

The influence of *Prosopis* canopies on understorey vegetation: Effects of landscape position

Schade, J.D.^{1*}; Sponseller, R.¹; Collins, S.L.² & Stiles, A.²

¹Department of Biology and ²Department of Plant Biology, Arizona State University, Tempe, AZ 85287-1501, USA;

*Corresponding author; E-mail john.schade@asu.edu

Abstract. The influence of canopy trees and shrubs on understorey plants is complex and context-dependent. Canopy plants can exert positive, negative or neutral effects on production, composition and diversity of understorey plant communities, depending on local environmental conditions and position in the landscape. We studied the influence of *Prosopis velutina* (mesquite) on soil moisture and nitrogen availability, and understorey vegetation along a topographic gradient in the Sonoran Desert. We found significant increases in both soil moisture and N along the gradient from desert to riparian zone. In addition, *P. velutina* canopies had positive effects, relative to open areas, on soil moisture in the desert, and soil N in both desert and intermediate terrace. Biomass of understorey vegetation was highest and species richness was lowest in the riparian zone. Canopies had a positive effect on biomass in both desert and terrace, and a negative effect on species richness in the terrace. The effect of the canopy depended on landscape position, with desert canopies more strongly influencing soil moisture and biomass and terrace canopies more strongly influencing soil N and species richness. Individual species distributions suggested interspecific variation in response to water- vs. N-availability; they strongly influence species composition at both patch and landscape position levels.

Keywords: Canopy-understorey interaction; Mesquite; *Prosopis velutina*; Soil resource.

Introduction

Interactions between canopy trees and shrubs and understorey plant communities depend on the history of a site and local environmental conditions (Callaway et al. 1991; Bertness & Callaway 1994; Anderson et al. 2001). In areas where shrubs and trees are encroaching upon grassland ecosystems, woody plant invasion may lead to a relatively rapid conversion of grassland to woodland, resulting in a loss of understorey productivity and diversity (Tiedemann & Klemmedson 1977; Petranka & McPherson 1979; Archer et al. 1988; Hoch et al. 2002). Conversely, in other areas, woody plants may have little effect or even enhance productivity and diversity of understorey species (Muller 1953; Whittaker et al. 1979; Collins & Good 1987). The magnitude and

direction of influence of woody species depend on their effects on the spatial distribution of soil nutrients (Schlesinger & Pilmanis 1998; Reynolds et al. 1999), soil moisture availability due to soil infiltration rates and rates of water loss (Tiedemann & Klemmedson 1977; Frost & McDougald 1989; Weltzin & Coughenour 1990; Reynolds et al. 1999), and the intensity of competition with understorey plants for soil nutrients and water (Belsky 1994). Thus, canopy-understorey interactions are complex, variable, and highly context dependent (Yavitt & Smith 1983; Tewksbury & Lloyd 2001; Callaway et al. 2002).

Analyses of canopy effects on structure of herbaceous vegetation have rarely considered how landscape context may affect pattern and process (Hibbard et al. 2001). Recent work by McAuliffe (1994) in the Sonoran Desert has shown that plant distributions are determined by both elevational gradients and local soil type and microclimate. In this project, we measured the effects of both position along a topographic gradient and the local effects of *P. velutina* trees on herbaceous understorey vegetation in the Sonoran Desert of central Arizona. Previous analyses have suggested that *P. velutina* and other woody species increased the abundance of some herbaceous species beneath their canopies (Muller 1953; Yavitt & Smith 1983; Tewksbury & Lloyd 2001), yet this interaction does not appear to be consistent throughout the desert landscape. Therefore, we tested the hypothesis that canopy effects on herbaceous vegetation would change in different landscape contexts as a function of differences in soil water and nitrogen availability underneath, versus outside, *Prosopis* canopies.

In the Sonoran Desert, one of the primary tree canopy species is *Prosopis velutina* (Velvet mesquite), an ecologically and economically important woody plant, which is common throughout the desert landscape from arid uplands to riparian zones (Stromberg et al. 1992). Both growth form and productivity of *P. velutina*, and a closely related species, *P. glandulosa*, vary considerably between habitat types, with individuals attaining maximum height and productivity in the riparian zone (Sharifi et al. 1982; Stromberg et al. 1992). These traits are influenced by

depth to groundwater (Stromberg et al. 1993), which varies greatly between desert and riparian habitats, and has been heavily influenced by human activities such as surface flow diversion and groundwater pumping (Stromberg et al. 1993). Furthermore, previous studies of *Prosopis* woodlands have shown a strong influence of *Prosopis* on herbaceous vegetation, including alteration of species distribution patterns (Yavitt & Smith 1983), as well as higher production and differences in species composition of plant communities growing under *Prosopis* canopies vs. in open areas (Whittaker et al. 1979). However, we still do not understand the mechanism by which these differences were generated. The wide-spread distribution of *P. velutina*, coupled with its well-documented response to changes in water table depth, provide an opportunity to investigate changes in the interaction between *P. velutina* canopy trees and herbaceous understory plants between habitat types which differ in depth to groundwater and availability of soil resources. We addressed the following questions: 1. How does *P. velutina* influence soil moisture and nitrogen availability? 2. How does its presence influence production and diversity of the herbaceous plant community? 3. How do these influences change with landscape position? 4. What is the relative importance of changes in soil moisture or nitrogen availability in explaining observed vegetation patterns?

Site description

Our study area encompassed ca. 2 km² within the Verde River watershed in Central Arizona. Sites were located along a topographic gradient on a gentle north-facing slope, and included desert scrub (desert), an intermediate terrace (terrace) and the riparian zone (riparian). The shrub and tree community in the desert scrub consists mainly of scattered, small individuals of *P. velutina*, *Ambrosia deltoidea*, *Larrea tridentata* and *Cercidium spec.* In the terrace, the only woody components are medium to large *P. velutina* trees. In the riparian zone, *P. velutina*, *Salix goodingii* and *Populus fremontii* form a more or less closed-canopy gallery forest. Large riparian *P. velutina* trees grow in discrete patches of ca. 500 m² situated between gallery forest and the upland terrace. These stands also include occasional individuals of *Tamarix ramosissima*, *Baccharis salicifolia* and *Hymenoclea monogyra*. In both desert and terrace, open areas separate individual mesquites. In the riparian zone, trees are larger and closer together and form a closed canopy over *P. velutina* dominated patches. In response to above average winter rains, a bloom of herbaceous vegetation occurred in all zones during February and March of 2001.

Methods

In March 2001, we established two 30 m transects, roughly 400-600 m apart in each zone (desert, terrace, and riparian) for measurement of both soil and plant community variables. Transects were located to intersect the canopies of at least two *P. velutina* trees and to include open areas between trees. In the riparian zone, transects spanned a single patch of *P. velutina* forest. One of the riparian transects was limited to 22 m in length due to limitations imposed by the size of the patch.

Soil moisture and nutrient availability

Soil moisture and nutrient availability were measured within 1 m of the trunk and either outside (desert and terrace) or at the edge (riparian) of the canopies of five trees growing within 15 m of either side of the transect, including trees used in herbaceous plant sampling (see next section). 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 samples were collected > 3m from trunks). Soil moisture was measured gravimetrically on samples collected in February and March to a depth of 10 cm using a bucket auger. Samples were returned to the lab, sieved through a 2 mm-mesh sieve, and subsamples of the < 2mm fraction were weighed before and after drying at 60 °C for 48 hr. Soil N availability was estimated at these same locations using cation exchange resins (CER) to estimate NH₄⁺ concentrations and anion exchange resins (AER) to measure NO₃⁻ concentrations (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 02.02.2001 and incubated for one month. On 02.03.2001, these bags were retrieved and replaced by a new set of bags, which were retrieved on 05.04.2001. All bags were returned to the lab and frozen for later analysis. The period of incubation was chosen to coincide with the bloom of herbaceous vegetation.

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 NaHCO₃ 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 in a lettuce spinner 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 ex-

tracted in 100 ml of 0.5 M HCl, cation exchange resins in 100 ml of 2 M NaCl. All extractant samples 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.

To compare soil moisture and nitrogen between zones, we performed separate analyses of variance for each month using means calculated for samples collected near each transect, giving a sample size of 2 for each zone. This was done for overall comparisons and for individual comparisons of canopy and/or open areas between zones. Differences between months were compared using separate analyses of variance for each zone. For comparison of patch types within zones, we used separate nested analyses of variance for each zone, in which patch type was nested within transect to reduce problems associated with pseudoreplication ($n = 5$ for each patch type in each zone). For patch type comparisons within zones, we also ran ANOVAs on each transect individually, but we do not report these results here, as they agree with the results from the nested ANOVAs. All multiple comparisons were performed using Tukey's test.

Production, diversity and species composition

At each m along each transect, we estimated percent cover of all herbaceous species within a 0.25 m² quadrat. Every 2 m, we clipped all above-ground herbaceous plant material from half of the quadrat. Herbaceous material collected from each quadrat was dried at 60 °C for 48 hours then weighed to estimate above-ground biomass. Biomasses of individual species were not distinguished.

Since herbaceous plants were essentially absent before the winter rains, we used total biomass as a measure of above-ground production during the study period. This should be viewed with some caution, since we are assuming that biomass is a good measure of productivity, which is not always the case (Patten 1978). We used species richness as a measure of diversity because other calculated indices gave the same results. For each transect, we calculated the average number of species per quadrat (species richness) and the total number of species found on each transect.

We used ANOVAs to compare total biomass, species richness, and total species per transect between zones. As for soil characteristics, means were calculated for each transect where appropriate and these means were used in the ANOVAs ($n = 2$ for each analysis). This was done for overall comparisons and for individual comparisons of canopy and/or open areas between zones. We compared patch types within zones for total biomass and species richness using separate nested analyses of variance for

each zone, in which patch type was nested within transect, similar to analyses for soil characteristics. We recognize the possibility that autocorrelation between quadrats complicates the interpretation of ANOVA results. To mitigate this problem, we ran ANOVAs on each transect individually. Autocorrelation would tend to blur the distinction between open and canopy quadrats within a transect, particularly at the edge of the canopy, and reduce our ability to detect differences between them. We report only the results of nested ANOVAs here because tests run on individual transects gave similar results. All multiple comparisons were performed using Tukey's test.

We used Detrended Correspondence Analysis (DCA) ordinations to summarize vegetation patterns both among and within zones along the topographic gradient (similar results were obtained with PCA and NMDS). To summarize patterns between zones, we combined abundance data from all quadrats along the six transects into a single species-by-sample matrix for ordination. All species were included in the ordination, but rare species were down-weighted in proportion to their abundances to reduce distortion. To summarize vegetation patterns within each zone, we analyzed transect data from each location separately by constructing species-by-sample matrices for each transect. For each transect, we conducted DCA ordinations using both abundance and presence-absence data to determine if vegetation patterns reflected differences in species abundances and/or species composition. We then plotted the DCA axis 1 scores against quadrat number along each transect (Whittaker et al. 1979; Shmida & Whittaker 1981) to visualize vegetation patterns within a given landscape position.

Soil-plant interactions

We used linear regression analyses on both the original and the log-transformed data to estimate the relative importance of soil moisture and soil N availability for productivity, species richness and species composition. For this analysis, mean values for biomass and species richness were calculated for quadrats grouped by patch type and transect within desert and terrace, and by transect regardless of patch type within the riparian zone. This gave a total of ten values for each regression. Biomass and species richness (species per quadrat) were each regressed against average soil moisture and soil N. Only significant regressions are reported here.

Results

Soil moisture and nutrient availability

In both February and March, soil moisture was significantly higher in the riparian zone than in both desert and terrace, which did not differ significantly from each other (Fig. 1). In the desert, moisture in canopy patches was significantly higher than in open patches in both months, while in the terrace, canopy patches were significantly lower in moisture in February (Fig. 1a) and significantly higher in March (Fig. 1b). Soil moisture was higher under desert canopy than terrace canopy in February, but not in March, and, overall the canopy effect on moisture was larger in the desert than the terrace. In the riparian zone, soil moisture was significantly lower near the trunk than at the edge of the canopy, but both patch types were higher than all samples from desert and terrace.

Soil nitrogen availability was higher in March in all zones and patch types, and varied significantly both between zones and between patches within desert and terrace in both February and March (Fig. 2). Nitrogen availability was significantly lower in the desert than terrace and riparian zone in both months. Canopy patches were significantly higher than open patches in both terrace and desert in both months, with terrace canopy patches significantly higher in N than all other patch types in February, and all but riparian edge patches in March. Desert open patches were significantly lower in N availability than all other patches in both months (Fig. 2). The terrace was enriched in N relative to the desert in both open and canopy patches, with terrace open patches as high as desert canopy patches. Furthermore, in contrast to soil moisture results, the effect of the canopy on N availability was higher in the terrace than in the desert.

Production, diversity and species composition

We found no difference in any plant community variables between canopy and edge of canopy in the riparian zone, hence no distinction was made between these patch types. Since we did find differences for at least one variable, the distinction between open and canopy is retained in terrace and desert for all variables. Herbaceous biomass was significantly higher in the riparian zone than the desert and the terrace, and was significantly higher under canopies than in open patches in both desert and terrace (Fig. 3a). Biomass under canopies in the desert was significantly higher than biomass under canopies in the terrace, and the difference in biomass between open and canopy patches was larger in the desert than in the terrace (Fig. 3a). Table 1

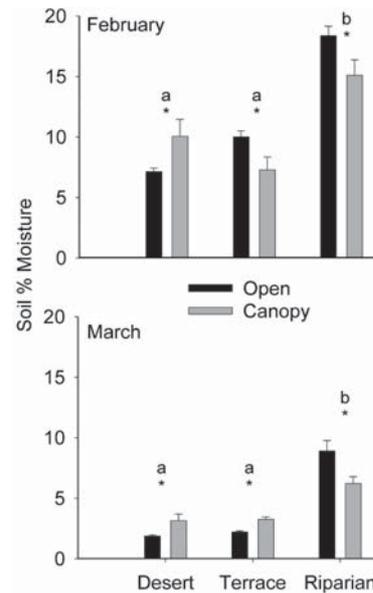


Fig. 1. Mean soil moisture for both landscape position and patch type in February and March. Stars indicate significant differences between patch types within a zone; letters indicate significant differences between zones after averaging across patch types.

shows all species observed and where they were present. Mean species richness per quadrat was significantly higher in the desert than terrace and riparian zone (Fig. 3b). Canopy and open patches were significantly different only in the terrace, with species richness lower under the canopy than in open patches. Canopy patches in the terrace were not significantly different from the riparian zone, while open patches in the terrace were significantly higher than the riparian zone (Fig. 3b). The total number of species found per transect also decreased down the landscape, with desert significantly higher than terrace, and terrace significantly higher than riparian zone (Fig. 3c).

The first two axes of the DCA ordination clearly separated samples from the three landscape positions (Fig. 4). Both axes had gradient lengths > 4.0 indicating that few species occur across the length of each gradient. DCA axis 1 reflected floristic differences between terrace, dominated by *Sphaeralcea coccinea* and *Erodium cicutarium*, desert, where *Pectocarya recurvata*, *Lepidium lasiocarpum*, *Ambrosia deltoidea* and *Bromus rubens* were common, and riparian zone, which was dominated by *Bowlesia incana* and *Hordeum leporinum*. The second DCA axis primarily separated desert from terrace and riparian zone, particularly the open patches in the desert. Also, it is evident in the figure that vegetation under *P. velutina* canopies differs from vegetation outside of canopies in both desert and terrace, and that canopy patches in these two zones differed from each other.

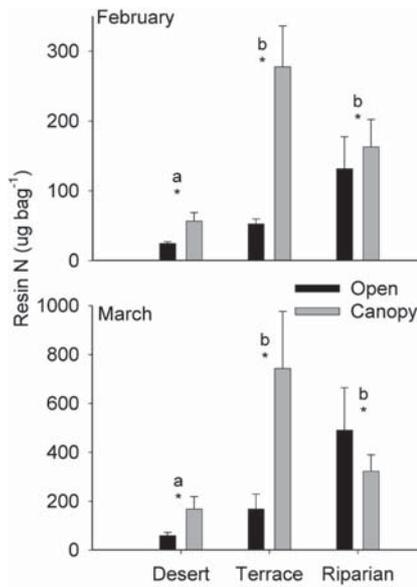


Fig. 2. Mean soil N availability for both landscape position and patch type in February and March. Stars indicate significant differences between patch types within a zone; letters indicate significant differences between zones after averaging across patch types.

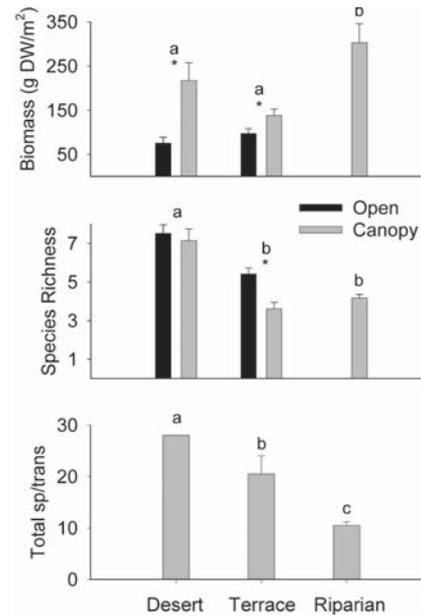


Fig. 3. Mean values for both landscape position and patch type for biomass, average number of species per quadrat, and number of species per transect. Stars indicate significant differences between patch types within a zone, letters indicate significant differences between zones after averaging across patch types.

Within zones, there is a strong effect of *P. velutina* canopies on vegetation in desert and terrace (Fig. 5a, b). Variation in DCA axis 1 scores in both desert and terrace is clearly associated with whether quadrats are located beneath or outside *P. velutina* canopies (Fig. 5a, b). In addition, traces for presence-absence and quantitative data were similar in both desert and terrace suggesting

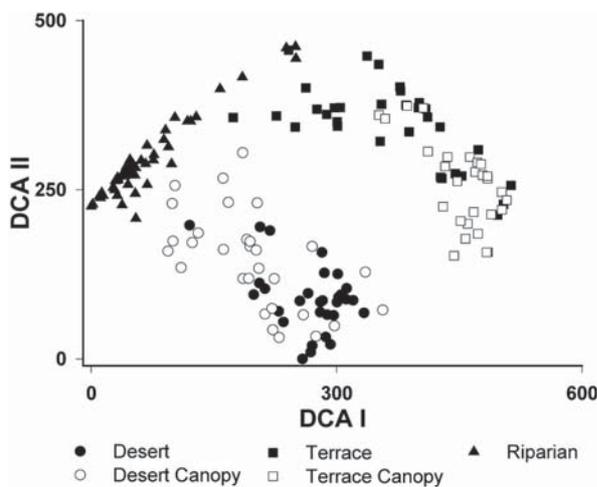


Fig. 4. Results of Detrended Correspondence Analysis (DCA) ordination for all quadrats from all transects combined. See text for description of plant species associated with the separation between zones.

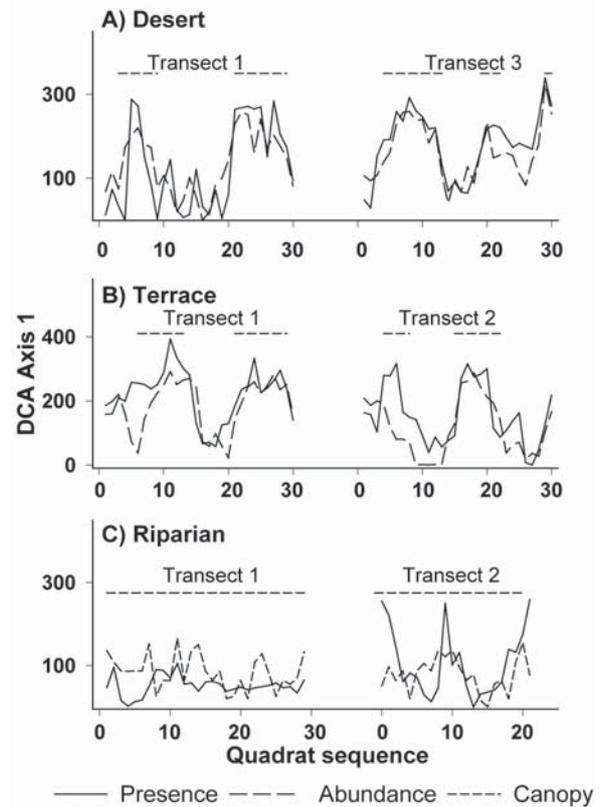


Fig. 5. Results of DCA analyses for individual transects. See text for description of plant species associated with differences between canopy and open patches for each zone.

Table 1. All taxa observed in our study, and the zone in which they were present.

Taxon	Desert	Terrace	Riparian
<i>Agrostis spec.</i>	X		
<i>Ambrosia deltoidea</i>	X		
<i>Amsinckia menziesii</i>	X	X	X
<i>Astragalus nuttallianus</i>	X	X	
<i>Avena fatua</i>			X
<i>Baccharis sarothroides</i>			X
<i>Bowlesia incana</i>	X		X
<i>Bromus arizonicus</i>	X		X
<i>Bromus rubens</i>	X	X	X
<i>Calandrinia ciliata</i>		X	
<i>Camissonia micrantha</i>	X		
<i>Castilleja exserta</i>	X		
<i>Crassula connata</i>	X	X	
<i>Cryptogamic lichen</i>	X	X	
<i>Cryptantha spec.</i>	X		
<i>Daucus pusillus</i>	X		
<i>Descurainia pinnata</i>	X		
<i>Draba cuneifolia</i>	X		
<i>Eriogonum inflatum</i>	X		
<i>Erodium cicutarium</i>	X	X	X
<i>Eucrypta chrysanthemifolia</i>	X		
<i>Filago arizonica</i>	X	X	
<i>Herniaria hirsuta</i>	X	X	
<i>Hordeum leporinum</i>	X	X	X
<i>Lasthenia californica</i>		X	
<i>Lepidium lasiocarpum</i>	X	X	
<i>Linanthus aureus</i>	X		
<i>Lotus humistratus</i>	X		
<i>Lupinus concinnus</i>	X		
<i>Lycium spec.</i>	X		
<i>Malva parviflora</i>		X	X
<i>Medicago polymorpha</i>			X
<i>Oenothera caespitosa</i>	X		
<i>Parietaria hespera</i>	X		
<i>Pectocarya recurvata</i>	X	X	
<i>Plantago patagonica</i>	X	X	
<i>Poa bigelovii</i>	X	X	
<i>Pterostegia drymarioides</i>	X		
<i>Schismus spec.</i>	X		
<i>Silene antirrhina</i>	X		
<i>Sisymbrium irio</i>		X	X
<i>Sonchus oleraceus</i>			X
<i>Sphaeralcea coccinea</i>		X	
<i>Uropappus lindleyi</i>	X		X
<i>Urtica spec.</i>			X
<i>Vulpia octoflora</i>	X	X	

that differences in vegetation along transects reflected not only changes in abundances but changes in composition, as well. In the desert, *Crassula erecta*, *Lepidium lasiocarpum*, *Erodium cicutarium*, *Pectocarya recurvata*, and desert crust were common outside the canopy, whereas *Ambrosia deltoidea*, *Amsinckia menziesii*, *Bromus rubens* and *Bowlesia incana* were found under *P. velutina* canopies. In the terrace, *Cryptantha spec.*, *E. cicutarium* and *Filago arizonica* were common outside the canopy, while *A. menziesii*, *Hordeum leporinum*, *Sisymbrium irio*, and *Sphaeralcea coccinea* were most abundant under *P. velutina* canopies. In the riparian zone, all quadrats were located under *P. velutina* canopy. Understorey vegetation in this zone was strongly dominated by *B. incana*, *H. leporinum*, and *A. menziesii*, with

scattered occurrences of *S. irio* and *B. rubens*. Traces for presence-absence and quantitative data were uncorrelated in the riparian zone suggesting that vegetation patterns within this zone are a function of shifts in abundance as well as the presence or absence of particular species (Fig. 5c).

Soil-plant interactions

Linear regression showed a significant and positive relationship between mean biomass and soil moisture ($r^2 = 0.628$; $p = 0.006$), while species richness was negatively related to soil N on a log-log scale ($r^2 = 0.480$; $p = 0.026$).

Discussion

We have shown that (1) *Prosopis velutina* canopies have significant effects on soil moisture and N availability in desert and terrace, (2) *P. velutina* canopies influence both production, species richness, and species composition of the herbaceous plant community, (3) there is a strong effect of landscape position on resource availability, the herbaceous plant community, and the influence of *P. velutina* and (4) the relative importance of soil moisture and N availability in explaining vegetation patterns appears to depend on the landscape context. Thus, interactions between canopy trees and herbaceous layer species may be positive, neutral or negative depending on landscape context.

We found relatively clear effects of both landscape position and patch type on productivity, composition and species diversity (Figs. 3-5). We also have shown evidence that these effects are caused by patterns in soil moisture and N availability at the scale of both landscape and patch type (Figs. 1 and 2). The positive relationship between biomass and soil moisture overall suggests that productivity of the herbaceous community is water limited. As one might expect, both soil moisture and biomass were highest in the lowest point in the landscape, the riparian zone, most likely due to proximity to the water table. More interestingly, the strong positive effect of desert canopy on both soil moisture and biomass contrasts with the lack of a consistent effect of terrace canopies on soil moisture and their weak effect on biomass. The difference in influence on soil moisture is particularly clear in February (Fig. 1a) when terrace canopies, in fact, had a negative effect on soil moisture. Since the bulk of herbaceous production occurred in February (Schade pers. obs.), these results suggest the possibility that positive effects of *P. velutina* canopy trees in the terrace may be reduced due to an increase in competition with understorey plants for water, while desert canopy trees are

facilitating herbaceous production by increasing water availability. Previous work suggests that increased moisture is most likely caused by increasing infiltration of water and/or water holding capacity of soils under desert canopy trees relative to open areas (Reynolds et al. 1999). Our results are consistent with a previous study by Belsky (1994), who also found weaker competition between canopy trees and understorey plants under drier conditions. She attributed this pattern to a deeper groundwater table leading to a deeper rooting zone for the canopy tree in drier areas, which resulted in a vertical spatial separation between roots of the canopy tree and the understorey. Since our terrace transects were located downslope of desert transects, it is likely that terrace *P. velutina* is growing in closer proximity to the water table, which would reduce the spatial separation between their roots and the rooting zone of the herbaceous plants, increasing the likelihood of competition between them.

Although changes in nitrogen availability did not correlate with herbaceous biomass, the negative relationship between species richness and soil N availability overall suggests that N availability has a strong influence on species diversity at both landscape and patch type scales. The lack of any relationship between soil moisture and species richness reinforces this conclusion. At the landscape scale, we suggest that lower N availability in the desert is the explanation for higher species richness per quadrat and per transect in this zone than either terrace or riparian zone (Fig. 3b, c). Interestingly, the terrace and riparian zone were not significantly different in average number of species per quadrat, but the terrace had more species per transect (Fig. 3c). This is likely because large variation in local habitat conditions led to large variation in species composition between canopy and open areas in the terrace (Fig. 5b, c), which were not evident in the riparian zone. In addition, the contrast between the significant negative effect of terrace canopies on species per quadrat and the lack of any effect of desert canopies (Fig. 3b) is probably due to large differences between these zones in the effects of canopies on soil N (Fig. 2). These results are all consistent with previous work, which showed lower species diversity of herbaceous plant communities at high nutrient supply (Tilman 1984, 1993; DiTommaso & Aarssen 1989; Gough et al. 2000).

Finally, our results suggest that shifts in species composition at both landscape and patch type scales may be due to variation in the response of individual species to both soil moisture and nitrogen availability. Both terrace and desert canopy patches had several abundant species in common with the riparian zone, but only one with each other (*A. menziesii*). We suggest that differences in species composition between desert and terrace canopy patches potentially result from interspecific variation in plant

responses to water vs. nitrogen availability. Common species in desert canopy and riparian patches (i.e. *B. incana*, *B. rubens* and *A. menziesii*) may respond more strongly to variation in soil moisture, while species in terrace canopy and riparian patches (i.e., *S. irio*, *H. leporinum* and *A. menziesii*) respond more to variation in soil N.

In conclusion, we found clear effects of landscape position and *P. velutina* canopies on herbaceous production, diversity and species composition, as well as on soil moisture and N availability. We observed a shift in the magnitude of the influence of *P. velutina* along the riparian to upland gradient. The main influence of *P. velutina* in the desert is through increased soil moisture under the canopy, while in the terrace, the main influence is through its effect on soil N availability. Previous work has shown that *P. velutina* production also changes with landscape position (Stromberg et al. 1993). On terraces, *P. velutina* grows in closer proximity to the water table than in the desert, which increases their potential growth rate, water use, and possibly N-fixation rate relative to those growing in the desert (Stromberg et al. 1993). The combination of higher rates of water use and N fixation may have caused lower moisture and higher N availability under canopies on the terrace relative to the desert; particularly in the shallow soils used by herbaceous understorey plants.

Overall, these results are consistent with McAuliffe's (1994) conclusion that species distributions change in complex ways along resource gradients in arid environments. We add here that these distributional patterns are at least partly the result of variation in the strength of species interactions, both between canopy and understorey plants, and between understorey species. We observed clear effects of landscape position on the influence of *P. velutina* on soil moisture and N availability. These shifts in the relative availability of water and nitrogen create a spatially variable physical template upon which herbaceous plant communities develop, leading to variation in productivity, species diversity and species composition between patches and zones. Our results clearly show that canopy-understorey interactions may be positive, negative or neutral, depending on both the landscape context and on characteristics of the interacting species. These complex and highly context-dependent outcomes highlight the challenges of predicting pattern and change in diversity and productivity as woody vegetation continues to increase in arid areas worldwide.

Acknowledgements. We thank Dana Swoveland, Jill Koehler, Luis Herrera and Kathy Goodhart for invaluable assistance in both field and lab. We thank Sarah Hobbie for help with soil protocols. We also thank the Genes-to-Ecosystems research group for early comments on the project. Finally, our thanks go out to Dr. Exequiel Ezcurra and two anonymous reviewers for excellent comments that greatly improved the paper. This work was funded by the NSF-IRCEB Biological Stoichiometry Genes-to-Ecosystems project directed by Jim Elser.

References

- Anderson, L.J., Brumbaugh, M.S. & Jackson, R.B. 2001. Water and tree-understorey interactions: a natural experiment in a savanna with oak wilt. *Ecology* 82: 33-49.
- Archer, S., Scifres, C., Bassham, C.R. & Maggio, R. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecol. Monogr.* 58: 111-127.
- Belsky, A.J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology* 75: 922-932.
- Bertness, M.D. & Callaway, R. 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9: 191-193.
- Callaway, R.M., Nadkari, N.M. & Mahall, B.E. 1991. Facilitation and interference of *Quercus douglassi* on understorey productivity in central California. *Ecology* 72: 1484-1499.
- Callaway, R.M. et al. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844-848.
- Collins, S.L. & Good, R.E. 1987. Canopy-ground layer relationships of oak-pine forests in the New Jersey pine-barrens. *Am. Midl. Natur.* 117: 280-288.
- DiTommaso, A. & Aarssen, L.W. 1989. Resource manipulations in natural vegetation: a review. *Vegetatio* 84: 9-29.
- Frost, W.E. & McDougald, N.K. 1989. Tree canopy effects on herbaceous production of annual rangeland during drought. *J. Range Manage.* 42: 281-283.
- Gough, L., Osenberg, C.W., Gross, K.L. & Collins, S.L. 2000. Fertilization effects on species density and primary production in herbaceous plant communities. *Oikos* 89: 428-439.
- Hibbard, K.A., Archer, S., Schimel, D.S. & Valentine, D.W. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* 82: 1999-2011.
- Hoch, G.A., Briggs, J.M. & Johnson, L.C. 2002. Assessing the rate, mechanism and consequences of conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems* 5: 578-586.
- Lajtha, K. 1988. The use of ion-exchange resin bags for measuring nutrient availability in an arid ecosystem. *Plant Soil* 105: 105-111.
- McAuliffe, J.R. 1994. Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert Bajadas. *Ecol. Monogr.* 64: 111-148.
- Muller, C.H. 1953. The association of desert annuals with shrubs. *Am. J. Bot.* 40: 53-60.
- Patten, D.T. 1978. Productivity and production efficiency of an upper Sonoran Desert ephemeral community. *Am. J. Bot.* 65: 891-895.
- Petranka, J.W. & McPherson, J.K. 1979. The role of *Rhus copallina* in the dynamics of the forest-prairie ecotone in north-central Oklahoma. *Ecology* 60: 956-965.
- Reynolds, J.F., Virginia, R.A., Kemp, P.R., de Soyza, A.G. & Tremmel, D.C. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecol. Monogr.* 69: 69-106.
- Schlesinger, W.H. & Pilmanis, A.M. 1998. Plant-soil interactions in deserts. *Biogeochemistry* 42: 169-187.
- Sharifi, M.R., Nilsen, E.T. & Rundel, P.W. 1982. Biomass and net primary production of *Prosopis glandulosa* (Fabaceae) in the Sonoran Desert of California. *Am. J. Bot.* 69: 760-767.
- Shmida, A. & Whittaker, R.H. 1981. Pattern and biological microsite effects in two shrub communities, southern California. *Ecology* 62: 234-251.
- Stromberg, J.C., Tress, J.A. & Wilkins, S.D. 1992. Response of velvet mesquite to groundwater decline. *J. Arid Environ.* 23: 45-58.
- Stromberg, J.C., Wilkins, S.D. & Tress, J.A. 1993. Vegetation-hydrology models – implications for management of *Prosopis velutina* (velvet mesquite) riparian ecosystems. *Ecol. Appl.* 3: 307-314.
- Tewksbury, J.J. & Lloyd, J.D. 2001. Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia* 127: 425-434.
- Tiedemann, A.R. & Klemmedson, J.O. 1977. Effect of mesquite trees on vegetation and soils in the desert grasslands. *J. Range Manage.* 30: 361-367.
- Tilman, D. 1984. Plant dominance along an experimental nutrient gradient. *Ecology* 65: 1445-1453.
- Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* 74: 2179-2191.
- Weltzin, J.F. & Coughenour, M.B. 1990. Savanna tree influence on understorey vegetation and soil nutrients in north-western Kenya. *J. Veg. Sci.* 1: 325-334.
- Whittaker, R.H., Gilbert, L.E. & Connell, J.H. 1979. Analysis of two-phase pattern in a mesquite grassland, Texas. *J. Ecol.* 67: 935-952.
- Yavitt, J.B. & Smith, E.L. 1983. Spatial pattern of mesquite and associated herbaceous species in an Arizona desert grassland. *Am. Midl. Nat.* 109: 89-93.

Received 7 May 2002;

Revision received 4 December 2002;

Final version received 26 March 2003;

Accepted 26 March 2003.

Co-ordinating Editor: E. Ezcurra.