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ON THE SPATIAL PATTERN OF SOIL NUTRIENTS IN DESERT ECOSYSTEMS[1]

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Abstract. We examined the spatial distribution of soil nutrients in desert ecosystems of the southwestern United States to test the hypothesis that the invasion of semiarid grasslands by desert shrubs is associated with the development of "islands of fertility" under shrubs. In grasslands of the Chihuahuan Desert of New Mexico, 35–76% of the variation in soil N was found at distances <20 cm, which may be due to local accumulations of soil N under *Bouteloua eriopoda,* a perennial bunchgrass. The remaining variance is found over distances extending to 7 m, which is unlikely to be related to nutrient cycling by grasses. In adjacent shrublands, in which *Larrea tridentata* has replaced these grasses over the last century, soil N is more concentrated under shrubs and autocorrelated over distances extending 1.0–3.0 m, similar to mean shrub size and reflecting local nutrient cycling by shrubs. A similar pattern was seen in the shrublands of the Mojave Desert of California. Soil PO_4, Cl, SO_4, and K also accumulate under desert shrubs, whereas Rb, Na, Li, Ca, Mg, and Sr are usually more concentrated in the intershrub spaces. Changes in the distribution of soil properties may be a useful index of desertification in arid and semiarid grasslands worldwide.

Key words: Artemisia tridentata; Bouteloua eriopoda; Bromus tectorum; Chihuahuan Desert; desertification; desert soils; desert vegetation; geostatistics; Great Basin Desert; Larrea tridentata; Mojave Desert; nitrogen cycling; soil heterogeneity.

INTRODUCTION

Several years ago, we postulated that various processes, especially overgrazing, that create spatial heterogeneity in the soils of arid and semiarid grasslands may lead to the invasion of these communities by desert shrubs (Schlesinger et al. 1990). Shrubs may further localize soil fertility under their canopy, leading to the development of "islands of fertility," which characterize shrub–desert and steppe ecosystems worldwide (Crawford and Gosz 1982, Noy-Meir 1985). Our hypothesis suggested that the accumulation of nutrients under desert shrubs is an autogenic process that may promote the persistence of shrubs in the community and the desertification of grasslands that are invaded by shrubs (Reynolds et al., *in press*).

Implicit in this view was the assumption that the distribution of soil resources in grasslands was relatively uniform. Hook et al. (1991) found a fine-scale pattern of soil nitrogen in a semiarid grassland, suggesting that the changes in soils that accompany the transition from grassland to shrubland may be associated with a change in the *scale* of soil heterogeneity, rather than with the initial development of heterogeneity per se (cf. Tongway and Ludwig 1994). Thus, the main objective of this paper is to compare the scale of

soil heterogeneity in arid and semiarid grasslands to that in desert shrublands of the southwestern United States.

In this paper, we use geostatistics to describe the spatial variation in soil nutrient distribution in different ecosystems by the calculation of a semi-variogram (Fig. 1), which shows the average variance found in comparisons of samples taken at increasing distance from one another, the *lag* interval. For randomly distributed data, one would expect little change in the semi-variance (γ) encountered with increasing distance (i.e., the total sample variance is found at all scales of sampling), and the semi-variogram is essentially flat (Rossi et al. 1992, Robertson and Gross 1994; Fig. 1, curve *a*). For patterned data, the semi-variogram first rises from comparisons of neighboring samples that are similar and autocorrelated and then levels off at the *sill*, indicating the distance beyond which samples are independent (Fig. 1, curve *b*). A spherical model is often used to fit this form of semi-variogram (Webster 1985, Issaks and Srivastava 1989). Statistics from the spherical model indicate the *range* over which samples show spatial autocorrelation (A_0 in Fig. 1), an index of the scale of spatial pattern in the community involved. Variance that exists at a scale finer than the field sampling is found at 0 lag distance and is known as *nugget* variance (C_0). A high nugget variance indicates that most variance occurs over short distances, and a high
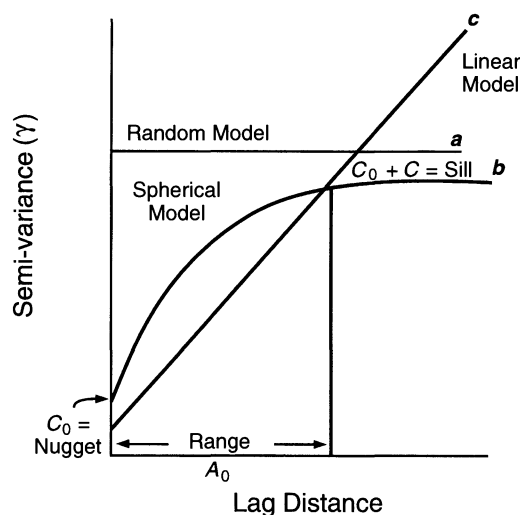
FIG. 1. Theoretical interpretations of semi-variograms, showing the proportion of variance (semi-variance, γ) found at increasing distances of paired soil samples (lag distances). Curve a is expected when soil properties are randomly distributed. Curve b is expected when soil properties show spatial autocorrelation over a range (A_0) and independence beyond that distance. Variation that is found at a scale finer than the field sampling is nugget variance (C_0). Curve c is found when there is a large-scale trend in the distribution of soil properties, but no local pattern within the scale of sampling.

ratio of nugget variance (C_0) to sill variance ($C_0 + C$) is an indication of a random pattern among the data (Trangmar et al. 1985).

We examined soil nutrient distributions in 11 sites representing arid and semiarid habitats of the southwestern United States (Table 1). We sampled grassland and shrubland sites at the Sevilleta National Wildlife Refuge ($n = 1$ each) and the Jornada Experimental Range ($n = 2$ each) in the Chihuahuan Desert of New Mexico, where various desert shrubs, including *Larrea tridentata,* have invaded perennial grasslands, dominated by *Bouteloua eriopoda,* during the last century (Buffington and Herbel 1965). We compare the distribution of soil nutrients in these shrubland communities to that in two sites dominated by *Larrea tridentata* in the Mojave Desert of California, where desert shrublands have existed in conditions of extreme drought for millennia (Thorne 1986) and some individual *Larrea tridentata* appear >10 000 yr old (Vasek 1980). We also compare the distribution of soil nutrients in the *Bouteloua eriopoda* communities of the Chihuahuan Desert to that in the short-grass steppe, dominated by *Bouteloua gracilis,* at the site sampled by Hook et al. (1991) in the Central Plains Experimental Range of northeastern Colorado.

We hypothesized that the distribution of soil nutrients in desert shrublands would show spatial autocorrelation up to the average size of the dominant individuals. This pattern should be seen for biologically essential elements, especially those that are limiting in desert ecosystems (e.g., N), but spatial autocorrelation

TABLE 1. Environmental conditions of the field sites.

Site	Latitude (N)	Longitude (W)	Parent material	Slope (%)	Plant cover* (%)	Dominant species
Chihuahuan Desert						
Sevilleta						
Shrubland	34°19′	106°42′	Metasedimentary	1	35	*Larrea tridentata* *Gutierrezia sarothrae*
Grassland	34°22′	106°41′	Metasedimentary	1	60	*Bouteloua eriopoda*
Jornada†						
Shrubland 1	32°31′	106°47′	Quartz monzonite	3	41	*Larrea tridentata* *Gutierrezia sarothrae*
Shrubland 2	32°28′	106°44′	Mixed volcanics	2	30	*Larrea tridentata* *Gutierrezia sarothrae*
Grassland 1	32°35′	106°51′	Floodplain alluvium	1	46	*Bouteloua eriopoda*
Grassland 2	32°33′	106°47′	Floodplain alluvium	0	66	*Bouteloua eriopoda*
Mojave Desert						
Coxcomb Mountains	33°54′	115°23′	Granodiorite	3	13	*Larrea tridentata* *Ambrosia dumosa*
Ludlow	34°44′	115°41′	Granite	4	17	*Larrea tridentata* *Ambrosia dumosa*
Great Basin Desert						
Shrubland	39°35′	119°50′	Metavolcanics	14	42	*Artemisia tridentata*
Grassland	39°35′	119°50′	Metavolcanics	28	ND	*Bromus tectorum*
Central Plains						
Grassland	40°49′	107°47′	Eolian	0	92	*Bouteloua gracilis*

* Number of random points under vegetation as a percentage of 109 sample points at each site.
† There is no explicit pairing of the shrubland and grassland sites at the Jornada.

could be seen for nonlimiting, mobile elements (e.g., Na, Li, and Cl) as well, if physical processes (e.g., wind erosion) are important to the development of shrub islands. For grassland ecosystems, in which grass clumps are typically <20 cm diameter, our hypothesis was that most of the variance in soil nutrients would be found at a distance less than our smallest lag, 20 cm, and we expected that the semi-variogram would show a high nugget-to-sill ratio, indicating a random pattern, for all elements.

We also sampled two sites in the Great Basin Desert of Nevada, where large areas of sagebrush (*Artemisia tridentata*) have been replaced by an exotic annual grass (*Bromus tectorum*), which promotes frequent fire in this region (Billings 1990). As a contrast to the hypothesized changes in soils that accompany the invasion of grasslands by shrubs in New Mexico, we hypothesized that the loss of sagebrush from our site by a fire in 1947 (Billings 1990) would be reflected by a change in soil nutrient distribution, from a heterogeneous distribution of nutrient-rich islands in sagebrush (Wikeem and Pitt 1982, Bolton et al. 1993) to a relatively homogeneous distribution of soil nutrients in the *Bromus* grassland.

METHODS

Field sampling

We established an 8 × 12 m plot in each of the 11 sites (Table 1). In each case, we attempted to sample a level and apparently topographically uniform field site (e.g., no rills) to avoid anisotropic effects in the geostatistical analysis. In each plot, a sampling grid of 109 points was established at two spatial scales. First, the plot was divided into 48 cells, each 1.5 × 1.5 m in size, and a sampling point was located randomly in each cell. Four additional points were then cast randomly in the 8 × 12 plot, and each was used to locate a 2 × 2 m subplot that was divided into 16 0.5 × 0.5 m cells, in which a sampling point was located randomly. During these procedures three points fell outside the 8 × 12 plot; when these were deleted, the final sampling array contained 109 points. Each sample was a 2 cm diameter soil core taken from 0 to 12 cm depth. For each sample we noted whether it was taken from beneath vegetation or from the bare soil between plants. In Nevada, the abundance and small size of *Bromus* in the grassland made differentiation of bare and vegetated patches impossible.

Laboratory analysis

In the laboratory each air-dried soil sample was sieved (<2 mm) and analyzed for Ca, Mg, Na, K, Li, Sr, Rb, NH_4, F, Cl, Br, NO_3, PO_4, and SO_4. In this paper, we focus on N and P, which are the most commonly limiting biological elements in desert ecosystems (Crawford and Gosz 1982). The other elements were included to deduce the importance of biotic vs. physical

processes in the development of soil heterogeneity. We consider the sum of NH_4-N and NO_3-N to be an index of total available N (N_{avail}). Although extractable forms of N are often not an ideal index of the nutrient dynamics in the soil, in previous work we found a significant positive correlation between N_{avail} and total N in 321 soil samples from the Chihuahuan Desert ($r = 0.52$) and in 45 samples from the Chihuahuan, Mojave, and Great Basin Deserts ($r = 0.37$) (Peterjohn 1990).

The cationic elements, except for NH_4, were extracted by shaking a 6-g subsample of soil with 30 mL of 1 mol/L $NH_4C_2H_3O_2$ solution, adjusted to pH 7.0. The extract was filtered through a 0.4-μm polycarbonate Nucleopore filter and analyzed for Ca and Mg by atomic absorption spectrophotometry and the remaining cations by flame emission on a Perkin Elmer Model 3100 Atomic Absorption Spectrophotometer. NH_4 was extracted by shaking a separate subsample of 6 g of soil with 30 mL of 2 mol/L KCl, filtering the extract with a Seraclear filter, and analyzing the supernatant using Traacs 800 autoanalyzer methods (Bran and Luebbe 1986). Anions were extracted by shaking a third 6-g subsample with 30 mL of distilled water, and analyzing the filtered extract (as above) on a Dionex 2010i ion chromatograph. All data were expressed as micrograms per gram of soil. Mean values for each site are given in the Appendix, and the complete data set for 14 constituents measured in 109 samples at each site is available.[2]

In nearly all samples, Br was below analytical sensitivity, so data for Br were not subjected to further analysis; Li was frequently near sensitivity and these values should be interpreted with caution. We also omit any discussion of F, for which we experienced considerable analytical interference by soluble organic compounds during ion chromatography. We checked the efficiency of the water extraction for NO_3 and PO_4, compared to traditional "strong-anion" extractions for these ions. At one site (Mojave-Coxcomb), NO_3 measured by autoanalyzer methods on the 2 mol/L KCl extract was highly correlated ($r = 0.99$, slope ± SE = 1.03 ± 0.015) to NO_3 in the water extract. In Mojave-Coxcomb samples, PO_4 measured in a 0.5 mol/L $NaHCO_3$ extract (Olsen et al. 1954) on the autoanalyzer was highly correlated ($r = 0.85$) to PO_4 analyzed by ion chromatography in the water extract. The bicarbonate extraction yielded values that were 2.52 ± 0.14 (SE) times greater than those from the water extraction (cf. Sharpley et al. 1988), but the strong correlation suggests that the water extract should be a robust index of PO_4 availability.

[2] See ESA Supplementary Publication Service Document Number 9504 for supplementary material. This material is available on a 3½″ diskette. For a copy of this diskette, contact the senior author or order from the Ecological Society of America, 118 Prospect Street, Suite 212, Ithaca, New York 14850-5616. There is a small fee for this service.

TABLE 2. Ratio of the mean concentration of elements measured under vegetation to that measured between vegetation in various deserts of the southwestern United States

Element	Mojave Coxcomb shrubland	Mojave Ludlow shrubland	Sevilleta Shrubland	Sevilleta Grassland	Jornada Shrubland‡	Jornada Grassland‡	Central Plains grassland	Great Basin‡ shrubland
N_{avail}	2.25	2.22*	2.93*	1.17	1.71*	1.49*	1.53*	1.11
					1.65*	0.97		
PO_4	3.31*	3.09*	3.44*	1.12	1.93*	1.09	0.71	1.66*
					1.52*	1.40		
Cl	2.80*	5.45*	2.36*	1.38	1.20	1.77*	2.39*	7.66*
					1.27	1.58		
SO_4	2.39*	2.97*	2.14	1.05	1.72	1.60	1.35	2.94*
					2.13*	1.32		
K	1.53*	1.59*	1.11*	0.86*	1.21*	1.01	1.13	1.48*
					1.14*	0.91		
Rb	1.02	1.01*	0.89*	0.88*	1.00	0.94	1.03	1.02
					1.05	1.10		
Na	1.25	0.80	0.74*	0.91	0.69*	0.84*	1.18	1.09
					0.93	0.95		
Li	1.02	0.86*	0.82*	0.83	0.78*	0.77*	ND	0.97
					0.95*	ND		
Ca	0.98	1.02	0.90*	0.79*	0.87*	0.79*	1.02	1.08
					0.98	0.92*		
Mg	1.06	0.77*	0.82*	0.85*	0.92*	0.90*	1.05	1.00
					1.05	0.91*		
Sr	1.10	0.82	0.81*	0.76*	0.93*	0.84*	1.00	1.05
					0.96	1.08		

* Indicates a significant difference in these mean concentrations (t test, $P < 0.01$). ND = not determined.

† Differentiation of bare vs. vegetated soils was not possible in the Great Basin grassland.

‡ Values presented are for Shrubland 1 and Grassland 1 above, and Shrubland 2 and Grassland 2 below.

Statistical analysis

For each element, we calculated the mean concentration in samples taken under plants or between plants in each community, and the ratio between these values (Table 2). A t test was used to deduce significant differences between these means. To avoid Type I errors in the multiple use of t tests, we selected a conservative critical value ($P < 0.01$) to test for significance. We also calculated the coefficient of variation (CV) for the entire sample ($n = 109$), as a general index of variability among the samples taken at each site. Pearson product-moment correlations were calculated between all combinations of soil constituents at each site.

GS$^+$ software (Version 2.0; Gamma Delta, Plainwell, Michigan) was used to calculate semi-variograms from the field data and to fit various models to isotropic semi-variograms. (Having chosen our field sites in uniform topography, we did not pursue anisotropic semi-variograms and other alternatives to the traditional omni-directional variogram.) We adjusted each data set to approximate a normal distribution using a $\log_e + 1$ transformation. We used a lag interval of 20 cm, which resulted in a minimum of nine samples in the smallest lag interval (0–20 cm) and a maximum of 223 pairs in the 440–460 cm interval. Our analysis extends to a lag of 700 cm, 50% of the maximum lag interval. In this paper we focus only on the spherical model for the semi-variogram, because it has proven especially useful in the interpretation of two-dimensional spatial data (Webster 1985). In the spherical model, if $h < A_0$, then

$\gamma = C_0 + C[1.5(h/A_0) - 0.5(h/A_0)^3]$, where h is the lag interval, A_0 is the range, C_0 is the nugget variance, and C is the structural variance. If $h > A_0$, then $\gamma = C_0 + C$.

In nearly all cases in which the spherical model was significant, the semi-variance calculated at the sill, $C_0 + C$, included >90% of the total variance in the data (Barnes 1991). If the spherical model was not significant (i.e., $r^2 < 0.18$; $P > 0.05$; $F < 3.30$ with 2 and 32 df) for a particular element, we examined a linear fit for the semi-variogram (Fig. 1, curve c). However, no linear models were significant (i.e., $r^2 > 0.12$), so we interpreted these patterns as random.

RESULTS

Mean values

Available nitrogen, PO_4, and K were significantly more concentrated in samples taken under shrubs than in samples from the barren spaces between shrubs in the *Larrea tridentata* communities of the Chihuahuan Desert of New Mexico (Table 2). Chloride was also more concentrated under shrubs at the Sevilleta, as was SO_4 in one site at the Jornada. The mean concentration of cations (other than K) under shrubs was always less than or equal to the concentration in the shrub interspaces at these sites.

This distribution of elements in the Chihuahuan Desert shrublands is similar to that seen in both Mojave Desert shrublands, also dominated by *Larrea tridentata* (Table 2). In the Mojave Desert, N_{avail}, PO_4, Cl, SO_4, and K were always more concentrated under shrubs,

TABLE 3. Coefficient of variation [(SD ÷ mean) × 100%] for the overall mean concentration of soil elements at various sites in the southwestern United States. $n = 109$.

Element	Mojave Coxcomb shrubland	Mojave Ludlow shrubland	Sevilleta Shrubland	Sevilleta Grassland	Jornada Shrubland*	Jornada Grassland*	Central Plains grassland	Great Basin Shrubland	Great Basin Grassland
N_{avail}	91	99	103	60	68	43	92	88	48
					90	68			
PO_4	98	81	99	33	67	32	69	59	53
					52	82			
Cl	117	137	123	403	234	104	205	257	61
					100	98			
SO_4	120	79	131	68	134	88	31	132	38
					102	127			
K	51	74	17	20	20	25	17	39	27
					17	27			
Rb	26	19	11	18	15	14	22	23	26
					13	84			
Na	97	36	38	27	38	27	57	34	62
					21	18			
Li	34	20	15	80	20	29	ND	14	17
					9	ND			
Ca	42	18	10	33	21	30	20	18	18
					8	15			
Mg	26	19	16	20	11	16	24	24	29
					10	18			
Sr	32	86	17	28	14	23	24	16	16
					15	83			

* Values presented are for Shrubland 1 and Grassland 1 above, and Shrubland 2 and Grassland 2 below.

usually significantly so, whereas the concentrations of Rb, Ca, Mg, Na, Li, and Sr under shrubs were less than or equal to the concentrations in the shrub interspaces. A similar pattern was seen in the Great Basin Desert of Nevada.

Mean values for N_{avail}, PO_4, Cl, and SO_4 under grass clumps at the Sevilleta were not significantly different from the mean concentration in bare soils between grasses (Table 2). A similar pattern was seen at the Jornada, although at one site, the concentration of N_{avail} and Cl was higher under grass clumps. In all three Chihuahuan Desert grasslands, the concentrations of cations under grasses were always less than or equal to the concentrations in bare soils between grasses. The *Bouteloua gracilis* community at the Central Plains site also showed higher concentrations of N_{avail} and Cl under grass clumps, and no significant differences between samples taken from under grasses or bare soils for the remaining elements.

Coefficient of variation

The coefficient of variation (CV) associated with the mean concentration ($n = 109$) of each soil constituent offers an index of the overall variation of the soils at each site (Table 3). In Mojave, Chihuahuan, and Great Basin Desert shrublands, CVs were highest for N_{avail}, PO_4, Cl, and SO_4, and nearly always <40% for the remaining elements. In Chihuahuan Desert grasslands, the highest CVs were found for Cl and SO_4; a high CV for Cl was also seen in the Central Plains and Great Basin grasslands. CVs for N_{avail} and PO_4 in the Sevilleta and Jornada grasslands were lower than CVs for these

constituents in adjacent shrublands, with the exception of PO_4 in one Jornada grassland. Overall, CVs for cations were relatively low, suggesting that these elements have relatively similar concentrations among the samples taken in each community. Higher CVs for N_{avail}, PO_4, Cl, and SO_4 suggest that these constituents are more variable, especially in the soils of shrublands.

Correlations

There were significant, positive correlations among the concentrations of N_{avail}, PO_4, Cl, SO_4, and K in the Sevilleta shrubland. A similar pattern was seen in both Jornada shrublands, but the correlations were not always significant. At these Chihuahuan Desert sites, Rb, Ca, Mg, Na, Li, and Sr showed positive correlations, and these constituents were nearly always negatively correlated to N_{avail}, PO_4, Cl, SO_4, and K. A similar pattern (i.e., positive correlations among N_{avail}, PO_4, Cl, SO_4, and K and negative or no correlation of these to Rb, Ca, Mg, Na, Li, and Sr) was seen in the shrubland at Mojave-Ludlow; at Mojave-Coxcomb all constituents were positively correlated among the 109 samples.

Significant positive correlations were found among N_{avail}, PO_4, Cl, SO_4, and K in the Chihuahuan Desert grasslands. Rb, Ca, Mg, Na, Li, and Sr also showed positive correlations that were frequently significant, and, as in shrublands, the members of this group typically showed significant negative correlations to N_{avail}, PO_4, Cl, SO_4, and K. A similar pattern was seen among the samples from the Central Plains grassland, except for SO_4, which was positively correlated to all cations at that site.

TABLE 4. Spherical model geostatistics for semi-variograms expressing the distribution of constituents in Chihuahuan Desert soils. Ellipses indicate that the spherical model was not significant ($r^2 < 0.18$; $P > 0.05$). All semi-variograms were constructed using 20-cm lag intervals to a maximum lag of 700 cm. N:S is nugget-to-sill ratio; A_0 is the range. ND = not determined.

Element	Shrublands			Grasslands		
	N:S	A_0	r^2	N:S	A_0	r^2
Sevilleta NWR						
N_{avail}	0.35	102	0.25	0.35	294	0.55
PO_4	0.00	125	0.64	...	...	...
Cl	...	...	...	...	...	...
SO_4	...	...	...	0.35	230	0.35
K	...	...	...	0.03	121	0.62
Rb	0.30	218	0.56	0.40	555	0.64
Li	0.00	123	0.58	0.00	77	0.20
Na	0.00	46	0.39	0.44	605	0.65
Ca	0.35	>700	0.71	0.27	140	0.36
Mg	0.26	149	0.47	0.31	329	0.67
Sr	0.10	117	0.50	0.20	141	0.52
Jornada Experimental Range						
N_{avail}	0.61	183	0.23	0.76	555	0.25
	0.12	304	0.55	0.44	698	0.60
PO_4	0.35	>700	0.60	0.41	242	0.60
	0.23	349	0.83	0.00	48	0.46
Cl	0.09	>700	0.71	...	...	...
	0.17	298	0.61	0.21	>700	0.76
SO_4	0.59	187	0.19	0.07	272	0.45
	0.24	225	0.50	...	...	...
K	0.05	213	0.43	0.18	137	0.52
	0.30	249	0.57	0.00	125	0.67
Rb	0.20	>700	0.73	0.37	180	0.53
	0.69	288	0.23	...	...	...
Li	0.00	113	0.69	0.10	131	0.61
	0.23	>700	0.99	ND	ND	ND
Na	...	...	...	0.33	116	0.51
	0.52	>700	0.59	0.45	319	0.30
Ca	0.00	122	0.57	0.00	72	0.70
	0.16	>700	0.83	0.00	126	0.42
Mg	0.19	114	0.52	0.54	110	0.22
	0.38	222	0.64	0.17	189	0.65
Sr	0.00	128	0.52	0.00	71	0.46
	0.27	669	0.80	0.00	316	0.28

Geostatistics

For the Sevilleta grassland, a spherical model provides a significant fit to the semi-variogram of most soil constituents (Table 4). The nugget-to-sill ratio for N_{avail} indicates that only 35% of the variation is found at a scale <20 cm, but the remaining variance is found over a 294-cm range of autocorrelation (A_0), which does not appear to be associated with the mean size of grass clumps at that site (Fig. 2). Na is autocorrelated over a distance of ≈6 m, and PO_4 and Cl are essentially random (i.e., no fit to the spherical model; Fig. 3). These geostatistical observations are consistent with the observation that the concentrations of Na, PO_4, and Cl are similar in bare soils and under grasses (Table 2).

In the adjacent shrubland, N_{avail} and PO_4 are autocorrelated over distances of 102 and 125 cm, respec-

tively, close to the mean size of *Larrea tridentata* at the Sevilleta (142 cm, Cross 1994), suggesting that the spatial distribution of these elements may be associated with biotic processes operating at the scale of shrub islands. The semi-variograms for K, Cl, and SO_4, other elements with higher concentrations under shrubs (Table 2), show no spatial autocorrelation in the Sevilleta shrubland. Rubidium, Mg, Na, Li, and Sr have relatively low nugget-to-sill ratios and a limited range of spatial autocorrelation (49–218 cm) in the Sevilleta shrubland. The spatial autocorrelation of these elements is likely to be associated with the higher concentration of these elements in the shrub interspaces.

A similar pattern is seen in comparisons of N_{avail} between grasslands and shrublands at the Jornada Experimental Range (Table 4). In the two grassland sites, N_{avail} is autocorrelated over distances of 555 and 698 cm, and nugget-to-sill ratios indicate that 76 and 44% of the variance is found at distances <20 cm, respectively. In the two shrublands, the ranges of autocorrelation for N_{avail} are 183 and 304 cm, somewhat larger than the mean diameter of *Larrea tridentata* at the Jornada (88 cm; Ludwig et al. 1975), but much shorter than in grasslands. Unlike the Sevilleta, in the Jornada shrubland there is no evidence that biotic processes have "focused" the distribution of PO_4 at a scale that is associated with the size of *Larrea*. Na and Cl are also random, or autocorrelated over long distances, in both Jornada shrublands.

The spherical model provides a good fit to the semi-variogram for most soil constituents in the Mojave-Coxcomb shrubland (Table 5). The range of spatial autocorrelation for N_{avail} is within 2 SD of the mean diameter of *Larrea tridentata* shrubs measured during previous work at the Coxcomb site [140 ± 40 cm (Schlesinger and Jones 1984)]. At Mojave-Ludlow, N_{avail}, Cl, SO_4, and K are autocorrelated over a range that is less than or equal to the mean size of *Larrea tridentata,* consistent with observations of higher concentrations of these constituents under shrubs (Table 2). Autocorrelations in the distribution of cations, other than K, in the Mojave Desert shrublands are typically larger than the mean shrub diameter and likely to reflect the average size of intershrub spaces, in which they are more concentrated (Table 2).

Most soil constituents at the Central Plains grassland are autocorrelated over ranges >200 cm (Table 6), much larger than the mean diameter of *Bouteloua gracilis* or patches of bare soil (Hook et al. 1991). An exception is N_{avail}, for which 100% of the variance among samples is found within a range of 0–80 cm, perhaps related to root activity that extends for a radius of 30 cm around individual *Bouteloua gracilis* at this site (Milchunas et al. 1992). This coarse-scale distribution of soil N at the Central Plains site is in marked contrast to the pattern seen in the various grassland sites in the Chihuahuan Desert (Table 4).

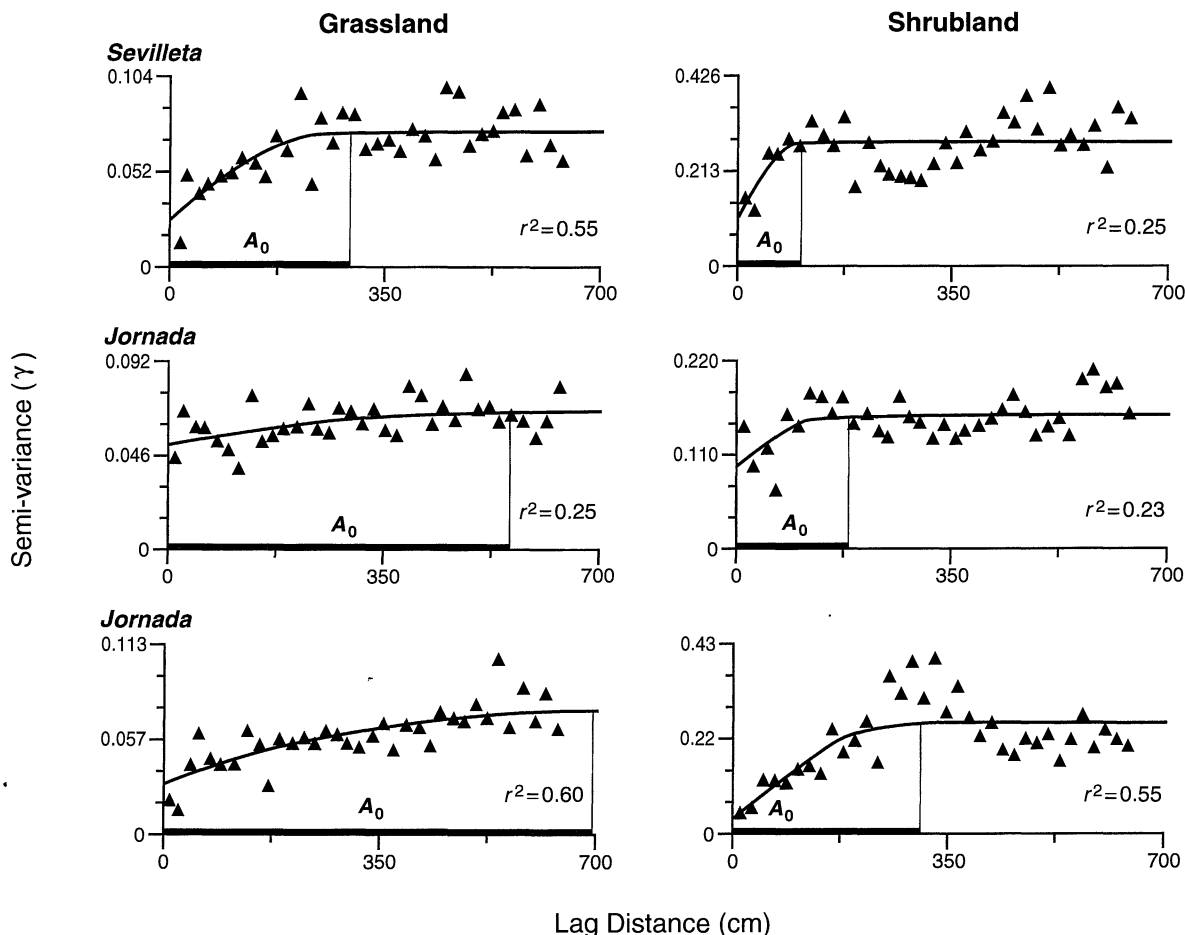With the exception of PO_4, all soil nutrients in the

FIG. 2.   Spherical model semi-variograms for the distribution of soil N_{avail} in grassland and shrubland soils at the Sevilleta National Wildlife Refuge and the Jornada Experimental Range in the Chihuahuan Desert of New Mexico.

Artemisia tridentata shrubland of the Great Basin desert are autocorrelated over distances of <350 cm (Table 7). Samples taken from the nearby *Bromus* grassland show a slight increase in the nugget-to-sill ratio for N_{avail} (cf. 0.44 vs. 0.00) and in the range of autocorrelation (cf. 215 vs. 193 cm), suggesting limited dispersal of N since the replacement of sagebrush by *Bromus* at this site. For SO_4, Cl, K, Ca, Mg, Li, and Sr the range of autocorrelation is shorter in grassland than in the shrubland, although the differences are not striking.

DISCUSSION

Although the application of geostatistics to study regional variations of soil properties is fairly common, relatively few workers have provided high-resolution analyses of the spatial dependence of plant nutrients in soils. Palmer (1990) found that most elements showed spatial autocorrelation within 5 m in forest soils of North Carolina, with P showing spatial dependence within 1 m. Lechowicz and Bell (1991) found that soil pH, K, and NO_3 were autocorrelated within a distance of 2 m in a forest in southern Quebec, where

the pattern of soil fertility helped to define plant distributions and the extent of gene flow between local populations. Stratton (1994) also related genetic variation among *Erigeron annuus* to fine-scale variations in soils in an old field in New Jersey. The distance of spatial autocorrelation in soils is typically longer under a uniform cover of grassland than in areas of woody vegetation. Robertson (1987) found that NH_4 and NO_3 were autocorrelated to distances of 20 m in an old-field community in Michigan.

Significantly, geostatistics allowed us to determine the scale of spatial dependence in the distribution of soil N in Chihuahuan Desert grasslands, and changes in the distribution of N_{avail} that are associated with the invasion of these grasslands by *Larrea tridentata*. Geostatistics indicate that 35–76% of the variation in N_{avail} in the three Chihuahuan Desert grasslands is found at a scale <20 cm, which may be due to local accumulations of soil N under *Bouteloua eriopoda*, a perennial bunchgrass. This high nugget variance suggests a fine-grained pattern in the distribution of N_{avail} in grasslands; the remaining variance is found over dis-
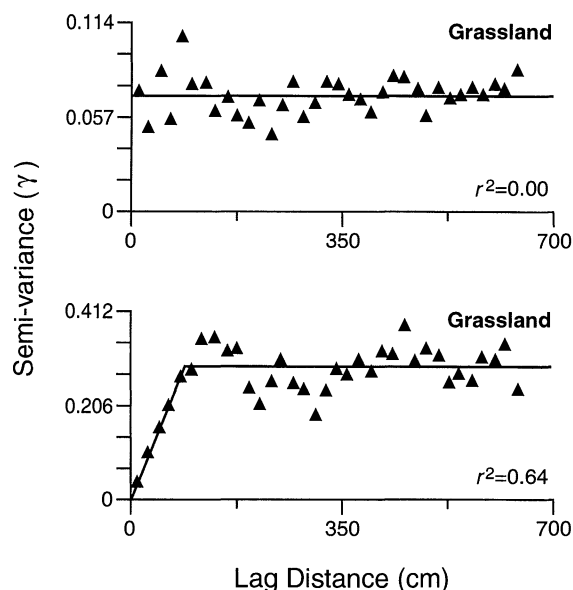
FIG. 3. Spherical model semi-variograms for the distribution of soil phosphate in grassland and shrubland soils at the Sevilleta National Wildlife Refuge, New Mexico.

tances from 20–300 cm (Sevilleta) or 20–700 cm (Jornada), which is unlikely to be related to nutrient cycling by grasses. In adjacent shrublands, in which *Larrea tridentata* has replaced these grasses over the last century, soil N_{avail} is more concentrated under shrubs (Table

TABLE 5. Spherical model geostatistics for semi-variograms of constituents in Mojave Desert soils. All parameters are described in the Table 4 legend.

Element	N:S	A_0	r^2
Coxcomb Mountains			
N_{avail}	0.29	199	0.49
PO_4	0.53	206	0.58
Cl	0.03	81	0.51
SO_4	0.33	195	0.54
K	0.01	144	0.67
Rb	0.19	122	0.42
Li	0.36	241	0.57
Na	0.28	>700	0.60
Ca	0.23	254	0.69
Mg	0.15	191	0.68
Sr	0.11	186	0.68
Ludlow			
N_{avail}	0.27	104	0.21
PO_4	···	···	···
Cl	0.00	46	0.22
SO_4	0.00	37	0.29
K	0.00	80	0.33
Rb	0.37	396	0.72
Li	0.28	489	0.58
Na	0.60	536	0.44
Ca	0.38	254	0.55
Mg	0.39	410	0.68
Sr	···	···	···

TABLE 6. Spherical model geostatistics for soil constituents in the Central Plains grassland. All parameters are described in the Table 4 legend.

Element	N:S	A_0	r^2
N_{avail}	0.00	80	0.27
PO_4	0.71	201	0.19
Cl	0.06	272	0.51
SO_4	0.19	250	0.31
K	0.29	>700	0.85
Rb	0.00	>700	0.83
Na	···	···	···
Ca	0.19	>700	0.86
Mg	0.07	>700	0.94
Sr	0.04	>700	0.94

2) and autocorrelated over distances extending to a maximum of 100–300 cm, which is likely to be due to biotic processes, i.e., biogeochemical cycling, acting at the scale of individual shrubs. As the shrubs develop "islands of fertility," they are more likely to be resistant to environmental perturbation and more likely to persist in the community (Reynolds et al., *in press*). Thus, changes in the distribution of soil properties may be a useful index of desertification in arid and semiarid grasslands worldwide (Schlesinger et al. 1990, Tongway and Ludwig 1994).

The islands of fertility associated with shrubs that have recently invaded areas of the Chihuahuan Desert are not as well developed as those found in the Mojave Desert, where some individual *Larrea tridentata* have existed for thousands of years (Vasek 1980). In the Mojave Desert, N_{avail}, PO_4, Cl, SO_4, and K are more concentrated under shrubs (Table 2); all are also autocorrelated over distances that are less than or equal to the mean diameter of *Larrea* at each site (Table 4; except PO_4 at Mojave-Ludlow). In contrast, in the Sevilleta shrubland, N_{avail}, PO_4, Cl, and K are more concentrated under shrubs than in the shrub interspaces, but only N_{avail} and PO_4 show significant autocorrelations, over distances of 102 and 125 cm, which may

TABLE 7. Spherical model geostatistics for semi-variograms for soil constituents in the Great Basin Desert near Reno, Nevada. All parameters are described in the Table 4 legend.

Element	Shrubland			Grassland		
	N:S	A_0	r^2	N:S	A_0	r^2
N_{avail}	0.00	193	0.71	0.44	215	0.58
PO_4	···	···	···	0.56	>700	0.57
Cl	0.33	202	0.37	0.62	158	0.25
SO_4	0.32	173	0.53	0.27	93	0.38
K	0.00	254	0.31	0.00	125	0.60
Rb	0.46	208	0.32	0.42	>700	0.67
Li	0.37	270	0.39	0.14	181	0.61
Na	0.58	239	0.25	0.15	406	0.79
Ca	0.20	240	0.65	0.00	196	0.70
Mg	0.42	344	0.62	0.22	261	0.74
Sr	0.33	272	0.48	0.34	252	0.56

be related to local nutrient cycling by shrubs. We speculate that "islands of fertility" may develop most rapidly for the elements that are typically the most limiting to plant growth in desert soils.

Smith et al. (1994) report spatial autocorrelation in nitrogen mineralization potential and other soil properties over distances of ≈100 cm in a sagebrush desert in Washington, and Jackson and Caldwell (1993) used geostatistics to demonstrate autocorrelation within 100 cm in the distribution of N, P, and K under shrublands of the Great Basin Desert of Utah. The autocorrelations for soil nutrients in our Great Basin shrubland frequently extended to 200 cm. When these desert shrubs are eliminated, the "islands of fertility" are slow to disappear. Burke et al. (1987) found little change in the distribution of soil nutrients 14 yr after the elimination of *Artemisia tridentata* from a desert in Wyoming. Forty-five years after the loss of sagebrush in our site near Reno (Billings 1990), soil N_{avail} is still autocorrelated over distances of 0–200 cm in the *Bromus* grassland that has replaced it (Table 7).

Shrub islands are the locus of biotic activity and biogeochemical cycling in desert ecosystems on all continents (e.g., Gerakis and Tsangarakis 1970, Noy-Meir 1985, Mazzarino et al. 1991, Tongway and Ludwig 1994, Herman et al. 1995). Despite their widespread occurrence, we know relatively little about the processes leading to their formation. Both physical and biological factors may be important (Garner and Steinberger 1989, Tongway and Ludwig 1994). Where desert shrubs have recently invaded grassland habitats, the islands may represent a residual or "lag" deposit that remains following the erosion of soil from the intershrub spaces (Rostagno et al. 1989, Abrahams and Parsons 1991). Alternatively, analyses of soil particle size suggest that the fine-grained soils in many shrub islands may result from the deposition of windblown materials that are captured by the shrub canopy (Elkins et al. 1986, Coppinger et al. 1991). Differential rainsplash, as a result of the dissipation of raindrop energy in the shrub canopy, also results in the directional transport of soil materials toward shrub islands (Parsons et al. 1992). Finally, the uptake of soil nutrients by vegetation, and the subsequent deposition of litter and throughfall under the canopy, biogeochemical cycling, may result in an accumulation of elements that are important to plant nutrition (West and Skujins 1977).

High concentrations of N, P, and K under vegetation in various *Larrea tridentata* shrublands speak strongly for the importance of biotic processes in the development of "islands of fertility" in deserts. Nitrogen is limiting to net primary production in soils of the Chihuahuan (Fisher et al. 1987) and Mojave Deserts (Sharifi et al. 1988), potentially selecting for efficient local recycling of nitrogen by desert shrubs. The accumulation of K under shrubs indicates selective biotic accumulation and cycling of K (vs. other cations) during the development of shrub islands. It is noteworthy that

Rb, which is often used as a tracer for K in studies of plant nutrition (Smith and Epstein 1964, Hafez and Stout 1973), shows no tendency to accumulate under shrubs (Table 2).

Accumulations of Cl and SO_4 under shrubs suggest that indirect factors associated with the presence of shrubs may also affect the distribution of some constituents in desert soils. These ions may move passively in the mass flow of water driven by plant transpiration, accumulating in shrub islands over long periods of time. Chloride is strongly concentrated under shrubs and autocorrelated over distances less than the mean shrub size in the Mojave Desert (Tables 2 and 5). If physical processes alone determined the distribution of Cl, we would expect a random distribution or a distribution that would be highly correlated to that of other mobile ions (e.g., Na and Li) in surface soils.

We suggest that physical processes are important determinants of the distribution of most cations in desert shrublands; however, the distribution of these ions is nonrandom. Calcium, Mg, Na, Rb, Li, and Sr were often slightly more concentrated in the soils between shrubs, especially in the recently desertified sites in the Chihuahuan Desert (Table 2). At the Sevilleta, erosion of the surface soil from the shrub interspaces has exposed fractured portions of the underlying soil calcic horizon, potentially leading to high concentrations of exchangeable Ca in these soils. Soil cations may also be transported locally by overland flow, which accumulates and evaporates in the shrub interspaces. Romney et al. (1980) and Virginia and Jarrell (1983) also report that exchangeable Na was more concentrated in the shrub interspace than under vegetation for sites in the Mojave and Sonoran Deserts.

We suggest that comparisons of soil heterogeneity are a useful index of desertification. Grassland ecosystems show a fine-scale distribution of soil constituents, whereas desert shrublands show a coarse-grained distribution, in which the pattern for essential, limiting plant nutrients is autocorrelated to the area of biogeochemical cycling under the shrub canopy.

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APPENDIX

The mean concentration of soil constituents measured in bare soils (between vegetation) in the field sites. All values are in micrograms per gram, determined by various methods of extraction given in the *Methods: Laboratory analysis.* To calculate the mean value for samples taken under vegetation, multiply these values by the respective values in Table 2.

Element	Mojave Coxcomb shrubland	Mojave Ludlow shrubland	Sevilleta Shrubland	Sevilleta Grassland	Jornada Shrubland*	Jornada Grassland*	Central Plains grassland	Great Basin Shrubland	Great Basin Grassland
N_{avail}	2.32	1.97	1.45	1.14	2.01 / 3.94	1.54 / 0.92	5.16	6.32	12.11
PO_4	1.70	3.11	1.07	3.46	4.32 / 3.48	1.89 / 0.54	4.29	9.37	10.65
Cl	1.89	2.11	1.37	0.25	5.91 / 2.39	1.36 / 1.42	1.82	1.05	3.41
SO_4	4.96	2.02	3.53	0.94	1.05 / 3.34	0.89 / 2.47	8.26	3.85	8.12
K	94.1	176.5	258.0	137.2	210.8 / 313.8	139.7 / 267.0	189.2	186.3	274.3
Rb	0.14	0.33	0.57	0.24	0.31 / 0.07	0.34 / 0.07	0.69	0.32	0.63
Na	3.53	3.31	1.80	1.87	1.65 / 1.73	0.97 / 1.27	9.62	7.10	19.09
Li	0.05	0.08	0.10	0.06	0.06 / 0.12	0.08 / ND	ND	0.04	0.08
Ca	977.5	893.8	3141.8	841.6	1432.4 / 2639.3	1672.9 / 2792.8	1557.0	1003.6	1960.0
Mg	44.8	136.5	122.6	119.4	119.8 / 114.3	84.2 / 111.3	267.7	271.8	487.9
Sr	6.4	11.2	8.5	5.4	7.3 / 1.1	6.7 / 8.6	1.3	10.7	18.7
n	95	91	71	44	64 / 76	59 / 37	9	63	109

* Values presented are for Shrubland 1 and Grassland 1 above, and Shrubland 2 and Grassland 2 below.