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Depth Distribution and Seasonal Populations of Mesquite-Nodulating Rhizobia in Warm Desert Ecosystems

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ABSTRACT

Deeply rooted woody legumes are common in desert ecosystems yet little is known about the distribution of their rhizobial symbionts in relation to their roots and soil properties of the systems. The distribution of mesquite (*Prosopis glandulosa* Torr.)–nodulating rhizobia was investigated to depths of 13 m in warm desert ecosystems. Soils were collected under mesquite from sand dune and playa ecosystems in the California Sonoran Desert, and from sand dune, playa, arroyo, and grassland ecosystems in the Chihuahuan Desert of southern New Mexico. A *Larrea tridentata* (DC.) Coville (creosote bush) ecosystem in New Mexico, containing no mesquite, was sampled as a reference. Three intact soil cores from each ecosystem were removed during the winter, spring, and fall from the New Mexico sites, and the winter from the California sites. Significant rhizobial population densities were measured in soil from 1- to 4-m depths at the sand dune, arroyo, and playa ecosystems. At the playa ecosystem in New Mexico population densities $>10^5$ cells kg^{-1} were measured in soils from 8-m depth, and root nodules containing rhizobia were recovered in soil samples from 3-, 4-, and 7-m depths. Multiple-regression analysis of rhizobial concentration against soil NH_4-N, PO_4-P, electrical conductivity, and gravimetric water content indicated that no single soil factor was related significantly to rhizobial concentration across the ecosystems. Rhizobial densities varied with season in the dune and arroyo ecosystems. In these desert ecosystems significant rhizobial populations, root nodules, and presumably symbiotic N_2 fixation occur at soil depths rarely studied.

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IN ARID AND SEMIARID ecosystems, low soil N availability often limits primary plant production (West and Klemmedson, 1978). Woody legumes, which are

frequently important components of desert ecosystems, might be potential sources of symbiotically fixed N for these ecosystems. Because few root nodules have been observed in surface soil near woody legumes, the importance of symbiotic N_2 fixation in desert ecosystems has been questioned (Farnsworth et al., 1978). Recent studies, however, indicate that woody legumes such as mesquite fix significant quantities of N_2 in deserts (Shearer et al., 1983). Nitrogen fixation was probably associated with deep roots since nodulation was inferred from a large subsurface population of rhizobia in a moist, phreatic soil zone above a water table (Virginia et al., 1986). In other warm desert ecosystems, however, such as arroyos, playas, and dunes, mesquite does not have access to a continuously recharged source of groundwater as the mesquite woodland in California that Virginia et al. (1986) studied.

Although symbiotic N_2 fixation is evidently a significant factor in the N cycle of desert ecosystems dominated by woody legumes (Hoegberg, 1986; Shearer et al., 1983) the depth distribution and seasonal fluctuations of rhizobia in deserts that differ in the distribution of soil water and host plant roots are not known. The woody legume mesquite, which is nodulated by both fast- and slow-growing cowpea rhizobia (Jenkins et al., 1987, 1989), occurs in four different systems in the Chihuahuan Desert of New Mexico. Since these systems vary in the depth of potential rooting, time of mesquite occupancy, soil properties, and water distribution, they offer an ideal series of systems in which to examine factors that regulate the distribution and potential significance of rhizobia in desert soils.

We have hypothesized that large rhizobial population densities can occur at considerable depths in woody legume systems where deep moisture also occurs. However, associated with deep soil environments are low concentrations of soil nutrients (Virginia and Jarrell, 1983; Virginia, 1986) that might affect nodulation and also limit survival of free-living rhizobia. The objectives of this study were to (i) determine if results from a previous study of a mesquite woodland utilizing groundwater in the California Sonoran Desert (Virginia et al., 1986) were generalizable to mesquite systems in other deserts where root depth varied with ecosystem type and (ii) examine possible relationships of soil properties and host-plant phenology to rhizobial concentrations.

MATERIALS AND METHODS

Site Description

Four mesquite ecosystems were studied: playa, coppice dune, arroyo, and grassland. An ecosystem dominated by the nonlegume, *Larrea tridentata*, and lacking mesquite was included as a reference. The arroyo, grassland, *Larrea*, and a playa site were located on the NSF Jornada Long Term Ecological Research (LTER) site situated 40-km north of Las Cruces, NM, in the northern Chihuahuan Desert. A coppice dune site was located on the adjacent USDA Jornada Experimental Range about 15 km from the above sites. A second dune and playa site were located in the Sonoran Desert of California at Borrego Sink near Borrego Springs.

Precipitation at the New Mexico sites averages 230 mm yr^{-1} with half occurring during the summer months from intense, convective thunderstorms. The frost-free period is about 200 d, and mean annual temperature is about 14 °C. At the California sites precipitation averages 65 mm yr^{-1}. From May through July there is generally <1 mm of precipitation, and mean annual temperature is about 22 °C.

Both of the playa systems are fringed with dense stands of mesquite and flood at irregular intervals. Standing water reaches the edge of these mesquite stands and recharges the soil profile. Large mesquite trees at low densities are found in the arroyo that dissects an extensive bajada. Both dune systems are dominated by mesquite that grows as low, multistemmed shrubs on dunes and entraps windblown sand to form "coppice" dunes 1- to 3-m tall. The grassland is dominated by a mix of shrubs (*Larrea, Yucca, Ephedra, Prosopis*) and grasses (*Bouteloua, Aristida, Erioneuron*). *Prosopis* plants are scattered throughout the grassland, but are considerably smaller than plants in the playa and arroyo systems. Precipitation is the main source of water to these plants. Portions of the bajada slope at the LTER site are dominated by nearly pure stands of *L. tridentata. Larrea,* unlike mesquite, is shallow-rooted, evergreen, and not capable of symbiotic N_2 fixation.

The general classification of the soils at the study sites on the Jornada have been reported by Gile (1979) and Wierenga et al. (1987). The New Mexico playa, grassland, and *Larrea* soils are Haplargids; the dune is a Torripsamment; and the arroyo is a Torrifluvent. The California playa consists of lacustrine deposits, and the California dune is a Torripsamment. Virginia and Jarrell (1983) described the general characteristics of the soils similar to those at the Borrego Sink study sites.

Sampling Methods

Undisturbed soil cores from the rooting zone of three trees in each ecosystem were removed using a split steel, continuous sampling tube, 1.56-m long with 6.5-cm i.d. This coring device, mounted on a truck, was modified from Kelley et al. (1947). Similar systems have been used to sample shallow aquifers, and to isolate and quantify the abundance of soil organisms from subsurface environments (Wilson et al., 1983). The split-tube bit fits into an outer, rotating auger bit that served as a continuous casing to prevent cave-in. As the outer bit cut through the soil, the inner, nonrotating bit was pressed into the soil. Cores were collected at the edge of the mesquite canopy. The core retainer and the two halves of the split sampling tube were cleaned of all residual soil. Their interior surface was flame sterilized with 95% ethanol before being put together for sampling. Soil samples were removed from the surface 1 m of soil in 0.5-m increments, and thereafter in 1-m increments. Flame sterilized trowels and spatulas were used to place each depth increment into a clean plastic bag. These were put into ice-cooled chests, and transported to the Univ. of California, Riverside, where they were subdivided for analyses.

Drilling depth for each core was determined by either the absence of roots in two consecutive 1.56-m sampling tube lengths, or the presence of coarse, dry loose soil that could not be retained in the tube. The number of cores (three per ecosystem per sampling) collected was limited by the expense of obtaining the specialized drilling equipment used in this study. Sampling dates at New Mexico were in January 1986, the midpoint of the dormant season; late May 1986, during peak growth; and early October 1986 following the summer rains. Soil samples were collected in California in January 1987 when the trees were dormant.

Soil Analysis

Each bag of soil representing a depth increment was mixed thoroughly before subsampling. Using trowels and spatulas flame sterilized with 95% ethanol, each soil sample was sub-

Table 1. Properties of soils at our study sites.†

Depth	NH_4-N‡	NO_3-N‡	PO_4-P§	Roots¶	pH#	EC
m	mg/kg					dS/m
	New Mexico playa					
0-0.5	2.00	2.86	14.54	1185.3	7.8	0.42
0.5-1	2.09	2.53	5.29	262.0	7.7	0.33
1-2	1.62	1.69	6.11	96.0	7.8	0.31
2-3	1.54	1.07	11.13	113.0	7.7	0.26
3-4	1.47	0.36	5.47	16.8	7.8	0.26
4-5	1.79	0.29	2.54	6.8	7.7	0.28
5-6	1.26	0.30	0.66	10.8	7.8	0.24
6-7	0.94	0.30	0.35	76.5	8.1	0.21
7-8	0.84	0.26	0.50	33.0	8.0	0.21
8-9	0.89	0.23	0.86	70.2	7.8	0.27
9-10	0.89	0.26	0.31	14.1	7.7	0.22
10-11	0.71	0.33	0.17	163.7	8.0	0.23
11-12	0.49	0.23	0.14	11.2	8.3	0.15
12-13	0.41	0.32	0.16	0	8.2	0.08
	New Mexico arroyo					
0-0.5	2.38	1.43	5.31	152.6	7.9	ND
0.5-1	2.68	0.51	2.45	21.5	8.1	0.34
1-2	2.07	0.67	1.77	81.5	8.0	0.33
2-3	1.49	0.65	1.07	31.0	8.1	0.34
3-4	1.51	0.48	0.79	80.0	8.5	0.41
4-5	1.41	0.58	2.13	24.3	8.7	0.65
5-6	1.22	0.48	0.99	10.9	9.1	0.60
6-7	1.11	0.38	0.57	32.4	9.0	0.68
7-8	1.27	0.41	1.24	ND††	8.9	ND
8-9	1.21	0.36	0.73	ND	8.9	ND
	New Mexico dune					
0-0.5	2.32	3.07	3.43	736.4	7.7	0.58
0.5-1	2.05	3.09	1.91	207.8	8.0	0.62
1-2	1.05	3.47	0.77	286.9	7.9	2.31
2-3	0.87	0.54	0.13	146.6	8.0	3.69
3-4	1.75	1.55	0.08	118.1	7.8	5.85
4-5	0.67	0.08	0.07	435.3	7.9	4.92
5-6	0.73	0.08	0.13	ND	8.3	1.20
	New Mexico grassland					
0-0.5	3.06	1.00	2.64	1457.3	7.4‡‡	ND
0.5-1	2.04	0.62	2.01	247.5	7.3‡‡	ND
1-2	1.48	53.76	2.00	180.5	7.2‡‡	ND
2-3	1.34	82.86	0.68	21.9	7.3‡‡	ND
	New Mexico *Larrea*					
0-0.5	1.89	1.29	4.73	1021.9	8.0	0.50
0.5-1	1.92	13.90	2.06	421.2	8.1	0.88
1-2	1.26	43.24	2.38	124.6	7.8	1.54
2-3	1.14	20.19	1.35	54.3	8.0	4.80
	California playa					
0-0.5	3.32	19.38	1.93	1078.5	7.9	3.70
0.5-1	1.96	2.03	0.13	234.4	8.1	2.61
1-2	1.32	1.75	0.10	145.2	8.7	2.40
2-3	0.89	3.77	0.20	51.3	9.1	2.14
3-4	1.58	1.38	0.17	189.6	9.1	1.19
4-5	2.19	0.34	0.17	8.8	8.9	0.63
5-6	2.40	0.72	0.27	62.9	8.2	0.52
6-7	1.84	0.49	0.27	80.0	8.7	0.29
7-8	1.61	0.31	0.23	12.1	8.6	0.19
8-9	3.08	1.00	0.87	42.9	8.3	0.36
9-10	3.67	1.27	0.63	18.7	8.4	0.37
10-11	3.32	1.30	0.43	32.0	8.4	0.35
11-12	3.10	1.06	0.40	30.4	8.7	0.30
	California dune					
0-0.5	2.13	11.62	2.23	2301.3	8.6	0.14
0.5-1	1.70	29.55	1.07	590.3	8.7	0.22
1-2	1.60	11.80	0.30	106.7	9.1	0.32
2-3	1.57	3.53	0.47	20.8	8.8	0.62
3-4	1.66	2.05	0.53	6.6	8.5	0.86
4-5	1.49	0.77	0.50	47.7	8.4	0.90
5-6	1.64	0.59	0.43	20.4	8.7	0.91

† Data on chemical properties except in grassland were from analysis of winter soil samples (means of thee soil cores per depth per site). Chemical properties in grassland system, and all root mass data, were from spring soil samples.
‡ 2 *M* KCl extract.
§ 0.5 *M* $NaHCO_3$ extract (pH 8.5).
¶ mg fresh wt. kg^{-1}.
# Saturated paste.
†† No data.
‡‡ 1:1 (w/v), 0.01 *M* $CaCl_2$.

divided for various analyses. Gravimetric water content of the soil samples was determined at the time of subsampling. Soils for chemical analysis were then air-dried in a glasshouse, ground to break-up clay and caliche aggregates, and passes through a 2-mm sieve. Soil saturation extracts (U.S. Salinity Laboratory Staff, 1954) were prepared, and electrical conductivity (EC) was measured using a temperature compensating conductivity meter. Soil pH was measured either using a glass electrode on soil prepared as a saturated paste or a 1:1 (w/v) 0.01 *M* $CaCl_2$ method as described by McLean (1982). Potassium chloride-extractable NH_4-N and NO_3-N(Keeney and Nelson, 1982), and $NaHCO_3$-extractable P (Olsen and Dean, 1965) were measured colorimetrically using a Technicon Autoanalyzer (Technicon Instruments Corp., Tarrytown, NY). Roots were separated from field-moist soil without sieving by flotation using an elutriator fitted with a 20-mesh sieve (Byrd et al., 1976).

Estimations of Rhizobial Population Densities

Concentrations of mesquite-nodulating rhizobia in field-moist soil samples were estimated using the plant-infection, most probable-number (MPN) technique (Vincent, 1970). Tenfold dilutions (10^{-1} to 10^{-6}), starting with 10 g of subsample in 90 mL of sterile, buffered saline (0.15 *M* NaCl, 0.002 *M* KH_2PO_4, 0.004 *M* Na_2HPO_4, pH 7), and four replicate mesquite plants per dilution, were used for the MPN tests. Mesquite seedings were germinated from seed collected from the Jornada. Seeds were surface sterilized and scarified by exposure to concentrated sulfuric acid for 3 min followed by six washes in sterile, distilled water. One sterilized seed was planted in sterile vericulite contained in plant tubes (Garvin and Lindemann, 1983). The plant tubes had been sterilized with 0.5% sodium hypochlorite and rinsed thoroughly in sterile water. Each mesquite seedling was inoculated with 1 mL of an appropriate soil dilution. After inoculation, the plants were randomized, and grown in a glasshouse where temperatures ranged from 25 to 35 °C under natural lighting conditions. During winter, supplemental light (cool-white fluorescent lamps) situated 1-m above the plants was provided to maintain a 14-h daylength. On alternate days the plants were irrigated with sterile, 0.25-strength Hoagland's nutrient solution lacking N. Noninoculated plants served as controls. Plants were grown for 6 to 8 wk before they were examined for nodulation. The MPN for each sample was calculated using Table 3.5A in Vincent (1970). All MPN values are reported on a soil dry weight basis.

Statistics

The common logarithms of rhizobial population densities were used for all calculations. First order regression models were calculated for soil properties effects on rhizobia using a stepwise regression search (StatView for Macintosh, BrainPower, Calabasas, CA). Differences in log numbers of rhizobia and gravimetric water by depth were determined by one-way analysis of variance (ANOVA) and means were separated by the least significant difference (LSD).

RESULTS AND DISCUSSION

Soil Properties

The soils of the playa, grassland, and *Larrea* ecosystems have distinct horizons; some high in clay, indicating that they are more developed than the arroyo and both the New Mexico and California dune systems, all three of which are Entisols. The playa sites were characterized by distinct layers of widely varying texture, the consequence of periodic flooding and soil deposition.

Concentrations of total salts (EC) and extractable N and P decreased with increasing depth at each site (Table 1). Exceptions were increasing NO_3-N concentrations with depth in the New Mexico *Larrea* and grassland systems, an accumulation of NH_4-N between 9 and 12 m at the California playa, and an increase in EC at the New Mexico dune site.

The California playa and dune ecosystems had lower PO_4-P concentrations than the New Mexico sites (Table 1) that were derived from parent materials high in P (Lajtha and Schlesinger, 1988). Below 5-m depth PO_4-P concentrations were generally <1 mg kg^{-1}, however. The sites were variable in total salts (EC). The highest mean EC was found at 2 to 5 m in the New Mexico dunes. The highly leached arroyo, and the New Mexico playa contained few soluble salts. There was little variation among sites in mean concentrations of NH_4-N. Concentrations of soil NO_3-N were high at 1- to 3-m depth in the grassland and *Larrea* ecosystems, and in the upper 2 m at the California dune ecosystem.

Distribution of soil water (Fig. 1) varied considerably between ecosystems. There were significant differences with depth on the grassland, both California and New Mexico dune, arroyo, and New Mexico playa ecosystems. With the exception of the *Larrea* and grassland systems, the largest quantities of gravimetric water occurred at depth: 2 to 4 m at the New Mexico dunes, 3 to 5 m at the California dunes, 1 to 5 m and 8 to 11 m at the New Mexico playa, 1 to 4 m and 8 to 12 m at the California playa, and 1 to 7 m at the arroyo.

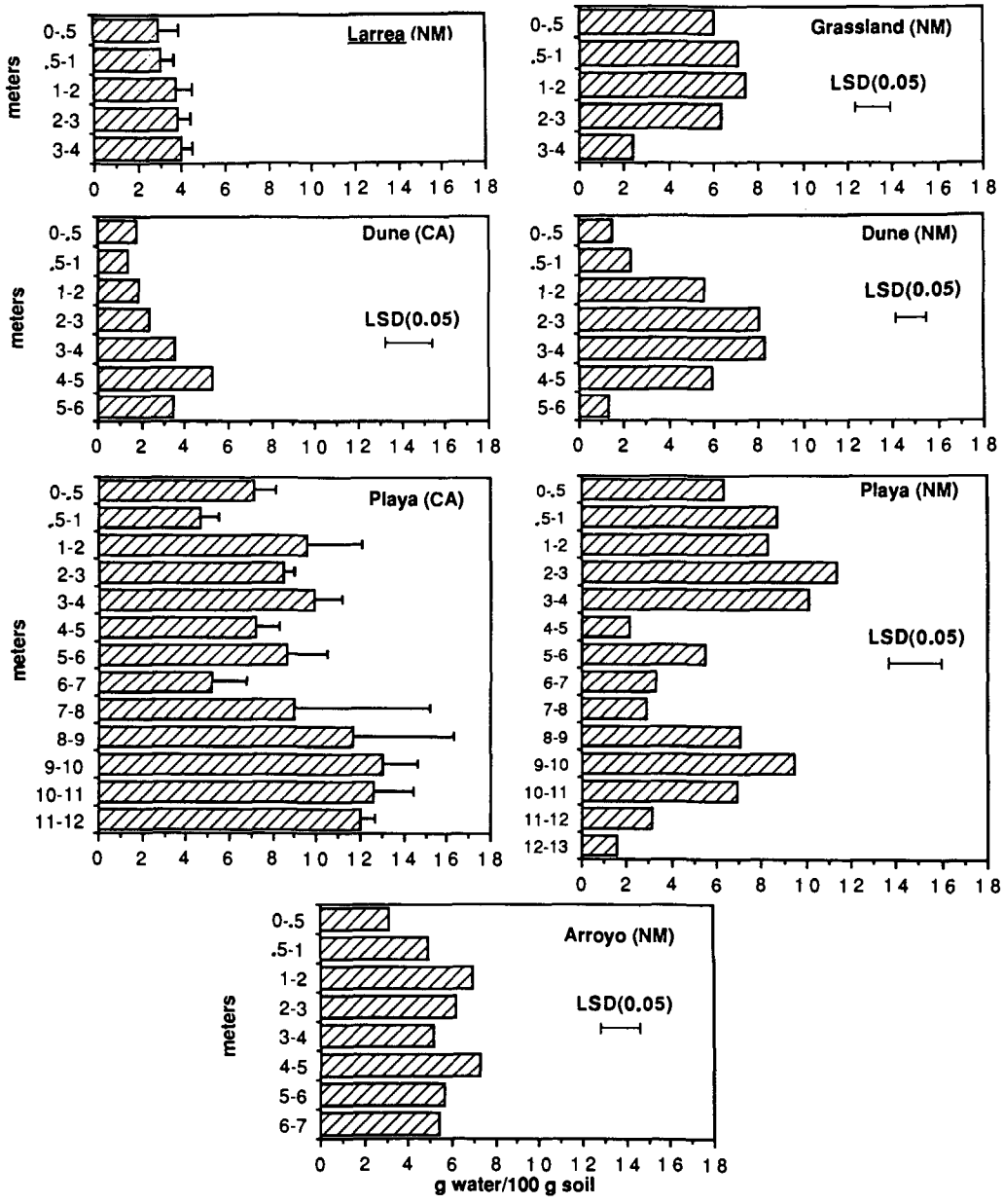

Fig. 1. Distribution of soil water with depth in New Mexico and California ecosystems. Values are means of nine cores, three cores per sampling date. Where ANOVA indicated significant differences between depth increments, LSD (0.05) values are shown; otherwise, error bars representing standard deviations of the means are shown.

Roots were recovered as deep as 12 to 13 m at the New Mexico playa; but were not observed below 6 m at the arroyo and dune systems, or below 3 and 4 m at the grassland and *Larrea* systems, respectively. Mean root mass to the depth of root recovery was greatest in the California dunes and lowest in the arroyo (Table 1).

Rhizobia Populations-Depth Distribution

Concentrations of rhizobia ranging from 10^5 to 10^7 cells kg^{-1} were measured between 1 to 5 m at both California and New Mexico dune and playa ecosystems, and 0.5 to 2 m at the arroyo (Fig. 2). At the New Mexico sites these rhizobial concentrations were significantly greater than those associated with surface (0.5 m) soil and with soil depths > 8 to 9 m.

Rhizobial population densities at the grassland and *Larrea* systems were barely detectable, or not detectable. Since the noninoculated control plants lacked nodules, the low number of inoculated plants that were nodulated were probably not the result of contamination, but reflect population densities just above the limit of detectability according to the MPN tables of Vincent (1970). The lowest detectable MPN was < 600 cells kg^{-1} (log = 2.78), which represents one nodulated replicate at the 10^{-1} dilution. However, since MPN estimates are known to be less reliable at the low end of the scale (Fisher and Yates, 1963), MPN estimates of 10^3 cells kg^{-1} or less should be interpreted only as indicating the presence of a small rhizobial population.

Nodulation may occur even though rhizobial population densities are low or undetectable using MPN

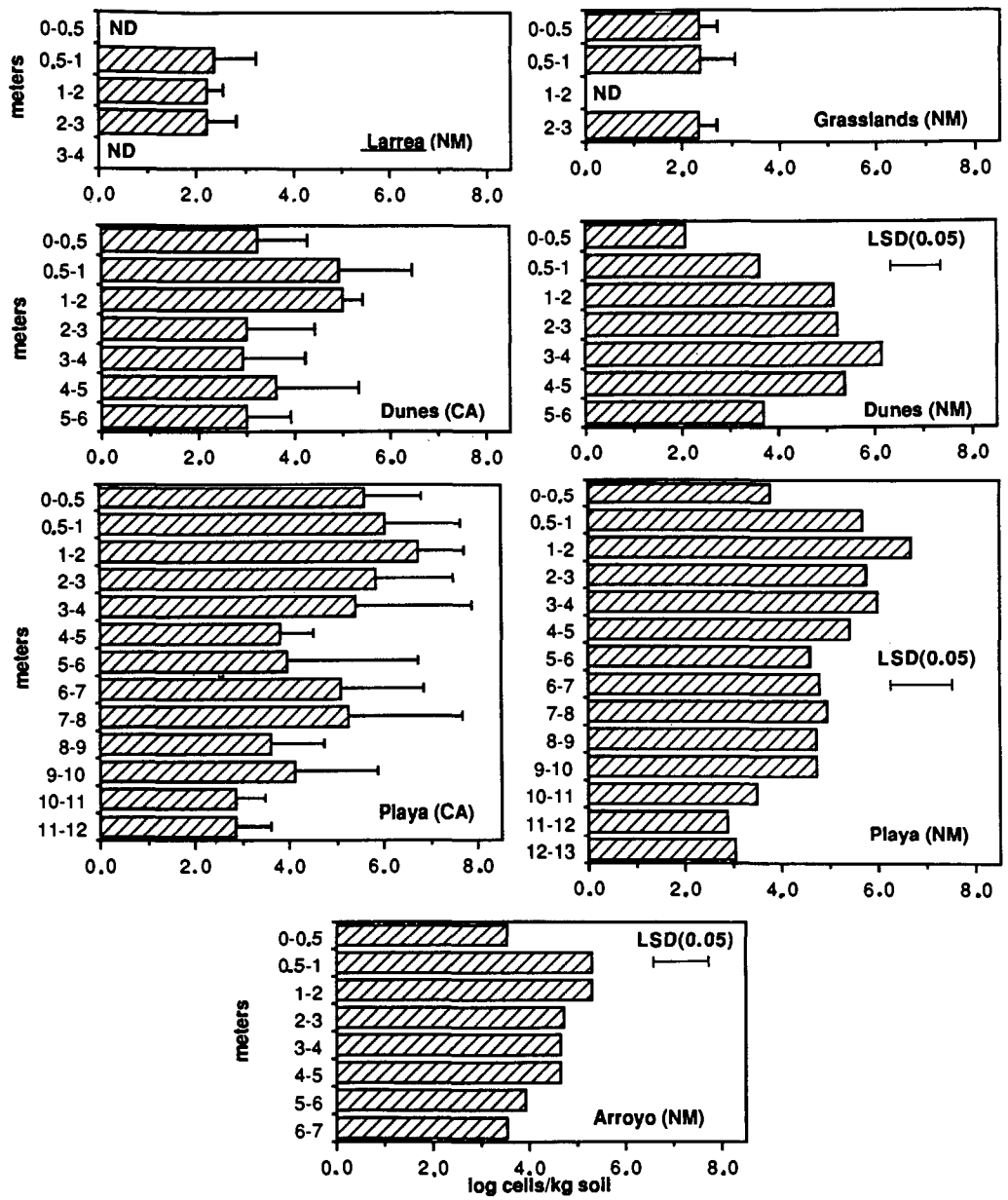

Fig. 2. Distribution of mesquite-nodulating rhizobia with depth for the ecosystems in New Mexico and California. Values are means of nine cores, three per sampling data. Where ANOVA indicated significant differences between depth increments, LSD (0.05) values are shown; otherwise, error bars representing standard deviations of the means are shown. ND = not detectable.

techniques. Roots of mesquite seedings found in the California Sonoran Desert growing in soil with barely detectable rhizobial populations were effectively nodulated (Jenkins et al., 1987), as were seedlings of the woody legume *Psorothamnus spinosus* growing in a Sonoran Desert arroyo in soil with an undetectable rhizobial population (Jenkins et al., 1988).

The low to undetectable rhizobial populations at the *Larrea* and grassland systems are not surprising since the lack of legumes precludes a build up of rhizobial populations (Beadle, 1964). Few annual and no woody legumes occur in the *Larrea* ecosystem, and the density of mesquite in the grassland is low (<10% cover). Nevertheless, detectable rhizobial populations even in the *Larrea* system indicate that mesquite plants establishing in this system may nodulate.

The populations of many soil bacteria decrease with increasing soil depth. Exceptions may be rhizosphere bacteria, especially symbionts, whose numbers increase in the presence of plant roots (Rovira, 1965). We found the rhizobial populations associated with mesquite increased with depth.

The increase in rhizobial concentration occurred generally 2 m or more below the surface 0.5 m of soil where the greatest root mass developed. There was no correlation between root mass and rhizobial population densities. In other studies, high soil NO_3–N (Hoegberg, 1986), EC values >0.4 dS m^{-1} (Yousef et al., 1987), high soil temperatures (Marshall, 1964), and low water potential (Fuhrmann et al., 1986) have been associated with low rhizobial numbers. However, we detected a substantial surface (0- to 0.5-m depth) rhizobial population at the California playa site where levels of soil NO_3–N and EC values were high, surface temperatures often exceeded 40 °C, and the soil water potential was below −1.5 MPa.

The primary difference between the ecosystems investigated in this study and the groundwater system at Harper's Well, CA, which Virginia et al. (1986) studied is the lack of a permanent source of deep soil water. High populations of mesquite-nodulating rhizobia at Harper's Well were associated only with the moist soil (22 g H_2O 100 g^{-1}) contiguous with the groundwater and in which mesquite roots occurred (Virginia et al., 1986). In the present study, significant rhizobial populations occurred at depth but in broader zones than the Harper's Well groundwater ecosystem.

Table 2. Mean rhizobial population densities of three cores per site to the depth of rooting as a function of season.

Ecosystem	Depth	Population densities		
		Winter	Spring	Fall
	m	log cells kg^{-1}		
Larrea (NM)	4	ND†	2.39b‡(a)§	2.07b(a)
Grassland (NM)	3	--	2.20b(a)	2.23b(a)
Dune (CA)	6	3.61a	--	--
Dune (NM)	6	4.05ab(a)	5.66a(b)	4.86a(ab)
Arroyo (NM)	7	4.18ab(a)	5.11a(b)	4.22a(a)
Playa (CA)	12	4.60b	--	--
Playa (NM)	13	4.77b(a)	4.97a(a)	4.62a(a)

† Not detectable.
‡ Means that lack common letters between ecosystems are significantly different at the 0.05 level based on Fisher's protected LSD test.
§ Means that lack common letters in parentheses within a row (seasonal differences by site) are significantly different at the 0.05 level based on Fisher's protected LSD test.

The thickness of these soil zones of elevated rhizobial numbers varied between ecosystems (Fig. 2).

Root nodules containing rhizobia were isolated from depths of 3, 4, and 7 m at the New Mexico playa. Recovery of nodules in situ supports the assumption that natural legume woodlands capable of nodulating actually develop root nodules in the field (Hoegberg, 1986). Deeply rooted woody legumes, such as mesquite, probably nodulate as deep as 10 m.

Rhizobia Populations-Intersite Comparisons

Rhizobial population densities varied between sites from the same region and with season for individual sites. For the winter sampling, the California dune system had a significantly smaller population than the playa systems. Seasonal variations were apparent only for the New Mexico dune and arroyo systems (Table 2). In each case rhizobial populations at the spring sampling were the greatest, which was the period of most rapid aboveground growth.

Seasonal trends in nodulation of desert legumes have been correlated to rains or soil moisture (Beadle, 1964). Lawrie (1981) speculated that the depth of nodulation may be a factor in the magnitude of variation in nodulation between seasons. Nodules occurring at depth should have greater longevity since they are less likely to be affected by the extremes of desiccation and temperature than shallower nodules. Deep rhizobial populations associated with groundwater ecosystems may fluctuate less than surface populations (Virginia et al., 1986), and the same may be true for deep populations in ecosystems recharged by runoff and infiltration.

Rhizobia-Soil Relationships

Linear regression equations were developed to examine multifactor relationships between soil properties expected to influence saprophytic survival of rhizobia and rhizobial population densities (Table 3). Regression analyses were performed only on data from the dune, playa, and arroyo ecosystems in which large rhizobial concentrations were observed.

No factor was related significantly to rhizobial populations across all the ecosystems. Gravimetric water was a significant factor in the New Mexico playa and dune systems. Electrical conductivity was a significant factor in the New Mexico dune system during the winter, as well as in both California ecosystems. Ammonium was a significant factor in the arroyo and California dune systems. Soil PO_4–P was correlated negatively with rhizobial density at the New Mexico dune system during the spring. The most significant

Table 3. Multiple regression models relating rhizobial concentrations [log (cells kg^{-1})] to soil properties at the dune, arroyo, and playa ecosystems.

Ecosystem	Season	Regression equations	R
Dune (CA)	Winter	= 10.27 − 2.83(NH_4-N) − 3.24(EC)	0.724***
Dune (NM)	Winter	= 1.96 + 0.28(EC) + 0.22(%H_2O)	0.833***
	Spring	= 6.68 − 1.19(PO_4-P)	0.891***
Arroyo (NM)	Winter	= 2.82 + 0.81 (NH_4-N)	0.516**
Playa (CA)	Winter	= 3.82 + 0.76(EC)	0.460**
Playa (NM)	Winter	= 3.23 + 0.21 (%H_2O)	0.572***
	Spring	= 3.69 + 0.18(%H_2O)	0.552***

,* Significant at the 0.01 and 0.001 probability levels, respectively.

correlations were for both dune ecosystems, followed by the New Mexico playa, California playa, and arroyo ecosystems.

Although regression models indicated a significant relationship between rhizobial populations, and gravimetric soil water for the winter sampling at both the New Mexico dune and playa sites, no such relations existed at the California sites. This apparent lack of consistency suggests that soil moisture may not have been a primary factor in determining rhizobial populations.

Beadle (1964) hypothesized that the lack of legumes and detectable rhizobial populations in some desert ecosystems could be attributable to soils with low phosphate. We found that the distribution of rhizobia in the ecosystems studied was not related to levels of soil phosphate with the apparent exception of the New Mexico dune system. The negative relationship between bicarbonate-extractable phosphate and the rhizobial numbers at the New Mexico dunes may be the result of competition between roots and soil microflora for uptake of this limiting mineral nutrient.

Rhizobial populations and root nodulation of mesquite occur at depths >0.5 m in ecosystems where there are sources of deep soil water other than ground water. Population densities of mesquite-nodulating rhizobia appeared to be related, though not consistently, to soil water, NH_4-N, PO_4-P, and EC. Fluxes in concentrations of rhizobia in deep soil may be related more to host plant activity than levels of mineral nutrients. The seasonal fluxes in concentrations of rhizobia were more evident in the dune and arroyo ecosystems, suggesting that the playa ecosystem, with its greater potential to store deep water, is more stable. Persistence of nodules and the maintenance of a large soil population of rhizobia may be greater in the very deep-rooted playa systems.

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