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FERTILE ISLAND DEVELOPMENT AROUND PERENNIAL SHRUBS
ACROSS A MOJAVE DESERT CHRONOSEQUENCE

John D. Bolling[1,2] and Lawrence R. Walker[1]

ABSTRACT.—Spatial heterogeneity has been examined only recently as a factor in studies of ecosystem processes. The effect of this factor on desert organisms is exemplified in the "fertile island"—a concentration of essential soil nutrients under perennial shrubs. In this study we examined fertile island patterns in undisturbed desert areas and on abandoned roadways to see at what rate and magnitude these fertile patches reappeared after disturbance. Small-scale examination of patterns of soil P, organic matter, moisture, and bulk density showed that soils beneath *Larrea tridentata* (DC.) Cov. shrubs on the roads lacked the tight circular gradient in these variables that was characteristic of soils beneath control shrubs, even 88 years after road abandonment. The nature of the initial soil disturbance altered both spatial patterns of soil N and temporal patterns of fertile island development. Fertile island patterns for total soil N, available P, and organic matter were more circular than patterns for bulk density, texture, or pH. We suggest that patterns of soil heterogeneity may develop first for elements that may be limiting to desert shrub growth (N, P, organic matter), followed by spatial development in other less limiting soil factors (bulk density, texture, pH).

Key words: *disturbance,* Larrea tridentata, *revegetation, soil recovery, succession.*

The realization of the important role of spatial heterogeneity in the study of ecosystem processes has been a fairly recent development (Armesto et al. 1991, Dutilleul and Legendre 1993, Schlesinger et al. 1996). One example of spatial heterogeneity is differences in soil factors adjacent to shrubs in desert ecosystems. The abrupt change in soil factors such as nitrogen (N), phosphorus (P), and organic matter from beneath perennial shrub canopies to intershrub spaces is called the "fertile island" effect (García-Moya and McKell 1970). Fertile island formation is primarily a biological process (Garner and Steinberger 1989) whereby plants and animals concentrate mineral nutrients from a wide area to the island and into plant biomass (Binet 1981).

Soil properties of fertile islands are well documented. Organic matter and pH are spatially variable because of fertile islands (Jackson and Caldwell 1993a), and the availability of N and P increases under shrubs (Romney et al. 1980, Skujinš 1981). These changes are especially important because N and P are the elements considered most limiting to plant growth in arid regions (Schlesinger et al. 1996). On a microscale, soil conditions can change drastically within centimeters. For example,

heterogeneity for N at small scales can be expected because of the susceptibility of NH_4 and NO_3 to local microbial transformations (Jackson and Caldwell 1993b). The highest level of microbial activity in deserts occurs around plant roots (Vollmer et al. 1973, Binet 1981).

Ecologists generally agree that the consideration of spatial heterogeneity is critical in studies of pattern and process at many scales. The functional significance of spatial heterogeneity is not well understood, however. A clear grasp of spatial heterogeneity can contribute to the understanding of some of the mechanisms behind apparent successional changes (Armesto et al. 1991). Spatial heterogeneity, or the lack thereof, likely has a strong impact on vegetation development through time.

Plant succession has not been thoroughly examined in desert ecosystems. Most previous studies have dealt only with plant community recovery after a single disturbance event (Wells 1961, Webb and Wilshire 1980, Prose et al. 1987), and aside from studies of compaction, no attempt has been made to study mechanisms of desert succession. The slow rate of vegetation development in deserts suggests that the general dogma about successional trends,

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such as an increase in nutrient availability through time, may not hold in this system. Difficulties in applying successional theories to deserts may also be due to the extreme nature of the desert environment. Plant life is overwhelmingly influenced by drought. Soil structure can be fragile and is very slow (on a human time scale) to recover after disturbance. Soil development processes are on the order of centuries to millennia (McAuliffe 1991, McAuliffe and McDonald 1995, Bolling and Walker 2000), not decades as in more mesic systems.

The study of desert succession is further confounded by the question of how to study such a heterogeneous system. The effect of disturbance on these spatially heterogeneous patterns has been examined only recently (Schlesinger et al. 1996). In general, disturbances can either increase or decrease the heterogeneity of the landscape (Risser 1987). The nature of the disturbance is likely to have some effect on rates of recovery of natural patterns of spatial heterogeneity.

The purpose of this study was to examine the development of spatial patterns in soil factors around *Larrea tridentata* (DC.) Cov. shrubs using geostatistical techniques. *Larrea*, a dominant species in the Mojave Desert scrub community, has obvious spatial effects on soil properties (fertile islands) and has a very long life span (Vasek 1980), which makes the presence of this species indicative of long-term recovery from disturbance. *Larrea* growth is supposedly limited by N in this system (Fisher et al. 1988, Sharifi et al. 1988) but may not be limited by P (Lajtha 1987).

Our study examined 3 abandoned road sites along a chronosequence of 21–87 years and was conducted in the context of soil and plant community restoration efforts being done by the National Park Service. Restoration efforts have been under way for some time in this region, but none has yet proven successful on a time scale measurable by a single researcher. For this reason it is important to examine natural patterns of vegetation recovery following disturbance.

In this paper we seek to ascertain whether fertile islands appear on disturbed roads in the Mojave Desert and, if so, how long they take to develop. Finally, we seek to determine how spatial scale affects nutrient heterogeneity.

METHODS

Three unpaved roads, abandoned in 1907, 1940, and 1974, were chosen for this study. The roads are located within the Cottonwood Valley (35°N, 115°W; 240–450 m elevation), adjacent to Lake Mohave in the Lake Mead National Recreation Area in southern Nevada and western Arizona, USA (Fig. 1). We selected 3 roads within the same watershed in an attempt to minimize geological, climatic, and elevational differences among the roads. Records of National Park Service land acquisitions and reports from National Park Service personnel (Jim Riley, Bill Burke) were used to determine the time since road abandonment. Road 1 (21 years since abandonment) was "bladed"; i.e., topsoil was removed by a bulldozer, and the road was characterized by the presence of lateral berms. Road 2 (55 years since abandonment) was a track-type road, impacted only by surface vehicular traffic and with a characteristic raised center berm. This road may have had intermittent use since its nominal abandonment date. Road 3 (88 years since abandonment) was a railroad bed that had ties and track removed before abandonment. Thus, it was similar to road 1 where surface soils had been pushed to the sides to form lateral berms.

All sites in the study are located on loamy sand alluvium derived from basalt (Volbroth 1973, Anderson 1978) that is classified as a shallow, hyperthermic aridisol (Soil Conservation Service 1993). All soils are underlain by a layer of hardpan caliche at 1–2 m depth. The climate is typical of the Mojave Desert, with hot summers, cool winters, and low episodic rainfall (Ehleringer 1985). Most precipitation occurs in the winter; the mean yearly precipitation at Cottonwood Cove is 10.9 cm (Soil Conservation Service 1993). Variance around this mean is extraordinarily high, with small and spatially heterogeneous summer rainstorms. Mean monthly temperatures at Cottonwood Cove range from 10.1°C in January to 33.4°C in July (Soil Conservation Service 1993).

Small-scale Spatial Analysis

During 1994 we subjectively chose 1 individual *Larrea* shrub in the center of each of the 3 roads and in adjacent control areas for analysis of the small-scale structure of fertile islands. Paired control shrubs were chosen from
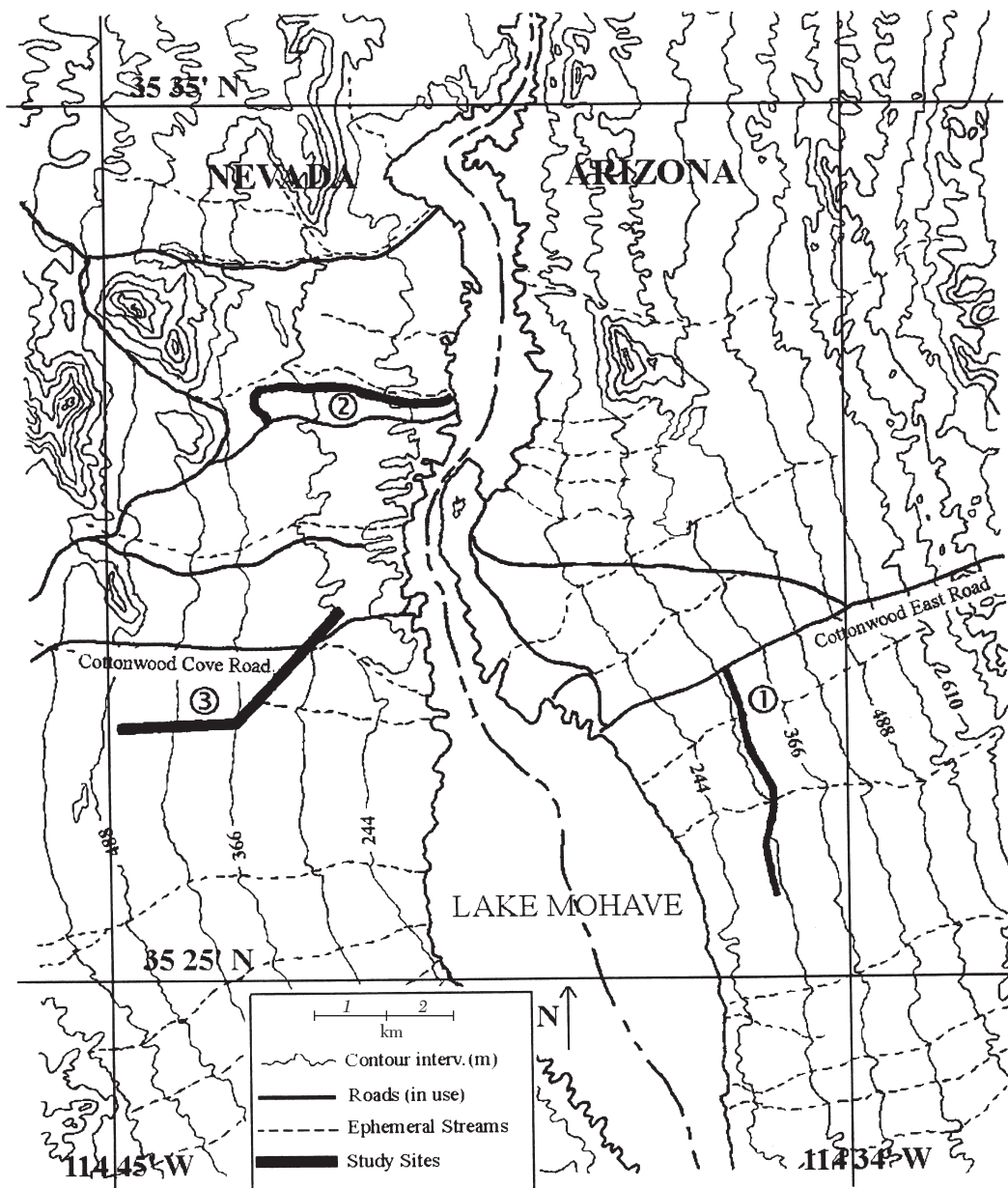
Fig. 1. Cottonwood Valley region, Lake Mead National Recreation Area, Nevada and Arizona, with road locations.

the adjacent undisturbed desert; these shrubs were similar in area and volume to road shrubs ($P > 0.05$; data not shown). Control shrubs were all located within 50 m of the road shrub, but at least 30 m away from the road. The longest canopy radius of each shrub was doubled to define the boundaries of a square plot in which we obtained soil samples from a grid (Fig. 2; $n = 36$ points · shrub^{-1}). After removing surface litter, we collected soils from 2 depths (0–7.5 cm and 7.5–15 cm). Moisture, organic matter, pH, and total N were determined for each soil sample, as described under laboratory methods.

Medium-scale Spatial Analysis

For the more extensive portion of this study, all *Larrea* shrubs on each road were identified, and 10 shrubs per road were selected based on location (no shrubs in gullies were chosen) and size (no shrubs <10 cm height). Only 9 were available on road 3. Paired control shrubs were again chosen in the adjacent, undisturbed desert as described above. Soils were sampled from 3 positions: directly under the shrub and at the canopy edge in July 1995, and in the intershrub spaces in May 1995. All soil sampling sites were located on 2 sides of the shrub in the directions paralleling the road. After removing surface litter, we collected soils from 2 depths (0–7.5 cm and 7.5–15 cm; $n = 2$ samples per position per shrub) at the under shrub and canopy edge positions, and then composited the samples per position after passage through a 2-mm sieve. This yielded 4 samples per shrub not counting the intershrub space sampling. A subsample of the thoroughly mixed composite sample was placed in a sealed soil tin and refrigerated at 5°C prior to analysis within 72 hours. For each soil sample, we determined moisture, organic matter, pH, total N, particle size, bulk density, available N, and available P as described under laboratory methods. The shrub-standardized design allowed comparisons of spatial heterogeneity of soil factors due to shrub processes alone, regardless of shrub size.

Large-scale Spatial Analysis

Large-scale spatial analysis involved examining and manipulating data collected in the previous section. Values for each parameter were pooled and means for each shrub combined to reveal a mean and variance value across all 3 roads.

Laboratory Methods

After removing 20 g of fresh soil for analysis of KCl extractable N, we weighed the soils from the medium-scale spatial analysis, dried them in a 105°C oven until they reached a constant mass, and reweighed them to determine fine soil bulk density and soil moisture content. Soil pH was determined with a glass electrode on a 5-g sample of dry soil saturated with 5 mL deionized H_2O (McLean 1982). After oven-drying, a 0.5-g sample of each soil was digested in sulfuric acid with a mercuric
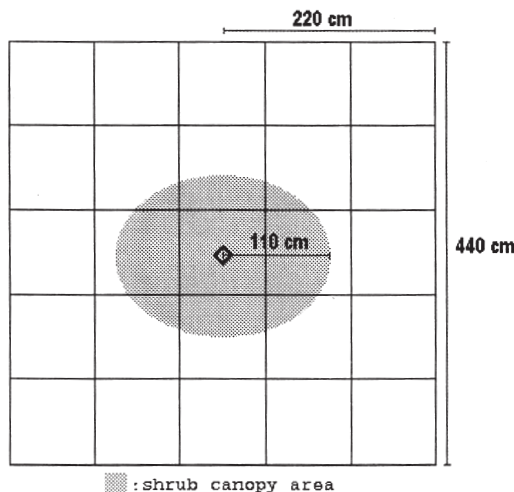

Fig. 2. Depiction of sampling grid for small-scale spatial heterogeneity work. Sampling points were established at each line intersection ($n = 36$ points per shrub). Samples were collected at 2 depths (0–7.5 cm and 7.5–15 cm) for a total of 72 samples per shrub. This figure depicts an example shrub that measures 110 cm across.

oxide catalyst, then analyzed colorimetrically for total Kjeldahl nitrogen using an automated salicylate procedure (U.S. EPA 1984). Particle size determinations were done on a subset of samples (3 shrubs per road) using the Bouyoucos hydrometer method (Day 1982). We determined organic matter content of oven-dried soils by mass loss after ignition at 550°C for 4 hours (Black 1965).

The available nitrogen pool was determined on 10 g of fresh soil after extraction in 100 mL of 2M KCl for 4 hours on a benchtop shaker. The supernatant was analyzed for inorganic N (Keeney and Nelson 1982) using an automated Cd reduction procedure (NO_2 and NO_3) and an automated phenol procedure (NH_4; Alpkem 1991). An additional 10 g of fresh soil was placed into a 40-mL tube that was then filled with distilled H_2O and placed in a 40°C oven for 1 week, after which NH_4 levels were again determined. Nitrogen mineralization was then calculated as the difference between postincubation and preincubation $NH_4 + NO_2 + NO_3$ concentrations (Keeney 1982, Lober and Reeder 1993) and reported as molecular N.

Phosphorus availability was assessed using 3 g of bicarbonate-treated Dowex 1-X8 anion exchange resin enclosed in a nylon mesh bag (Sibbesen 1978, Lajtha 1988). This procedure

is a measure of only the most biologically available forms of phosphorus (Lajtha and Schlesinger 1988).

Statistical Analyses

Data to assess spatial variability on a microscale were examined visually because attempts to use Kriging—a method of assessing structure in spatially arranged data (Fry 1993)—resulted in flat semi-variograms (an indication that variation did not increase with distance). For the medium-scale spatial analysis data, we used a principal components analysis (PCA; SAS Institute 1987) to compare fertile island structure around shrubs from the 3 roads. Five soil variables (bulk density, available P, total N, organic matter, and pH) at 3 positions (under shrub, canopy edge, intershrub space) were used for this analysis.

Particle size data were excluded from this analysis due to incomplete data (soils around only 3 shrubs per road examined for this), and moisture and N mineralization were excluded due to different collection times; levels of moisture and N mineralization likely changed between May and July 1995. For each observation and each principal component (PC) score, we subtracted road values from paired control values, and these differences were subjected to a multiple analysis of variance (MANOVA), with road number and position as main effects (StatSoft, Inc. 1995). This type of analysis allows the comparison of fertile island structure across roads given any background structural differences in control fertile islands. The MANOVA analyses of soil factors were run on the 2 depths separately.

Soil variables not included in the PCA (moisture, N mineralization, sand, clay) were individually subjected to a 3-way analysis of variance (ANOVA), with treatment (road, control), road number (1–3) and position (1–3) as main effects (StatSoft, Inc. 1995). Sand and clay values were compared across all 3 positions, but for moisture and N mineralization, only the under shrub and canopy edge positions were compared.

Coefficients of variation were examined for all soil factors on the medium-scale data, pooling all positions (under shrub, canopy edge, intershrub space) per shrub. Spatial variance in total soil nitrogen was examined at small (36 points around individual shrubs), medium (within each road; all points around each shrub pooled), and broad (across roads; poolings of each shrub pooled per road) scales. Statistical comparisons of variance across the scales could not be performed for these data because $n = 1$ value of variance per group.

RESULTS

Concentrations of total soil N showed more pronounced patterns around shrubs (Figs. 3, 4) than any other soil parameter. Kriging was successful on the road 1 control shrub, showing autocorrelation at a distance of approximately 1 m (data not shown). Fertile island structure around the single shrub where it could be properly examined was thus similar to the structure found by Schlesinger et al. (1996), who found autocorrelation at distances of 1–3 m for soil N around *Larrea* shrubs. We expect that decreases in autocorrelation distance occur as fertile patches form in this region.

Patterns of total soil N differed visually among roads, but there were no clear temporal patterns. In general, control shrubs appeared to show a more pronounced island effect in soil N than road shrubs (tighter circular gradients; Figs. 3, 4). Only the fertile island around the road 2 (intermediate age) shrub showed a pattern of soil N that was more pronounced than its paired control shrub (Figs. 3c, 3d). The road 3 shrub unexpectedly showed a lack of development of a natural soil N fertile island pattern altogether, despite its being the oldest road.

The PCA of soil factors showed very even component loadings for PC axis 1 (Table 1). This axis was not heavily dependent on the levels of any single soil parameter, but rather was defined by an even combination of all parameters. Changes in fertile island structure thus involve changes in a complex combination of the soil factors measured in this study. PC2, on the other hand, showed a strong dependence on the level of available soil phosphorus (high PO_4 = high PC2 levels). Individual variables did emerge as influential for PC axes 3–5, but these axes each expressed <10% of the total variance in the data set. PC axes 1 and 2 expressed 54% and 20% of the variance, respectively.

No significant road or treatment effects were seen in the MANOVA analyses of PC score differences for depth 1 (0–7.5 cm; Table 2). A
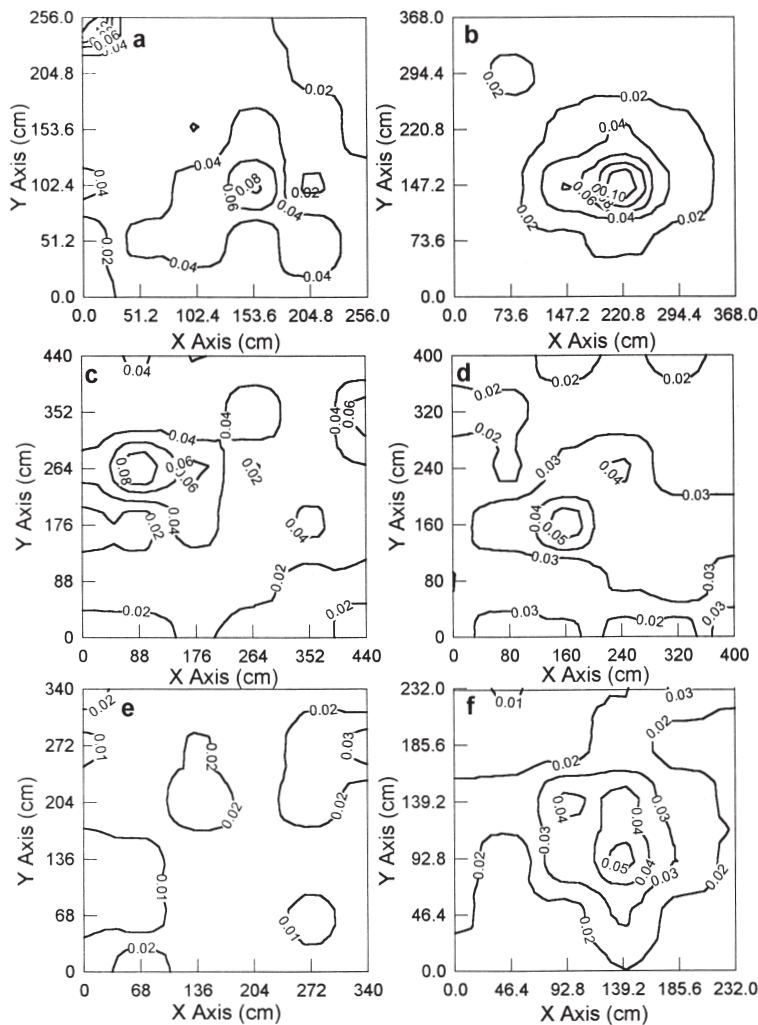
Fig. 3. Small-scale total soil nitrogen patterns (%) around individual *Larrea* shrubs (0–7.5 cm depth). Labels indicate sampling locations; shrub base is in exact center of plot (a = road 1; b = road 1 control; c = road 2; d = road 2 control; e = road 3; f = road 3 control). Road age increased with road number.

significant road-by-position interaction was seen for this depth, however. This shows that overall fertile island structure varies across the roads in terms of these variables at 0–7.5 cm depth. Both a road effect and a road-by-position interaction were found for depth 2 (7.5–15 cm; Table 2). The effects seen here were not unidirectional across time, however, yielding no meaningful successional relationship.

The presence of road-by-treatment interactions led us to examine PCs on a one-by-one basis. PC2 emerged as the most important factor to explain differences in road and position for both depths. This factor was dominated by

the levels of soil PO_4 (Table 1). Road 2 (55 years since abandonment) was the only site where a positional difference in the control PC2 minus road PC2 value was found for 0–7.5 cm depth (Fig. 5a). At 7.5–15 cm depth, this was true only for road 3 (Fig. 5b).

Soil factors not included in the PCA (soil moisture content, N mineralization, percent sand, and percent clay content) were subjected to a 3-way ANOVA, which showed no significant trends with time or treatment. The comparisons of coefficients of variation across all sites and treatment types showed that total N, available P, and soil organic matter had

Fig. 4. Small-scale total soil nitrogen patterns (%) around individual *Larrea* shrubs (7.5–15 cm depth). Labels indicate sampling locations; shrub base is in exact center of plot (a = road 1; b = road 1 control; c = road 2; d = road 2 control; e = road 3; f = road 3 control). Road age increased with road number.

TABLE 1. Eigenvectors for principal component analysis of soil variables.

Variable	PC1	PC2	PC3	PC4	PC5
Percent variance	54	20	8	7	5
Bulk density	−0.451	0.292	0.755	0.362	0.101
Total N	0.494	0.200	−0.167	0.826	−0.082
Available P	0.192	0.914	−0.071	−0.350	−0.002
pH	−0.499	0.147	−0.541	0.216	0.625
Organic matter	0.517	−0.133	0.322	−0.136	0.770

higher levels of spatial variation than the other soil parameters measured (excluding N mineralization and soil moisture that may measure temporal variability as well; Tables 3A, 3B).

Soil clay content also had relatively high variation. Fertile island structure was therefore based mostly on changes in the most variable parameters.

TABLE 2. *P* levels for MANOVA effects: principal components 1 through 5.

Effect	0–7.5 cm	7.5–15 cm
Road	0.122	**0.000244**[a]
Position	0.23555	0.541221
Road * position	**0.000545**	**0.000002**

[a]Significant effects are in boldface type.

Spatial variation across different scales was compared by examining total soil N around individual shrubs (small scale), across 10 shrubs on one road (medium scale), and across all roads (large scale). Successional trends were apparent at the 0–7.5 cm depth only, with variance decreasing as time since road abandonment increased (Fig. 6). Although samples were collected during different months, levels of total soil N are not subject to broad annual fluctuations (Wallace et al. 1978); thus, this comparison is based solely on spatial variation rather than on spatial and temporal variance combination. Control soils across the region also differed, with the highest variance in soil N seen at the control sites for road 1 in 3 of 4 comparisons. At the medium scale of depth 2 (7.5–15 cm), control soils for road 3 had higher variance for soil N than any other area. Trends in depth 2 are difficult to explain. The variance did not tend to decrease as spatial scale increased, as depth 1 showed (Fig. 6).

DISCUSSION

We did not find significant chronosequence trends in fertile island development. These results confirm the findings of a broader study which found no apparent successional changes in a range of soil variables across 8 roads (Bolling and Walker 2000). Total soil N levels, and thus fertile island magnitude, were higher and more spatially distinct under road 2 shrubs than either of the other 2 roads. Roads 1 and 3 were initially disturbed by blading, which removed surface soils and destroyed vegetation. Road 2, however, was subjected only to surface vehicular traffic, leaving a characteristic "center berm." This center berm was where all perennial vegetation on the road was later found. Surface soils and fertile island structure thus were likely preserved, and *Larrea* individuals may have resprouted from root crowns after removal of aboveground structures.
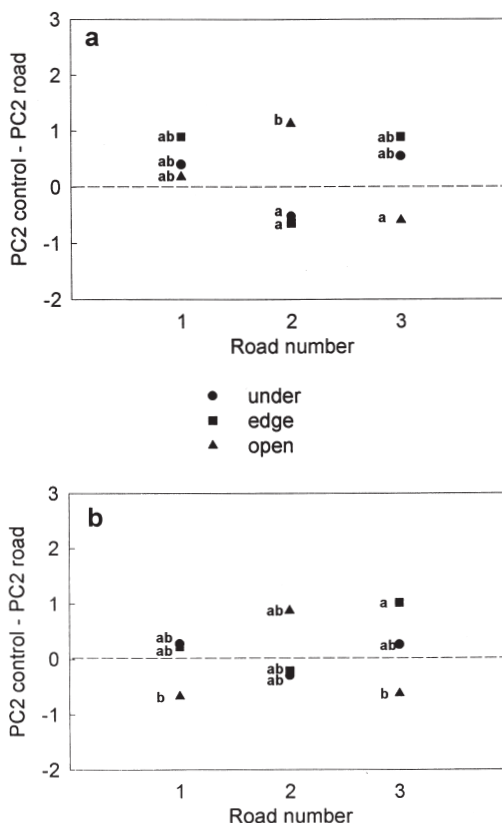

Fig. 5. PC2 differences for (a) 0–7.5 cm depth and (b) 7.5–15 cm depth as a result of MANOVA analysis. PC2 is defined primarily by the level of available soil phosphorus. Values above the dashed line have higher PC2 levels in control soils than road soils, and vice versa. Values are means of 10 samples · road^{-1} for roads 1 and 2, and 9 samples for road 3. Pairwise differences between means are not significant ($P < 0.05$) when preceded by the same letter.

Application type is more influential than time in determining spatial patterns and concentrations of available soil P and organic matter content, both of which were higher on road 2 than on the other 2 roads. The raised center berm on road 2 may have facilitated the aeolian deposition of organic materials on center berms (as described by Allen 1988). The effect of the central berm might also have had an impact on soil water relationships and nutrient content, as microtopography can have strong effects on water infiltration and runoff on desert watersheds (Schlesinger and Jones 1984).

In the medium-scale examination of 10 shrubs per road, road 2 had higher available P

TABLE 3. Coefficients of all soil parameters.

Parameter units	n[a]	Road number					
		1		2		3	
		Road	Control	Road	Control	Road	Control
A 0–7.5 cm depth[b]							
Total N (%)	30	66.0	66.2	56.8	46.5	50.1	63.0
Available P							
($\mu g \cdot g^{-1}$ soil)	30	44.2	57.6	88.2	40.0	34.0	43.7
Organic matter							
(%)	30	40.7	38.5	15.8	16.2	42.6	26.7
Bulk density							
($g \cdot cm^{-3}$)	30	10.3	10.2	6.3	7.7	9.8	7.0
Clay (%)	9	21.4	25.9	22.5	26.7	11.4	23.6
Sand (%)	9	5.4	15.4	9.2	17.3	4.9	9.1
pH	30	2.4	2.0	1.7	1.4	1.9	1.6
Moisture (%)	30	77.4	91.0	69.7	73.1	60.7	46.2
N mineralization							
($\mu g \cdot g^{-1} \cdot wk^{-1}$)	30	264.9	209.9	−264.5	−5544.3	−145.9	−182.1

[a]All positions (under shrub, canopy edge, intershrub space) combined. Negative values for N mineralization are due to net immobilization. Intershrub soils data collected 5/95; canopy edge and under shrub soils collected 7/95. Therefore, moisture and N mineralization data measure temporal variability as well as spatial and should be interpreted with caution.
[b]For all data except sand and clay, $r = 27$ for road 3 and road 3 controls.

than paired controls. This was true for both depths, although only significant for the shallow depth (Figs. 5a, 5b; PC2 is dominated by the levels of PO_4 [see Table 1]). Phosphorus acquisition and cycling were thus more efficient in the road 2 shrubs than in paired controls. Road 3, in contrast, showed the opposite pattern: fertile island soils on roads had less available P than their paired controls, whereas intershrub samples had more. This pattern was observed again for both depths, although significant only for the deeper soils (Figs. 5a, 5b). This result may have been caused by reduced P uptake on road 3 because of less belowground biomass. An examination of belowground processes (water movement, annual and perennial root dynamics) may help explain these results.

Total N, available P, and organic matter have higher coefficients of spatial variation than the other soil parameters (Tables 3A, 3B). Jackson and Caldwell (1993a) found similar patterns in southern Utah. The ultimate causes of fertile island formation are biological (Garner and Steinberger 1989) and are affected by shrub processes (growth and abscission of roots and shoots), decomposition, and physical transport of organic materials by animals. Proximate causes might include changes in soil texture and aeolian effects. It is reasonable to expect biologically important soil nutrients

to be more spatially dependent than less limiting factors.

Successional trends were found in the analysis of variance of total soil N. However, variance in total soil N decreased as time since road abandonment increased (Fig. 6). This was most apparent at the smallest scale and at the shallower depth. Variance in soil N also changed across control sites, indicating that soils in this region are inherently different. Variance also tended to decrease as spatial scale increased, showing general convergence of patterns at larger scales. This result exemplifies the importance of small-scale spatial heterogeneity (i.e., around individual shrubs) in the Mojave Desert ecosystem.

Whether soil heterogeneity is caused by shrubs, or shrub occurrence is controlled by soil heterogeneity is a matter of speculation. Some aridland species (e.g., *Artemisia tridentata* ssp. *vaseyana* [Rydb.] Beetle and *Agropyron desertorum* [Fisch. ex Link] Schult.) can effectively exploit preexisting fertile patches (Caldwell et al. 1985), while others (e.g., *Larrea*) can clearly affect the soils around them. There is a need for future studies to address the issue of spatial resource heterogeneity in the Mojave Desert.

Broad temporal fluctuations in nutrient mineralization and moisture were apparent in this study. The climate in this region is charac-

TABLE 3. Continued.

Parameter units	n^a	Road number					
		1		2		3	
		Road	Control	Road	Control	Road	Control
B 7.5–15 cm depth[b]							
Total N (%)	30	54.8	47.8	57.0	33.1	45.5	82.8
Available P							
($\mu g \cdot g^{-1}$ soil)	30	48.6	61.2	67.3	46.6	38.6	60.9
Organic matter							
(%)	30	25.8	20.6	19.4	18.3	20.8	30.7
Bulk density							
($g \cdot cm^{-3}$)	30	6.3	7.1	5.4	4.0	9.9	8.2
Clay (%)	9	26.7	20.6	19.2	25.0	19.4	13.0
Sand (%)	9	5.9	11.9	6.1	14.9	7.6	4.4
pH	30	1.4	1.3	2.2	1.6	1.5	1.7
Moisture (%)	30	44.9	67.1	95.1	83.3	39.6	58.4
N mineralization							
($\mu g \cdot g^{-1} \cdot wk^{-1}$)	30	−1068.2	274.1	−210.8	−280.9	−138.4	−139.0

terized by long, dry periods punctuated by short and spatially heterogeneous rainstorm events. This likely causes a release of mineralized nutrients from organic matter, followed by rapid uptake and immobilization (Skujinš 1981). This immobilization was shown in soils collected in May 1995 but not July 1995. The appearance of broad fluctuations in N mineralization exemplifies the importance of sampling over a short time span to make valid comparisons among sites in terms of spatial patterns.

The importance of patterns of heterogeneity in soil factors turned out to be critical to interpreting our observations. Schlesinger et al. (1996) found that, over the last century, the effects of desertification on New Mexico desert soils included an increase in soil N under *Larrea* shrubs compared to open spaces. A grassland system showed an increase in nutrient heterogeneity, but on a smaller scale than the desert ecosystem. These results and our study suggest that patterns of heterogeneity may develop first for elements limiting to desert shrub growth, followed by spatial development in other abiotic factors. The development time of these patches will vary with location, climate, and initial disturbance type.

In a 12-year study of succession in the sagebrush steppe, McLendon and Redente (1990) found that type of disturbance affected the direction of succession, but suggested that over a longer time frame successional pathways might converge. Convergence did not

occur during the 88 years of this study. Long-term change was noted by McAuliffe (1991) on Sonoran Desert bajadas formed between 500 and 4000 years ago. Over millennia, Mojave Desert communities can also be expected to change from sites dominated by short-lived ruderal species to long-lived perennials. Another possibility is that succession may never be "completed"; instead, community evolution may continue indefinitely (Vasek 1979/80). These changes will be difficult to examine in the scale of human lifetimes, and longer time scales involve broader issues such as climate change. Experimental studies will have to carefully address issues of temporal heterogeneity in climate to successfully describe small-scale changes in soil factors.

Studies of natural patterns of establishment of desert plants can guide restoration efforts following disturbance. The soil factors of critical interest to restoration in this system include soil N, P, and organic matter. Because of their critical effects on desert plants, mycorrhizal fungi probably play a significant role as well. "Ripping" of compacted soils (Kay and Graves 1983) and subsequent stabilization with annual plants would be a useful first step to community restoration (Marble 1985). Once erosional gullies form on unstable ground, they are difficult to redirect. Without restoration efforts, successional trajectories will be permanently altered after severe anthropogenic disturbance because of changes in surface hydrology and soil fragility (Marble 1985).
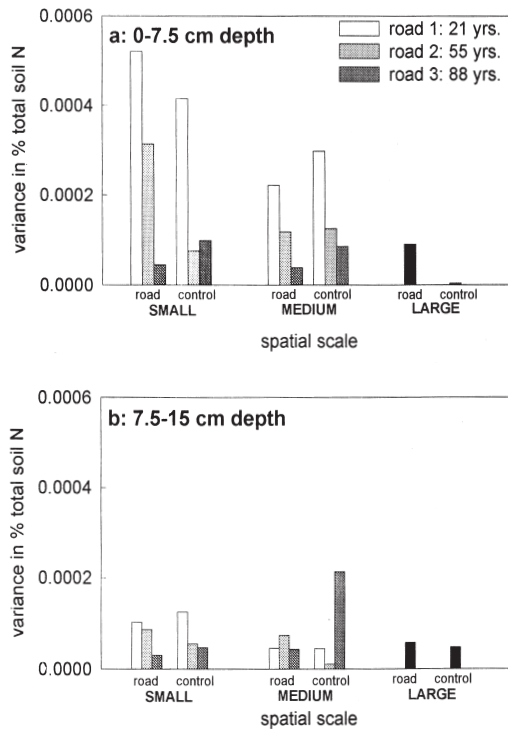
Fig. 6. Variance for total soil N at 3 spatial scales. For small scale, variance of the mean of 36 points around individual shrub. For medium scale, all positions at each shrub pooled, all poolings compared (1 value of variance for each road). For large scale, poolings of each shrub pooled per road; 1 value of variance for all roads derived from 3 means.

Because most biological activity in these soils occurs within the top 5 cm (Wallace et al. 1978, Skujinš 1981), restoring soil layering and horizontal heterogeneity is also important. Reestablishment of these natural patterns of microtopography and spatial patchiness is critical to restoring natural communities. Additionally, as soil heterogeneity appears on many scales in this region, future studies should not overlook this important fact. Only then can important ecosystem processes be properly assessed (e.g., landscape-level nutrient cycling).

Stochastic processes (unpredictable rains, long dry spells) have important effects on the direction of succession in this region. Differing initial disturbance types also play an important role. Regardless of successional stage, these factors alone may cause significant changes in small-scale patterns of soil heterogeneity. Future mechanistic studies of desert succession must be conducted over multiple decades

on individual sites or through careful comparative studies of chronosequences on individual watersheds. This will be necessary to reduce the overriding influence of spatial and temporal heterogeneity seen in this study.

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