaceae	P	3	0	3
Mentzelia multiflora (Nutt.) A. Gray	Loasaceae	P	3	0	3
Oxalis corniculata L.	Oxalidaceae	P	3	0	3
Setaria viridis (L.) Beauv.	Poaceae	A	3	0	3
Datura wrightii Regel	Solanaceae	P	3	1	2
Physalis philadelphica Lam.	Solanaceae	A	3	1	2
Xanthisma gracile (Nutt.) D.R.Morgan & R.L.Hartm.	Asteraceae	P	3	1	2
Agave palmeri Engelm.	Asperagaceae	SS	2	0	2
Agave parryi Engelm.	Asperagaceae	SS	2	0	2
Cirsium wheeleri (A. Gray) Petr.	Asteraceae	P	2	0	2
Cosmos parviflorus (Jacq.) Pers.	Asteraceae	A	2	0	2
Coursetia caribaea (Jacq.) Lavin	Fabaceae	S	2	0	2
Cylindropuntia spinosior (Engelm.) F.M. Knuth	Cactaceae	SS	2	0	2
Dasylirion wheeleri S. Watson	Liliaceae	S	2	0	2
Desmodium neomexicanum A. Gray	Fabaceae	A	2	0	2
Echinocereus rigidissimus (Engelm.) Haage f.	Cactaceae	SS	2	0	2
Euphorbia dentata Michx.	Euphorbiaceae	A	2	0	2
Lactuca serriola L.	Asteraceae	A	2	0	2
Lobelia fenestralis Cav.	Campanulaceae	A	2	0	2
Pseudognaphalium arizonicum (A. Gray) A. Anderb.	Asteraceae	P	2	0	2
Pseudognaphalium macounii (Greene) Kartesz, comb. nov. ined.	Asteraceae	A	2	0	2

Solanum adscendens Sendtner	Solanaceae	A	2	0	2
Sporobolus cryptandrus (Torr.) A. Gray	Poaceae	P	2	0	2
Tephrosia tenella A. Gray	Fabaceae	P	2	0	2
Xanthium strumarium L.	Asteraceae	A	2	0	2
Zornia gemella Vogel	Fabaceae	P	2	0	2
Croton pottsii (Klotzsch) Muell.-Arg.	Euphorbiaceae	P	2	1	1
Echeandia flavescens (J.A. & J.H. Schultes) Cruden	Asparagaceae	P	2	1	1
Phoradendron californicum Nutt.	Santalaceae	P	2	1	1
Portulaca oleracea L.	Portulacaceae	A	2	1	1
Adenophyllum cancellatum Kuntze	Asteraceae	S	1	0	1
Apodanthera undulata A. Gray	Cucurbitaceae	V	1	0	1
Celtis laevigata Willd. var. reticulata (Torr.) L.D. Benson		T	1	0	1
Chamaesaracha coronopus (Dunal) A. Gray	Solanaceae	P	1	0	1
Cheilanthes lindheimeri Hook.	Pteridaceae	P	1	0	1
Cryptantha barbigera (A. Gray) Greene	Boraginaceae	A	1	0	1
Cyperus amabilis Vahl	Cyperaceae	A	1	0	1
Cyperus esculentus L.	Cyperaceae	P	1	0	1
Cyperus squarrosus L.	Cyperaceae	A	1	0	1
Ditaxis neomexicana (Muell.-Arg.) Heller	Euphorbiaceae	P	1	0	1
Eriogonum abertianum Torr.	Polygonaceae	A	1	0	1
Froelichia gracilis (Hook.) Moq.	Amaranthaceae	A	1	0	1
Hackelochloa granularis (L.) Kuntze	Poaceae	A	1	0	1
Hesperidanthus linearifolius (A. Gray) Rydb.	Brassicaceae	P	1	0	1
Juncus interior Wiegand	Cyperaceae	P	1	0	1
Linum puberulum (Engelm.) Heller	Linaceae	A	1	0	1
Monarda citriodora Cerv. ex Lag.	Molluginaceae	P	1	0	1
Polygala obscura Benth.	Polygalaceae	P	1	0	1
Polygonum aviculare L.	Polygonaceae	A	1	0	1
Thalictrum fendleri Engelm. ex A. Gray	Ranunculaceae	P	1	0	1
Thelesperma megapotamicum (Spreng.) Kuntze	Asteraceae	P	1	0	1
Verbena gracilis Desf.	Verbenaceae	A	1	0	1
Machaeranthera sp. Nees	Asteraceae		2	2	0
Carlowrightia arizonica A. Gray	Acanthaceae	S	1	1	0
Linum aristatum Engelm.	Linaceae	A	1	1	0
Physalis hederifolia A. Gray	Solanaceae	P	1	1	0
Asclepias asperula (Decne.) Woodson	Apocynaceae	P	2	3	-1
Eriogonum polycladon Benth.	Polygonaceae	A	1	2	-1
Hymenothrix wislizeni A. Gray	Asteraceae	A	1	2	-1
Macroptilium gibbosifolium (Ortega) A. Delgado	Fabaceae	P	1	2	-1
Opuntia chlorotica Engelm. & Bigelow	Cactaceae	SS	1	2	-1
Vulpia octoflora (Walter) Rydb.	Poaceae	A	1	2	-1
Boerhavia coulteri (Hook. f.) S. Watson	Nyctaginaceae	P	0	1	-1
Heliomeris multiflora Nutt.	Asteraceae	P	0	1	-1

Hopia obtusa (Kunth) Zuloaga & Morrone	Poaceae	P	0	1	-1
Ipomoea purpurea (L.) Roth	Convolvulaceae	V	0	1	-1
Tradescantia pinetorum Greene	Commelinaceae	P	0	1	-1
Trianthema portulacastrum L.	Aizoaceae	A	0	1	-1
Zinnia grandiflora Nutt.	Fabaceae	P	0	1	-1
Mirabilis linearis (Pursh) Heimerl	Nyctaginaceae	P	1	3	-2
Heterotheca rutteri (Rothr.) Shinners	Asteraceae	P	1	4	-3
Polygala alba Nutt.	Polygalaceae	P	0	3	-3
Berlandiera lyrata Benth.	Asteraceae	P	0	4	-4
Erigeron arisolius G.L. Nesom	Asteraceae	A	0	4	-4
Erigeron neomexicanus A. Gray	Asteraceae	P	0	4	-4
Chamaesyce albomarginata (Torr. & A. Gray) Small	Euphorbiaceae	P	0	5	-5