Biogeochemistry (2005) 73: 541–553
DOI 10.1007/s10533-004-1718-1

Spatial and temporal variation in islands of fertility in the Sonoran Desert

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Received 12 January 2004; accepted in revised form 29 July 2004

Key words: Islands of fertility, Microbial biomass C and N, N biogeochemistry, Nitrogen mineralization, Net nitrification, *Prosopis velutina*

Abstract. In many arid and semi-arid ecosystems, canopy trees and shrubs have a strong positive influence on soil moisture and nutrient availability, creating islands of fertility where organic matter and nutrients are high relative to areas outside the canopy. Previous studies of canopy effects on soil processes have rarely considered how landscape context may modulate these effects. We measured the effects of velvet mesquite trees (*Prosopis velutina*) on soil moisture and the biogeochemistry of nitrogen at different positions along a topographic gradient from upland desert to riparian zone in the Sonoran Desert of central Arizona. We also examined how landscape position and patterns of precipitation interact to determine the influence of *P. velutina* on soil moisture, N availability assessed using ion exchange resins, net N mineralization and net nitrification, and microbial biomass C and N. *P. velutina* clearly created islands of fertility with higher soil organic matter, net N mineralization and net nitrification rates, and microbial biomass under mesquite canopies. These effects were consistent across the landscape and showed little temporal variability. Magnitude and direction of effect of mesquite on soil moisture changed with landscape position, from positive in the upland to negative in the terrace, but only when soil moisture was $>4\%$. Resin N showed responses to mesquite that depended on precipitation and topographic position, with highest values during wet seasons and under mesquite on terraces. We suggest changes in proximity of *P. velutina* to groundwater lead to shifts in biogeochemical processes and species interactions with change in landscape position along a topographic gradient.

Introduction

In many arid and semi-arid ecosystems, canopy trees and shrubs have a strong positive influence on soil moisture and nutrient availability, creating islands of fertility where organic matter and nutrients are high relative to areas outside the canopy (Schlesinger et al. 1996; Reynolds et al. 1999; Schade et al. 2003). A number of physical and biological mechanisms cause these increases in resource availability, including the concentration of materials due to litter production, root sequestration, and the trapping of materials during physical transport (Schlesinger and Pilmanis 1998). Canopy trees also significantly alter the movement of water through these ecosystems, generally by increasing infiltration rates into arid and semi-arid soils (Ludwig and Tongway 1997; Puigdefabregas et al. 1999).

Much of what is known about these processes comes from studies of grassland–shrubland transition zones and changes in patterns of resource availability during encroachment of shrubs into grasslands (Kieft et al. 1998). In general, the transition from grassland to shrubland leads to greater spatial heterogeneity in soil resource levels (Schlesinger et al. 1996). Resulting patterns of water, nutrient and organic matter availability have significant consequences for microbial processes, often increasing rates of nitrogen mineralization, nitrification (Kieft et al. 1998), and denitrification (Wainwright et al. 2002), and the production and diversity of understory plant communities (Schade et al. 2003). These effects have been documented in several different types of ecosystems, ranging from desert shrublands to oak savannas. However, little is known about these processes in shrublands of the Sonoran Desert.

Analyses of canopy effects on soil processes and understory plant communities have rarely considered how landscape context may affect pattern and process, even though canopy shrub or tree species often occur in a wide variety of communities and topographic positions (Hibbard et al. 2001). Recent work suggests that the effects of canopy trees on understory plant production can switch from facilitative to competitive down topographic gradients, due in part to an increase in proximity of the canopy tree to the water table (Belsky 1994; Schade et al. 2003). These authors hypothesize that greater access to the water table leads to higher productivity of the canopy tree, which leads to greater water use and depletion of water availability in surface soils, reducing productivity of understory plants. Schade et al. (2003) also show declines in species diversity and changes in species composition of plant communities growing under mesquite trees along a topographic gradient in the Sonoran Desert. They suggest these changes are due to increases in nitrogen availability under mesquite at low points in the landscape. These studies highlight how canopy-understory interactions change with landscape position, and suggest these changes are due to indirect effects of the canopy tree on water and nutrient availability. In this study, we further explore the influence of landscape position by measuring the effects of velvet mesquite trees (*Prosopis velutina*) on soil moisture, organic matter and the biogeochemistry of nitrogen at different positions along a topographic gradient in the Sonoran Desert of central Arizona.

In addition, we examined how intra-and interannual patterns of precipitation interact with landscape position to determine the influence of *P. velutina* on soil moisture, organic matter and biogeochemistry of N. Both water and N availability in desert soils exhibit high temporal variability (Kieft et al. 1998; Xie and Steinberger 2001) because of strong responses to seasonal and interannual variation in precipitation. Precipitation in the Sonoran Desert shows a distinct seasonal pattern, with most rain falling from June to September (monsoon rains) or from December to March (winter rains). Monsoon rainstorms are generally shorter in duration and more intense than winter storms.

Velvet mesquite (*Prosopis velutina*) is an ecologically and economically important woody plant that is common throughout the Sonoran Desert landscape from arid uplands to riparian zones (Stromberg et al. 1992). Both growth form and productivity of mesquite trees vary considerably among habitat types, with individuals attaining maximum height and productivity in the riparian zone (Sharifi et al. 1982; Stromberg et al. 1992). These traits are strongly influenced by depth to groundwater (Stromberg et al. 1993), which decreases from upland to riparian habitats, and which has been heavily influenced by human activities such as surface flow diversion and groundwater pumping (Stromberg et al. 1993). Previous studies of mesquite woodlands have shown a strong influence of mesquite on herbaceous vegetation, including alteration of species distribution patterns (Yavitt and Smith 1983; Schade et al. 2003), as well as higher production and differences in species composition of plant communities growing under mesquite canopies versus in interplant areas (Whittaker et al. 1979; Schade et al. 2003).

The mechanism underlying these differences is unclear, although, as mentioned above, variation in effects of mesquite on soil water and nutrient availability has been clearly implicated (Schade et al. 2003). The widespread distribution of velvet mesquite, coupled with its well-documented response to changes in water table depth, provides an opportunity to investigate changes in the interaction between mesquite canopy trees and soil resources in different landscape contexts arrayed along a topographic gradient. In this paper, we address the following three research questions: (1) how does mesquite influence soil moisture and organic matter content, nitrogen availability, and microbial biomass C and N, (2) how do these influences change with topographic position, and (3) how do seasonal changes in precipitation alter the local effects of mesquite along a topographic gradient?

Site description

Our study area encompassed roughly 2 km^2 located within the Verde River watershed in Central Arizona, roughly 30 miles north of the city of Phoenix. Sites were located along a topographic gradient on a gentle north-facing slope, and included desert scrub (upland), an intermediate terrace (terrace) and the riparian zone (riparian). The shrub and tree community in the upland scrub consists mainly of scattered, small individuals of mesquite, bursage (*Ambrosia deltoidea*), creosote bush (*Larrea tridentata*), and paloverde (*Cercidium sp.*). In the terrace, the only woody components are medium to large mesquite trees. In the riparian zone, mesquite, willow (*Salix goodingii*) and cottonwood (*Populus fremontii*) form a gallery forest. Large riparian mesquite trees grow in discrete patches of several individuals, roughly 500 m^2 in area, situated between gallery forest and the terrace. These stands also include occasional individuals of tamarisk (*Tamarix ramosissima*), seepwillow (*Baccharis salicilifolia*) and burrobush (*Hymenoclea monogyra*). In both upland and terrace, interplant areas (interplant) separate individual mesquites. In the riparian zone, trees are larger and closer together and form a closed canopy over mesquite-dominated patches. Winter rainfall in 2001 was above average, coinciding with a bloom of herbaceous vegetation in all zones during February and March of 2001.

Methods

Soil moisture, microbial processes, and nutrient availability were measured within 1 m of the trunk and either outside (upland and terrace) or at the edge (riparian) of the canopies of 10 trees in each zone. In the riparian zone, we sampled where the canopy edges of adjacent trees met to maximize the distance from the trunk of the trees (all edge and interplant samples were collected >3 m from trunks). Soil samples were collected bimonthly from May to September 2000, and from February to December 2001 to a depth of 10 cm using a bucket auger. Samples were returned to the laboratory, sieved through a 2 mm-mesh sieve, and all succeeding analyses were performed on the $<$ 2 mm fraction. On all soil samples, 40–50 g subsamples were weighed before and after drying at 60 °C for 48 h to measure soil moisture, then combusted at 500 °C for 4 h and weighed for the determination of organic matter content estimated as loss on ignition, reported here as ash-free dry mass (AFDM). This method overestimates organic matter content due to loss of carbonates during ashing.

Soil N availability was estimated at these soil sampling locations in July and September 2000 and monthly between February and December 2001 using cation (CER) and anion (AER) exchange resins to estimate NH_4^+ and NO_3^- availability, respectively (Lajtha 1988). At each field location, a pair of resin bags, consisting of a single AER and a single CER bag, was buried in the soil to a depth of 10 cm by cutting a slit in the soil using a shovel to minimize soil disturbance. Bags were initially placed in the ground on the 2nd of February 2001. After 1 month, these bags were retrieved and replaced by a new set of bags, and this process was repeated monthly through the end of December. All bags were returned to the laboratory and frozen for later analysis.

Resin bags were constructed by weighing 4 g of either AER or CER into a small nylon bag. AER bags were rinsed three times and soaked overnight in 0.5 M $NaHCO_3$ to convert them to the bicarbonate form. CER bags were washed and soaked overnight in 0.5 M HCl. All bags were rinsed thoroughly with distilled water and spun dry before transportation to the field. After retrieval and subsequent freezing, all resin bags were removed from the freezer and rinsed to remove soil particles. Anion exchange resins were extracted in 100 ml of 0.5 M HCl, cation exchange resins in 100 ml of 2 M NaCl. All extracts were adjusted to neutral pH. NO_3 was measured on AER extracts on a Lachat Quick Chem 8000 Flow Injection Analyzer. CER extracts were analyzed for NH_4 concentration on a Bran & Luebbe TrAAcs 800 Autoanalyzer.

In April and September 2001, we estimated net potentially mineralizable N and net potential nitrification rates in all soil samples using laboratory incubations. From each sample two 10 g subsamples were collected. One subsample was immediately extracted in 2 M KCl to determine initial NO_3 and NH_4 concentrations. The second subsample was placed in a plastic sample bottle, wet to approximately 15% moisture content with distilled water, and incubated for 30 days. Distilled water was added as necessary to maintain moisture content at 15% in all samples. After 30 days, incubated subsamples were extracted in 2 M KCl to determine final NO_3 and NH_4 concentrations. All extracts were filtered and frozen until analysis for NO_3 and NH_4 on a Bran and Leubbe TRAACS 800 autoanalyzer. Net mineralizable N was calculated as the difference between final and initial dissolved inorganic N (NO_3 + NH_4), and net nitrification as the difference between final and initial NO_3 concentrations.

In May, July, and September 2000, and April and September 2001, we estimated soil microbial biomass C and N using chloroform fumigation direct extraction (CFDE, Brookes et al. 1985). Two 10 g subsamples were collected from each soil sample. One subsample was extracted immediately with 1 M K_2SO_4, and the second was fumigated with chloroform in a cabinet dessicator for 72 h followed by extraction with 1 M K_2SO_4. All extracts were filtered and frozen until analysis for total dissolved N using persulfate followed by ultraviolet digestion on a Lachat QuikChem 8000 autoanalyzer and dissolved organic carbon (DOC) on a Shimadzu TOC 5000.

We used repeated measures analysis of variance to compare zones and patches across months for soil moisture and organic matter, resin N, and microbial biomass C and N. To establish the effect of monthly precipitation on N availability we preformed separate simple linear regressions for each patch type within each zone (a total of 6 regressions). When relationships appeared non-linear, or to meet assumption of constant variance, we natural-log transformed the dependent variable. Analysis of variance was used to compare net N mineralization and net nitrification rates between zones and patches for each month separately.

Results

Soil moisture was generally low ($<4\%$), with peaks in February and December in all zones and also in April in the riparian zone (Figure 1a–c). Temporal patterns in soil moisture correspond generally with seasonal patterns in rainfall, although moisture was not significantly correlated with monthly precipitation. Mesquite had little influence on soil moisture when soil moisture was low (Figure 1a–c). In February and December, soil moisture was higher under mesquite in the upland, lower under mesquite in the terrace, and was not affected by mesquite in the riparian zone. Soil moisture content was higher in the riparian zone, particularly, in February and April.

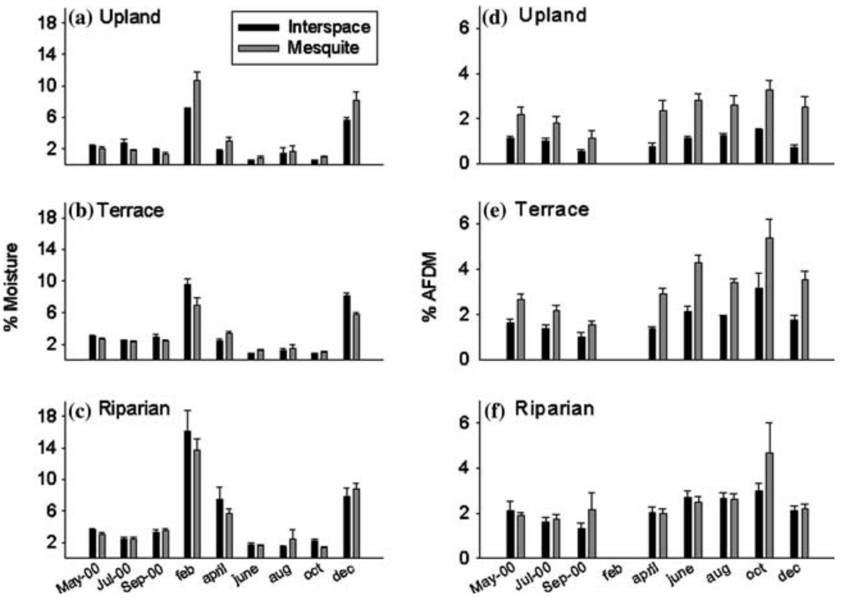

Figure 1. Monthly mean soil moisture (a–c) and AFDM (d–f) in soils from interplant and mesquite patches from all zones. Lines at bottom indicate the year measurements were taken. *Significant differences between patches within a particular month. **Patch differences across all months. All other differences are not statistically significant (repeated measures ANOVA followed by Tukey's test; for all significant differences $p < 0.01$).

Organic matter content (AFDM) was higher under mesquite in both upland and terrace, but not in the riparian zone (Figure 1d–f). In interplant patches, AFDM was significantly lower in the upland than terrace or riparian zone, while mesquite patches were not significantly different between zones (repeated measures ANOVA, followed by Tukey's test; all significant differences $p < 0.01$). As a result, the positive effect of mesquite on AFDM relative to interplant patches was greater in the upland than in the terrace or riparian zone (Figure 1d–f). Temporal patterns in AFDM differed between the 2 years. In 2000, we found a significant decrease between May and September in upland and terrace, while in 2001, AFDM increased between April and October in these zones.

In both upland and terrace, nitrogen availability assessed using ion-exchange resins (resin N) was significantly higher under mesquite during spring and fall, but there was never a difference between interplant and mesquite patches in the riparian zone (Figure 2a–c). Resin N increased in interplant patches down the landscape from upland to terrace to riparian zone, but peaked in the terrace under mesquite (Figure 2a–c). The difference in N availability between interplant and mesquite patches was much larger in the terrace than the upland. In all three zones, resin N tended to increase in spring and fall when rainfall was high, and spatial patterns along the topographic gradient and within zones

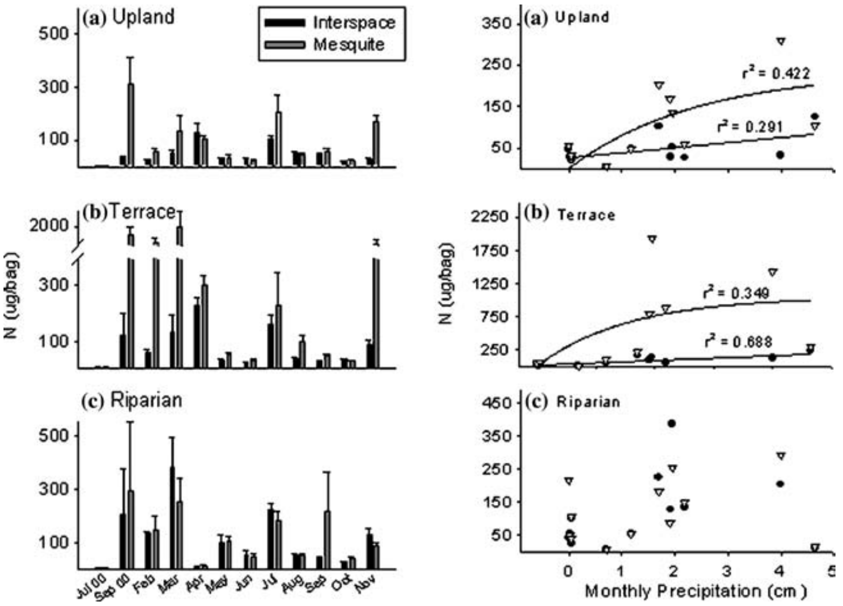

Figure 2. Monthly mean nitrogen (a–c), as measured using ion-exchange resin bags, and the relationship between monthly precipitation and resin nitrogen for each patch type within each zone. *Significant differences between patches within a particular month ($p < 0.01$). Monthly precipitation data from the National Climatic Data Center.

were accentuated. The relationship between resin N and monthly precipitation differed between patches and zones (Figure 2d–f). In mesquite patches in upland and terrace, resin N was significantly positively related to monthly precipitation, but the relationship was curvilinear (Figure 2d, e). In these two zones, interplant patches showed a weaker, but significant linear relationship. In the riparian zone, there was no clear relationship between precipitation and resin N (Figure 2f).

In upland and terrace, rates of both net N mineralization and net nitrification were significantly higher under mesquite than in interplant patches in both April and September, but we found no significant difference between patches in the riparian zone in either month (Figure 3). No differences between zones were significant, although in April we observed a trend toward higher rates of both processes in terrace mesquite patches. Rates of both processes were generally higher in September than April, particularly in interplant patches.

As with microbial processes, microbial biomass carbon and nitrogen were higher in mesquite patches than interplant patches in upland and terrace, although for microbial C this effect was restricted to May and July 2000, and April 2001. Both microbial C and N were significantly lower in the upland than terrace and riparian zones in interplant patches (Figure 4). Microbial N was significantly higher in the terrace than upland and riparian zones in mesquite

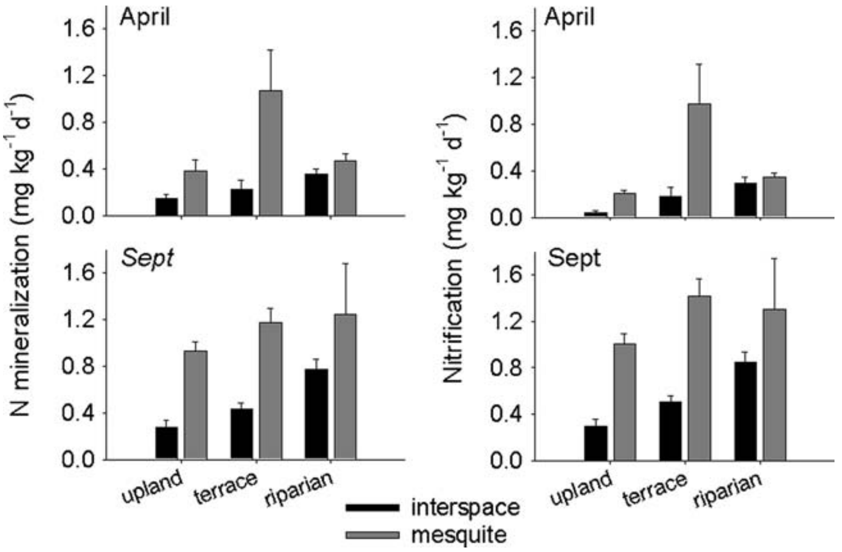

Figure 3. Net potential nitrogen mineralization and net nitrification rates measured using laboratory incubations of soils collected in April and September 2001. *Significant differences between patches ($p < 0.01$).

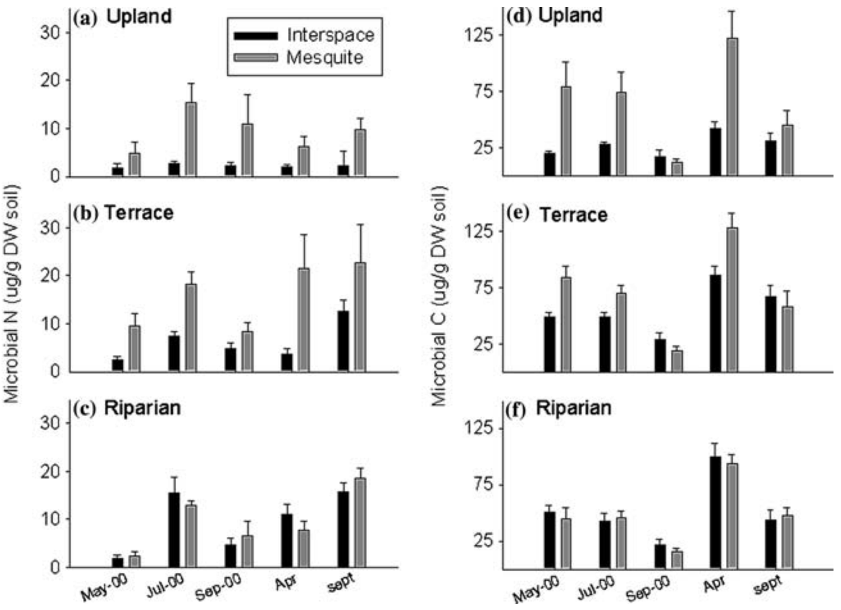

Figure 4. Soil microbial biomass nitrogen (a–c) and carbon (d–f) measured using CFDE. *Significant differences between patches within a particular month ($p < 0.01$).

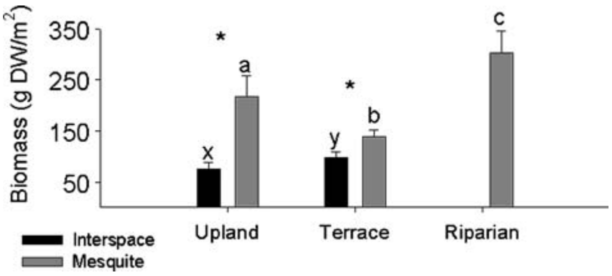

Figure 5. Mean values for understory plant biomass for both landscape position and patch type. Since all patches showed negligible biomass at the beginning of the winter rain season, spatial variation in total biomass at the time of collection should correlate with variation in plant production. Letters indicate significant differences between zones for each patch type (a–c for mesquite, x–y for interplant), stars indicate differences between patches within a zone. No differences were found between edge and canopy patches in the riparian zone, therefore these patches were lumped for all subsequent analyses. Modified from Schade et al. (2003).

patches, but we found no differences between zones in microbial C. We found no strong temporal patterns in microbial N in any zone or patch, however, microbial C declined in September in both years, particularly in mesquite patches in upland and terrace.

Discussion

We found clear indication of the existence of islands of fertility for soil N availability and transformation rates under mesquite canopies in upland and terrace zones, but not in the riparian zone. In particular, organic matter content, net potential N mineralization and net nitrification rates, and microbial biomass C and N were all higher under mesquite than in interplant patches in upland and terrace, consistent with recent studies on mesquite and other canopy species in a number of ecosystems (Kieft et al. 1998; Schlesinger and Pilmanis 1998; Hibbard et al. 2001; Reyes-Reyes et al. 2002). We also observed little temporal variation in these variables, suggesting they are well-buffered against changes in precipitation and are tied to long-term accumulation of organic matter under mesquite. In particular, CFDE assesses total, not active, microbial biomass C and N, and would not be expected to show strong responses to precipitation. The lack of a canopy effect in the riparian zone is likely because trees form a closed canopy in this zone, resulting in a lack of true interplant spaces. Our sampling strategy in the riparian zone was designed to maximize distance from the trunks of trees, but it is certainly possible that soils unaffected by mesquite do not exist in these riparian mesquite patches.

Interestingly, landscape position influenced levels of these soil variables in interplant patches, but not under mesquite, where zones did not differ significantly. As a result, the magnitude of the difference between mesquite and interplant decreased down the topographic gradient from upland to terrace to riparian zone. This may be explained in part by spatial patterns of understory production in interplant patches. In a previous study at this site, Schade et al. (2003) demonstrated that understory production was high in February and March 2001, and increased down the topographic gradient in interplant patches (Figure 5), suggesting understory production is driven by moisture availability. Although the difference between upland and terrace in understory production is small, it is possible that higher understory plant biomass may have increased organic matter content, net potential N mineralization and net nitrification rates, and microbial biomass C and N in interplant spaces, obscuring the difference between patch types in the terrace and riparian zone.

When we shift our attention to soil moisture and resin N, the picture becomes a bit more complex. Unlike soil organic matter and microbial processes discussed above, these variables varied greatly from month to month. Obviously, soil moisture is expected to vary with precipitation, and since water movement is likely to influence what accumulates on ion-exchange resins, resin N should also respond strongly to precipitation patterns. Although monthly precipitation and soil moisture were not significantly related, it is clear from Figure 1 that soil moisture is higher during the rainy seasons of the year. Both the magnitude and direction of effect of mesquite on soil moisture changed with landscape position, from positive in the upland to negative in the terrace to neutral in the riparian zone. This pattern only existed when soil moisture was above 4%, which occurred in February and December 2001 in upland, terrace, and riparian zone, and in April in the riparian zone.

Although mesquite effects on soil moisture were restricted in time, most of the growth in understory vegetation occurred in February and March 2001, when these effects were the strongest. In a previous paper, we observed higher production of understory vegetation under mesquites in the upland than in the terrace (Figure 5), most likely because of higher soil moisture under upland mesquites (Schade et al. 2003). The difference between mesquite and interplant production was also higher in the upland. Clearly, the effects of mesquite on soil moisture depend on topographic position, probably as a result of closer proximity to the water table of trees at low points in the landscape. Belsky (1994) suggests that trees with greater access to the water table are more productive and use more water, depleting surface soil moisture down to levels that negatively affect shallow-rooted understory plants. Our data showing lower soil moisture under terrace mesquites than desert mesquites (Figure 1) are consistent with this explanation.

Resin N also showed responses to mesquite that depended on precipitation and topographic position. Resin N peaked during the rainy seasons in all zones and patches (Figure 2). Values were similar to those reported in a Hawaiian montane rain forest (Schuur 2001; 7.8–53.1 μg bag^{-1} d^{-1} versus 0.21–64.17 μg bag^{-1} d^{-1} in this study), and suggest high N availability during wet seasons. Positive effects of mesquite were evident then in both upland and terrace. The magnitude of mesquite effects on resin N was influenced by topographic position, with terrace showing a much stronger positive effect of mesquite than the other zones. Increasing N under mesquites has been shown previously to reduce species diversity and alter species composition of understory vegetation during the same bloom of production in spring 2001, with the largest effects occurring under terrace mesquites (Schade et al. 2003). Clearly, both temporal and spatial variation in these nutrients changes with landscape context, and these changes have a strong influence on the interaction between mesquite and understory plant communities.

The pattern of interaction between soil N and monthly precipitation also varies with landscape position (Figure 2d–f). The pattern of response of N to precipitation under mesquites in upland and terrace and in both patch types in the riparian zone suggests a shift in processes influencing N availability. At low to moderate rainfall, increases in soil moisture probably lead to increases in net N mineralization or direct remobilization of available N. In all mesquite patches, increases in N leveled off, or in fact may have reversed in the riparian zone, at high precipitation (Figure 2). Leveling off of N could simply indicate that net nitrogen mineralization or remobilization exhibits a saturating response to increases in moisture over the range measured here. Alternatively, at high precipitation, increases in understory plant production (Figure 5; Schade et al. 2003) may increase consumption of available N, or soil moisture may become high enough to cause anoxia in organic-rich soils, leading to dissimilatory processes like denitrification that would reduce N availability.

The intensity of the response of N to the presence of mesquite in the terrace indicates strong control by plant production on biological and physical processes in this zone. Mesquite trees are bigger, more productive, and may fix nitrogen at higher rates, in terrace and riparian zones, where the water table is closer to the soil surface. Root production is likely to be higher, which could explain higher levels of microbial C and N under mesquite in the terrace. Higher microbial biomass, in turn, could lead to strong biological control on soil N cycling that is reflected in the strong response of availability of N (measured by resins) to precipitation.

In summary, we have clearly shown a strong effect of mesquite on soil moisture, resin N, net potential N mineralization and net nitrification rates, and microbial biomass C and N. However, these effects are dependent on both the landscape context in which they occur and temporal patterns in precipitation. In particular, position along a topographic gradient had a large influence on both direction and magnitude of mesquite effects on soil moisture and the magnitude of the positive effect of mesquite on other soil variables. These results highlight the role of landscape position in mediating ecosystem processes, and their responses to temporal variability in environmental conditions.

Acknowledgments

We thank Tiffany Miley, Jill Koehler, Dana Swoveland, Marcia Kyle, Ayoola Folarin, Amy Novotny, Cathy Kochert and Tom Collela for invaluable assistance in field and laboratory. Ryan Sponseller made valuable comments on an early version of the manuscript that significantly improved our interpretation of the data. We thank Jim Elser, Bill Fagan, and other members of the genes-to-ecosystems team for assistance with the development of the ideas behind this project. This work was funded by the NSF-IRCEB Biological Stoichiometry Genes-to-Ecosystems project (IBN-9977047) directed by Jim Elser.

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