Plant response to variations in nitrogen availability in a desert shrubland community

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Abstract. Spatial variations in nitrogen availability were studied in a desert community codominated by *Larrea tridentata* (DC.) Cov. and *Prosopis glandulosa* Torr. Measurements of natural $\delta^{15}N$ values in tissues suggested that *Prosopis* obtains approximately half of its nitrogen through direct symbiotic fixation. Soils were collected under 1) *Prosopis* shrubs, 2) *Larrea* shrubs ≤ 2 m from *Prosopis* (LP), and 3) *Larrea* ≤ 2 m from other *Larrea* but > 5 m from the nearest *Prosopis* (LL). *Prosopis* soils showed significantly higher rates of nitrogen mineralization than LL soils in both A and B horizons. Rates of mineralization in LP soils were significantly higher than rates in LL soils only in the B horizon and were not significantly different from rates in *Prosopis* soils. Leaf nitrogen concentrations were significantly higher in LP shrubs (2.06%) than in LL shrubs (1.78%), although $\delta^{15}N$ values did not differ between the two shrub types. Nitrogen concentrations in *Perezia nana* Gray, a perennial herb, were greater in plants under *Prosopis* shrubs (2.09%) than under LP shrubs (1.93%) or LL shrubs (1.67%). Despite apparent differences in nitrogen availability, biomass of *Larrea* and density of *Perezia* did not differ significantly among these sites.

Introduction

Shrub-induced spatial patterns of nutrients have been observed in many desert soils (Klemmedson and Barth, 1975; Tiedemann and Klemmedson, 1973; Charley and West, 1975). Causes of these nutrient mosaics include localized patterns of litter accumulation around widely spaced shrubs, and a lack of nutrient redistribution by leaching (Virginia and Jarrell, 1983). The enrichment of nitrogen in soils beneath shrub canopies may be among the most significant consequences of these heterogeneous distributions, as nitrogen has been shown to limit net primary productivity in many desert ecosystems (Ettershank et al., 1978; Romney et al., 1978).

Localized concentrations of soil nutrients have been found in communities dominated by both nitrogen-fixing and non nitrogen-fixing shrubs. In three widely separated locations in Utah, Charley and West (1977) found that rates of nitrogen mineralization in laboratory incubations were from 1.17 to 2.20 times higher in the surface soils beneath *Atriplex* canopies than in the open spaces between shrubs. Using a pot culture technique, Tiedemann and

Klemmedson (1973) found that the availability of nitrogen to understory plants was up to 15 times higher in soils underneath *Prosopis* shrubs than in the intershrub spaces. However, there have been few attempts to compare nitrogen availabilities in soils beneath various shrub species in mixed communities and to assess the significance of these nutrient mosaics to understory vegetation.

In this study, we tested the hypothesis that nitrogen availability would be greater beneath canopies of *Prosopis glandulosa*, a potential nitrogen fixer, than beneath canopies of *Larrea tridentata*, a shrub that does not fix nitrogen, and that both shrubs and understory herbs would respond to the increased nitrogen availability near *Prosopis*. We also examined $^{15}N/^{14}N$ ratios in plant tissues to determine the extent of symbiotic nitrogen fixation by *Prosopis* in this ecosystem (similar to Shearer et al., 1983).

Methods

Study site

This research was carried out in the Chihuahuan Desert at the New Mexico State University Experimental Ranch about 40 km NNE of Las Cruces, New Mexico. The study site was located on an east-facing alluvial piedmont of the Dona Ana Mountains, with a slope of 3%. Numerous shallow washes dissect this slope, which is a Jornada II geomorphic surface of late Pleistocene age (Gile et al., 1981). The soil, a Typic Haplargid, is a sandy loam with a well-developed caliche layer below the argillic B horizon. *Prosopis glandulosa* Torr. (honey mesquite) and *Larrea tridentata* (DC.) Cov. (creosotebush) are codominants of this community, comprising about 90% of the perennial plant cover. Numerous annual herbs occur seasonally both between and underneath the shrubs. The most common perennial herb, *Perezia nana* Gray (dwarf desert holly), is found primarily beneath shrub canopies.

Field sampling

Two categories of *Larrea* shrubs were defined and used in this study: 1) an LL shrub was defined as a *Larrea* whose center was ≤ 2 m from the center of another *Larrea*, but ≥ 5 m from the center of a *Prosopis*; 2) an LP shrub was defined as a *Larrea* that was ≤ 2 m from a *Prosopis*. The *Prosopis* nearest each LP shrub (a PL shrub) was also sampled.

Shrubs were sampled according to a stratified random design in a 1-ha area in this community. Ten parallel sampling lines, each 100 m long, were placed at 10-m intervals. On 9 of these lines, all *Larrea* shrubs intersected by the sampling line were sampled if they fit either the LL or LP category. The tenth line was used to bring the number of shrubs in each category up to 27.

Instead of direct growth measurements, we chose to use shrub biomass as a measure of the potential effect of any differences in nitrogen availability

to *Larrea* shrubs, as any *net* differences in growth rates between shrubs should be reflected in cumulative shrub biomass. Also, if increases in nutrient availability are most critical during the early growth of shrubs, then potential differences between shrub sites will not be detected in measurements of adult twig elongation.

For each shrub, maximum canopy height and average canopy diameter (mean of two perpendicular measurements) were measured and were converted to volume estimates using the assumption that *Larrea* canopies generally fit the shape of an inverted cone (Ludwig et al., 1975). Thus, $V = \pi/3 * r^2 * h$. These size measurements (cm^3) were then converted to biomass (g) using a regression equation based on the harvest of 60 shrubs in a nearby plot (Fonteyn et al., in prep.):

$$\text{Biomass} = 58.12 + 0.00179 * \text{volume} \qquad (r^2 = 0.91)$$

In addition, distance to nearest neighbor (shrub center to shrub center) and total number of *Perezia* growing underneath the canopy of each shrub were measured. Density of *Perezia* was expressed as individuals/m^2 of shrub canopy area. At each sampling location, both shrub leaves and whole *Perezia* plants were collected for tissue analysis.

Since it was thought that differential water availability to LL versus LP shrubs might affect growth or potential responses to nitrogen availability, pre-dawn xylem water potentials were measured on all shrub types on August 3, 1984 using the Scholander pressure bomb method (Waring and Cleary, 1967).

Soil sampling

Samples of A horizon (0–10 cm) and upper B horizon (10–30 cm) soils were collected under 10 shrubs within each category on July 3, 1983. All soils were collected from the east side of each shrub near the canopy center, as significant east-west differences in soil nutrients have been found around the base of shrubs in this area, presumably due to wind-blown litter accumulation patterns (Parker et al., 1982). All soils were collected dry ($< 4\%$ water by weight) and were stored in paper bags for 6 weeks prior to laboratory incubation experiments.

Analytical techniques

Plant samples were dried at 65 C and ground in a Wiley Mill to pass a 20-mesh screen. Samples were digested using a sulfuric acid-hydrogen peroxide flux (Lowther, 1980) and analyzed for total nitrogen using standard Technicon AutoAnalyzer methods (Technicon, 1977a).

Laboratory mineralization rates were used as a relative index of nitrogen availability in these soil types (Powers, 1980). Although it would be preferable to use an *in situ* mineralization index, techniques currently being employed in the field, such as closed buried bags, may not be suitable for

desert soils in which water potentials fluctuate sharply between infrequent rainstorm events and long intervening dry periods. Soils were passed through a 2-mm screen, and samples were incubated at a soil water potential of -0.05 MPa for 30 days to determine mineralization potentials following the procedures of Montes and Christensen (1979). Initial and incubated samples were extracted with $2N$ KCl at a 1:4 (dry soil mass:extraction solution) extraction ratio. Filtrates were analyzed for NH_4 and NO_3 colorimetrically using a Technicon AutoAnalyzer (Technicon, 1977b; 1978). Net mineralization was defined as the difference between the initial mineral N content ($NH_4 + NO_3$) and the post-incubation value.

   $^{15}N/^{14}N$ values for *Larrea* and *Prosopis* tissue, expressed as $\delta^{15}N$ (parts per thousand ^{15}N excess relative to atmospheric nitrogen standards), were analyzed by Dr. Georgia Shearer at Washington University using a VG Micromass 602E mass spectrometer (Shearer et al., 1983).

   Statistical analyses used the one-way *ANOVA* procedure of *SAS* corrected for nested *ANOVA* designs. When the *ANOVA* indicated statistical significance, Duncan's multiple range test was used to sort out differences among the sites.

Results

Larrea shrubs with *Prosopis* shrubs as nearest neighbors had a significantly greater leaf nitrogen concentration than did *Larrea* shrubs that had other *Larrea* shrubs as nearest neighbors (Table 1). Differences in the distance to nearest neighbor did not affect this result, as the mean distances for LL and LP pairs were nearly identical (106.1 cm vs. 105.6 cm). Although the mean LP shrub biomass was 26% less than the mean LL biomass, these differences were not significant ($p > 0.2$) due to a great range of shrub sizes. The nitrogen concentrations in *Perezia* tissues were significantly different among the three shrub types, with the highest leaf nitrogen concentrations found in plants underneath *Prosopis* canopies (Table 1). However, *Perezia* density did not differ among shrub categories.

   Prosopis tissue had significantly lower $\delta^{15}N$ values than did *Larrea* shrubs, suggesting that *Prosopis* obtained a significant percentage of its nitrogen through direct symbiotic fixation (Shearer and Kohl, 1978). Although LP shrubs had a slightly lower mean $\delta^{15}N$ value than LL shrubs, this difference was not statistically significant (Table 1).

   Prosopis soils had the highest initial mineral nitrogen levels in both the A and B horizons, but the initial NH_4 and NO_3 levels did not differ between the two *Larrea* soil categories (Table 2). Nitrification and mineralization rates appeared higher in LP soils than in LL soils, but this difference was statistically significant only in B horizon incubations. *Prosopis* soils, however, had significantly higher rates of mineral nitrogen production than did LL soils in both horizons.

Table 1. Some attributes of *Prosopis glandulosa*, *Larrea tridentata*, and *Perezia nana* in three microsite conditions in the Chihuahuan Desert. All values are mean ± 1 S.E.; underlined values are not significantly different by Duncan's multiple range test after one-way nested ANOVA analysis (p < 0.05)

	Shrub Category		
	LL	LP	PL
Leaf N Concentration (%)			
Prosopis			3.07 ± 0.31
Larrea	1.78 ± 0.28	2.06 ± 0.25	
Perezia	1.67 ± 0.19	1.93 ± 0.28	2.03 ± 0.22
$\delta^{15}N$ of tissues	5.34 ± 0.92	5.05 ± 0.73	2.17 ± 1.08
Shrub water potentials (MPa)	− 4.2 ± 0.5	− 4.1 ± 0.2	− 1.7 ± 0.8
Density of *Perezia* (individuals m^{-2} of shrub canopy)	13 ± 14	8 ± 12	13 ± 22
Biomass of *Larrea* (g)	2100 ± 1722	1557 ± 1225	
Distance to nearest neighbor (cm)	106.1 ± 31.2	105.6 ± 22.8	

Nitrogen concentrations in *Larrea* and *Perezia* leaf tissues were weakly correlated with the rates of mineral nitrogen production measured in soils. Mineralization in A horizon incubations showed the best correlations, yet rates explained only 22% of the variance in *Larrea* leaf nitrogen concentrations, and only 28% of the variance in *Perezia* nitrogen concentrations (p = 0.037 and 0.034, respectively). However, within each shrub category, mineralization

Table 2. Mineralization of nitrogen in soils found beneath shrubs in the Chihuahuan Desert. All data are $ugN\,g^{-1}$ ± 1 S.E. Underlined values are not significantly different by Duncan's multiple range test after one-way nested ANOVA analysis (P < 0.05)

	Shrub Category		
A HORIZON SOILS	LL	LP	PL
Initial Concentrations			
NH_4^+	0.78 ± 0.13	0.98 ± 0.20	1.24 ± 0.34
NO_3^-	2.03 ± 0.28	2.65 ± 1.14	3.79 ± 1.70
Total Mineral N	2.83 ± 0.41	3.64 ± 1.34	5.02 ± 2.04
Change during incubation			
Net nitrification	24.0 ± 6.6	37.6 ± 23.2	37.5 ± 12.6
Net mineralization	23.7 ± 6.4	37.3 ± 23.4	36.7 ± 12.1
B HORIZON SOILS			
Initial Concentrations			
NH_4^+	0.68 ± 0.10	0.76 ± 0.08	0.91 ± 0.15
NO_3^-	1.08 ± 0.11	1.14 ± 0.11	2.05 ± 1.61
Total Mineral N	1.77 ± 0.21	1.90 ± 0.19	2.96 ± 1.75
Change during incubation			
Net nitrification	6.3 ± 2.3	8.8 ± 2.0	10.2 ± 2.6
Net mineralization	6.5 ± 2.5	9.3 ± 2.3	10.6 ± 3.0

rates were not significantly correlated with leaf concentrations for either species. Similarly, the nitrogen concentration in *Perezia* was significantly correlated with the nitrogen concentration in the *Larrea* shrub under which the *Perezia* had been collected, although there was a great deal of scatter ($r^2 = 0.25$, p = 0.005). Even when *Prosopis* tissue and its associated *Perezia* plants were included in the analysis, the r^2 value did not improve ($r^2 = 0.24$, p = 0.0008). Within site types, however, only LP sites showed a significant correlation between % N in *Perezia* tissue and % N in *Larrea* tissue. ($r^2 = 0.30$, p = 0.03).

The xylem water potentials measured for *Prosopis* shrubs ($\bar{x} = -1.7$ MPa) were significantly less negative than those for *Larrea* shrubs. Measured potentials for *Larrea* clustered quite closely around the mean value of -4.2 MPa, with no significant difference between the two *Larrea* shrub categories (Table 1).

Discussion

The relatively low δ^{15}N value of *Prosopis* found at our site, coupled with the high mean nitrogen concentration in *Prosopis* leaves (3.07%) relative to the nitrogen concentration in *Larrea* leaves, strongly suggests that fixation contributes to the nitrogen content of *Prosopis*. Using the assumptions of Shearer et al. (1983) that a) their experimentally measured value of -1.3 δ^{15}N represents the ^{15}N abundance of purely fixed nitrogen in *Prosopis* leaves, and b) the δ^{15}N abundance of control, non-fixing plants (LL shrub values for this study) represents the ^{15}N abundance of nitrogen contributed from other sources, then it can be calculated that in this ecosystem *Prosopis* is obtaining approximately 48% of its nitrogen through direct symbiotic fixation. This figure lies well within the range of percentages (43–61%) found by Shearer et al. (1983) in their landscape transect near Harpers Well in the Sonoran Desert. Although LP shrubs had a significantly higher %N in their tissue than LL shrubs and were presumably taking advantage of the high soil nitrogen derived from *Prosopis* litter, this pattern was not reflected in the δ^{15}N tissue values. These results are consistent with the findings by Shearer et al. (1983) that soil ^{15}N values did not differ between *Prosopis* canopy and inter-shrub sites, and with Binkley et al. (1985) who found that alder-fixed nitrogen could not be traced in soil nitrogen pools. Isotope fractionation is known to occur during such soil processes as mineralization, nitrification, immobilization, nitrate leaching, denitrification, and plant uptake (Blackmer and Bremner, 1977; Delwiche and Steyn, 1970), and thus the unique δ^{15}N values of *Prosopis*-fixed nitrogen could be lost upon entering the general soil pool.

Based on patterns that have been found in forested mesic systems, one would predict that the nitrogen-rich leaves of *Prosopis* would produce litter that is more readily utilized by decomposers than *Larrea* leaves that have

high concentrations of waxy resins (Swift et al., 1979). Thus the low C:N ratio of *Prosopis* litter should result in higher rates of nitrogen mineralization than decomposing *Larrea* litter (Melillo et al., 1982). These predictions are supported by the high rates of nitrogen mineralization found in soils underneath *Prosopis* shrubs, and further suggest that litterfall remains relatively localized in this system. Yet it should be noted that in a 1-year litterbag study, Schaefer et al. (1985) reported that *Prosopis* litter exhibited the lowest rate of decomposition of six desert species, including *Larrea,* and that there were no correlations between rates of mass loss and percent lignin, C:N ratio, or lignin:N ratio in any of the species. However, these results are not necessarily inconsistent with mineralization results reported here. Initial rates of litter decomposition are complicated by such factors as soil water content and the activities of detritivorous animals. Similarly, nitrogen mineralization rates in soils are not determined exclusively by the decomposition rates of the litter that forms the soil organic matter, but also can be affected by rates of nitrogen release by the turnover and decomposition of roots of the dominant plant species. It would be interesting to know if the patterns found by Schaefer et al. (1985) would hold over a more long-term decomposition study. There are few studies that have followed litter decomposition long enough to cover the continuum between fresh plant debris and soil humus formation (Melillo, 1985).

The dependence of certain understory plants on the canopies of shrubs in deserts has been observed by several authors (Went, 1942; Muller and Muller, 1956). This phenomenon has been linked to various chemical, physical, and microclimatic properties of soils beneath shrubs, such as increases in nutrient availability and reduced evapotranspiration (Barth and Klemmedson, 1978). In this study we have shown that while nitrogen concentrations in *Perezia nana* are greatest under *Prosopis* and higher under LP shrubs than under LL shrubs, these differences in nitrogen availability did not affect the density of *Perezia*. Similarly, the nitrogen concentration in *Larrea* leaves was significantly greater when shrubs occurred near *Prosopis*, although no size differences were observed.

These results are surprising in the light of the fertilization studies of Ettershank et al. (1978) and current research by Dr. W.G. Whitford, which show strong plant response to experimental nitrogen additions on a piedmont surface close to the one used in this study. Since xylem water potentials of LL and LP shrubs were virtually identical and significantly more negative than values for the phreatophytic *Prosopis* shrubs, it is unlikely that differential water competition with *Prosopis* played a role in the results of this study. It is possible that with long-term fixed nitrogen inputs by *Prosopis*, the nitrogen capital of this system has been built up sufficiently such that nitrogen is no longer the limiting element to plant productivity. While only a direct fertilization experiment could either prove or disprove this possibility, the nitrogen concentrations found in *Larrea* leaves here are

similar to those found in *Larrea* shrubs that have responded to nitrogen additions by increases in both growth and tissue nitrogen levels. This suggests that shrubs are not experiencing excess nitrogen availability, and offers the possibility that other factors, such as phosphorus availability, might limit the relative growth of shrubs in this system.

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