



## Hot spots and hot moments of carbon and nitrogen dynamics in a semiarid riparian zone

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[1] Riparian ecosystems are characterized by spatial and temporal heterogeneity in physical and biological attributes, with consequences for nutrient cycling. We investigated the responses of carbon (C) and nitrogen (N) cycling processes to the hydrogeomorphic template in the riparian zone of the San Pedro River, Arizona, a large (catchment area  $\sim 11,500 \text{ km}^2$ ), free-flowing, semiarid river. Over an annual period we documented spatial and temporal patterns in soil, shallow groundwater, and stream nutrient chemistry as well as rates of N-transforming processes in soils of the surface (0–17 cm) and region of seasonal saturation (RoSS). A hot moment of N retention and removal was indicated by elevated rates of microbial processes during the summer monsoon season. At the same time, elevated C was observed in soil microbial biomass for both surface soils and soils in the RoSS. Analyses of C-use profiles for soil microbes, coupled with trends in stream and shallow-groundwater chemistry, further suggest that this hot moment of N removal was fueled by newly available, labile organic material. In a spatial context, patchiness in soil resources, microbial biomass, and potential denitrification were best explained by variation in microtopography; low-elevation landscape positions were hot spots of resource availability and microbial activity. Vertical heterogeneity also corresponded with variation in the factors influencing N transformation rates. Organic matter was more frequently a significant factor explaining N transformation rates in RoSS soils whereas soil water content was more often important in surface soils. Together, these patterns suggest that understanding the points on the hydrogeomorphic template, both in space and in time, that bring together water and labile organic matter will lead to greater predictive capability regarding C and N cycling in semiarid river-riparian corridors.

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### 1. Introduction

[2] Ecosystem ecologists have frequently taken a “black-box” approach to understanding carbon and nutrient cycling by constructing input-output budgets [e.g., Fisher and Likens, 1973; Likens et al., 1970], which have been effective for characterizing biogeochemistry at particular scales of study and within single ecosystem types (e.g., aquatic or terrestrial). Efforts to scale up to larger spatial or temporal extents, or selection of less homogenous study ecosystems benefit from inclusion of principles developed by landscape ecologists [Pickett and Cadenasso, 1995]. In particular, a patch-dynamics perspective emphasizes how composition and structure of patches within an ecosystem influence internal nutrient-cycling processes and ultimately whole-ecosystem budgets of materials [Malard et al., 2002; Poole, 2002]. For example, patches may serve as sources or sinks for nutrients or may exhibit physical conditions that differ

from neighboring patches, leading to high reaction rates at patch boundaries [Clement et al., 2003; Hedin et al., 1998]. Further, connections among patches may result in locations or time periods of higher biogeochemical activity relative to the surrounding spatial locations or times, termed hot spots and hot moments [McClain et al., 2003]. Understanding which aspects of heterogeneity influence patterns in nutrient transport, transformation, and removal remains a challenge in moving toward a predictive biogeochemistry that can encompass both terrestrial and aquatic features of landscapes [Grimm et al., 2003]. Here we address the consequences of spatial and temporal heterogeneity in the hydrogeomorphic template for hot spots and hot moments of resource transport, transformation, and removal in the riparian zone of a large, semiarid river. The hydrogeomorphic template consists of both temporal variation in hydrology (i.e., the hydrologic regime), and spatial variation conferred by landform [Hauer and Smith, 1998].

[3] Riparian zones constitute an appropriate laboratory in which to evaluate the effects of heterogeneity on biogeochemical processes because they are spatially and temporally dynamic. For example, hydrologic vectors redistribute both water and materials among riparian zones and sur-

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rounding stream and upland ecosystems [Gregory *et al.*, 1991; Naiman and Décamps, 1997]. Along a horizontal axis, riparian zones exhibit heterogeneity in a variety of features that are known to influence nutrient cycling, including: soil water content [Groffman *et al.*, 1992; Simmons *et al.*, 1992]; soil organic matter content [Sobczak *et al.*, 1998]; redox conditions [Gallardo, 2003; Hedin *et al.*, 1998]; soil nutrient concentrations [Gallardo, 2003; Hill *et al.*, 2000]; soil texture [Maitre *et al.*, 2003; Pinay *et al.*, 2000]; plant species composition [Clement *et al.*, 2002; Lyon and Sagers, 2002]; and microclimate [Brosofske *et al.*, 1997]. For low-order channels, heterogeneity may occur primarily on a stream-upland gradient with sharp contrasts in nutrient transformations at the boundaries of each subsystem. Examples include hot spots of denitrification at the stream-riparian interface [Hedin *et al.*, 1998] or riparian-upland interface [Haycock and Pinay, 1993; Peterjohn and Correll, 1984]. For higher-order channels, patchiness often occurs across the riparian zone due to geomorphic legacy effects of previous flood events or fluctuations in channel form and position [Latterell *et al.*, 2006; Parsons *et al.*, 2005]. A network of hydrologic flowpaths overlying this patchiness has consequences for the timing and locations of C and N transformations within the riparian zone, and for recipient ecosystems.

[4] Riparian zones also exhibit heterogeneity in the vertical dimension. In addition to vertical gradients typical of developed soils in such variables as physical structure, organic matter, water, and nutrient chemistry, vertical heterogeneity in riparian zones is increased by a fluctuating water table. This creates permanently saturated, seasonally saturated (i.e., region of seasonal saturation, hereafter, “RoSS”), and unsaturated regions within the soil profile [Baker *et al.*, 2000]. A fluctuating water table results in vertical changes in redox conditions as well as water and material availability to plants and soil microbes. In regions where the annual hydrograph is punctuated by large discharge events, such as those characterized by distinct snowmelt or storm seasons, inundation of riparian soils by a rising water table or floodwater results in flushing of labile dissolved organic carbon (DOC) [Baker *et al.*, 2000; Boyer *et al.*, 1997] or nutrients [Heffernan and Sponseller, 2004] from the soil. Increased C availability during these periods may fuel microbial activity, contributing to a hot moment of N removal via denitrification or microbial immobilization.

[5] Characterizing the effects of the multidimensional heterogeneity inherent to riparian zones will enable prediction of the timing and spatial locations of nutrient transport, transformation, and removal. Several conceptual and numerical models describing how spatial and temporal variability interact to influence biogeochemical processes in streams and watersheds have potential to contribute to such a synthesis. For example, models derived to explain hillslope- or catchment-scale nutrient dynamics emphasize lateral connectivity and seasonal dynamics in precipitation as agents influencing material transport [e.g., Belnap *et al.*, 2005; Stieglitz *et al.*, 2003]. Similar models describing processes within the stream-riparian corridor have emphasized vertical in addition to lateral hydrologic connectivity [Fisher *et al.*, 1998], and also have identified the potential role of spatial arrangements of patch types [Fisher and Welter, 2005]. Such models have less often been applied

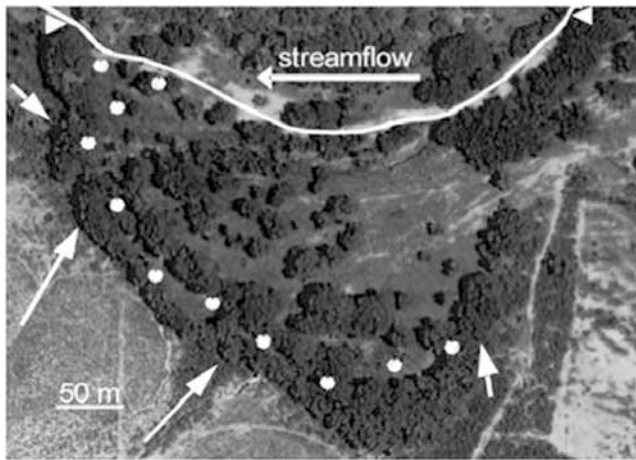
within riparian zones, where temporal variability in both lateral and vertical hydrologic connectivity may contribute to the formation of hot spots and hot moments of biogeochemical activity via several mechanisms. These include redistribution of substrates within the riparian zone [Sponseller and Fisher, 2006], import of upland- or stream-derived substrates [Schade *et al.*, 2005], and fluvial reorganization of the physical conditions of patches [Steiger and Gurnell, 2002]. Together, these observations underscore the importance of hydrologic flowpaths for material transformations but suggest that water may act to both homogenize resources and establish or maintain patchiness in riparian zones. Understanding the balance of these mechanisms is central to predicting how nutrient cycling may change under altered hydrologic regimes.

[6] We investigated temporal and spatial variation in C and N pools and microbial N transformations in riparian soils of a semiarid riparian zone. Our objective was to understand the ways in which temporal, vertical, and horizontal heterogeneity in the hydrogeomorphic template influences resource availability and microbial activity. We consider how the influences of the hydrogeomorphic template may change seasonally by documenting temporal patterns over an annual period. Our study contrasts two soil depths, the surface and RoSS, which have differing amounts of soil resources, and receive water and substrate inputs from different hydrologic vectors. We address the influences of geomorphic setting on resource processing and storage by considering variation in microtopography. These analyses are used to determine the conditions required to establish hot spots and hot moments of biogeochemical activity.

## 2. Study Site

[7] The upper basin of the San Pedro River (7,600 km<sup>2</sup>) is drained by an unregulated, perennially flowing river near the Sonoran-Chihuahuan desert transition. The study site lies at approximately 1300 m elevation and receives 300 to 750 mm of precipitation annually, largely confined to two distinct seasons: winter rains (December–March) and summer monsoon storms (July–September). Mean daily stream discharge  $\sim 3$  km downstream from the study reach ranged 0.14–0.31 m<sup>3</sup> s<sup>-1</sup> in winter and 0.01–0.03 m<sup>3</sup> s<sup>-1</sup> during the summer dry season. The summer monsoon season of 2003 was punctuated by several floods in late July and August (instantaneous discharge 22–85 m<sup>3</sup> s<sup>-1</sup>; all flow data from USGS gage #09471000 at Charleston, Arizona), with peak flow persisting less than 1 d. During this study, floods did not result in inundation of the entire riparian zone, although areas near the stream and wash outlets were subject to short-term (hours-days) inundation.

[8] Field sampling was conducted in a wide riparian floodplain (>250 m) overlying a relict channel along a gaining reach [Baillie *et al.*, 2007] of the San Pedro River in southeastern Arizona, United States. A gaining reach has greater potential for nutrient transport via shallow groundwater flow than a losing reach [Harner and Stanford, 2003]. Such sites also feature high primary productivity, are hydrologically connected with the river, and are common within the Upper San Pedro Basin. Using riparian condition classes, Stromberg *et al.* [2006] estimate that 39% of the stream length within the San Pedro River National Conser-



**Figure 1.** Aerial photograph of study site depicting locations of groundwater, soil (circles); and surface water samples (triangles). Washes entering the floodplain are denoted by arrows. Note upland desert scrub in lower left, mesquite bosque in lower right, and individual cottonwood trees in the floodplain. The low-stature vegetation in the center is grass.

vation Area is bordered by riparian zones described by the wettest condition class. This class is characterized by perennial surface stream flow, shallow groundwater, abundance of hydric plant species, and productive vegetation. A complementary classification scheme identifying river reaches characterized as hydrologically gaining or losing indicates that 37% of the river length of the Upper San Pedro encompasses gaining reaches, beginning at the U.S.-Mexico border [Brooks and Lemon, 2007].

[9] Within the study site, we focused on the area encompassed by the relict channel because greater plant productivity, finer soil textures, and shallower groundwater suggested that this was the most biogeochemically active region of the floodplain. The riparian floodplain is bordered by the surface stream and a mesquite (*Prosopis velutina*) dominated terrace situated 3–5 m above the riparian zone (Figure 1). Several washes break the terrace wall, connecting the uplands to the riparian zone via channeled flow during floods. Flow in washes occurs in response to precipitation and is of short duration (hours). Soil texture is spatially heterogeneous for both surface and subsurface soils. Surface soils range from sandy to clay loams while subsurface soils are sandy loams with patches of sand and clay. The vegetative community is dominated by cottonwood trees (*Populus fremontii*), seepwillow shrubs (*Baccharis salicifolia* and *B. emoryi*), native bunchgrass (*Sporobolus wrightii*) and two invasive grasses: Johnson grass (*Sorghum halepense*) and Bermuda grass (*Cynodon dactylon*). Cottonwoods begin to leaf out in March and leaf fall occurs primarily in November. A deep litter layer (mean depth 10 cm) of cottonwood leaves covers the soil surface throughout much of the study site.

### 3. Methods

#### 3.1. Soil Analyses

[10] To address spatial and temporal heterogeneity in riparian N dynamics, we analyzed pools of C and N and

rates of soil microbial activity in riparian soils over an annual period, at sampling locations arrayed throughout the riparian zone. Soils were sampled beginning February 2003 and approximately every other month thereafter until Feb 2004 to capture seasonal dynamics. Additional sampling dates followed precipitation and flood events during the summer monsoon season. A mid-July sampling followed the first monsoon rains, before any floods occurred. Late July sampling followed the first small floods, and the early August sampling followed a large flood. Soils were collected from 11 locations,  $\pm 1$  m from groundwater wells (see below).

[11] We collected soils using an auger (17 cm  $\times$  8 cm diameter) from the surface (after removing unconsolidated litter) and from the region of seasonal saturation (RoSS). The location of the RoSS varied from 60 to 180 cm depth among sites and was estimated from a previously collected year-long data set of seasonal water-table elevations for a subset of the groundwater wells. These data showed that water table elevation varied on average 40 cm annually, creating a seasonally inundated layer during the summer monsoon and winter rains (J. D. Schade and D. B. Lewis, unpublished data). Soils were transported on ice to the laboratory and were processed within 24 hours of collection. Samples were passed through a 2-mm sieve to remove the coarse fraction and large roots. Soil water content was determined as mass loss after drying subsamples at 105°C for 48 h, and soil organic matter (SOM) content was determined as mass loss on ignition at 550°C for 4 h. We measured soil texture using a hydrometer method followed by sieving (53  $\mu$ m) to measure the sand fraction by weight [Robertson *et al.*, 1999]. This analysis was conducted once in the dry season (June) and once during the monsoon season (August). There were no significant differences in surface soil texture before and after the monsoons (paired t-test,  $P > 0.05$ ) and data from June were used in statistical analyses.

[12] Soil  $\text{NO}_3^-$  and  $\text{NH}_4^+$  concentrations were determined by extracting a subsample with 2M KCl by shaking for 1 h. Soil particles were removed from the extract by gravity filtration through preleached, ashless Whatman<sup>®</sup> 42 paper filters. Samples were frozen until analysis on a Braun+Luebbe TrAAcs autoanalyzer using the cadmium-reduction method for nitrate and the phenolate method for ammonium. We determined net N-mineralization and nitrification rates by incubating a subsample at room temperature in the dark for  $\sim 28$  d, with soil water adjusted to fresh content weekly. Rates were determined by the difference of preincubation and postincubation extractable ammonium and nitrate, respectively [Robertson *et al.*, 1999].

[13] We estimated microbial biomass C and N as the difference in extractable DOC and TN between a pre-fumigation and chloroform-fumigated subsample [Robertson *et al.*, 1999]. Soils were fumigated in the dark under a chloroform atmosphere for 3 days followed by extraction in 0.5 M  $\text{K}_2\text{SO}_4$ . Samples were frozen until analysis for dissolved organic carbon (DOC) and total dissolved N. DOC was measured on a Shimadzu TOC-5000 total organic carbon analyzer (combustion followed by  $\text{CO}_2$  measurement by nondispersive infrared gas analysis) and total dissolved N on a Lachat autoanalyzer (inline persulfate-UV digestion followed by cadmium reduction). During



periods of low soil water content, this method can yield negative biomass values. We set all negative microbial biomass values to 0 for statistical analyses.

[14] As an index of C substrates available to fuel heterotrophic microbial activity, we compared C-substrate utilization by soil microbes in the summer dry season and during the summer monsoon using Biolog EcoPlate<sup>®</sup> sole-source C-use microplates (Biolog, Hayward, California, USA). Biolog EcoPlates<sup>®</sup> contain replicated wells, each with a single C source, a nutrient medium, and a tetrazolium dye that becomes blue in proportion to the amount of C used and can be used to identify patterns in heterotrophic microbial metabolic capabilities [Garland and Mills, 1991]. Plates were inoculated in a sterile laminar-flow hood with the supernatant of soils that had been centrifuged with filter-sterilized Ringer's solution and sonicated to detach microbes from soil particles. Absorbance of well contents at 595 nm was measured on a microplate reader at 0, 4, 12, and 24 h, followed by daily measurement for one week. The approximate half-saturation point of color development occurred at 72 hours, and absorbance values for this time point were used in statistical analyses. Values were corrected for initial absorbance and for any color development present in the well containing no C substrate. Wells showing negative values following these corrections were set to 0. Finally, absorbance values were standardized by the inoculum size, as estimated by DAPI-stained cell counts [Porter and Feig, 1980]. Mean values for the three sets of replicate wells per soil sample were used in analysis.

[15] We assessed potential denitrification rates using the acetylene block method [Yoshinari *et al.*, 1977] on two sample dates in 2004: during the dry season preceding the summer monsoons (June) and during the monsoon-associated floods (August). Potential denitrification rate gives an estimate of the amount of N that could be lost from soils by denitrification in the absence of substrate limitation. We added incubation media to soils (100 mg C [as dextrose]/L, 100 mg NO<sub>3</sub><sup>-</sup>-N/L, and 10 mg chloramphenicol/L), induced anoxia by addition of N<sub>2</sub> gas, and blocked reduction of N<sub>2</sub>O by addition of acetylene. We collected initial samples of the headspace volume and final samples following a 4-hour incubation at room temperature, both after vigorous shaking. Resulting gas samples were analyzed for N<sub>2</sub>O on a Shimadzu 14A gas chromatograph with an electron-capture detector and Porapak-Q columns.

### 3.2. Groundwater and Surface Water Analysis

[16] To evaluate the relationships among processes occurring in riparian soils and connectivity to the aquatic ecosystem, we measured concentrations of C and N in shallow groundwater and surface water. Six groundwater sampling wells were installed in March 2001, and an additional 5 wells were installed in March 2003. Wells were configured to trace the arc of the relict channel (Figure 1) and could not be manually installed through the coarse alluvium deposits that occur in the interior of this arc. Thus, the study design focuses on the most biogeochemically active portion of the riparian zone. Wells were constructed of 5 cm (inner diameter) polyvinyl chloride (PVC) with 1-m screened sections in the zone of saturation and unscreened sections in the vadose zone. The interspace between the PVC and soil was filled with sand, followed by native substrate, and a

bentonite seal at the surface. One well became filled with silt within one month of installation, which precluded groundwater sampling on most subsequent sampling dates and two wells were occasionally dry. Water sampling dates coincided with collection of soils. On each sampling date we measured water-table elevation using an electrical current meter and converted these data to elevations using survey data of ground elevations and well heights, obtained with a Zeiss R50 total station. Triplicate groundwater samples were then collected by pumping for 1–2 min, enough time to purge standing water within the well before sample bottles were rinsed and samples collected.

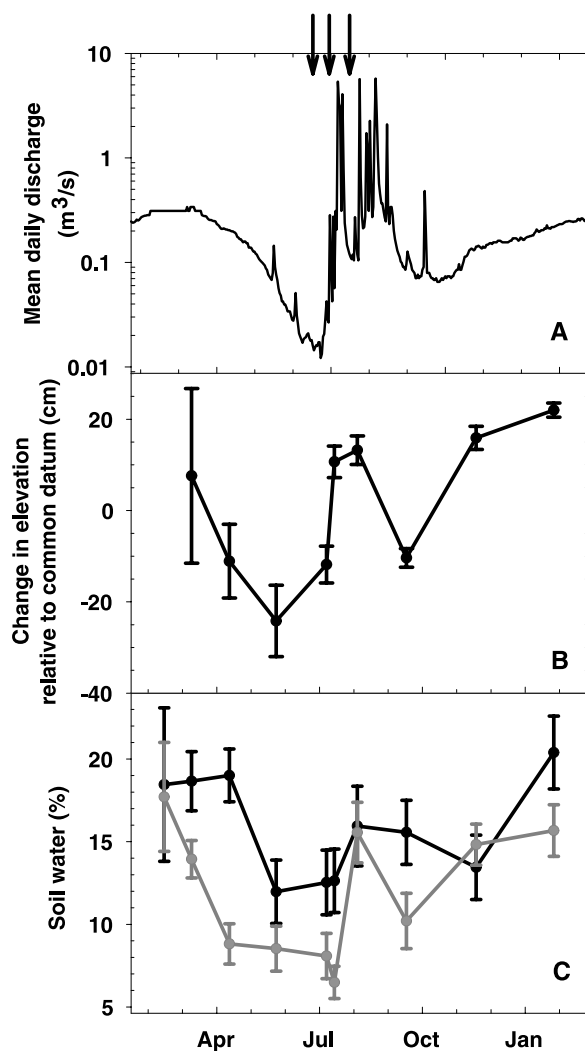
[17] Triplicate surface-water samples were collected upstream and downstream of visual knick points in channel geomorphology, which delineated the floodplain. These points were separated by 400 m (Figure 1). Water samples were collected at mid-depth in the center of the stream. Nutrient chemistry of surface water is not likely to fluctuate diurnally, except during floods. Both flood samples were collected on the falling limb of the flood hydrograph.

[18] Water samples were transported to the laboratory on ice and, within 24 hours of collection, samples were centrifuged or vacuum-filtered through ashed Whatman<sup>®</sup> GF/D and GF/F filters (nominal pore sizes 1 μm and 0.7 μm, respectively). Centrifuged samples were analyzed within 3 days of collection for nitrate (NO<sub>3</sub><sup>-</sup>-N; cadmium reduction method), and ammonium (NH<sub>4</sub><sup>+</sup>-N; phenolate method) on a Lachat flow-injection autoanalyzer. Filtered samples were analyzed for dissolved organic carbon (DOC) on a Shimadzu TOC-5000 total organic carbon analyzer within 7 days of collection and total dissolved N on a Lachat autoanalyzer (as previously described) within 30 days of collection. Dissolved organic N (DON) was calculated as the difference between total dissolved N and the sum of NO<sub>3</sub><sup>-</sup>-N and NH<sub>4</sub><sup>+</sup>-N.

### 3.3. Statistical Analyses

[19] We defined hot spots and hot moments as statistical outliers across sampling locations and times, respectively [Pennock *et al.*, 1992]. Hot spots and hot moments are thus defined relative to the spatial (10<sup>2</sup> m) and temporal (annual) extent of the study. Outliers are observations with values >1.5 times the range of the inner quartile of observations. Repeated-measures ANOVA was used to determine the effects of depth and time on soil chemical and microbial variables. Depth (surface or RoSS) was used as the between-subjects factor and time as the repeated measure. Because the sphericity assumption was unmet by these data, F-values were corrected using the Huynh-Feldt ε and corresponding P-values are reported. We used linear regression to evaluate the relationships among topography and soil N dynamics. For each response variable, we calculated a time-weighted mean for each sample location over the annual sampling period (n = 9–10 sample dates) to use in these regressions.

[20] Factors influencing soil microbial-biomass pools and net mineralization and nitrification rates were assessed using multiple linear regression. For C and N of microbial biomass, the set of predictor variables included concentrations of extractable soil N, DOC, NO<sub>3</sub><sup>-</sup>, and NH<sub>4</sub><sup>+</sup>; SOM, and soil water. For RoSS soils, we also considered the effects of groundwater chemistry by including dissolved oxygen, pH,



**Figure 2.** Temporal patterns in hydrologic descriptors. (a) Stream discharge. (b) Mean ( $\pm 1$  SE) change in water table elevation from previous sampling date. (c) Soil water content as mean ( $\pm 1$  SE) for surface (gray) and RoSS (black) soils,  $n = 11$ . Vertical arrows at the top of the figure indicate timing of the first rain, first flood, and first large flood of the monsoon season from left to right, respectively.

organic N, DOC,  $\text{NO}_3^-$ , and  $\text{NH}_4^+$  as predictors. For net N-mineralization rates, we excluded  $\text{NH}_4^+$  as a predictor and for net nitrification rates we excluded  $\text{NO}_3^-$ . We generated a set of candidate models by selecting models with adjusted  $R^2$  values  $>0.3$  from all possible subsets of models including four or fewer predictor variables. Final models were selected by adjusted  $R^2$  from those with all predictor variables explaining a significant fraction of variation given the other predictor variables included in the model. We evaluated the effects of potential multicollinearity among the predictors using tolerance values. The all subsets approach to multiple regression excludes the weaker correlates in cases of multicollinearity, thus this procedure seeks the strongest predictors but interpretations are not meant to imply that excluded variables are unimportant.

[21] For all statistical analyses, homogeneity of variance was evaluated via residual plots and normality was evalu-

ated based on normal probability plots of the residuals. The natural logarithm transformation was applied when these assumptions were not met and in some cases, the presence of many 0 values for the dependent variable prevented data from meeting these assumptions. In these cases, analyses were not performed. For all of the preceding statistical tests, results were considered significant when  $P \leq 0.05$ .

[22] Sole-source C-use data were analyzed by principal components analysis. Absorbance values for each C substrate were used as variables. Principal components analyses were conducted for premonsoon and postmonsoon C-use profiles. C substrates were considered to contribute strongly to components when loading scores were greater than  $|0.5|$ . All statistical analyses were performed in Systat v. 10, except for multiple regressions, which were performed in SAS, v. 8.

## 4. Results

### 4.1. Temporal Hydrologic Patterns

[23] Stream discharge, water-table elevation, and soil water content exhibited a predictable annual pattern, corresponding with precipitation (Figure 2). The monsoon season encompassed bankfull and overbank flash floods, during which near-stream sites were inundated and some sites were briefly inundated by flowing washes. Groundwater never reached the soil surface during this study. The water table was sloped toward the stream throughout the sampling period and changes in water-table elevation were conserved spatially. Depth to water table ranged approximately 30–200 cm beneath the surface across dates and locations. For nearly all sampling locations and dates, soil water content was greater in the RoSS than in surface soils (Figure 2).

### 4.2. Temporal Patterns in Soil Resources and Microbial Processes

[24] Soil physicochemical characteristics varied considerably over time in surface and RoSS soils (Table 1), with much of the temporal variation associated with the monsoon season (Figure 3). Extractable DOC concentrations oscillated over the annual sampling period in a similar pattern for both surface and RoSS soils (Figure 3a). Extractable  $\text{NH}_4^+$ -N dominated the soil inorganic N pool for much of the year in the RoSS, whereas extractable  $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ -N were equally available in surface soils. During the monsoon season,  $\text{NH}_4^+$ -N increased sharply in surface soils but decreased in RoSS soils (Figure 3b). Temporal contrasts between the two depths were significant (depth  $\times$  time interaction, Table 2). Soil extractable  $\text{NO}_3^-$ -N concentrations were near the limit of detection much of the year in RoSS soils but a 2–15 fold increase occurred during the monsoon season. In surface soils,  $\text{NO}_3^-$ -N concentrations decreased July through August and peaked following the conclusion of the monsoon floods (Figure 3c).

[25] Temporal changes in net N mineralization were significant, although spatial variability also contributed to high variance for both surface and RoSS soils (Table 2). A key observation from these trends was a large negative net N mineralization rate (i.e., immobilization) in surface soils during the monsoon season, which corresponded with the peaks in C and N of microbial biomass (Figure 4, N in

**Table 1.** Characteristics of Soil and Microbial Pools and Soil Fluxes, Summarized Over the Annual Sampling Period<sup>a</sup>

Constituent	Mean	CV <sub>temporal</sub> (%)	CV <sub>spatial</sub> (%)
<i>Surface</i>			
Moisture <sup>b,c</sup>	11.56	32.4	35.6
Organic matter <sup>d,c</sup>	39.35	12.3	31.7
Extractable TN <sup>e,c</sup>	9.65	19.0	46.6
Extractable DOC <sup>e,c</sup>	123.87	24.6	20.8
Extractable NH <sub>4</sub> <sup>+</sup> -N <sup>e,c</sup>	1.54	53.1	41.1
Extractable NO <sub>3</sub> <sup>-</sup> -N <sup>e,c</sup>	1.20	81.3	148.2
Microbial biomass N <sup>e,c</sup>	9.46	64.6	47.9
Microbial biomass C <sup>e,f</sup>	79.94	57.6	59.0
N mineralization <sup>g,f</sup>	-1.0*10 <sup>-3</sup>	881.9	1509.2
Nitrification <sup>g,f</sup>	0.15	31.4	68.4
Denitrification potential <sup>h</sup>	681.66	103.8	84.4
<i>RoSS</i>			
Moisture <sup>b,c</sup>	15.29	17.6	31.6
Organic matter <sup>d,c</sup>	17.93	26.5	56.3
Extractable TN <sup>e,c</sup>	2.53	18.3	60.6
Extractable DOC <sup>e,c</sup>	51.72	33.0	35.9
Extractable NH <sub>4</sub> <sup>+</sup> -N <sup>e,c</sup>	0.73	45.5	63.5
Extractable NO <sub>3</sub> <sup>-</sup> -N <sup>e,c</sup>	0.55	179.3	86.6
Microbial biomass N <sup>e,c</sup>	3.16	65.1	48.8
Microbial biomass C <sup>e,f</sup>	47.12	72.7	52.4
N mineralization <sup>g,f</sup>	0.02	168.7	179.7
Nitrification <sup>g,f</sup>	0.07	69.1	77.2
Denitrification potential <sup>h</sup>	88.79	155.5	149.2

<sup>a</sup>TN, total nitrogen; DOC, dissolved organic carbon. Variability in these parameters is compared using the coefficient of variation (CV) for samples collected over time and space. Denitrification potential is compared across the summer dry and monsoon seasons only.

<sup>b</sup>%.

<sup>c</sup>Here n = 10.

<sup>d</sup>g/kg dry soil.

<sup>e</sup>mg/kg dry soil.

<sup>f</sup>Here n = 9.

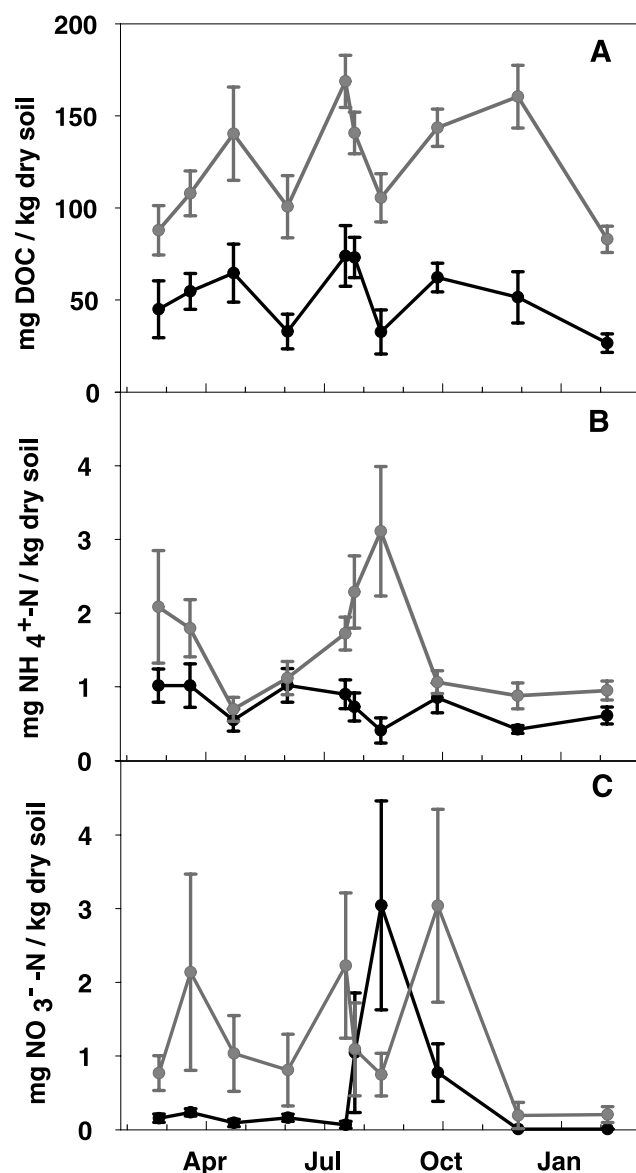
<sup>g</sup>mg/kg dry soil\*d.

<sup>h</sup>μg N/kg dry soil\*h.

biomass not shown). In contrast, net nitrification rates did not vary over time in RoSS soils, although rates were significantly lower compared to surface soils (Table 2). Microbial biomass and activity exhibited peak values during the monsoon season. Carbon in microbial biomass showed similar temporal patterns for both RoSS and surface soils (Figure 4). For both depths in the soil profile, significant temporal variability (Table 2) was punctuated by a sharp increase during monsoon flooding. Mean microbial biomass C was greater than mean soil extractable DOC concentrations during the monsoon floods for both surface and RoSS soils. This was also true of microbial biomass N in surface, but not RoSS soils, which showed little temporal variation in microbial biomass N (not shown). Potential rates of denitrification were significantly greater for surface compare to RoSS soils in both seasons. At both depths, rates were greater during the monsoon season (Table 2). Seasonal increases in these microbial processes constituted a hot moment, identified by statistical outliers. In surface soils, mean values of NH<sub>4</sub><sup>+</sup>-immobilization, microbial biomass N and microbial biomass C for August were outliers. The mean value of microbial biomass C in August was an outlier for RoSS soils.

[26] Sole-source assays of C use showed distinct patterns corresponding to the summer monsoon and dry seasons. Principal components analysis of sole-source C substrate-use patterns yielded three components (PC) that had strong

loadings ( $\geq 0.5$ ) for more than two C sources (Table 3) and captured 49, 10, and 9% of the total variation, respectively. Nearly all C sources loaded strongly and positively onto the first PC axis, but as it was not useful in differentiating samples we do not interpret it further. Phenolic compounds and a large amphipathic compound loaded positively onto the second PC axis while one carbohydrate loaded negatively. PC 3 was positively loaded by two small carbohydrates and negatively loaded by one phenolic and one large cyclic compound. Thus, PC 2 and 3 represent gradients of cyclic and small carbohydrate compounds. Carbon-use patterns for substrates represented by PC 2 and 3 differed sharply between premonsoon and monsoon samples, with an array of compounds used in the dry season and carbohydrate use predominating during the monsoon season (Figure 5).



**Figure 3.** Mean soil extractable (a) DOC, (b) NH<sub>4</sub><sup>+</sup>-N, and (c) NO<sub>3</sub><sup>-</sup>-N concentrations for RoSS (black) and surface soils (gray). Error bars are  $\pm 1$  SE, n = 11.

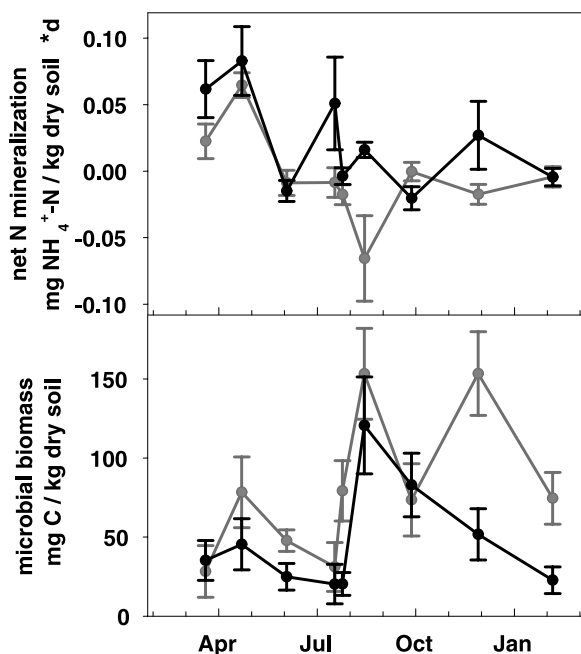
**Table 2.** F-Values (df) for Repeated-Measures ANOVA Analysis of Soil Characteristics and Microbial Attributes<sup>a</sup>

	Depth	Time	Depth x Time
Extractable total N	27.59 (1, 20)*	2.12 (8, 160)	1.62 (8, 160)
Extractable NO <sub>3</sub> <sup>-</sup> -N	0.58 (1, 19)	2.86 (8, 152)*	2.37 (8, 152)
Extractable NH <sub>4</sub> <sup>+</sup> -N	10.64 (1, 20)*	4.86 (8, 160)*	5.09 (8, 160)*
Extractable DOC	56.22 (1, 20)*	7.02 (8, 160)*	1.07 (8, 160)
Organic matter	15.42 (1, 19)*	2.72 (8, 152)*	0.66 (8, 152)
Soil moisture	5.38 (1, 18)*	7.81 (8, 144)*	3.57 (8, 144)*
Microbial biomass N	16.97 (1, 15)*	9.00 (8, 120)*	8.91 (8, 120)*
Microbial biomass C	2.54 (1, 17)	8.41 (8, 136)*	1.53 (8, 136)
N mineralization rate	4.40 (1, 16)	6.83 (8, 128)*	1.90 (8, 128)
Nitrification rate	9.79 (1, 16)*	0.91 (8, 128)	0.44 (8, 128)
Denitrification	27.64 (1, 18)*	23.98 (1, 18)*	0.82 (1, 18)

<sup>a</sup>February samples were removed from the analysis as sampling occurred for only a subset of locations on this sample date. Denitrification was measured as potential rate during the dry and monsoon seasons only. \* denotes  $P < 0.05$ .

### 4.3. Seasonal Patterns in Surface and Groundwater Chemistry

[27] Stream and groundwater DON and DOC were relatively invariant, except during the monsoon season when the highest concentrations occurred (Figure 6). Inorganic N concentrations were constant in time for both stream and groundwater with the exception of NO<sub>3</sub><sup>-</sup>-N which exhibited peak annual concentration in the stream following the onset of monsoon season floods (data not shown). Nitrate dominated the N pools of both the stream and groundwater except during the monsoon when nitrate and DON were present in approximately equal concentrations. Stream chemistry was less spatially variable than shallow groundwater chemistry; the two surface sites, which were separated by 400 m, showed nearly identical concentrations through-



**Figure 4.** Mean net N mineralization rates (top) and C pool size in microbial biomass (bottom) for RoSS (black) and surface (gray) soils. Error bars are  $\pm 1$  SE,  $n = 11$ .

out most of the annual sampling period. Following a large flood, however, concentrations of DON and DOC were higher downstream of the riparian floodplain than at the upstream site (Figures 6a and 6c).

### 4.4. Spatial Variation in Soil Characteristics and Microbial Activity

[28] Surface elevation correlated with physical characteristics of soils, resource concentrations, and microbial transformation rates of both surface and RoSS soils (Figure 7). The lowest points on the riparian landscape, which were distributed throughout the site, had the highest soil water content, extractable NH<sub>4</sub><sup>+</sup>-N concentrations, microbial biomass N pools, and finest soil texture in both surface and RoSS soils. For surface soils, spatial outliers occurred for at least one process on all but one sampled date and for all sampled dates in RoSS soils, identifying hot spots. Potential rates of denitrification in surface soils were negatively correlated with elevation both during the dry and monsoon seasons (Figure 7). Additionally, RoSS soils corresponding to low points in surface topography contained the highest organic matter content, extractable total N content, and rates of nitrification (data not shown).

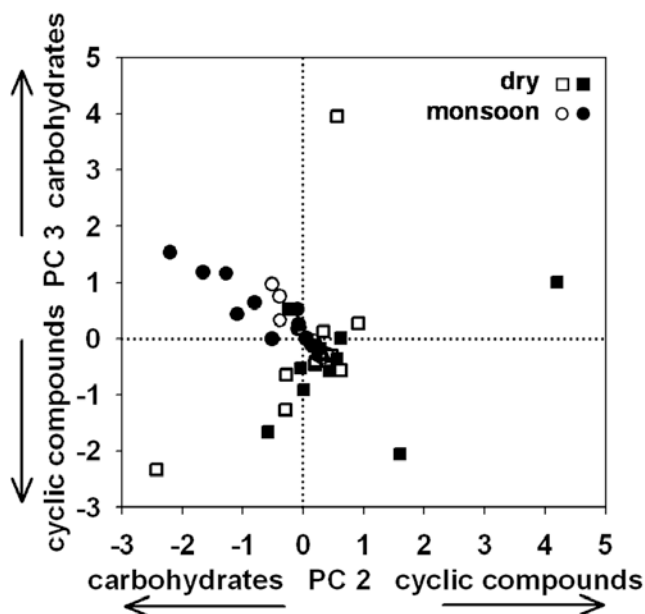
### 4.5. Factors Influencing Microbial Pools and N Transformation Rates

[29] Regression analysis revealed that a small group of soil characteristics explained most of the variation in microbial properties of soils and that these explanatory variables often differed for surface and RoSS soils (Table 4).

**Table 3.** Factor Loadings for Principal Components Analysis of Sole-Source C Substrate Use

Carbon Source	PC 1	PC 2	PC 3
$\beta$ -methyl-D-glucoside	0.634	-0.512	0.333
D-galactonic acid $\gamma$ -lactone	0.719	-0.444	0.208
L-arginine	0.615	0.104	-0.110
pyruvic acid methyl ester	0.913	0.039	0.045
D-xylose	0.795	0.368	0.138
D-galacturonic acid	0.725	-0.325	0.432
L-asparagine	0.707	-0.239	-0.266
tween 40	0.726	0.591	0.063
i-erythritol	0.755	-0.169	-0.345
2-hydroxy benzoic acid	0.415	0.523	0.380
L-phenylalanine	0.604	-0.255	-0.510
tween 80	0.725	0.203	0.217
D-mannitol	0.668	-0.158	0.508
4-hydroxy benzoic acid	0.832	0.325	-0.107
L-serine	0.580	-0.480	-0.369
$\alpha$ -cyclodextrin	0.610	0.018	-0.578
N-acetyl-D-glucosamine	0.868	-0.112	0.109
$\gamma$ -hydroxybutyric acid	0.774	0.257	-0.294
L-threonine	0.703	0.099	-0.223
Glycogen	0.526	0.248	0.142
D-glucosaminic acid	0.800	-0.163	-0.136
itaconic acid	0.816	0.096	-0.073
glycyl-L-glutamic acid	0.672	-0.446	-0.315
D-cellobiose	0.505	-0.353	0.648
glucose-1-phosphate	0.670	-0.283	0.382
$\alpha$ -ketobutyric acid	0.554	0.294	-0.157
phenylethylamine	0.713	0.612	0.008
$\alpha$ -D-lactose	0.363	-0.438	-0.298
D, L- $\alpha$ -glycerol phosphate	0.848	0.187	-0.133
D-malic acid	0.826	0.174	0.023
putrescine	0.758	-0.101	0.332





**Figure 5.** Principal component scores of sole-source carbon substrate use for RoSS (open symbols) and surface soils (solid symbols).

Organic matter, extractable N or  $\text{NH}_4^+$ , and water content primarily explained variation in C and N of microbial biomass, net N-mineralization rates, and nitrification rates. Soil water content was a significant predictor of all measured microbial pools and N transformations in surface soils for at least one time point whereas in the RoSS, soil water was a significant predictor in only one instance, for one response variable. In contrast, organic matter was often a

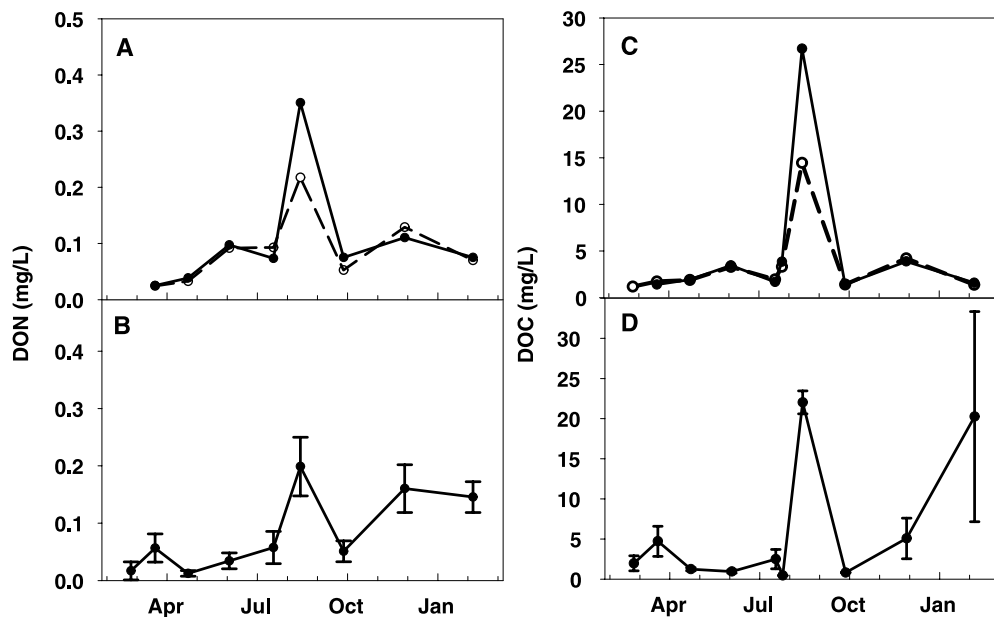
significant predictor of microbial pools and N transformations in RoSS soils.

## 5. Discussion

[30] In deserts, hot spots and hot moments of nutrient transformations may account for the majority of nutrient cycling activity on the landscape or over an annual period [Belnap *et al.*, 2005]. The riparian zone is often considered a hot spot in the larger desert landscape and within the riparian zone, heterogeneity conferred by the hydrogeomorphic template creates hot spots. Hot spots of nutrient transformations occurred at low-elevation sites within the riparian zone, which also harbored the highest concentrations of soil resources. On an annual timescale, we observed a hot moment of microbial activity in the riparian floodplain concurrent with summer monsoon floods. This coincided with annual maxima in soil C and N concentrations. Thus the hydrogeomorphic template, via its influences on water and material availability, was a significant driver of nutrient transformations in both space and time (Figure 8).

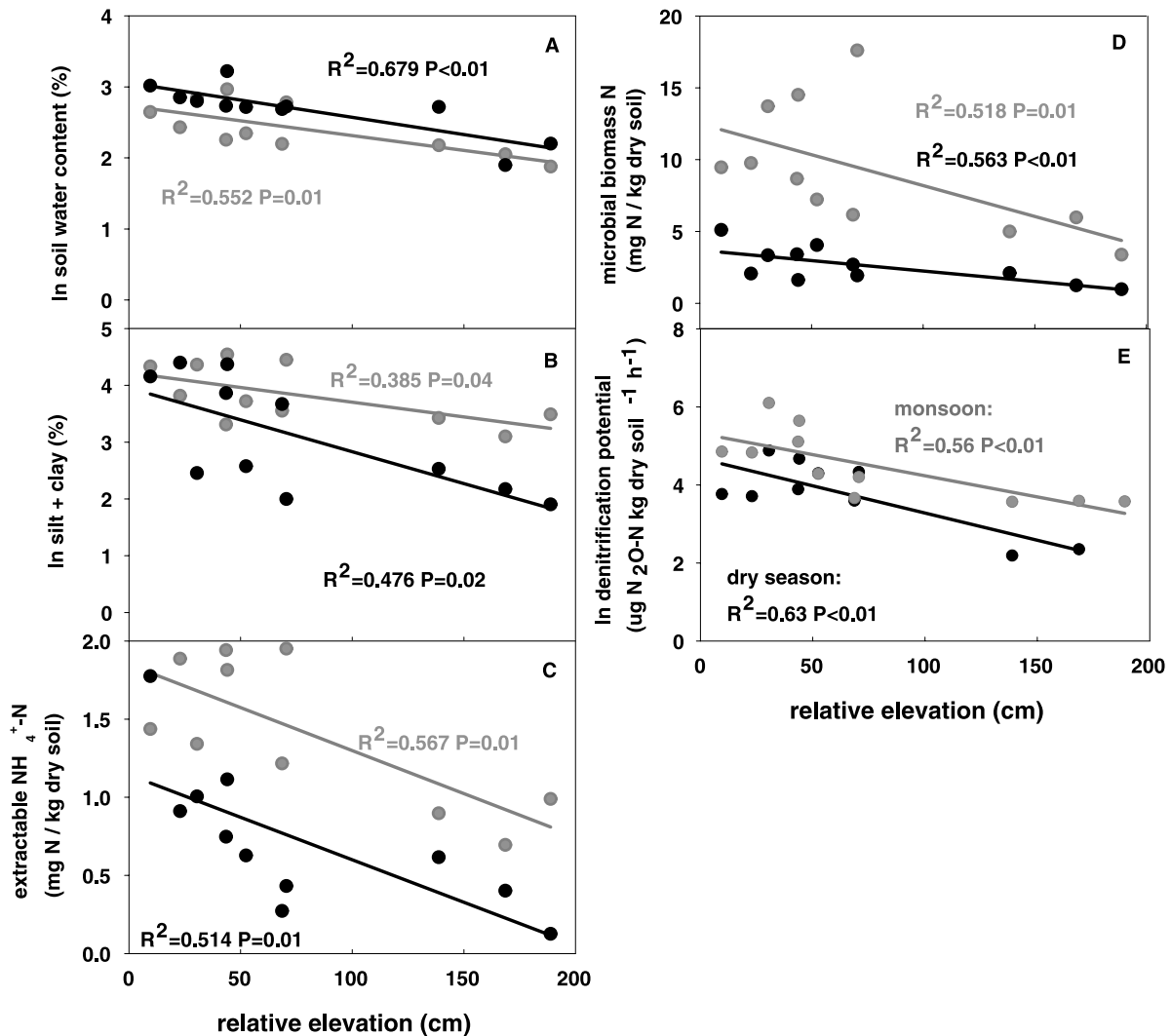
### 5.1. Temporal Patterns

[31] Seasonal patterns in soil microbial activity and nutrient chemistry implicate the intersection of hydrologic vectors with biologically active regions of the soil profile as a factor contributing to a hot moment of nutrient retention and removal in this semiarid riparian zone. Hydrologic vectors include flow of shallow groundwater through the RoSS and overbank or overland flow across surface soils (Figure 8). We contend that, after a long dry period, hydrologic vectors alleviate water limitation while simultaneously bringing reactants together through transport within the riparian zone. In this riparian floodplain, increased microbial immobilization of C (both in surface and RoSS



**Figure 6.** Surface water (a) DON and (c) DOC concentrations for points upstream (dashed) and downstream (solid) of the riparian floodplain. Shallow groundwater (b) DON and (d) DOC concentrations within the floodplain are means across all wells ( $n = 10\text{--}11$ ), error bars are  $\pm 1\text{SE}$ .





**Figure 7.** Relationships between soil characteristics ((a) water content, (b) silt + clay, (c) extractable ammonium, (d) N in microbial biomass) and surface elevation relative to a common datum for surface (gray) and RoSS (black) soils. (e) Relationships for denitrification for surface soils during the monsoon (gray) and dry (black) seasons.

soils) and N (in surface soils) occurred during the summer monsoon season. Net immobilization of  $\text{NH}_4^+$  in laboratory assays of surface soils corroborated this result during the summer monsoon. Further, potential rate of denitrification was greater during the monsoon season than during the dry season. Thus, retentive processes operating within the floodplain during the monsoon season have potential to alter the quantity and quality of materials available for transport to downstream ecosystems.

[32] Several lines of evidence suggest that peak microbial processing of C and N resulted from reestablishment of hydrologic connectivity between resource pools and soil microbes during monsoonal flooding. The stimulatory effect of precipitation on soil microbes is well documented in semiarid and arid regions [Austin *et al.*, 2004]. However, our observations suggest that alleviation of water limitation is a necessary but not sufficient condition for nutrient removal and retention. We sampled following the first rain storm of the monsoon season, the first small floods of the

monsoon season, and following the first large flood. A hot moment of microbial activity was detected only following the first large flood. Although it is plausible that high rates of activity may have been attained following subsequent floods, observations in other desert catchments suggest that available substrates are quickly depleted following pulse events, resulting in declines in peak rates following sequential storms [Meixner *et al.*, 2007; Sponseller, 2007].

[33] We observed a strong seasonal shift in microbial community C use, from greater use of cyclic compounds during the summer dry season to preferential use of non-cyclic carbohydrates during the monsoon season. These patterns correspond to hypothetical seasonal changes in available C pools. During the dry season, lack of water likely limits availability of C from soil organic matter, root exudates, and litter. Water may mobilize C during the monsoon season, and root exudation is likely increased due to growth of mesic plant species [Bagstad *et al.*, 2005]. Use of labile C sources corresponds temporally with

**Table 4.** Comparison of Best Fit Multiple-Regression Models for Estimates of Microbial Biomass N<sup>a</sup>

Month	Surface			RoSS		
	Predictors	R <sup>2</sup>	P	Predictors	R <sup>2</sup>	P
<i>Microbial Biomass C</i>						
Mar 2003	<sup>b</sup>			NA <sup>c</sup>		
Apr	NA <sup>c</sup>			NA <sup>c</sup>		
Jun	OM	0.50	0.01	moisture, N	0.85	<0.01
Jul (first rain)	<sup>b</sup>			NA <sup>c</sup>		
Jul (first flood)	OM	0.72	<0.01	<sup>b</sup>		
Aug	moisture	0.52	0.02	OM	0.73	<0.01
Sep	OM	0.76	<0.01	N	0.63	<0.01
Nov	OM, moisture	0.82	<0.01	<sup>b</sup>		
Feb 2004	NH <sub>4</sub> <sup>+</sup>	0.46	0.02	NA <sup>c</sup>		
<i>Microbial Biomass N</i>						
Mar 2003	NA <sup>c</sup>			NA <sup>c</sup>		
Apr	NA <sup>c</sup>			NA <sup>c</sup>		
Jun	C	0.50	0.02	NA <sup>c</sup>		
Jul (first rain)	<sup>b</sup>			OM	0.83	<0.01
Jul (first flood)	moisture <sup>d</sup>	0.69	<0.01	<sup>b</sup>		
Aug	moisture, NH <sub>4</sub> <sup>+</sup>	0.80	<0.01	OM	0.45	0.02
Sep	NH <sub>4</sub> <sup>+</sup>	0.65	<0.01	OM	0.80	<0.01
Nov	moisture, OM	0.96	<0.01	<sup>b</sup>		
Feb 2004	OM <sup>d</sup>	0.59	<0.01	NA <sup>c</sup>		
<i>N Mineralization</i>						
Mar 2003	NA <sup>c</sup>			N	0.41	0.03
Apr	OM	0.50	0.02	OM	0.92	<0.01
Jun	NA <sup>c</sup>			NA <sup>c</sup>		
Jul (first rain)	NA <sup>c</sup>			OM	0.74	<0.01
Jul (first flood)	moisture	0.51	0.01	NA <sup>c</sup>		
Aug	N	0.51	0.02	OM	0.51	0.01
Sep	moisture	0.65	<0.01	NA <sup>c</sup>		
Nov	NA <sup>c</sup>			<sup>b</sup>		
Jan 2004	NA <sup>c</sup>			<sup>b</sup>		
<i>Nitrification</i>						
Mar 2003	N	0.47	0.03	N <sup>d</sup>	0.72	<0.01
Apr	<sup>b</sup>			NA <sup>c</sup>		
Jun	NA <sup>c</sup>			OM	0.57	<0.01
Jul (first rain)	moisture	0.87	<0.01	<sup>b</sup>	0.61	<0.01
Jul (first flood)	<sup>b</sup>			OM	0.60	<0.01
Aug	NA <sup>c</sup>			NA <sup>c</sup>		
Sep	NA <sup>c</sup>			<sup>b</sup>		
Nov	NA <sup>c</sup>			<sup>b</sup>		
Jan 2004	NH <sub>4</sub> <sup>+</sup>	0.57	0.01	N	0.58	<0.01

<sup>a</sup>R<sup>2</sup> denotes values adjusted for the number of parameters in the model, n = 10–11. C, N, and NH<sub>4</sub><sup>+</sup> refer to extractable fractions.

<sup>b</sup>Data do not meet the assumptions of a parametric test.

<sup>c</sup>NA designates no significant models.

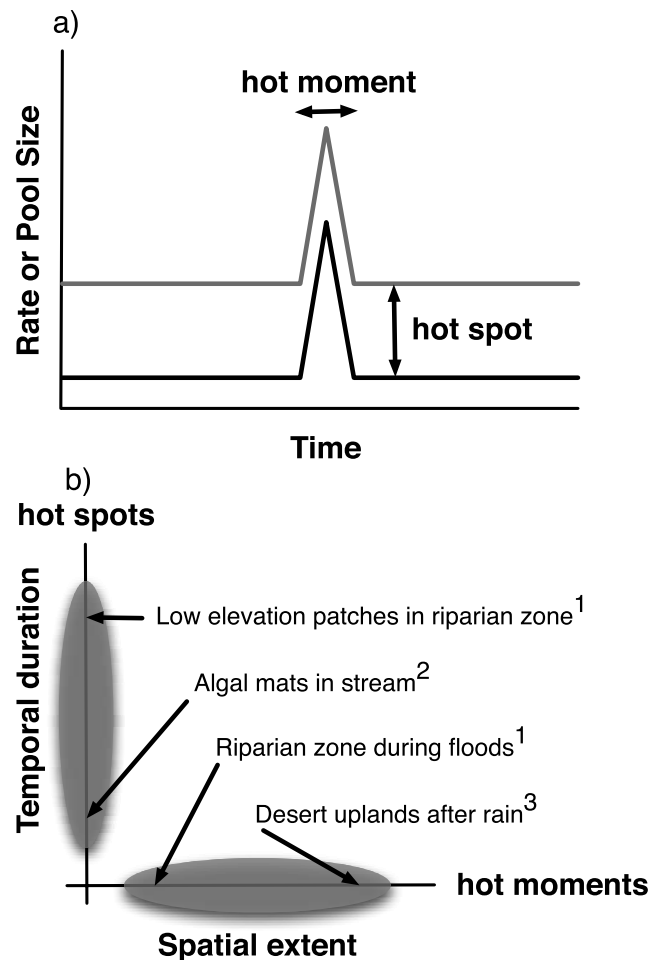
<sup>d</sup>One outlier removed.

peak annual microbial biomass, suggesting that available labile C substrates may fuel seasonal pulses in microbial activity. Observations in a diverse array of ecosystems support the notion that microbes track seasonal changes in C availability. Microbial C substrate-use patterns in lakes tracked seasonal patterns of carbohydrate versus amino and carboxylic acid availability [Grover and Chrzanowski, 2000]; bacterial production in arctic ecosystems responded to changes in the content of dissolved organic matter over short time scales [Judd *et al.*, 2006]; and, of particular significance to our study, soil microbial communities of the RoSS in a montane semiarid stream used DOC that was flushed from soils as they became inundated during snowmelt [Baker *et al.*, 2000]. Thus, temporal patterns in C-use

provide indirect evidence that the observed seasonal pulse of C contains a significant labile fraction with potential to fuel microbial processes.

## 5.2. Spatial Patterns

[34] Microbial biomass and activity (e.g., potential denitrification rates) were greater and average pools of organic matter and extractable C and N were 2–3 times larger in



**Figure 8.** Illustration of hot spots and hot moments. Over time, a hot moment exhibits disproportionately high process rates or storage of nutrients; however, different components of the system (here, surface and RoSS soils, high and low elevation patches) may respond similarly in time even though their baseline differs significantly (a). Hot spots are places on the landscape that exhibit high rates of processes or storage of materials, in this case associated with low-elevation sites. Hot spots and hot moments have characteristic scales (b). Although a hot moment is an episode of very high reaction rates relative to other time periods, the spatial extent over which they are active can vary from riparian zones to the vast expanse of desert uplands. Considering the desert landscape in which stream-riparian corridors are embedded, low-elevation sites in the riparian zone are hot spots that are active over long periods of time, in contrast to mats of stream algae. References: 1, this study; 2, Grimm and Fisher [1989] and Belnap *et al.* [2005]; 3, Welter *et al.* [2005] and Sponseller [2007].

surface than RoSS soils. Greater microbial activity fueled by relatively larger stores of materials suggests that surface soils may strongly contribute to the amount and forms of materials transported to downstream ecosystems. However, surface soils are only sporadically connected to downstream ecosystems, whereas soils in the permanently saturated zone are continuously connected to the river. Connectivity between surface soils and downstream ecosystems occurs via percolation of water to shallow groundwater followed by downstream transport, returning overbank flows, and overland flows. During the study period, overbank flows occurred only within meters of the stream and overland flows from upland washes were of short duration (hours) and infiltrated rapidly once within the riparian zone. In contrast, RoSS soils of this gaining reach were hydrologically connected to the stream during the time periods when they were inundated (January–March, July–August). Spatial patterns in water table elevation demonstrated a hydrologic gradient with flow oriented toward the stream over the entire study period. Additionally, in-stream bromide-tracer studies conducted in the study reach indicate increases in stream discharge along the reach ranging from 11 to 20% seasonally, with the greatest increase following the monsoon season (R.A. Martin, T. K. Harms, and N.B. Grimm, unpublished data). Thus, the seasonally saturated region of the soil profile directly links the riparian floodplain with the surface stream via shallow groundwater flow over seasonal time scales, whereas surface soils are connected only during storms.

[35] Microbes in soils of the surface and RoSS are influenced by different factors due to vertical stratification in soil resources. Although peak microbial biomass and activities were associated with elevated water, organic C, and N availability overall, activities and biomass of microbes in surface soils were strongly correlated with soil water and N. In contrast, subsurface microbes showed statistical patterns consistent with limitation by N and organic C. These patterns correspond with differences in organic C and water availability between the two depths. Surface soils have twice as much organic matter and extractable DOC as RoSS soils, on average, whereas RoSS soils contain greater soil moisture that varies less seasonally than in surface soils. Hydrologic flows potentially support a hot moment in these soil horizons either directly by providing water, or indirectly by transporting C and N.

[36] Low points within the riparian zone had high rates of biogeochemical processes and large pools of C and N, a spatial pattern supported by detection of hot spots as statistical outliers. On hillslopes, nutrient transport in hydrologic flows can produce distinct patches along topographic gradients [Giblin *et al.*, 1991]. Spatial patterns in this semiarid floodplain are consistent with such observations, despite an elevation gradient of less than 2 m. Within the floodplain, landscape positions at lower elevations have longer hydrologic residence times and, during our study, were sites of pooled surface water following the monsoon floods. Prolonged inundation likely supported increased rates of nutrient cycling within surface soils of low-elevation patches at annual timescales. In addition to altering redox conditions and delivery of nutrients and labile C substrates, as water velocity slows, fine-sediments are deposited. These particles can account for a large proportion

of N inputs in semiarid riparian zones [Adair *et al.*, 2004]. Particle size influences physical retention of C and N [Bechtold *et al.*, 2003; Steiger and Gurnell, 2002] as well as soil water and oxygen content, leading to strong relationships between fine particles and denitrification [Pinay *et al.*, 2000]. Patches of fine sediments in turn are sinks for additional nutrient inputs. Microbial and nutrient pools of RoSS soils also exhibited strong negative correlations with elevation. Although soils at depth are not subject to the same downslope hydrologic transport as surface soils, the RoSS is nearer to the surface in low-elevation patches, resulting in soils that are richer in nutrients and organic material. The locations described in this study encompass a broad range of conditions, although subsequent investigations of the study site have encompassed patches of coarser soils and less organic matter than those studied here (T.K. Harms, unpublished data). These expanded studies support the idea that the locations studied here do encompass hot spots relative to the spatial extent of the floodplain. Hot spots supported higher rates of microbial activity relative to surrounding patches, but they too exhibited temporal fluctuations linked to water and substrate availability described previously.

### 5.3. Sources of C and N

[37] Peak concentrations of C and N observed within the floodplain during the summer monsoon may have derived from four sources: the riparian ecosystem, upstream ecosystems (terrestrial and aquatic), precipitation, or deep groundwater. We infer a riparian source of C and N, supported by the large upstream-downstream difference in stream water nutrient chemistry during the monsoon. Potential contributions of C and N from precipitation may vary on an event-specific basis in semiarid watersheds [Welter *et al.*, 2005; Edmonds, 2004]. In a temperate forest ecosystem, precipitation could account for only a small fraction of the seasonal flush of DOC observed in shallow groundwater [Hinton *et al.*, 1998] and we do not consider it further here. Infiltrating stream water carrying nutrients derived from upstream ecosystems may contribute to peak C and N concentrations during the summer monsoon. However, this mechanism is likely to be most significant in losing, rather than gaining reaches such as the study site [e.g., Schade *et al.*, 2002]. Upstream ecosystems do contribute to the observed seasonal peak nutrient concentrations, as evidenced by seasonal increases in stream nutrient concentrations both upstream and downstream of the riparian floodplain. However, organic C and N concentrations were substantially greater downstream of the riparian floodplain during the period of large floods in August, suggesting a local source of these materials. Further, because instream production is halted during flooding, organic materials are not likely originating within the stream reach [Holmes *et al.*, 1998]. Finally, deep groundwater inputs to the reach may contribute to the observed resource pulse; however, extensive mixing of stream and alluvial groundwater occurs during the monsoon season in this basin [Brooks and Lemon, 2007], which would produce homogeneous concentrations of dissolved streamwater constituents. Thus, we infer a floodplain source of the peak concentrations of organic C and N observed during the period of large monsoon flash floods, which originated from within the local floodplain study site.



[38] The temporally dynamic nature of C and N availability and coincidence of peak concentrations with monsoon-season floods suggest that inundation of the riparian zone leads to a release of nutrients. Carbon and nitrogen are often released following inundation of previously dry soils and sediments in stream-riparian ecosystems, including semiarid regions [Baker *et al.*, 2000; Heffernan and Sponseller, 2004; Meixner *et al.*, 2007]. Here we document pulses of organic C and N to the stream, associated with the riparian floodplain. Sources of these organic materials include labile substrates derived from photosynthesis [McDowell and Likens, 1988], soil leachate [Vázquez *et al.*, 2007], or mycorrhizae [Harner *et al.*, 2004]. Using an increase in discharge due to water input from the riparian zone of 20% (from the postmonsoon time period, R. Martin, T. Harms, and N. Grimm, unpublished data), we estimated the daily load of DON and DOC contributed by the watershed as the difference between the load upstream of the floodplain during the monsoon floods and the previous sampled date. The riparian contribution was estimated as the difference between loads upstream and downstream of the riparian floodplain. For the sampled day, the riparian zone is estimated to have contributed 35% of the DOC and 37% of the DON in the stream downstream of the floodplain. Using these estimates, water entering the stream from the floodplain must have contained 31 mg/L C as DOC and 0.5 mg/L N as DON. These values are within the range of concentrations observed in runoff from desert catchments [Fisher and Grimm, 1985], suggesting that our estimates are reasonable for a mixture of shallow groundwater, overland flow, and interflow. Although we observed increased rates of soil microbial processes that contribute to retention or removal of C and N, this floodplain exports dissolved organic C and N to the stream during monsoon-season floods. These organic materials may fuel microbial processes in less productive downstream ecosystems.

#### 5.4. A Hydrogeomorphic Framework of Semiarid Riparian Biogeochemistry

[39] Interactions of hydrologic flowpaths with geomorphology may be the ultimate driver of spatial and temporal heterogeneity in nutrient cycling in stream-riparian corridors. Geomorphology determines the attributes of hydrologic flowpaths, such as residence time and velocity, which influence contact times of solutes with soil microbes. Within the riparian zone, heterogeneity conferred by the hydrogeomorphic template creates hot spots in low elevation patches. The geomorphic template directs hydrologic delivery of fine-textured particles and labile resources to these patches resulting in sustained periods of relatively high biogeochemical activity. The characteristic temporal domain of these riparian hot spots contrasts with those of the bordering stream ecosystem, where hot spots occur within mats of algae (Figure 8b). Algal mats slow water velocity relative to the majority of stream flow, facilitating biogeochemical reactions. However, they are subject to higher water velocities than the floodplain, and are frequently removed by flash floods [Grimm and Fisher, 1989]. In contrast to temperate and tropical ecosystems, hydrologic transport in semiarid ecosystems is extremely variable in time. Flashiness in the hydrologic template results in pulsed microbial activity, as floods make both water and labile

resources available over short time scales. Compared to an annual temporal extent, times following floods constituted a hot moment of microbial activity in this study. In the context of the broader desert landscape, the combination of water and labile substrates may also result in hot moments in the uplands following monsoon storms [Sponseller, 2007]. Although these hot moments occur over a large spatial extent, they are extremely brief in duration likely due to limited supplies of labile substrates compared to riparian floodplains (Figure 8b).

[40] Most large rivers in the semiarid U.S. Southwest are impounded, and efforts to restore or mitigate dammed rivers require some reference state or ecosystem. Remaining free-flowing rivers, such as the San Pedro, provide a reference and indicate the critical factors that may be considered in conservation and management of semiarid rivers. Strong links between hydrologic connectivity and biogeochemical activity such as those reported here have important implications for ecosystem functions resulting from alteration of the hydrologic regime. Because soil-derived nutrients become available during periods of contact with groundwater, declines in water table elevation could lead to reduced rates of microbial processes associated with N retention or changes in the dominant biogeochemical pathways [Hefting *et al.*, 2004]. Changes in the timing of floods inundating the riparian zone and disruption of river-riparian hydrologic connectivity due to channel modifications may alter the rates of biological processes in floodplains with consequences for the flux of materials downstream [Valett *et al.*, 2005]. Evaluation of ecosystem functions in the context of spatial and temporal aspects of the hydrogeomorphic template may allow for improved accuracy in anticipating changes under altered hydrology.

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