

Resource Islands Predict the Distribution of Heterotrophic Bacteria in Chihuahuan Desert Soils

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The resource island hypothesis predicts that soil resources such as nitrogen, phosphorus, and water will be distributed evenly in grasslands but have a patchy distribution focused around plants in shrublands. This hypothesis predicts that microorganism numbers will follow resources and be (i) evenly distributed in grasslands, (ii) concentrated around individual plants in shrublands, and (iii) higher where resources are higher when comparing the same vegetation type. This study enumerated total heterotrophic bacteria and a subset of these, the nitrogen-efficient guild (NEG), in three shrublands (playa fringe mesquite, tar bush, and creosote) and two grasslands (playa and bajada). Both heterotrophs and NEG members followed the distribution pattern predicted by the resource island hypothesis. There were no significant differences in heterotroph or NEG numbers comparing at-plant and interplant samples for both the playa and bajada grasslands. Furthermore, populations were generally higher in nutrient-rich playa grasslands than nutrient-poor bajada grasslands. In contrast, both heterotroph and NEG numbers were higher at shrubs than between shrubs in all three shrub sites. These results suggest that resource abundance in resource islands predicts the distribution of heterotrophic bacterial numbers in desert soils.

In arid environments, water and (or) nitrogen are the most common abiotic factors which limit plant growth. These resources vary both temporally and spatially in distribution (17). The spatial distribution of these resources appears to be important in determining the vegetation in arid environments (5, 32, 33). In the American Southwest, desertification is usually associated with the conversion of grasslands to scrub shrublands. Associated with this conversion is a redistribution of nitrogen, water, and other soil resources from a relatively homogeneous pattern in grasslands to a highly variable and patchy distribution associated with individual shrub canopies (25).

These shrub-focused resource islands represent locations where nutrients tied up in on-site primary productivity are made available by mineralization. They serve as barriers where organic matter is trapped and made available for mineralization. In addition, they are foci where the biological community modifies the water status of the island soils (3, 4, 12, 18, 29). Once shrubs invade grasslands, these processes produce a positive feedback loop reinforcing the resource island around the shrub and diminishing resources in the interplant spaces (25). Thus, shrubs contribute to the construction of their own islands and precipitate the conversion from even to patchy distribution of resources. Using a geostatistics approach, Schlesinger et al. (24) have recently shown that lag distances for nutrient distribution in grasslands of the Sevilleta and Jornada sites of southern and central New Mexico are consistent with an even distribution, while those in shrublands are consistent with patches approximately the size of shrub canopies.

This study tests whether the resource island hypothesis predicts the distribution of total heterotrophic bacteria and a subset of these heterotrophs, members of the nitrogen-efficient guild (NEG) (8). NEG members are oligotrophic organisms capable of activity in low-N environments either through free-

living N fixation or via efficient uptake of low concentrations of available soil N. About 25% of NEG members from Jornada soils are diazotrophs, while 75% are efficient nitrogen scavengers (8).

The hypothesis would predict that if resources are patchy, microbial populations will be high where resource availability is high and lower where it is not. If resources are relatively equable, then there should be relatively little difference in microbial counts. Specifically, the hypothesis predicts little or no difference in microbial numbers when comparing at-plant and interplant samples in grasslands. In contrast, counts from at-plant samples should be greater than interplant sample counts in shrublands.

MATERIALS AND METHODS

Site characteristics. Field studies were carried out on the Jornada long-term ecological research (LTER) area 40 km north-northeast of Las Cruces, N. Mex. (R1E T21S, Doña Ana County, N. Mex.). This site is typical of the extension of the Chihuahuan Desert into southern New Mexico. The most common vegetations found include upland bajada grasslands dominated by *Bouteloua eriopoda* (black grama) with significant amounts of *Sporobolus flexuosus* (mesa dropseed), playa grasslands dominated by tobosa grass (*Hilaria mutica*) and burrograss (*Scleropogon brevifolius*) or vine mesquite (*Panicum obtusum*), mesquite (*Prosopis glandulosa*) shrublands, tar bush (*Flourenzia cernua*) shrublands, and creosote (*Larrea tridentata*) shrublands. Weather data have been collected at the Jornada Experimental Range headquarters since 1915. The climate is arid, with average annual rainfall of 230 mm · year⁻¹, while mean open pan evaporation is 2,290 mm · year⁻¹. On average, 52% of the rainfall occurs between 1 July and 30 September. June is typically the warmest month (average daily maximum, 36°C), and January is the coldest (average daily maximum, 13°C). While there is local heterogeneity in rainfall for any given event, there are no consistent climatic differences between sites. In general, bajada site soils are Ustollic Haplargids, slope shrublands are Typic Haplargids (13), and lowland sites are Typic Torretts (34). Soil nutrient data were collected adjacent to 15 permanent LTER net primary productivity plots (29a). Values for a depth 0 of 10 cm for the five sites adjacent to the present study are shown in Table 1.

Media. All NEG enumerations were carried out on almost-nitrogen-free malate-mannitol medium (NF/MM) plates, a modification of *Azospirillum* semi-solid nitrogen-free malate medium (26). The composition of solid NF/MM was (in grams per liter): KH₂PO₄, 0.4; K₂HPO₄, 0.1; MgSO₄, 0.097; NaCl, 0.1; CaCl₂, 0.0196; FeCl₃ · 6H₂O, 0.017; NaMoO₄ · 2H₂O, 0.002; yeast extract, 0.001; L-malic acid, 3.58; mannitol, 5.0; and agar, 15. The medium pH was adjusted to 7.0 with KOH prior to the addition of the agar. Known N addition from yeast extract represents a concentration of <1 μM, with the agar impurities providing an

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TABLE 1. Selected soil nutrients in the top 10 cm of soil from Jornada soils collected at and between plants^a

Vegetation	Location	PO ₄ (mg kg ⁻²)	Total Kjeldahl N (g kg ⁻²)	K (mg kg ⁻²)
Creosote	Interplant	3.07 ± 0.35	0.38 ± 0.01	0.25 ± 0.01
Creosote	At plant	4.64 ± 0.42	0.46 ± 0.03	0.96 ± 0.09
Tarbush	Interplant	1.94 ± 0.19	0.42 ± 0.02	0.35 ± 0.03
Tarbush	At plant	2.05 ± 0.36	0.50 ± 0.04	1.27 ± 0.20
Mesquite	Interplant	2.27 ± 0.32	0.21 ± 0.01	0.22 ± 0.02
Mesquite	At plant	5.70 ± 0.84	0.35 ± 0.03	1.13 ± 0.12
Bajada	Interplant	5.54 ± 1.17	0.46 ± 0.05	0.28 ± 0.06
Bajada	At plant	4.80 ± 0.27	0.56 ± 0.06	0.44 ± 0.05
Playa	Interplant	18.60 ± 4.78	1.34 ± 0.20	0.51 ± 0.10
Playa	At plant	17.54 ± 3.35	1.23 ± 0.19	0.77 ± 0.13

^a Values are means ± standard deviations.

additional source of N in unknown quantities. Total heterotrophs were estimated in most-probable-number (MPN) tubes. The broth in MPN tubes contained the following nutrients: tryptone, 5 g liter⁻¹; yeast extract, 2.5 g liter⁻¹; and glucose, 1 g liter⁻¹. MPNs were estimated with the three-tube series table from Harrington and McChance (7).

Sample collection. Pairs of plants were selected for each of the five vegetation types. Duplicate soil cores were collected at the edge of the plant crown and in the middle of the interplant space, at a point at least 45 cm from the nearest plant. Cores were collected with a 19-mm (inside diameter) Oakfield soil probe. To eliminate variability associated with surface disturbance, the top 5 cm of each core was discarded and the soil between a depth of 5 and 10 cm was stored in plastic bags and brought back to the laboratory for analysis. The probe was flamed between each collection.

Cores were broken manually and mixed in their plastic bags. A 1-g sample from each core was aseptically weighed and transferred to a dilution bottle containing 100 ml of sterile deionized water. Bottles were allowed to stand for 15 min and shaken manually for 15 s. Two dilution series per bottle were made onto solid NF/MM or into MPN tubes. The results of these two pseudo-replicates were averaged to obtain a sample value for each core. Values reported represent the means and standard errors of the means (SEM) of the four replicate cores per treatment. Final dilutions ranged from 1:10,000 to 1:10,000,000. Soil samples were weighed, dried for 24 h at 105°C, and reweighed to calculate percent moisture.

Statistics. All data were analyzed by analysis of variance and multiple analysis of variance by SAS general liner model procedures (23) on log-transformed data. Groups were considered significantly different when the *P* was <0.05.

RESULTS

The population numbers of NEG members and total heterotrophs in grassland soils are shown in Fig. 1 and 2. The patterns of population estimates in grasslands were similar for both the bajada (Fig. 1) and playa (Fig. 2) sites. Neither NEG members nor general heterotrophs were significantly more numerous at plants than they were in interplant spaces in either grassland. This pattern was particularly striking in the playa, where interplant numbers exceeded at-plant numbers 50% of the time. NEG members were significantly more numerous in both the at-plant and interplant samples from the playa than they were from comparable bajada samples. This tendency was also apparent for general heterotrophs, but not significantly so.

Shrublands showed a different pattern of microbe distribution. In all cases, populations at plant crowns were significantly greater than numbers in interplant spaces. This was true for both heterotrophs and NEG members at all three shrubland sites. The tar bush site showed the least dramatic differences (Fig. 3). However, even here, populations of both NEG members and total heterotrophs were greater near the shrubs than in interplant spaces on an annual basis and in all but two sampling periods each in pair-wise comparisons. Both mesquite (Fig. 4) and creosote (Fig. 5) showed dramatic differences in populations of bacteria when at-plant and interplant samples were compared. For the mesquite site, both groups of bacteria were more numerous near plants on an annual basis

and in all but one pair-wise comparison of sampling dates. This pattern was most striking in the creosote shrubland. NEG members were more numerous in at-plant samples than in interplant spaces over the year and in all but one pair-wise comparison. Most dramatically, general heterotrophs were significantly more abundant near plants on an annual basis and at each sampling period.

If populations are nearly evenly distributed in space, a ratio of the at-plant number of organisms divided by the number in

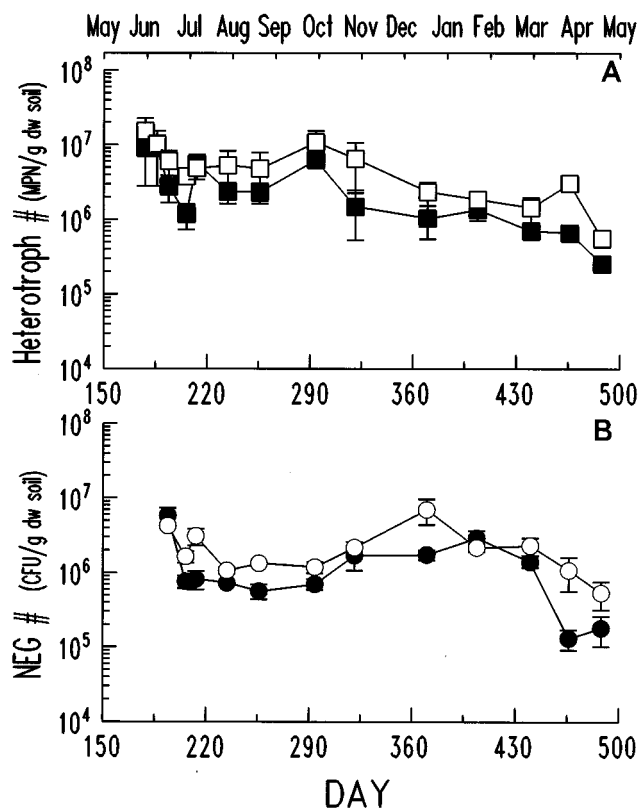


FIG. 1. Heterotroph numbers (A) and NEG member numbers (B) over time in bajada grassland soils. Day 1 is 1 January 1993. The approximate month reference is on the second abscissa. Plant crown samples (□ and ○) and interplant samples (■ and ●) are represented. All points are the means of four determinations ± SEM. There were no significant differences on an annual basis (*P* ≥ 0.05) between plant crown and interplant samples for either heterotrophs or NEG members. dw, dry weight.

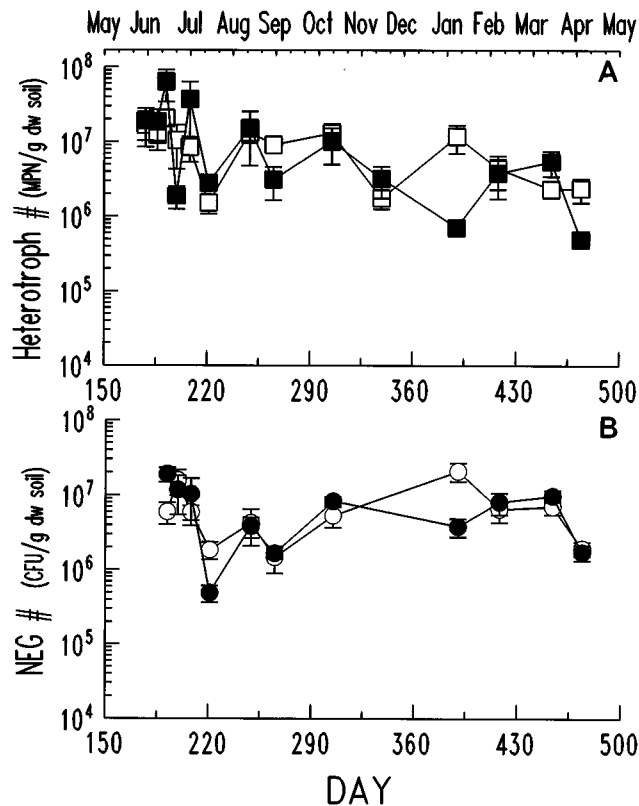


FIG. 2. Heterotroph numbers (A) and NEG member numbers (B) over time in playa grassland soils. Day 1 is 1 January 1993. The approximate month reference is on the second abscissa. Plant crown samples (\square and \circ) and interplant samples (\blacksquare and \bullet) are represented. All points are the means of four determinations \pm SEM. There were no significant differences on an annual basis ($P \geq 0.05$) between plant crown and interplant samples for either heterotrophs or NEG members. dw, dry weight.

interplant samples would be expected to be near unity. If the organisms are concentrated near plants, ratios of substantially greater than 1 would be expected. Figure 6 illustrates these ratios at each sample period for the bajada grassland and the creosote shrubland. The ratio in the grassland is consistent and low. The ratio in the creosote shrubland, while variable, is generally 5 or greater, with mean values of 17.11 and 12.91 for heterotrophs and NEG members, respectively. Table 2 shows the mean values of the ratios for all sites. The ratios in all shrubland sites are significantly higher than those in the grassland sites.

DISCUSSION

The distribution of microorganisms in soil is under complex control. One primary spatial controller of microbial population number in soils appears to be the distribution of nutrient resources (16, 31), including organic matter (1, 9, 11, 14, 15, 20, 31), nitrogen (1, 11, 28, 31), and soil moisture or water potential (2, 11, 27, 31). The resource island hypothesis predicts that these resources will all be concentrated around shrubs to form resource islands while they will be distributed relatively evenly in grasslands (25). By extension, this hypothesis predicts that microorganism numbers will follow resources and be (i) evenly distributed in grasslands, (ii) concentrated around individual plants in shrublands, and (iii) higher where resources are

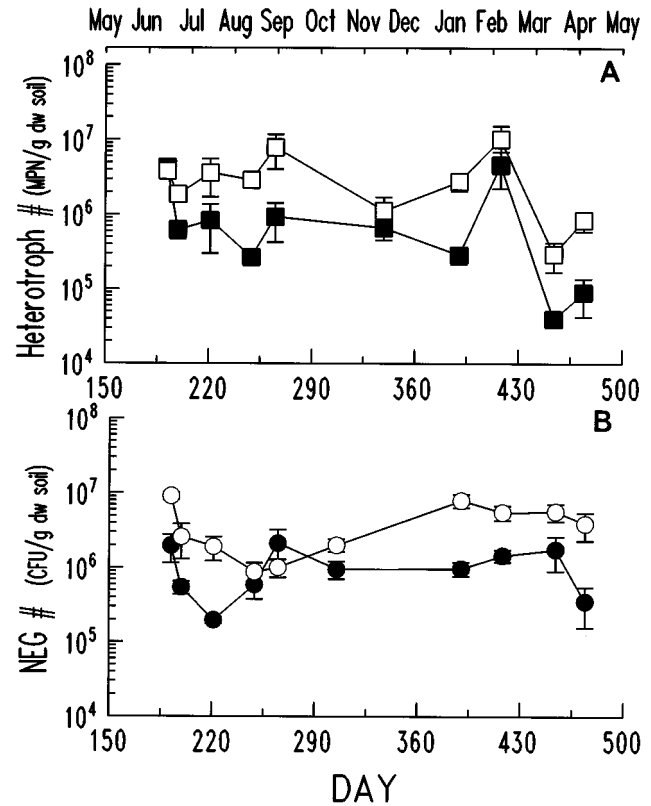


FIG. 3. Heterotroph numbers (A) and NEG member numbers (B) over time in tar bush shrubland. Day 1 is 1 January 1993. The approximate month reference is on the second abscissa. Plant crown samples (\square and \circ) and interplant samples (\blacksquare and \bullet) are represented. All points are the means of four determinations \pm SEM. On an annual basis, numbers in plant crown samples were significantly greater ($P < 0.05$) than in interplant samples for both heterotrophs and NEG members. dw, dry weight.

higher, for example, in playa grasslands compared with bajada grasslands.

Because of methodological difficulties, we were unable to test a fourth prediction, that oligotrophic NEG members would represent a smaller proportion of total heterotrophs in nutrient-rich sites compared with nutrient-poor sites. The fact that we were forced to estimate total heterotrophs via MPN because of the presence of swarming on all solid media tested made direct comparison of NEG member and total numbers impossible.

The NEG members and general heterotrophic bacteria sampled in this study clearly showed similar spatial distribution patterns with respect to proximity to plants. Both grassland sites, bajada (Fig. 1) and playa (Fig. 2), showed no significant differences in numbers between at-plant and interplant samples. In sharp contrast, all three shrubland sites, i.e., tar bush (Fig. 3), playa fringe mesquite (Fig. 4), and creosote (Fig. 5), had significantly higher numbers of microorganisms in the at-plant samples than in the interplant samples. As predicted, the average ratio (Fig. 6) for the bajada grassland is near unity (2.1 ± 0.37 and 2.2 ± 0.73 for heterotrophs and NEG members, respectively), demonstrating only small differences between at-plant and interplant sample numbers. On the other hand, the ratio for the creosote shrubland is well above unity (17.1 ± 3.3 and 12.9 ± 2.0 for heterotrophs and NEG members, respectively). While not as dramatically different, the ratios in

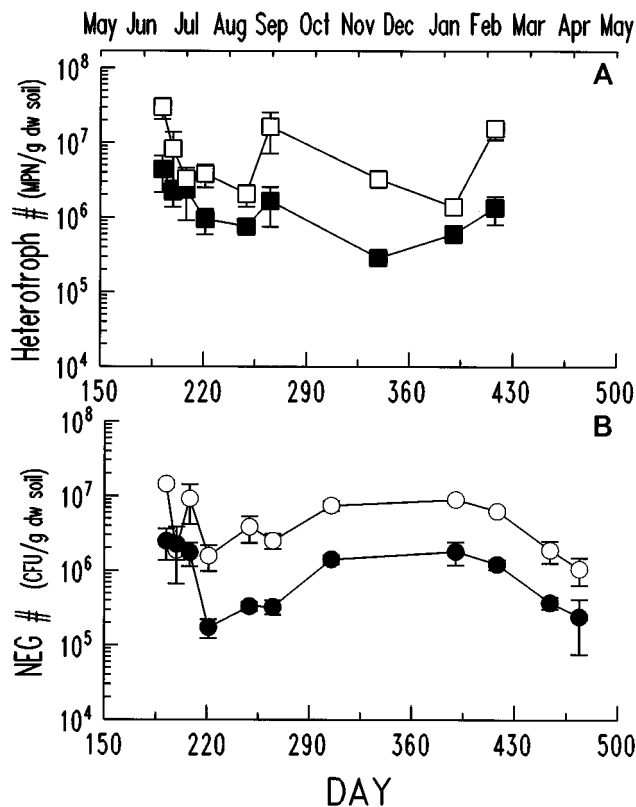


FIG. 4. Heterotroph numbers (A) and NEG member numbers (B) over time in playa fringe mesquite shrubland. Day 1 is 1 January 1993. The approximate month reference is on the second abscissa. Plant crown samples (\square and \circ) and interplant samples (\blacksquare and \bullet) are represented. All points are the means of four determinations \pm SEM. On an annual basis, numbers in plant crown samples were significantly greater ($P < 0.05$) than in interplant samples for both heterotrophs and NEG members. dw, dry weight.

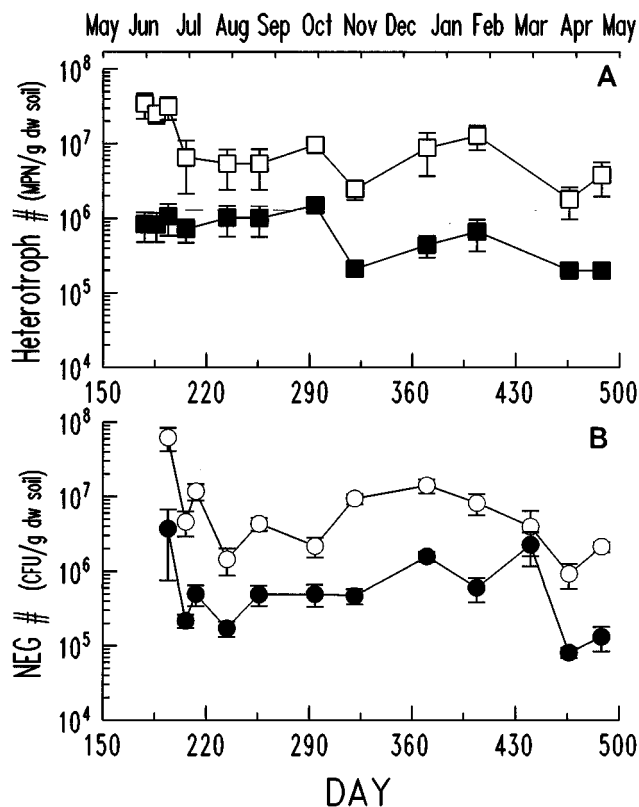


FIG. 5. Heterotroph numbers (A) and NEG member numbers (B) over time in creosote shrubland. Day 1 is 1 January 1993. The approximate month reference is on the second abscissa. Plant crown samples (\square and \circ) and interplant samples (\blacksquare and \bullet) are represented. All points are the means of four determinations \pm SEM. On an annual basis, numbers in plant crown samples were significantly greater ($P < 0.05$) than in interplant samples for both heterotrophs and NEG members. dw, dry weight.

the other two shrub sites are significantly higher than both grassland site ratios (Table 2).

There have been few studies designed to directly test the resource island hypothesis on microbial populations. However, there are a number of resource island studies where biomass or process data which may relate to microbe population status have been collected. Many of these studies support increased microbial populations, while others are ambiguous or non-supportive.

In a directly comparable study, our group (8) found that there were no significant differences in NEG numbers between at-plant and interplant samples in the same bajada grassland, a result confirmed in the present study. Gallardo and Schlesinger's (6) biomass nitrogen measurements indicated consistently higher microbial biomass under shrubs than between shrubs in all sites examined at the Jornada. These results are consistent with our findings of higher numbers of bacterial groups in at-shrub samples.

When studies move from direct measures of numbers or biomass to surrogate measures such as N transformations or respiration, the picture becomes less clear-cut. Soil respiration, N mineralization, and nitrification potential did not show a resource island effect in a mixed mountain sage brush (*Artemisia tridentata*)-bluebunch wheatgrass (*Pseudoroegneria spicata*) cool desert, although respiration did show an island effect when only sage plots were considered (10). Peterjohn (21) found that denitrification activity was greater in soils taken

from under shrubs than from intershrub soil in the Jornada, supporting the island of fertility associated with shrubs. When Peterjohn and Schlesinger measured in situ denitrification, they did not find the same island effect and suggested that the high sample variability may have obscured other trends (22). In contrast, in situ denitrification in the Sonoran Desert showed a strong honey mesquite resource island effect (30). Finally, N mineralization, nitrification, and N turnover were greater in soils under canopies than in intercanopy spaces in piñon-juniper woodlands (19).

A rhizosphere effect on numbers might be invoked to explain the pattern of microbe distribution which we see in this study. For this to be the case, the following conditions would have to be met: (i) roots in the sample soil volume would have to be relatively homogeneous in the grassland zone or the roots would have to have a large zone of influence, and (ii) roots in the sampled soil volume would need to be different in at-plant and interplant samples in the shrub zone. Roots in the depth zone of 5 to 10 cm at the Jornada site do not conform to either of these requirements. There were large differences in the quantity of roots in at-plant and interplant samples from bajada grasslands. At-plant soils contained 307.6 g m^{-2} , while interplant samples contained only 32.5 g m^{-2} , a 9.5-fold difference (8). Furthermore, these roots exerted a strong effect on numbers (10- to 40-fold higher than surrounding bulk soil), but the effect was limited to root-adhering soils (8). This difference in the quantity of rhizosphere-influenced soil might explain the

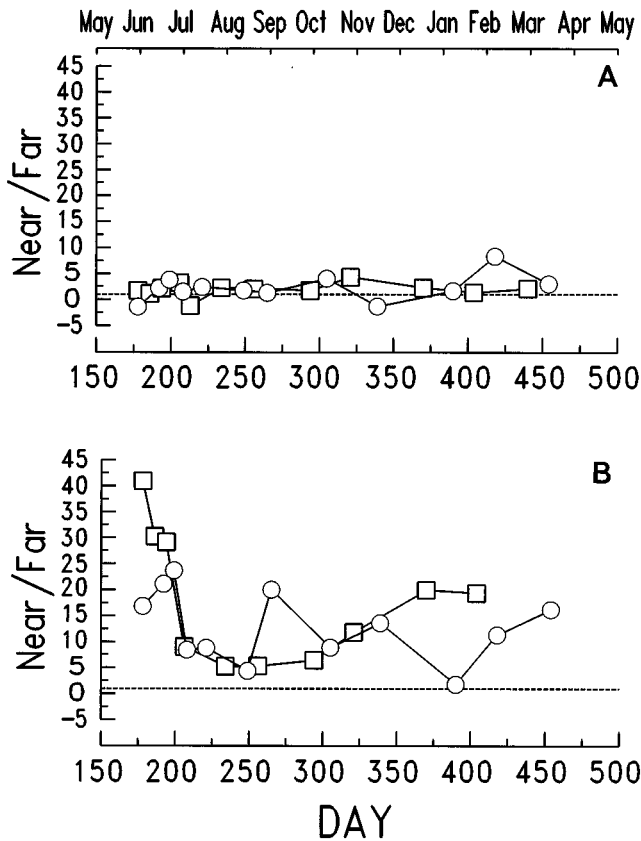


FIG. 6. Ratios of near-plant to far-plant sample numbers for bajada grassland (A) and creosote shrubland (B). Ratios for total heterotrophs (□) and NEG members (○) are shown for each site. Day 1 is 1 January 1993. The approximate month reference is on the second abscissa.

fact that the at-plant/interplant population ratios in grasslands were greater than the one predicted by homogeneous resource distribution but are the opposite of what would be required to explain the relatively even distribution of microorganisms by a rhizosphere explanation. Because the shrubs encountered in this study are deep rooted, few roots were contained in either at-plant or interplant samples taken in the shrub zones, again suggesting that rhizosphere effects cannot explain our observed microbe distribution pattern.

Our direct examination of both NEG members and total heterotrophic bacteria are clearly consistent with the three predictions derived from the resource island hypothesis. In general, counts were higher in nutrient-rich (playa) than nutrient-poor (bajada) grasslands [prediction (iii)]. They were not different at or between plants within a grassland [predic-

tion (i)]. Finally, all shrub sites studied showed concentrations of bacteria at shrubs [prediction (ii)]. The extent to which these differences in numbers also represent differences in community composition or metabolic abilities remains to be investigated.

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TABLE 2. Mean at-plant/interplant ratios for heterotrophs and NEG members in the five vegetation types

Vegetation	At-plant/interplant ratio (mean ± SD)	
	Heterotrophs	NEG
Bajada	2.28 ± 0.29	2.59 ± 0.60
Playa	2.63 ± 1.16	1.52 ± 0.48
Creosote	17.11 ± 3.32	12.91 ± 1.97
Tarbrush	5.81 ± 1.19	4.93 ± 1.13
Mesquite	5.96 ± 1.34	5.91 ± 0.83

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