

Drainage Size, Stream Intermittency, and Ecosystem Function in a Sonoran Desert Landscape

Ryan A. Sponseller* and Stuart G. Fisher

School of Life Sciences, Arizona State University, Tempe, Arizona 85287, USA

ABSTRACT

Understanding the interactions between terrestrial and aquatic ecosystems remains an important research focus in ecology. In arid landscapes, catchments are drained by a channel continuum that represents a potentially important driver of ecological pattern and process in the surrounding terrestrial environment. To better understand the role of drainage networks in arid landscapes, we determined how stream size influences the structure and productivity of riparian vegetation, and the accumulation of organic matter (OM) in soils beneath plants in an upper Sonoran Desert basin. Canopy volume of velvet mesquite (*Prosopis velutina*), as well as overall plant cover, increased along lateral upland–riparian gradients, and among riparian zones adjacent to increasingly larger streams. Foliar $\delta^{13}\text{C}$ signatures for *P. velutina* suggested that landscape patterns in vegetation structure reflect increases in water availability along this arid stream continuum.

Leaf litter and annual grass biomass production both increased with canopy volume, and total aboveground litter production ranged from $137 \text{ g m}^{-2} \text{ y}^{-1}$ in upland habitat to $446 \text{ g m}^{-2} \text{ y}^{-1}$ in the riparian zone of the perennial stream. OM accumulation in soils beneath *P. velutina* increased with canopy volume across a broad range of drainage sizes; however, in the riparian zone of larger streams, flooding further modified patterns of OM storage. Drainage networks represent important determinants of vegetation structure and function in upper Sonoran Desert basins, and the extent to which streams act as sources of plant-available water and/or agents of fluvial disturbance has implications for material storage in arid soils.

Key words: Sonoran Desert; intermittent streams; primary production; soil organic matter; scale; *Prosopis velutina*.

INTRODUCTION

Understanding the relationships between fluvial ecosystems and the catchments they drain has been a major research focus in stream ecology for over 30 years (Hynes 1975; Fisher and others 2004). Recently, efforts have focused on learning how the spatial structure of channel networks influences ecological patterns in streams (Power and Dietrich

2002; Benda and others 2004), and the surrounding terrestrial landscape (Fisher and others 2001). Arid landscapes are heavily dissected by drainage networks (Graf 1988), and the influence of aquatic ecosystems on terrestrial biota is evident from the conspicuous growth of riparian vegetation along streams and rivers that drain catchments that are otherwise poorly vegetated. Flow regimes within arid stream networks vary dramatically in space and time (Stanley and others 1997), however, and the importance of these hydrologic dynamics to ecological patterns considered at basin scales is largely unknown.

Received 7 December 2004; accepted 11 February 2005; published online 13 April 2006.

*Corresponding author; e-mail: rsponse@asu.edu

A variety of biotic and abiotic factors may influence plant communities in arid landscapes (McAuliffe 1994; Whitford 2002), but water availability is considered the prominent driver of vegetation pattern and process (for example, Noy-Meir 1973; Schlesinger and Jones 1984; Reynolds and others 1999). Water is routed across arid basins via a continuum of channels that drain subcatchments of increasingly greater area, and constitute a gradient in stream intermittency (Fisher and others 2001). The smallest channels (that is, rills) in the stream network receive runoff from surrounding hillslopes when rainfall is in excess of infiltration in soils, and thus support surface flow only in direct response to precipitation. Infiltration losses in the beds of rills can be substantial (for example, Parsons and others 1999); this water moves downstream along subsurface flow paths and represents an important mechanism for the recharge of alluvial aquifers (for example, Khazaei and others 2003). Surface and subsurface discharge from alluvial aquifers in turn supports intermittent and perennial flow in high-order stream and wetland ecosystems. Because channels divert water vertically and laterally, the productivity of near-stream vegetation can be augmented relative to that in upland habitats (for example, Ludwig 1987; Martinez-Yrizar and others 1999). It is not known how this disparity in production varies along the entire continuum flow regimes, which includes not only ephemeral washes, but also large intermittent and perennial streams.

Landscape gradients in plant productivity that result from differential access to water may in turn influence the storage of material in arid soils. Historically, research in desert ecosystems has emphasized the role of plants in sequestering carbon (C), nitrogen (N), and other nutrients into 'islands of fertility' (for example, Crawford and Gosz 1982; Schlesinger and others 1996). This concentration of material beneath vegetation is thought to derive from local plant productivity, the capture of dissolved and particulate components of overland sheet flow, and the trapping of particles transported by wind (Schlesinger and Pilmanis 1998). Therefore, to the extent that material storage beneath plants is driven by local production, the concentration of organic matter (OM) and nutrients in soils should increase along landscape gradients in plant productivity. Deposition and scour during floods, however, may further influence the storage of material in soils beneath vegetation in productive riparian habitats (Malanson 1993). These fluvial processes are likely to be particularly important in arid catchments, where rivers

are characterized by flash floods that represent important agents of disturbance along channel margins (for example, Stromberg and others 1991).

In this paper, we seek to better understand the role of stream networks in arid landscapes by exploring how stream size and intermittency affect the structure and function of riparian zones in an upper Sonoran Desert basin. Our first objective was to determine how differences in drainage area influence vegetation size, cover, and production in streamside habitats, as well as the strength of lateral upland-riparian gradients in plant structure. A second objective was to learn whether gradients in plant size and productivity influence the concentration of resources in underlying soils, and determine how relationships between vegetation structure and soil properties in riparian zones change with stream size and hydrologic regime. To meet these objectives, we quantified plant and soil features in upland and riparian habitats of subcatchments drained by streams that encompass the range of flow characteristics commonly found in arid basins of the upper Sonoran Desert. We then used a scaling analysis (*sensu* Ludwig and others 2000) to determine whether soil organic matter (SOM) concentration increases with plant size, and to evaluate how these plant-soil relationships change as the window of observation is expanded to include increasingly larger catchments, with more frequently flooded riparian terraces.

METHODS

Study Site

Sycamore Creek is located 52 km northeast of Phoenix, AZ, USA, and drains a 505-km² basin that ranges in elevation from 427 to 2,164 m. Mean annual precipitation varies with elevation, ranging from approximately 30 cm at 500 m to approximately 60 cm above 1,200 m (Thomsen and Schumann 1968). Annual precipitation is distributed bimodally, with approximately 70% of rainfall associated with Pacific frontal storms (November–April), and 30% associated with convective monsoon storms in the summer (June–September; Welter 2004). Stream flow across the Sycamore Creek basin is spatially and temporally intermittent (Stanley and others 1997). Surface water in the mainstem is typically continuous throughout the winter and spring (for example, December–April), but can be reduced by more than 50% during summer months. The largest tributaries to the mainstem may also support surface flow for extended periods of time (for example, weeks to

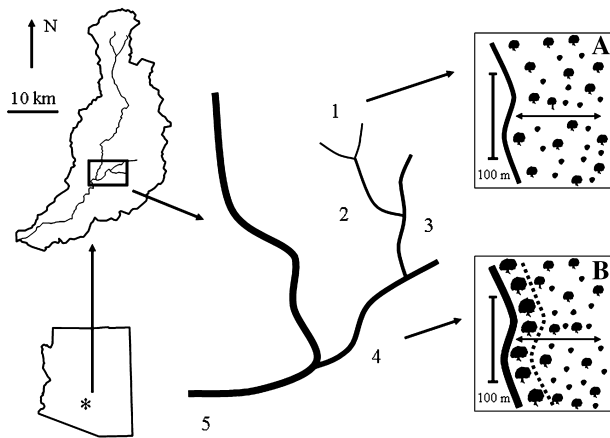


Figure 1. Depiction of study sites in the Sycamore Creek basin, located NE of Phoenix, AZ, USA. Sites were organized along a stream continuum, and site numbers (1–5) and line thickness correspond to increased catchment area and stream size: site 1 = 0.006 km², site 2 = 0.05 km², site 3 = 0.6 km², site 4 = 40.0 km², site 5 = 390.0 km². Each site consisted of a 100 m stream reach; plant and soil features were quantified from stream channel to ridge-top. Site 1 was an upland catchment with no apparent riparian terrace (*inset A*); sites 2–5 all had obvious streamside terraces (*inset B*, shown as *dotted line*).

months) during the winter and spring. For the vast majority of smaller channels in the stream network, however, surface flow is ephemeral and coincides with precipitation events.

We quantified vegetation structure, litter production, and SOM storage from five nested subcatchments ranging in area from 0.006–393.0 km² (sites 1–5, Figure 1). We selected sites drained by channels that encompass the spectrum of flow regimes found in the basin. Channels at sites 1–3 drain relatively small subcatchments (0.006–0.6 km²), and produce surface flow for short periods of time, only in response to precipitation. Previous research at these sites has shown that flow characteristics and drying patterns for channel sediments are tied to the characteristics of the precipitation regime (that is, the duration, magnitude, and intensity of events; Welter 2004). Site 1 had no obvious riparian terrace, and was only used for a subset of the analyses described below.

Channels at sites 4 and 5 drain larger subcatchments and can retain streamflow long past individual precipitation events. Site 4 lies adjacent to one of the major tributaries of Sycamore Creek (drainage area = 40 km²). The stream here can sustain surface water for months at a time during the winter and spring—sufficient to support a

variety of benthic fish and invertebrates (Stanley 1993). Following the cessation of surface flow, subsurface flow continues through early summer, although this eventually becomes restricted to deeper (> 3 m) strata (Thomsen and Schumann 1968; Clinton 1996). Site 5 is located on Sycamore Creek proper (390 km²). Here the stream retains some surface water throughout the year, in all but the driest years, and supports a diverse assemblage of benthic and hyporheic organisms, as well as obligate wetland and riparian vegetation. In addition to these five sites, we also completed a broader survey of plant structure in nine additional riparian zones from six major subcatchments in the Sycamore Creek basin (drainage size range = 0.02–50 km²).

Velvet Mesquite as a Model System

We used velvet mesquite (*Prosopis velutina*) as a model system to ask how stream intermittency influences the structure and function of riparian zones. *P. velutina* is a deciduous legume that is ubiquitous across upper Sonoran desert landscapes, being a common member of the Arizona upland desert–scrub association, and the dominant tree species along intermittent and permanent stream channels (Campbell and Green 1968; Stromberg and others 1993). *P. velutina* is a facultative phreatophyte (Campbell and Green 1968), meaning that it is able to access deep groundwater sources where possible, but can also utilize water from upper soil layers when deeper sources are not available (for example, Snyder and Williams 2000). In addition to this, *Prosopis* sp. in the Sonoran desert are known to (1) facilitate the growth of understory annual grasses (Yavitt and Smith 1983; Schade and others 2003), and (2) accumulate C, N, and other nutrients in underlying soils, relative to interplant spaces (for example, for *P. glandulosa*, Virginia and Jarrell 1983; for *P. velutina*, Schade and Hobbie 2005). For these reasons, *P. velutina* is ideal for investigating relationships between basin scale patterns in water availability and above-ground productivity, and asking how these interactions influence the accumulation of materials in soil beneath desert plants.

Survey of *P. velutina* Canopy Volume and Plant Cover

In each of the five subcatchments, we identified a study site bounded by a 100-m stream reach, extending laterally from channel-edge to ridge-top (Figure 1, inset). Within these boundaries, we

estimated *P. velutina* canopy volume for all individuals using:

$$V(\text{m}^3) = \frac{2}{3} \times \pi \times H \times \left(\frac{A}{2} \times \frac{B}{2} \right)$$

Where H represents tree height, and A and B the major and minor axes measured at 50% H (as developed for rangeland shrubs by Thorne and others 2002). Heights and widths of small individuals were measured with a meter stick; dimensions for larger individuals were estimated using a clinometer and meter tape.

We used data from sites 2–5 to compare *P. velutina* size between upland and riparian zones, and to ask whether this disparity varies with longitudinal position. For this, *P. velutina* were classified as either upland or riparian based on their position relative to the terrace–upland slope-break. Mean canopy volume was compared among sites and habitats (upland vs. riparian) using a two-way ANOVA, followed by t tests and a one-way ANOVA to compare averages between upland and riparian habitats within sites, and among riparian zones of increasingly larger streams, respectively. The total number of individuals sampled at these sites ranged from 38 (site 2) to 116 (site 3); canopy volume data were not normally distributed, and log-transformed values were used for analyses.

To further evaluate the influence of stream size on vegetation structure, we quantified total plant cover in upland and riparian habitats at sites 2–5 using the line intercept method (Mueller-Dombois and Ellenberg 1974). Total cover, relative cover by *P. velutina*, and the total number of plant patches (hereafter referred to as patch number) were quantified from three 100 m transects that ran parallel to the stream channel at each site and for both habitats (that is, upland and riparian terrace). We compared mean plant cover variables among sites and habitats using a two-way MANOVA. This was followed by two-way ANOVAs for each dependent variable separately, and post-hoc analyses as described for canopy volume.

To determine how riparian *P. velutina* size varies across a more complete range of drainage areas, canopy volume was surveyed from nine additional streams draining subcatchments of variable size, shape, slope, and parent material. For this, 100 m stream reaches were selected near the base of each subcatchment. Using the methods described above, canopy volume was measured for all individuals within the riparian zones of these study sites (within site n range = 15–34). Bivariate regression on site means was used to relate riparian canopy volume to drainage area.

Water Availability and Aboveground Productivity

To determine whether changes in stream size translate to increased water availability for *P. velutina* growing on adjacent terraces, we surveyed foliar $\delta^{13}\text{C}$ in riparian zones for three consecutive years. Stable C isotope signatures provide a temporally integrative descriptor of water use efficiency (WUE), and have been used widely to describe patterns in water stress, where low water availability leads to reduced stomatal conductance, less discrimination of ^{13}C , and heavier C isotopic signatures in C3 plants (for example, Ehleringer and Cooper 1988; Stewart and others 1995; Wainwright and others 2002). We include here the results of a pilot study conducted in August of 2002, where three to five trees were sampled from the riparian zone of sites 2, 4, and 5. In May 2003 and 2004, we expanded this survey to include ten trees at each site (that is, sites 2–5). For all 3 years, samples were also taken from upland individuals at site 1. Leaves were collected from five individual stems at the north side of each plant; individuals were selected that encompassed the spectrum of *P. velutina* size at each site. Leaves were dried, ground by ball mill, and $^{13}\text{C}/^{12}\text{C}$ ratios measured on a PDZ-Europa Hydra GSL 20/20 Isotope Ratio Mass Spectrometer (Europa Scientific, Cheshire, UK). Carbon isotope ratios in parts per thousand (‰) are expressed relative to Pee Dee Belemnite (PDB) as:

$$\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000]$$

where $\delta^{13}\text{C}$ is the C isotope ratio of the sample; R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ ratios of the sample and standard (peach leaf, NIST # 1547), respectively. Within years, one-way ANOVA was used to compare $\delta^{13}\text{C}$ among sites. Linear regression was used with data from all years to ask how foliar $\delta^{13}\text{C}$ signatures in riparian terraces varied as a function of drainage size.

We estimated *P. velutina* leaf litter production in the fall and spring of 2002–2003 and 2003–2004. For both years, litter fall was quantified from approximately 25 trees across the Sycamore Creek basin. The objective was to select trees that encompassed the range of habitats (that is, upland and riparian) and canopy volumes found in the broader survey, and then use statistical relationships between plant size and litter fall to estimate patterns of leaf production for each site and habitat. In 2002–2003, we used individual *P. velutina* from sites 1, 2, and 3, and from the riparian zone of an adjacent catchment approximately 50 km² in area. For 2003–2004, we used five individuals each from

sites 1–5. At each tree, circular (0.02 or 0.03 m²) litter traps were placed along two transects extending from the bole to the canopy edge. Litter was collected from traps monthly (leaves only) from October to April, encompassing the entire duration of leaf fall for *P. velutina* in this system. Leaves were dried at 60°C, and ashed to determine organic content.

The aboveground biomass of winter annuals was also quantified beneath *P. velutina* at the peak of growing season in 2003 and 2004. Because herbaceous plants are essentially absent prior to the winter rain season, we used grass biomass at the end of the growing season as a proxy for the production of winter annuals (for example, Schade and others 2003). For both years, we quantified grass biomass beneath 20 trees, 5 each from sites 1, 2, 4, and 5. Individuals selected from sites 2, 4, and 5 were located in the riparian terrace; all individuals from site 1 were located in upland habitat. Triplicate grass samples were harvested from beneath each tree using a 0.25 m² quadrat. Material was dried, and ashed to determine organic content. Linear regression was used to relate winter annual grass biomass production to *P. velutina* canopy volume; as described previously, regression equations were then used to estimate grass production for each site and habitat.

Resource Accumulation in Soils

Soil organic matter concentration at 0–2 cm depth was used as a proxy for material accumulation beneath *P. velutina*. Soils were sampled from beneath a subset of upland and riparian plants at sites 1–5. Site 1 included only upland individuals ($n = 33$); at sites 2–5, 18–20 riparian and 8–10 upland individuals were sampled. Triplicate samples were taken from within 1 m of the bole using a 10 cm diameter PVC core, inserted to 2 cm depth. Surface litter (O horizon) was removed before soils were collected. Interplant soils were also sampled at the same depth from five locations distributed across each upland and riparian site. Soils were air-dried in the laboratory and passed through a 2 mm sieve. The less than 2 mm fraction was subsampled, and OM content determined gravimetrically after combustion at 550°C for 4 h. Triplicate samples were averaged to generate an SOM concentration (% OM) for each tree. Within sites and habitats, we used *t* tests to compare mean % OM between plant and interplant patches. To determine whether patterns of SOM concentration were diagnostic for biogeochemically important

elements, we measured total N on a subset of soils ($n = 40$) used in the survey. For this, subsamples from sieved soils were ground by ball mill, and analyzed for total N on a Perkin-Elmer 2400 CHNS/O Analyzer (Perkin-Elmer, Wellesly, MA, USA). Linear regression was used to evaluate relationships between SOM and total soil N.

Regression scaling plots (sensu Ludwig and others 2000) with canopy volume on the *x*-axis and SOM concentration on the *y*-axis were used to ask (1) how the concentration of SOM beneath *P. velutina* changes with plant size, and (2) whether and how these plant–soil relationships change as the spatial extent of the analysis expands to include riparian plants from increasingly larger, more permanent streams. To answer this second question, we compared slopes of regression lines relating the (ln-transformed) accumulation of SOM and canopy volume from plant–soil pairs organized at five different spatial scales. To generate these plots, we started with data from site 1 only, and sequentially increased the spatial extent of the analysis by adding plant–soil pairs from the next largest subcatchment. The broadest spatial extent, therefore, was the entire Sycamore Creek basin (393 km² at the study site), and consisted of all plant–soil pairs generated in the study. ANCOVA was used to compare slopes of the relationship between canopy volume and SOM as we increased the spatial extent. A Bonferroni adjustment was used to control for Type I error in slope comparisons.

To determine the extent to which fluvial processes influence soil features in riparian zones, particle size distribution was quantified from beneath a subset of trees in upland and streamside habitats at sites 2–5 ($n = 5$ for upland, $n = 7$ for terrace). Here, a bucket auger was used to collect soils to 10 cm. Percent gravel was determined gravimetrically from the larger than 2 mm size fraction. Clay content was quantified from 50 g subsamples using the density hydrometer method and sand was determined gravimetrically after rinsing the same subsamples through a 53 μm sieve and drying at 60°C. Both % clay and sand then scaled to the original bulk soil sample. A two-way MANOVA was used to compare mean % gravel, sand, and clay among sites and habitat. As described for the analysis of plant cover, this was followed by univariate statistics for each variable separately. All statistical analyses were conducted with SYSTAT 10 (SYSTAT 2000). In all cases, transformations were used when bivariate relationships were nonlinear, or otherwise failed to meet regression assumptions.

Table 1. Summary Statistics for Canopy Volume and Line-transect Data from Upland and Riparian Habitats at Sites 2–5

Site	Habitat	2	3	4	5
Canopy volume (m ³)	U	28.7 (5.3)	28.2 (2.6)	32.0 (5.4)	14.7 (1.6)
Canopy volume (m ³)	R	47.4 (5.2) ^b	***72.2 (9.5) ^b	***150.7 (18.0) ^a	***201.1 (30.0) ^a
Plant cover (%)	U	45.5 (1.7)	38.4 (2.0)	37.7 (4.8)	41.1 (1.5)
Plant cover (%)	R	*52.6 (1.5) ^b	**52.8 (1.8) ^b	*63.3 (4.3) ^b	***77.8 (2.8) ^a
<i>P. velutina</i> (%)	U	20.7 (9.3)	21.7 (5.0)	22.5 (11.7)	22.1 (5.6)
<i>P. velutina</i> (%)	R	*57.8 (7.0) ^a	*63.0 (7.8) ^a	*78.3 (7.7) ^a	67.5 (16.3) ^a
Patch #	U	38.3 (0.9)	39.0 (3.8)	24.3 (1.5)	35.0 (0.6)
Patch #	R	***20.0 (0.6) ^b	**13.0 (1.2) ^{ab}	*13.3 (2.0) ^{ab}	***9.0 (2.5) ^a

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

RESULTS

Spatial Patterns in Vegetation Structure

Average canopy volume ranged from 14.7 m³ in the uplands at site 5 to 201.1 m³ in the riparian zone at site 5, and generally increased along both upland–riparian and upstream–downstream gradients (Table 1). Results from the two-way ANOVA with canopy volume showed no site effect ($F_{3,315} = 1.8$, $P = 0.146$), but did reveal significant habitat, and site by habitat effects ($F_{1,315} = 64.3$, $P < 0.001$, $F_{3,315} = 10.6$, $P < 0.001$, respectively). Multiple comparison tests show that average *P. velutina* canopy volume was greater in riparian zones when compared to adjacent uplands for sites 3, 4, and 5, but not site 2. Furthermore, average canopy volume varied among riparian zones ($F_{3,178} = 7.7$, $P < 0.001$); means at sites 2 and 3 were lower than those at sites 4 and 5 (Table 1). Results from the broader survey of riparian *P. velutina* canopy volume showed that average plant size increased with drainage area ($n = 13$, $r^2 = 0.82$, $P < 0.001$, Figure 2).

Vegetation cover and the number of plant patches varied among upland and riparian habitats. Percent cover generally increased (37.7–77.8 %), and patch number decreased (39–9) along both upland–riparian and upstream–downstream gradients (Table 1). The percentage of plant cover comprised by *P. velutina* also varied among sites and ranged from 20.7 (site 2, upland) to 78.3 (site 4, riparian). Taken together, we found significant differences in plant cover variables among sites (Wilks $\Lambda = 0.10$, $F_{9,34} = 5.9$, $P < 0.0001$), habitats (Wilks $\Lambda = 0.05$, $F_{3,14} = 84.9$, $P < 0.0001$), as well as a significant site by habitat interaction term (Wilks $\Lambda = 0.10$, $F_{9,31} = 6.2$, $P < 0.0001$). Similarly, univariate tests showed that, analyzed individually, total plant cover and patch number both varied

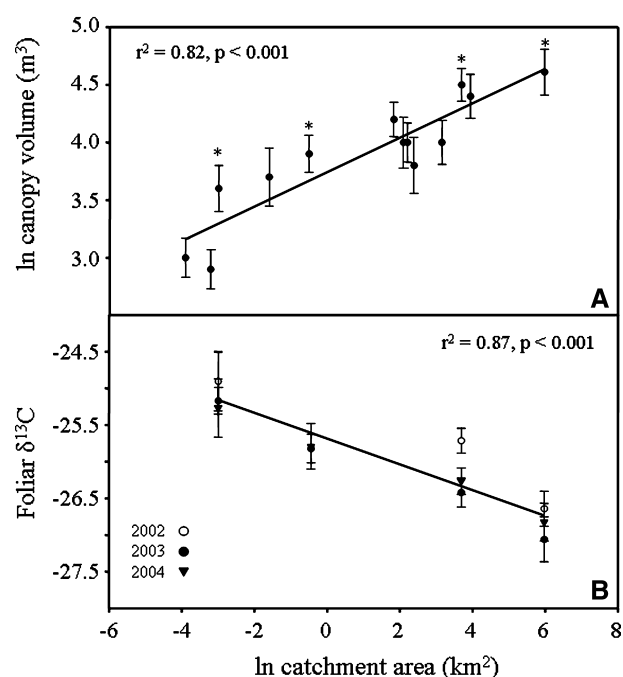


Figure 2. Relationships between riparian *P. velutina* canopy volume (m³) (**A**) and foliar $\delta^{13}\text{C}$ (‰) (**B**) and catchment area (km²). For (**A**), data are mean (\pm SE) for 13 streams of varying drainage area, points with asterisks represents sites also used in the intensive survey of plant and soil properties. For (**B**), data are mean (\pm SE) for surveys conducted in three consecutive years at four sites. Lines represent the best-fit least squared means regression equations.

among sites and habitats, with significant site by habitat interaction terms ($F_{3,16} = 10.6$, $P = 0.001$; $F_{3,16} = 6.9$, $P = 0.001$, respectively). For all sites, we found that percent cover was greater, and patch number lower, in riparian versus upland habitats (Table 1). There were also significant differences in plant cover and patch number among riparian

Table 2. Foliar $\delta^{13}\text{C}$ (‰) Values for *P. velutina* in Upland (site 1) and Riparian (sites 2–5) Habitat

Year	Site				
	1*	2†	3†	4†	5†
2002	-24.4 (0.12) ^c	-24.9 (0.4) ^{bc}	NA	-25.7 (0.17) ^{ab}	-26.6 (0.24) ^a
2003	-24.3 (0.12) ^d	-25.2 (0.18) ^c	-25.8 (0.19) ^{bc}	-26.4 (0.19) ^{ab}	-27.1 (0.30) ^a
2004	-24.7 (0.15) ^c	25.3 (0.39) ^{bc}	-25.7 (0.31) ^{bc}	-26.3 (0.18) ^{ab}	-26.8 (0.25) ^a

Values are mean (\pm SE). Within years, values that share superscripts are not significantly different from each other.

*Data from upland *P. velutina*.

†Data from riparian *P. velutina*.

zones ($F_{3,8} = 17.9$, $P < 0.001$; $F_{3,8} = 6.8$, $P < 0.01$, respectively). Percent cover by *P. velutina* typically increased along upland–riparian gradients, but not among riparian zones adjacent to different-sized channels (Table 1).

Water Availability and Aboveground Productivity

Average foliar $\delta^{13}\text{C}$ in riparian terraces ranged from -24.9‰ at site 2 (2002) to -27.1‰ at site 5 (2003); values for upland trees (site 1) ranged from -24.3‰ (2002) to -24.7‰ (2003) (Table 2). Within years, $\delta^{13}\text{C}$ values differed among sites (2002: $F_{3,11} = 19.4$, $P < 0.0001$; 2003: $F_{4,39} = 32.4$, $P < 0.0001$; 2004: $F_{4,43} = 9.2$, $P < 0.0001$). Furthermore, using data for all years, foliar $\delta^{13}\text{C}$ decreased in riparian zones with \ln catchment area ($r^2 = 0.87$, $P < 0.001$, Figure 2). Leaf litter production ranged from 21.4 to 187.3 g AFDM m^{-2} in 2003 and from 67.4 to 238.3 g AFDM m^{-2} in 2004, increasing both years with \ln canopy volume ($r^2 = 0.79$, $P < 0.001$, and $r^2 = 0.74$, $P < 0.001$, 2003 and 2004, respectively, Figure 3A). The biomass of winter annuals varied from 76.0 to 428.3 g AFDM m^{-2} in 2003, and from 34.7 to 175.4 g AFDM m^{-2} in 2004, again, increasing with \ln canopy volume both years ($r^2 = 0.76$, $P < 0.001$, and $r^2 = 0.89$, and $P < 0.001$, respectively, Figure 3B). We applied statistical relationships between canopy volume and litter and grass production to all upland trees from site 1 and riparian trees at sites 2–5, and estimated that total litter inputs (leaves + grass) beneath *P. velutina* ranged from 166.0 $\text{g m}^{-2} \text{y}^{-1}$ (site 1) to 446.4 $\text{g m}^{-2} \text{y}^{-1}$ (site 5) in 2003 and from 136.6 $\text{g m}^{-2} \text{y}^{-1}$ (site 1) to 341.8 $\text{g m}^{-2} \text{y}^{-1}$ (site 5) in 2004 (Table 3).

Average surface SOM concentration beneath *P. velutina* ranged from 5.4% at site 1, to 13.1% at site 4 (riparian); values in interplant spaces varied from 1.8% at site 5 (upland) to 5.3% at site 5 (riparian). SOM concentration was significantly greater beneath *P. velutina* when compared to

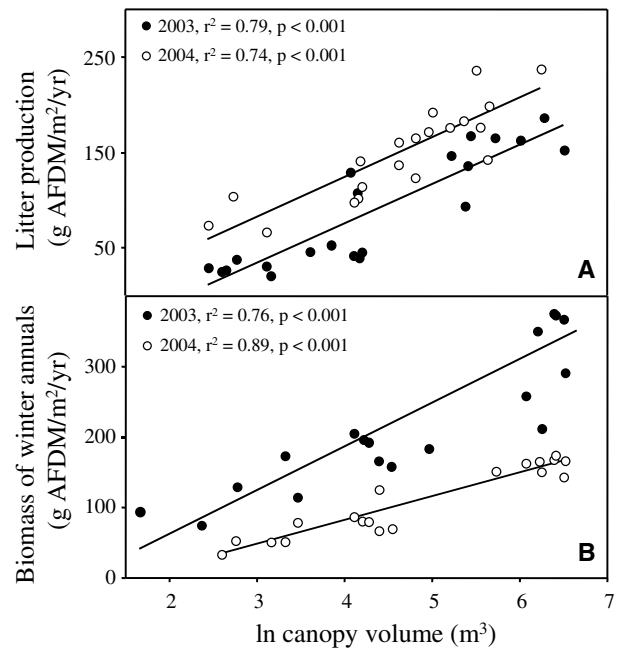


Figure 3. Relationship between \ln canopy volume of *P. velutina* (m^3) and **A** leaf-litter production ($\text{g AFDM m}^{-2} \text{y}^{-1}$), and **B** biomass production of winter annuals ($\text{g AFDM m}^{-2} \text{y}^{-1}$). Each panel includes data from two consecutive growing seasons. Lines represent the best-fit least squared means regression equations.

interplant spaces for all sites and habitats except in the riparian zone of site 5 (Table 4). Furthermore, \ln % SOM beneath *P. velutina* increased with \ln canopy volume across a broad range of subcatchment sizes (Figure 4A–E). We found that scaling relationships between *P. velutina* canopy volume and SOM content remained statistically constant across five orders of magnitude in drainage area (Figure 4A–D; F scores range: 0.31–1.9, P values range: 0.17–0.58, when comparing slopes). When evaluated at the scale of the entire basin, however, the slope of the relationship between canopy volume and SOM storage decreased significantly ($F_{1,255} = 10.4$, $P = 0.001$, Figure 4E). Finally, we

Table 3. Estimates of Leaf and Annual Grass Inputs (g AFDM/m²/yr) beneath *P. velutina* in Uplands (site 1), and Riparian Zones Adjacent to Increasingly Larger Streams (sites 2–5)

Season		Site				
		1*	2 [†]	3 [†]	4 [†]	5 [†]
2002–2003	Leaf	37.1 (3.4)	84.0 (5.0)	103.5 (5.5)	129.5 (6.7)	149.1 (5.6)
	Grass	128.9 (5.1)	199.2 (7.5)	228.9 (8.3)	267.9 (10.1)	297.3 (8.4)
	Total	166.0 (8.5)	283.3 (11.9)	332.6 (13.8)	397.5 (16.7)	446.4 (14.0)
2003–2004	Leaf	85.3 (3.4)	132.6 (4.8)	152.7 (5.6)	178.9 (6.7)	198.7 (5.7)
	Grass	51.4 (2.8)	89.6 (3.9)	105.8 (4.5)	127.0 (5.4)	143.1 (4.6)
	Total	136.6 (6.2)	222.3 (8.9)	258.5 (10.1)	305.6 (12.2)	341.8 (12.0)

Values are mean (± SE), and obtained by applying equations that describe relationships between leaf and grass production and canopy volume to all trees surveyed at each site.
 *Data for uplands.
 †Data for riparian habitat.

Table 4. Estimates of % SOM for Plant and Interplant Spaces, and the Difference between These Patch types, for All sites and Habitats (U = upland, R = riparian)

Site	Habitat	Plant	Inter-plant	Difference
1	U	5.39 (0.3)*	2.15 (0.1)	3.2
	R	NA	NA	–
2	U	5.48 (0.5)*	2.47 (0.2)	3.0
	R	9.10 (0.6)*	2.35 (0.06)	6.8
3	U	6.10 (0.4)*	2.98 (0.1)	3.1
	R	12.51 (1.2)*	2.37 (0.2)	10.1
4	U	7.83 (0.3)*	4.65 (0.2)	3.2
	R	13.10 (1.1)*	3.8 (0.9)	9.3
5	U	5.47 (0.4)*	1.8 (0.2)	3.7
	R	7.12 (0.8)	5.30 (1.0)	NS

Asterisks indicate where mean % SOM beneath *P. velutina* was significantly greater than that from interplant spaces. In this case, $P < 0.001$ for all significant *t* tests.

found that our measure of combustible OM successfully predicted patterns in total soil N, where: % N = 0.04 (% OM)–0.01 ($r^2 = 0.89$, $P < 0.001$).

Soil particle-size distribution varied significantly among sites and habitats (Table 5). Percent gravel ranged from 6.4 (site 5, riparian) to 41.4 (site 3, upland), % sand from 33.5 (site 4, upland) to 71.0 (site 5, riparian), and % clay from 4.8 (site 5, upland) to 9.7 (site 4, upland). Using the three variables simultaneously, we found significant differences in particle-size composition among sites (Wilks $\Lambda = 0.075$, $F_{9,92} = 19.55$, $P < 0.001$), habitats (Wilks $\Lambda = 0.52$, $F_{3,38} = 11.6$, $P < 0.001$), as well as a site by habitat interaction (Wilks $\Lambda = 0.51$, $F_{9,92} = 3.2$, $P = 0.002$). Univariate analyses indicated that, analyzed separately, average % gravel, sand, and clay each varied among sites ($F_{3,40} = 20.3$, $P < 0.001$; $F_{3,40} = 36.0$,

$P = 0.001$; $F_{3,40} = 7.05$, $P = 0.001$, respectively). Mean % gravel and sand also varied significantly among habitats ($F_{1,40} = 32.7$, $P < 0.001$; $F_{1,40} = 14.3$, $P = 0.001$, respectively). Only % gravel showed a significant site by habitat interaction ($F_{3,40} = 7.02$, $P = 0.001$). Relative to respective uplands, average % gravel was significantly lower in the riparian terrace of sites 4 and 5, and % sand was significantly greater in the riparian terrace of sites 3 and 5. There were also significant differences in mean % gravel and sand among riparian zones ($F_{3,24} = 17.9$, $P < 0.001$, $F_{3,24} = 27.4$, $P < 0.001$, respectively); here, % gravel was significantly lower in the terrace of site 5 when compared to all other sites. Similarly, average % sand was significantly greater in the riparian zone of site 5 when compared to all other terrace habitats.

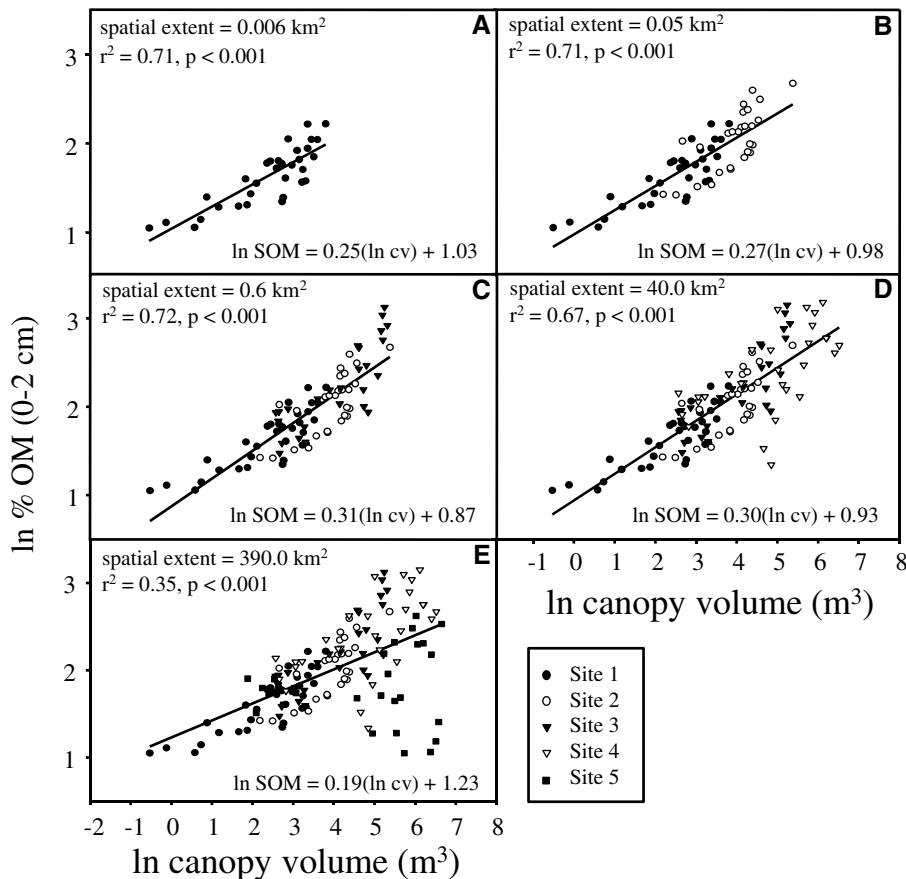


Figure 4. Scaling plots that show relationships between ln soil organic matter (% SOM) and ln *P. velutina* canopy volume (m³) at five spatial scales. **A** shows data from site 1 only; consecutive panels add all points from the next largest catchment, and **E** includes all data points in the survey. Regression lines represent the equations for scaling relationships at each spatial extent; results from the ANCOVA indicate that slope of the line in **E** is significantly different than those in all other panels ($F_{1,255} = 9.8, P = 0.002$).

Table 5. Percent Composition of Gravel, Sand, and Clay beneath *P. velutina* in Upland and Riparian habitats at sites 2–5

Site	Habitat	2	3	4	5
% Gravel	U	38.5 (2.4)	41.4 (2.3)	37.8 (2.5)	31.8 (2.8)
% Gravel	R	37.8 (1.8) ^c	32.9 (3.8) ^{cb}	*27.9 (2.2) ^b	***6.4 (1.9) ^a
% Sand	U	41.0 (2.2)	37.9 (2.4)	33.5 (2.2)	57.8 (2.7)
% Sand	R	42.5 (1.7) ^b	*47.5 (2.3) ^b	39.3 (3.3) ^b	*71.0 (3.4) ^a
% Clay	U	9.4 (0.6)	9.7 (1.0)	6.9 (0.6)	4.8 (0.5)
% Clay	R	8.2 (0.5)	8.3 (0.9)	9.2 (0.8)	6.5 (0.8)

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

DISCUSSION

Landscape Patterns in Plant Cover and Aboveground Production

The drainage networks that dissect arid landscapes influence basin-scale pattern of vegetation structure and function. In the Sycamore Creek basin, we found that the size and cover of dominant riparian vegetation increased 4- and 1.5-fold, respectively, along a channel continuum. These downstream changes in vegetation size and cover in turn increased the disparity in plant structure between

adjacent upland and riparian habitats. Because we do not have replication at the catchment level, caution should be used when attributing observed differences in plant characteristics to drainage area alone. Indeed, site-specific features acting independently of drainage size, such as geomorphic structure (for example, Hupp 1992), nutrient availability (for example, Harner and Stanford 2003), and disturbance (for example, Stromberg and others 1991) all likely interact to influence the dynamics of riparian vegetation at small spatial-scales. Results from the spatially extensive survey

of riparian canopy volume, however, support the idea that at basin scales the channel network is an important organizer of plant structure in arid landscapes (Caylor and others 2004).

Results from the survey of foliar $\delta^{13}\text{C}$ suggest that longitudinal and lateral patterns in plant size and cover are the consequence of increased water availability adjacent to larger intermittent and perennial streams. In all years, foliar $\delta^{13}\text{C}$ of *P. velutina* decreased among riparian zones adjacent to streams of increasing size and hydrological permanence. The observed change in C isotope values, from approximately -24% in uplands to approximately -27% in the riparian zone site 5, likely reflects increases in stomatal conductance and discrimination of ^{13}C by plants adjacent to streams with greater duration of surface and subsurface flow, as well as an increased capacity to store water in near-channel alluvial sediments. Other studies in arid environments have shown that features of intermittent drainage networks can influence plant–water relations. For example, Wainwright and others (2002) found that $\delta^{13}\text{C}$ signatures for *Larrea tridentata* were significantly higher for upland individuals when compared to those growing in depositional areas of upland rills (beads), which proved to be locations of high water infiltration and storage. Observed patterns of $\delta^{13}\text{C}$ for *P. velutina* among riparian habitats in this study are also consistent with the results from Snyder and Williams (2000) and Stromberg and others (1993) who found that predawn leaf water potentials for the same species were significantly lower in desert uplands and along ephemeral and intermittent streams than near perennial streams in southern Arizona.

Differences in plant size and water availability influenced patterns of leaf litter and understory annual grass production, which increased from 2.3- to 4-fold from desert uplands to perennial riparian zones. Values for leaf production across the landscape were within the range of those reported for *P. glandulosa* in the Sonoran Desert of California ($30\text{--}188\text{ g m}^{-2}\text{ y}^{-1}$, Sharifi and others 1982). Grass biomass values were similar to those reported by Schade and others (2003) in a nearby drainage ($150\text{--}325\text{ g m}^{-2}\text{ y}^{-1}$), and represented approximately 70 and 40% of the total litter production in 2003 and 2004, respectively. The observed range in total aboveground litter production (leaves + annual grasses) in this study corresponds well to that given by Martinez-Yrizar and others (1999) for upland ($60\text{ g m}^{-2}\text{ y}^{-1}$) and arroyo ($357\text{ g m}^{-2}\text{ y}^{-1}$) sites along a southern Sonoran desert drainage. Production numbers reported here also resemble

those given by Ludwig (1987) and Austin and Sala (2002) for total aboveground net productivity in upland and lowland habitats in the Chihuahuan Desert (range: $30\text{--}592\text{ g m}^{-2}\text{ y}^{-1}$), and along an aridity gradient in Patagonia (range: $15.9\text{--}338.4\text{ g m}^{-2}\text{ y}^{-1}$), respectively.

Previous research in arid landscapes has shown that plant productivity can be augmented along ephemeral stream channels, when compared to surrounding uplands (for example, Ludwig 1987; Martinez-Yrizar and others 1999). Ludwig (1987) suggests that precipitation regimes dictate these spatial patterns: when rainfall is sufficient to generate runoff in the rill network, transmission losses from low-order channels infiltrate terrace soils, and riparian plant productivity is stimulated. In dry years, stream flow in rills is limited, and rates of productivity along channels are unlikely to differ from those in adjacent uplands. This runoff/runon model would likely apply across the range of drainage sizes at Sycamore Creek where stream flow is tied directly to precipitation (for example, sites 1–3). Surface and subsurface flow in high-order streams of larger drainages, however, is supported by discharge from upstream alluvial aquifers, persists long past individual precipitation events, and acts to further stimulate the productivity of riparian vegetation. Our results also suggest that plants able to access these more permanent groundwater stores are less sensitive to intra-annual variation in precipitation. Between 2002 and 2003, estimates of *P. velutina* litter production in the uplands increased by 2.3-fold, corresponding to an approximate doubling in annual precipitation in the Sycamore Creek basin ($15.7\text{ vs. }32.5\text{ cm}$). For the same time interval, leaf production in the riparian zone of sites 4 and 5 increased by only 1.4- and 1.3-fold, respectively, suggesting that the availability of water at depth may effectively buffer climatically driven variation in productivity along more permanent stream channels.

We focused our efforts on a single, ubiquitous species so that we could ask questions about patterns of ecological function along landscape gradients using standardized response variables and metrics. Caution should be used, however, when extrapolating production estimates from a single species to a community that is (1) taxonomically and physiologically diverse, and (2) includes members that may respond to different aspects of the precipitation regime (for example, Ehleringer and others 1991; but also see Reynolds and others 1999). Our estimates of relative cover suggest this is particularly the case in the uplands, where *P. velutina* only represents about 20–25% of the total

assemblage. The remaining members of this community include other deciduous shrubs that may behave similarly to *P. velutina* (for example, Palo Verde, *Cercidium microphyllum*), as well as evergreen shrubs (for example, Jojoba, *Sommondsia chinensis*) and several species of cacti (*Optuntia* sp.) that may have different production dynamics. In riparian zones, however, relative cover by *P. velutina* ranges from about 60 to 80% of the total plant assemblage, thus the dynamics of this species may effectively represent those of streamside habitats as a whole.

Spatial Context for Islands of Fertility

Variation in plant size and productivity, along lateral upland–riparian gradients, and among riparian zones of increasingly larger streams, influenced the storage of SOM and N in soils beneath *P. velutina*. We found that the concentration of material in soils beneath plants increased with plant size (Ludwig and others 2000); these plant–soil scaling relationships were statistically similar across five orders of magnitude in catchment area. This represents a spatially extensive scaling domain (sensu Wiens 1989) within which material accumulation beneath *P. velutina* in both upland and riparian habitats increases as a constant function of patch size. Although Ludwig and others (2000) base predicted relationships between patch size and soil storage on the capture of material in runoff, in this study the concentration of soil resources beneath *P. velutina* is likely driven by local productivity (litter, roots, annual grasses, and so on), a finding consistent with research on isolated deciduous trees and shrubs in other arid and semiarid ecosystems (Belsky and others 1993; Facelli and Brock 2000). One consequence of increased material storage beneath larger plants is that the extent of fertility island development (that is, relative to interplant spaces) increases along both upland–riparian and upstream–downstream gradients. These results support the idea that fertility islands can spatial context (Schade and Hobbie 2005, in press); in this case, patterns of resource accumulation within this scaling domain reflect a landscape gradient in aboveground productivity.

Although material concentrated in soils beneath *P. velutina* may derive from local plant and grass production, mechanisms driving relationships between plant size and SOM concentration are likely to change with catchment size. In small upland catchments (for example, site 1), where plant size and productivity are unlikely to vary with proximity to channels, plant–soil scaling relationships likely arise from differences in the date of estab-

lishment, with older, larger individuals accumulating more resources in underlying soils (Facelli and Brock 2000). In larger subcatchments, stream channels provide a water source that stimulates the growth of riparian vegetation, and within-site relationships between SOM concentration and canopy volume likely reflect these lateral gradients in litter and grass production. With further increases in drainage area, longitudinal changes in SOM concentration with plant size correspond to downstream gradients in productivity of riparian plants that result from greater hydrologic permanence.

At the scale of the entire Sycamore Creek basin, we observed a shift in the statistical relationship between plant size and SOM concentration in underlying soils. Specifically, this scale-break occurs because SOM concentration beneath *P. velutina* in the riparian terrace of the perennial stream was lower than expected, given plant size and productivity. In addition, this was the only location where we found no significant differences in % SOM between plant and interplant spaces. These results suggest that, at the scale of the entire Sycamore Creek basin, additional processes emerge to alter the fate of detritus and the spatial pattern of material storage in soils. One potential explanation is that SOM turnover via biotic processes increases beneath trees in the riparian zone of site 5, when compared to other sites and patches. However, rates of litter decomposition and CO₂ flux from surface-soils (0–2 cm) at this site do not support this hypothesis (R.A. Sponseller, unpublished data). We argue that the scale-break is more likely the consequence of flooding in the riparian zone of site 5 that (1) removes and/or buries surface litter and SOM that would otherwise accumulate beneath vegetation (Steiger and others 2001), and (2) acts to homogenize the distribution of soil resources across terrace habitats. This hypothesis is supported by sediment particle size data, which show a dramatic reduction in percent gravel, and corresponding increase in percent sand, in the riparian zone of site 5, suggesting an abrupt increase in fluvial deposition at this site relative to riparian zones of smaller streams.

Riparian zones may act as sources or sinks for fluvial sediments, although deposition and sediment accrual typically outweigh erosion and sediment loss (Trimble and Knox 1984; Lowrance and others 1988; reviewed by Malanson 1993). Moreover, Graf (1985) suggests that, in arid catchments, phreatophytes growing along stream margins tend to augment sediment deposition onto riparian terraces. Our results indicate that depositional pro-

cesses are indeed important in the riparian zone of Sycamore Creek, and that these are likely to have implications for the fate of riparian detritus, and the trajectory of soil development beneath plants. Results from the survey of SOM and texture, however, suggest that fluvial processes adjacent to small and medium size streams used in this study do not have important consequences for soil structure. Flooding appeared to act as an important determinant of soil properties only in the riparian zone of the largest stream considered here. We hypothesize that the role of over-bank flooding as a driver of soil features in riparian zones emerges at some threshold in drainage size. This argument is consistent with principles of catchment hydrology that suggest increases in drainage area, from small to mid-sized catchments, correspond to a greater frequency and severity of floods and flood-associated disturbance (Graf 1988; Leopold 1994; Bendix 1997; Dodds and others 2004).

Conclusion: Stream Networks and Scale Dependencies

Our results support the hypothesis that, at basin scales, water availability (and stress) is the major driver of vegetation pattern in arid landscapes; these plant-water interactions are mediated in space by stream networks (Caylor and others 2004). In the Sycamore Creek catchment, we found that plant size, cover, and aboveground productivity increases along both upland-riparian and upstream-downstream gradients. Because differences in stream size have profound implications for the ecology of adjacent terrestrial habitats, the relative number and lengths of different-sized channels may influence functional properties (for example, net primary productivity) of the broader catchment. In other words, the geomorphic structure of drainage basins (for example, distribution of sizes, shape, slope, parent material), and the resulting drainage density and configuration of channel networks become significant landscape features to consider when evaluating the importance of arid streams to ecological patterns and processes at broad spatial scales (Benda and others 2004).

Results also show that patterns of plant size and productivity among upland and riparian habitats influence the development of fertility islands in arid landscapes. Moreover, the role of streams in arid landscapes, with respect to the accumulation of material beneath plants, shifts with drainage size. From small to mid-sized catchments, streams act to stimulate productivity and promote material

accumulation beneath plants. At some threshold in drainage area the frequency and magnitude of flooding acts to further influence the fate of riparian detritus—altering plant-soil scaling relationships and the spatial pattern of resource storage in soils. Thus, the accumulation of OM and nutrients beneath vegetation is driven by water as both a resource for plant growth and detritus production, and an agent of disturbance that buries, removes, and redistributes materials during floods. These contrasting modes of action are distributed in space by stream networks, and operate across a different range of catchment sizes.

ACKNOWLEDGEMENTS

This work was supported by grants from the National Science Foundation (NSF DEB 0075650, to SGF), and the Environmental Protection Agency Science to Achieve Results (STAR) Program (# 91613101, to RAS). Sam Norlin, Jim Heffernan, and John Schade provided assistance in the field and/or lab. Comments by David Lewis, Jim Heffernan, and two anonymous reviewers improved the quality of this manuscript.

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