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Plant and soil recovery along a series of abandoned desert roads

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Soil and vegetation dynamics were examined along roads abandoned for 5, 10, 21, 31, 55 and 88 years in southern Nevada in an attempt to elucidate factors controlling desert succession. None of the measured soil or vegetation parameters varied significantly with road age. Differences were found, however, between soils and vegetation on roads *vs.* nearby controls, and soils differed between roads created by surface vehicular traffic and bulldozing. Studies of recovery following disturbance in deserts must take into account natural patterns of plant and soil heterogeneity and initial disturbance type.

Keywords: disturbance; *Larrea*; Mojave Desert; revegetation; soil recovery

Introduction

Plant succession in North American deserts has been studied for more than half a century, but whether desert communities follow the predictable pathways of more mesic systems is still the subject of debate. Shreve and colleagues (Shreve & Hinckley, 1937; Shreve, 1942) suggested that perennial species cover in deserts changes little over decades. More recent work in abandoned town areas (Wells, 1961; Webb & Wilshire, 1980; Webb & Newman, 1982; Knapp, 1991) and military maneuver areas (Prose *et al.*, 1987) suggested that desert succession probably occurs, but at very slow rates and is strongly influenced by the nature and intensity of the initial disturbance. Knapp (1991) found significant differences in plant community structure between disturbed and undisturbed sites 77 years following disturbance on abandoned roadways in mining towns in Montana. The degree of soil compaction was a major determinant of the rate of recovery. In studying the vegetation of a ghost town in southern Nevada, Webb & Wilshire (1980) found that soils were still highly compacted after 51 years. The composition of vegetation in this disturbed site was predominantly short-lived perennials [e.g. *Stipa speciosa* and *Hymenoclea salsola* (Burrobush)). They noted the absence of *Larrea tridentata* (Creosote) on disturbed areas in their study, suggesting that it was incapable of establishment on compacted soils. These studies, however, were restricted to comparisons between disturbed and undisturbed plots at a single point in time. An exception to this trend was the work of Wallace *et al.* (1980), who examined the

*Present Address: 956 E. 42nd Ave., Spokane, WA 99203 development of vegetation on the Nevada Test Site 2, 5 and 11 years after nuclear test fallout debris disturbed a plant community.

Previous studies of succession in North American deserts have not adequately taken into account the role of soil characteristics in determination of plant community recovery rates. Rates of mineral cycling in deserts are high relative to input and output rates, giving these cycles low stability and long recovery periods following disturbance (Jordan *et al.*, 1972). Critical nutrients such as nitrogen and phosphorus are highly localized in soils of the Mojave Desert, limiting most biological activity to the top 3 cm of soil, especially under or near plant canopies (West, 1981). This horizontal and vertical heterogeneity of nutrients in desert soils has a strong impact on plant community structure (Schlesinger *et al.*, 1996).

Road cuts and the associated traffic have detrimental effects on soil nutrients and microbially controlled processes (e.g. N cycling) (Webb & Wilshire, 1980). These changes can then indirectly affect plant community development for many years after the disturbance. Although natural disturbances can have a catastrophic effect on vegetation in the Mojave Desert, roads are unique disturbances that compact soil, disturb soil structure, and kill vegetation. The type of road construction and the duration and intensity of road use modify road effects on the environment. The degree of soil compaction may be particularly important for determining succession (Knapp, 1991).

A series of economic booms and busts over the past nine decades in the Mojave Desert has left a record of impacts on native plant communities. These impacts have been recorded in the use and subsequent abandonment of unpaved roads. Our objective in this study was to examine patterns and mechanisms of plant and soil recovery on a time series of abandoned roads in the Mojave Desert over a span of 87 years. The use of a time series of abandonment is recognized as an acceptable method for studying succession when other types of analysis are not possible (Pickett, 1989; Matthews, 1992). An important assumption in this type of study is that variance in other factors (e.g. slope, parent material, climate) is similar across all sites. We hypothesized that perennial plant cover and density were positively correlated with time since road abandonment, and that community composition would change gradually, more closely resembling control vegetation with time since abandonment. We also hypothesized that changes in a combination of soil factors (e.g. increases in organic matter and nutrients) would be evident across the time series of roads.

Methods

Site description

Eight abandoned roads were chosen in Cottonwood Valley (35°N, 115°W; 210–480 m elevation), adjacent to Lake Mohave in both Nevada and Arizona in the Lake Mead National Recreation Area (LMNRA). This region is dominated by two perennial species; *Larrea tridentata* and *Ambrosia dumosa* (White Bur Sage). This species assemblage is typical of loose, sandy soils without a surface pavement (Beatley, 1976), and is generally considered a distinct community in the south-western deserts of the U.S.A. (MacMahon, 1992). All sites in the study were located on loamy sand alluvium derived from basalt (Volbroth, 1973; Anderson, 1978), and were shallow, hyperthermic aridisols (Soil Conservation Service, 1993). Soil types and geology are localized in the Mojave Desert (Volbroth, 1973); most in the Cottonwood valley were classified as Torriorthents. The climate is typical of the southern Mojave Desert, with hot dry summers and cool moist winters (Ehleringer, 1985). Most precipitation occurs in the winter; the mean yearly precipitation is 10·9 cm (Soil Conservation Service, 1993). The variance around this mean is extraordinarily high, with small and spatially heterogeneous summer rainstorms. The mean monthly temperatures range from 10·1°C in January to 33·4°C in July (Soil Conservation Service, 1993).

Aerial photography from the 1970's, records of National Park Service land acquisitions and reports from National Park Service personnel (B. Burke and J. Riley, pers. comm.) were used to determine the time since road abandonment for seven of the eight roads. The age of one road (Road 6) was estimated by dating similar disturbances within 1 km. Roads were chosen that had been abandoned in 1907, 1940, 1964, 1974, 1985 (2), and 1990. Typically, only one appropriate road of each age class was available for study in the Cottonwood Valley. Roads were excluded from the study if dates of abandonment were unknown (except Road 6), if road surfaces were initially paved, topped with gravel, or decompacted after the initial disturbance, if they fell outside the *Larrea-Ambrosia* plant community, or if they were still in use. By restricting the study to roads within a small geographic region (c. 50 km^2), geological, climatic, and elevational differences between sites were minimized. We believe these considerations are adequate to attempt to ascribe differences among the roads to age. Road ages refer to years prior to 1995, when field work was completed (Fig. 1, Table 1). The selected roads had one of two surface applications: 'bladed' roads were those with topsoil removed by a bulldozer and were characterized by the presence of lateral berms; and 'track' roads were impacted only by surface vehicular traffic and showed a characteristic raised centre berm.

The Cottonwood Valley was the scene of sporadic but intensive mining activity that started in the 1890's and continued into the 1980's. Water is of critical importance to the processing of gold ore, subsequently a narrow gauge railroad was built from Searchlight to the Colorado River in 1902. In 1907, ties and tracks were removed causing severe disturbance to surface soils. This disturbance is similar to blading, as the horizontal structure of the soil was destroyed. The abandoned railroad bed served as the oldest site in this study. In 1950, Davis Dam was installed, creating Lake Mohave, and in 1956 the area surrounding Lake Mohave became part of the LMNRA. Roads 4 and 5 were located on isolated inholdings that were ceded to the LMNRA in 1974 and 1964, respectively. Roads 1 and 2 were inadvertent disturbances within the protected recreation area, and Roads 3 and 7 were both track roads that were in use at one time but were closed by the Park Service in an effort to reduce human impacts.

Field methods

Areas of the selected roads that were highly dissected by arroyos or were on slopes greater than 20° were eliminated to reduce differences in overland runoff and water sheetflow among sites. Each road was divided into contiguous 50 m sections starting from a randomly chosen reference point. Ten 50 m sections were then randomly selected to be used as study plots ($n = 80$ road plots). If any of the ten plots had erosion channels > 20 cm in depth or side berms > 1 m above the road surface for > 3 m along the road, an alternate plot was chosen at random. On Road 1 the entire length was used because of limited overall length (approx. 500 m). An exception to these criteria was on Road 2, where both the road and control plots fell entirely within a broad arroyo. Paired control plots were located exactly 25, 35 or 45 m (closest place where selection criteria were met) from one side of the road (side chosen at random), and parallel to the road ($n = 80$ control plots). It was assumed that this was enough distance to ameliorate roadside edge effects. The road plots and the control plots were all 0·5 m in width and 50 m in length; road plots were located along the centre berm or the centre of the bladed area.

After removal of surface litter, soils were collected from two depths (0–7·5 cm and 7·5–15 cm; $n = 5$ samples per depth per plot) at random open locations within each plot, then composited per plot after passage through a 2 mm sieve. Random soil sample

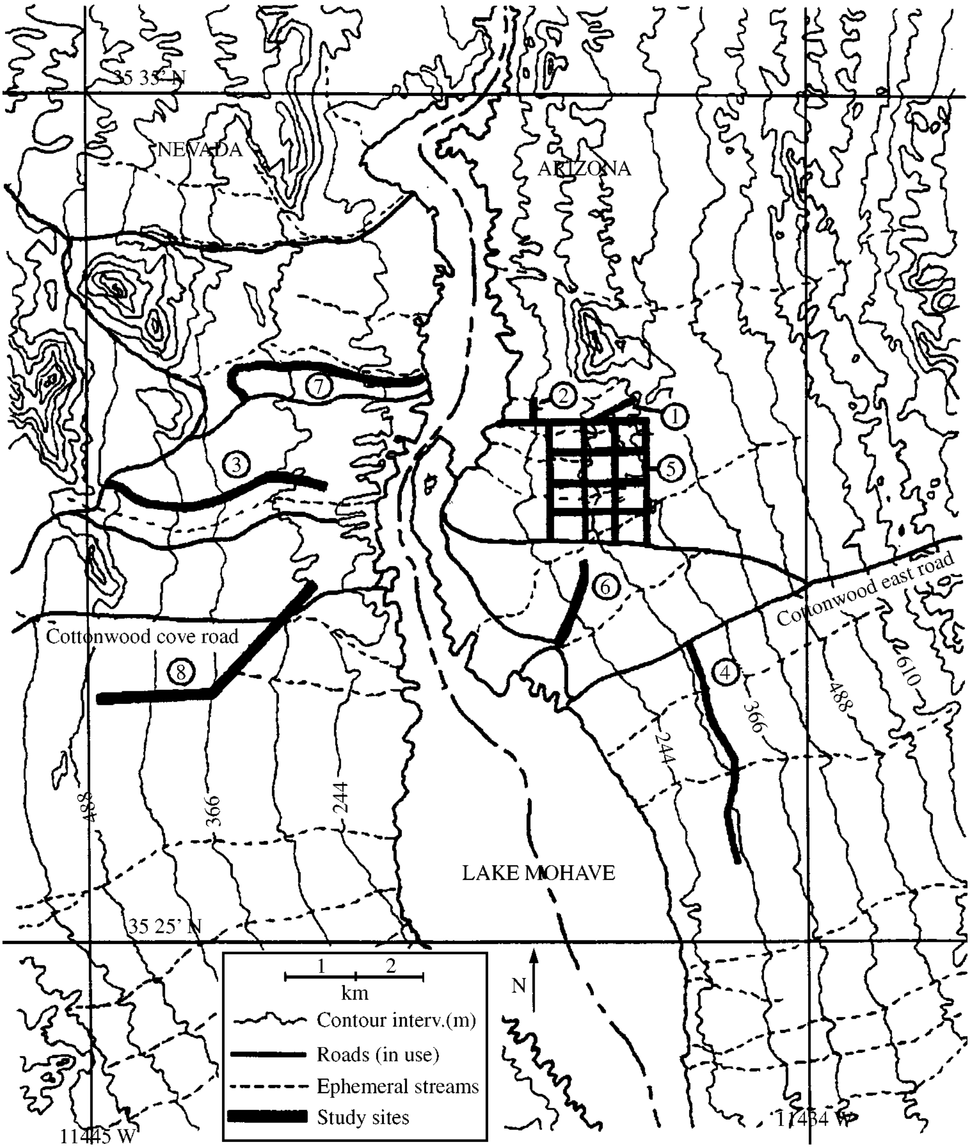

Figure 1. Cottonwood Valley region, Lake Mead National Recreation Area, Nevada and Arizona, with road locations.

locations were rejected if they were < 1 m from any shrub that was > 10 cm in height. This subsample design eliminated heterogeneity for nutrients at small scales due to variation in local microbial transformations (Jackson & Caldwell, 1993).

At five additional random locations per plot, surface compaction measurements were taken with a proving ring cone penetrometer (ELE Soil Test, Inc, Lake Bluff, IL U.S.A.). To ensure consistent technique, only one person used this instrument. One large pit (of variable size; 15 cm depth and 50 cm by 30–100 cm across; 0·23–0·72 m^3) was also excavated at an easily accessible location along each road for bulk density analysis. The contents of each pit were separated into a > 2 mm and a < 2 mm

Table 1. *Names, ages, and treatment types of the eight abandoned roads in the study*

Road number and map code	Road name	Age (yrs)*	Treatment type
1	Yuma Cove	5	bladed
2	Denman	10	bladed
3	Park Rte. 35	10	track
4	Oaxaca	21	bladed
5	Desert Rose	31	bladed
6	Mt. Davis	~ 40	track
7	Ridgeline	55	track
8	Railroad	88	bladed

*Equals years since abandonment, with the 1995 sampling season as a reference point.

fraction, and measured for weight and volume, yielding a 'whole soil' bulk density measurement (Vincent & Chadwick, 1994).

In the summer of 1995, mean canopy cover for all perennial shrubs > 10 cm in height and rooted in each plot was determined by measuring the maximum length of the shrub canopy paralleling the road, and the canopy diameter perpendicular to this measurement, even when the canopy extended outside the plot. Annual plants were not included in the sampling because of their ephemeral occurrence. The one-time measurement would have misrepresented their long-term contribution to plant cover.

The volume of perennial shrubs > 10 cm in height and rooted in each plot was calculated for most plants using the formula for the volume of a sphere ($[\pi r^2 h]/3$), where $h =$ height of the canopy. *Larrea* resembles an inverted cone (Ludwig *et al.*, 1975), so the formula for a cone was used ($[4\pi r^3]/3$). For the few occurrences of *Ferocactus acanthodes* (Barrel Cactus), the formula for the volume of a cylinder ($\pi r^2 h$) was used. Density of all perennial vegetation was determined, and individuals of *Larrea* were grouped into five size classes ($< 0{\cdot}15$ m^3, $0{\cdot}15$–$0{\cdot}30$ m^3, $0{\cdot}30$–$0{\cdot}45$ m^3, $0{\cdot}45$–$0{\cdot}60$ m^3, and $> 0{\cdot}60$ m^3 volume) to examine broad patterns of *Larrea* size across roads. Nomenclature followed Munz (1974).

Laboratory methods

A subsample of each thoroughly mixed composite sample was placed in a sealed soil tin and refrigerated at 5°C prior to analysis, which took place within 72 hours of collection. After removal of 20 g of soil sample for chemical analysis, the soils were weighed, dried in a 105°C oven until they reached a constant mass, and reweighed 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). Particle size determinations were done on a subset of samples (three per depth per road) using the Bouyoucos hydrometer method (Day, 1982). Organic matter content of soils was determined by mass loss after ignition at 550°C (Black, 1965). After oven drying, a 0·5 g sample of each soil was digested in sulfuric acid with a mercuric oxide catalyst, then analysed colorimetrically for total Kjeldahl nitrogen using an automated salicylate procedure (Environmental Protection Agency, 1984). Soil salinity was assessed on a saturation extract of a subset of 25 g subsamples (three per depth per road) from all roads with an electrical conductivity bridge (Rhoades, 1982).

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. After settling of the soil had occurred, the supernatant was analysed for available N (Keeney & 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. Water was added as needed to minimize headspace and ensure an anaerobic environment. Nitrogen mineralization was then reported as the difference between post-incubation and preincubation $NH_4 + NO_2 + NO_3$ concentrations (Keeney, 1982; Lober & Reeder, 1993). Binkley and Vitousek (1989) considered measurement of the release of mineralized nitrogen from organic matter a good method for providing an index of nitrogen availability. Anaerobic incubations are preferable for large-scale laboratory analysis of desert soils because they more closely match natural patterns and the mineralization produces only NH_4, simplifying analysis. *In-situ* methods for assessing available nitrogen are unsuitable for desert soils because water potentials fluctuate greatly between rainstorm events and long dry periods (Lajtha & Schlesinger, 1986). Additionally, net nitrogen mineralization cannot be measured directly in intact ecosystems because the sampling regime affects microbial processes and plant uptake (Vitousek *et al.*, 1989). Laboratory incubations allow the comparison of sites in terms of potential substrate quality as opposed to actual field conditions (Binkley & Vitousek, 1989).

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). Subsamples of 4·0 g of oven-dried soils were shaken in small jars and P was desorbed from the resin with 0·5 M HCl. Extracts were then analysed colorimetrically for PO_4 (Sibbesen, 1978). This procedure is a measure of only the most biologically available forms of phosphorus (Lajtha & Schlesinger, 1988). In desert soils, labile inorganic phosphorus is a small fraction of total soil phosphorus (Allen, 1988); most forms are locked up in calcium and magnesium phosphates and are unavailable to plants (Charley & Cowling, 1968; Lajtha & Schlesinger, 1988). All laboratory analyses had quality control checks run simultaneously to ensure consistent technique.

Statistical analyses

Before data analysis, 30 outliers from the N pool data (overall $n = 360$) and 24 outliers from the N mineralization data (overall $n = 360$) were removed according to the Mardia's kurtosis test (Schwager & Margolin, 1982), because a localized rain event immediately before sampling skewed the time zero estimates upwards. A Principal Components Analysis (PCA; SAS Institute, 1987) was run on nine of the soil variables measured (compaction, fine soil bulk density, moisture, pH, organic matter, total N, N pool, N mineralization, and available P). Particle size and salinity data were excluded from this analysis due to incomplete data. For each observation and each PCA score, road values were subtracted from paired control values, and these differences were subjected to a multiple analysis of covariance (MANCOVA), with application type (bladed road *vs.* track road) as the main effect and road age as the covariate (StatSoft, Inc., 1995). Although age was used as a covariate, this was not to remove the effect of age, but to appropriately test for the effects of age (a continuous variable). The MANCOVA analyses of soil factors were run on the two depths separately. The analysis of differences in PCA scores allowed the examination of changes in combinations of variables along the road series given the background soil heterogeneity. Whole soil bulk density pits were not replicated so statistics were not done on these data.

Multivariate comparisons of application types were followed by univariate analyses of each soil variable. Means for each application type (bladed, track, control) were

Table 2. *Results of Principal Components Analysis/Multiple Analysis of Covariance. Significant differences between applications (bladed vs. track roads; $p < 0{\cdot}05$) for each individual factor are in boldface type. Road age was used as the covariate*

Soils PCA depth 1		Soils PCA depth 2	
MANCOVA application effect: $p < 0{\cdot}0001$ Application* covariance effect: $p = 0{\cdot}255$		MANCOVA application effect: $p < 0{\cdot}0001$ Application* covariance effect: $p = 0{\cdot}223$	
Factor (control-road difference in application)	p values application	Factor (control-road difference in application)	p values application
PC1	**0·026**	PC1	**0·006**
PC2	0·408	PC2	0·961
PC3	**0·0001**	PC3	**<0·0001**
PC4	0·111	PC4	0·339
PC4	0·557	PC4	0·988
PC6	0·862	PC6	**0·025**
PC7	0·81	PC7	0·114
PC8	0·713	PC8	0·645
PC9	0·613	PC9	0·894

compared using a one way ANOVA or Kruskall-Wallis test (on normal and non-normal data, respectively).

Plant cover data was examined using the PCA/MANCOVA method as described above. Plant factors used in the PCA were cover values for the most abundant species (*Larrea tridentata, Ambrosia dumosa, Encelia farinosa* (Brittle Bush), *Hymenoclea salsola, Krameria parviflora* (Ratany)), and cover for the remaining 10 species ('other'). After the PCA/MANCOVA analysis yielded no meaningful trends across the road series, univariate comparisons of application types (bladed versus track versus control; ANOVA or Kruskall-Wallis) were done on cover values for each species independently. Total percent cover, density and shrub volume across all roads were also examined with one-way ANOVAs. *Larrea* recruitment, which was high on Road 1, was correlated with individual soil variables to see if edaphic conditions contributed to its higher occurrence on Road 1.

Results

The PCA/MANCOVA analyses on soils showed significant differences between bladed and track application types but no significant interaction by road age, indicating no significant trends along the road series for soil parameters at either depth (Table 2). Mean differences in PCA scores were significantly different in the MANCOVA analysis only for Principal Components (PC's) 1 and 3 between the two applications (Table 2). Bladed roads had PC differences close to zero, indicating their overall similarity to control soils (Fig. 2). No linear trends by road age were visible on Figure 2, further indicating the lack of trends in soil variables across the road series. Differences for the track roads diverged negatively for PC1 and positively for PC3. Axis PC1 was positively associated with pH and moisture and negatively associated with

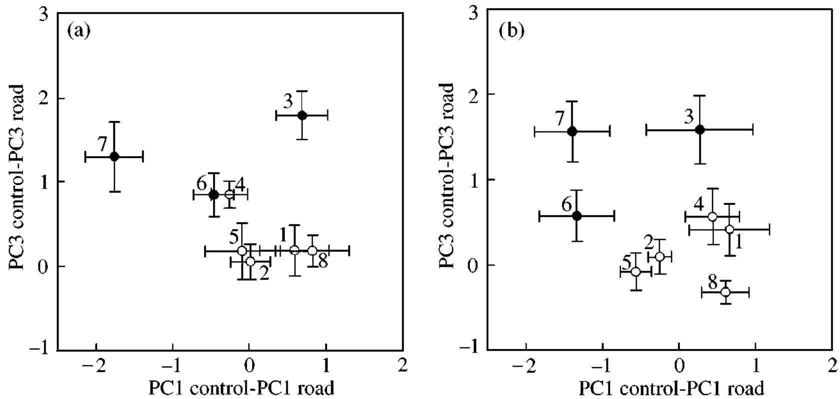

Figure 2. PCA plots for nine soil variables. Differences in principal component scores 1 and 3 were significantly different among applications. (a) 0–7·5 cm depth; (b) 7·5–15 cm depth. Bladed roads (○); Track roads (●).

Table 3. *Eigenvalues of Principal Component axes. The axes shown were the only ones to contribute significantly to the MANCOVA effects*

	PC1	PC3
Eigenvalue	3·1	1·2
Proportion of variance	0·34	0·13
Eigenvector		
moisture	0·39	− 0·07
bulk density	− 0·45	− 0·08
N pool	0·22	0·53
N mineralization	0·02	− 0·01
Available P	− 0·34	0·22
total N	0·25	0·5
organic matter	− 0·43	− 0·02
pH	0·44	− 0·11
compaction	0·21	− 0·63

bulk density, organic matter, and available P (Table 3). Axis PC3 was positively associated with the available N pool and total N and negatively associated with compaction (Table 3). Although it was not significant to the MANCOVA analysis, PC2 was positively associated with N mineralization, available P, and total N, and negatively associated with soil moisture.

Univariate comparisons between bladed, track and control treatments indicated that soils on track roads were more compacted, had higher clay content, lower total N and lower available P than soils from either bladed roads or control plots at both 0–7·5 and 7·5–15 cm depths (Fig. 3). Soils from track roads also had lower pH than bladed roads (7·5–15 cm depth; data not shown), higher organic matter (7·5–15 cm depth; Fig. 3(c)) and lower available N (0–7·5 cm depth; Fig. 3(e)) than bladed roads. No differences were found between track roads, bladed roads, or controls for bulk density,

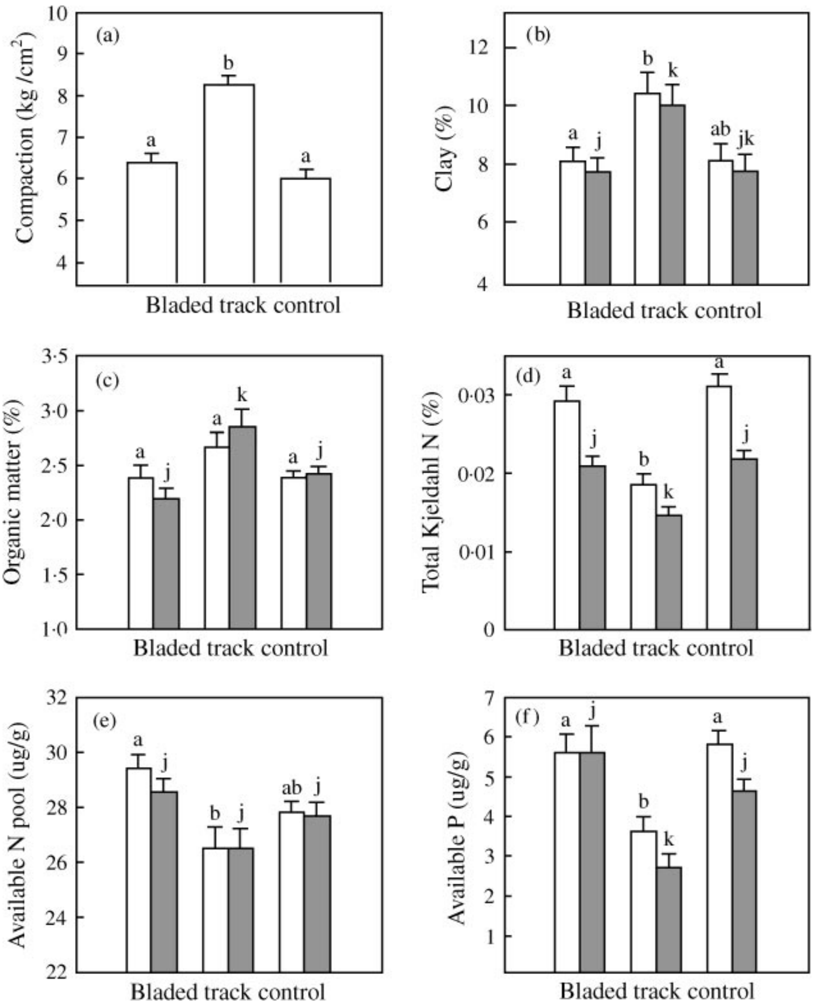

Figure 3. Means of soil parameters for each application type. Values are mean $\pm$ S.E. ($n = 50$ for bladed roads, $n = 30$ for tracks, and $n = 80$ for controls). For each depth, different letters above the bars indicate significant differences among means ($p < 0{\cdot}05$). 0–7·5 cm depth (□); 7·5–15 cm depth (■).

moisture, sand content or N mineralization (see Table 4 for complete data). The univariate analyses confirmed the PCA/MANCOVA results showing that bladed roads were more similar to control areas than track roads.

Soil salinity was below 4·0 dS m^{-1} for all samples (Table 4), which is considered non-saline (U.S. Salinity Laboratory Staff, 1954). Salinity levels in the subset of soils tested showed no significant differences among roads or between applications, and no road by application interaction. Overall bulk density of soils also varied randomly between sites, reflecting the differing aggregations of alluvial debris size (data not shown).

PCA/MANCOVA results for the plant cover data showed no overall application (bladed *vs*. track) effect, and no application by road age interaction (data not shown), indicating no clear time series trend in vegetation development. When differences in PC3 values between control and road plots were compared (Fig. 4), bladed and track

Table 4 (a). *Mean & S.E. of soil parameter, 0– 7·5 cm depth*

	Compaction (kg/cm^2)		Bulk density (g/cm^3)		Moisture (%)		pH		Sand (%)		Clay (%)		Organic matter (%)	
n =	10		10		10		10		3		3		10	
Road #:														
Application	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
1: bladed	6·139	0·175	1·365	0·023	0·379	0·038	7·865	0·04	67·417	5·193	7·833	1·483	2·485	0·098
1: control	6·432	0·169	1·325	0·026	0·389	0·051	7·765	0·03	63·750	2·366	9·000	0·408	2·937	0·145
2: bladed	6·500	0·237	1·561	0·024	0·383	0·049	7·945	0·04	85·000	3·240	3·833	0·414	2·708	0·135
2: control	6·705	0·221	1·514	0·019	0·417	0·067	7·895	0·04	79·417	7·825	4·833	1·293	2·377	0·143
3: track	8·762	0·211	1·661	0·020	0·259	0·048	7·965	0·05	71·250	5·651	10·333	1·396	2·293	0·171
3: control	6·808	0·283	1·570	0·011	0·305	0·045	7·915	0·07	69·500	2·208	10·167	0·649	2·431	0·150
4: bladed	7·691	0·285	1·635	0·022	0·152	0·012	8·08	0·02	78·833	2·109	5·250	0·717	1·804	0·070
4: control	6·202	0·271	1·634	0·021	0·095	0·018	8·09	0·03	74·667	5·377	6·583	0·802	1·976	0·059
5: bladed	7·358	0·214	1·492	0·034	0·579	0·159	7·94	0·05	69·917	1·464	6·750	0·514	2·996	0·152
5: control	6·646	0·204	1·500	0·017	0·644	0·244	7·89	0·04	72·833	1·717	5·583	0·446	2·748	0·142
6: track	8·334	0·240	1·508	0·020	0·197	0·020	7·97	0·03	70·417	0·785	7·917	0·476	2·334	0·149
6: control	6·408	0·137	1·504	0·015	0·121	0·025	7·98	0·02	68·000	2·273	7·417	0·710	2·117	0·099
7: track	7·863	0·202	1·513	0·019	0·578	0·046	7·92	0·06	57·667	3·145	13·167	1·063	3·355	0·178
7: control	5·349	0·215	1·519	0·013	0·417	0·046	7·99	0·02	56·250	3·082	13·667	1·002	2·547	0·112
8: bladed	4·172	0·243	1·671	0·025	0·143	0·02	8·23	0·03	80·417	0·379	7·333	0·476	1·938	0·418
8: control	3·833	0·141	1·562	0·022	0·149	0·023	8·16	0·01	76·667	0·981	8·000	0·408	1·963	0·131

$n =$ Road #:	Total N (%) 10		Salinity (dS/m) 3		N pool (ug/g) 10		N mnz. (ug/g/wk) 10		Available P (ug/g) 10	
Application	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
1: bladed	0·0405	0·0038	0·620	0·016	30·130	1·208	2·447	2·270	2·587	0·731
1: control	0·0436	0·0032	0·708	0·045	30·873	1·027	2·432	2·950	4·641	0·898
2: bladed	0·0305	0·0025	0·722	0·084	30·938	0·785	12·363	2·206	4·624	0·804
2: control	0·0360	0·0040	0·682	0·028	29·058	0·489	11·409	1·665	5·930	0·707
3: track	0·0193	0·0029	0·625	0·039	25·405	0·546	− 5·134	3·317	3·388	0·423
3: control	0·0291	0·0016	0·732	0·117	31·295	0·809	− 4·598	4·662	4·047	0·700
4: bladed	0·0219	0·0021	0·691	0·067	26·050	0·735	5·900	2·484	9·080	0·603
4: control	0·0242	0·0018	0·767	0·187	26·934	0·335	7·658	2·207	9·886	0·961
5: bladed	0·0377	0·0041	0·779	0·089	29·571	1·481	10·032	4·406	4·115	0·744
5: control	0·0445	0·0075	0·742	0·123	26·726	1·979	19·552	2·460	3·960	0·682
6: track	0·0143	0·0017	0·831	0·106	25·417	1·181	9·148	2·492	4·913	0·568
6: control	0·0171	0·0008	0·839	0·156	24·875	0·349	9·418	2·040	4·757	0·777
7: track	0·0219	0·0019	0·626	0·053	30·112	2·646	− 6·447	4·901	2·553	0·600
7: control	0·0301	0·0024	0·556	0·044	25·713	0·931	− 0·406	3·042	7·382	0·776
8: bladed	0·0152	0·0026	0·670	0·123	30·412	0·297	− 10·679	1·113	7·641	0·468
8: control	0·0237	0·0026	0·625	0·053	28·588	0·36	− 5·546	1·136	5·786	0·591

Table 4(b). *Mean & S.E. of soil parameter, 7·5–15 cm depth*

	Bulk density (g/cm^3)		Moisture (%)		pH		Sand (%)		Clay (%)		Organic matter (%)		Total N (%)	
n =	10		10		10		3		3		10		10	
Road #:														
Application	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
1: bladed	1·362	0·014	0·901	0·126	7·975	0·04	66·917	2·724	7·250	1·021	2·554	0·162	0·0261	0·0025
1: control	1·299	0·033	0·861	0·077	7·91	0·04	67·250	1·947	8·667	0·491	2·95	0·197	0·0306	0·0030
2: bladed	1·547	0·014	0·814	0·125	8·085	0·03	83·667	3·664	4·000	0·656	2·486	0·197	0·0192	0·0019
2: control	1·526	0·014	0·601	0·066	8·105	0·03	84·167	5·407	3·833	1·227	2·381	0·144	0·0209	0·0015
3: track	1·575	0·031	0·517	0·093	7·935	0·05	70·083	5·483	11·500	1·620	2·374	0·214	0·0175	0·0015
3: control	1·519	0·034	0·485	0·113	7·905	0·07	71·167	2·008	9·917	0·68	2·522	0·228	0·0249	0·0021
4: bladed	1·592	0·014	0·255	0·023	8·15	0·02	80·667	2·607	5·167	0·476	1·674	0·043	0·0148	0·0022
4: control	1·598	0·016	0·199	0·025	8·145	0·03	75·000	3·682	6·833	0·691	2·071	0·131	0·0165	0·0015
5: bladed	1·461	0·031	0·532	0·051	8·01	0·05	72·417	1·569	7·000	0·624	2·750	0·132	0·0278	0·0024
5: control	1·488	0·020	0·547	0·075	8·005	0·04	75·667	1·396	5·75	0·118	2·595	0·134	0·0247	0·0044
6: track	1·463	0·031	0·412	0·034	8·025	0·03	73·917	0·720	7·333	0·593	2·849	0·355	0·0084	0·0009
6: control	1·568	0·019	0·452	0·019	8·085	0·03	73·000	3·169	6·667	0·557	2·021	0·115	0·0101	0·0012
7: track	1·416	0·017	1·100	0·091	7·87	0·06	62·917	1·668	11·250	0·408	3·316	0·165	0·0179	0·0014
7: control	1·435	0·016	0·815	0·121	7·91	0·05	59·917	3·185	12·333	0·531	2·841	0·145	0·0275	0·0028
8: bladed	1·646	0·025	0·303	0·034	8·235	0·03	76·917	0·245	7·583	0·297	1·537	0·13	0·0167	0·0018
8: control	1·576	0·042	0·286	0·035	8·225	0·02	76·667	0·297	8·417	0·18	1·97	0·126	0·0191	0·0016

	Salinity (dS/m)		N pool (ug/g)		N mnz. (ug/g/wk)		Available P (ug/g)	
n =	3		10		10		10	
Road #:								
Application	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
1: bladed	0·669	0·061	29·197	0·855	– 4·976	1·942	2·171	0·557
1: control	0·586	0·032	31·285	1·319	– 8·254	2·344	3·275	0·622
2: bladed	0·555	0·083	28·964	0·505	– 2·241	1·108	3·955	0·658
2: control	0·724	0·032	28·981	0·427	– 3·292	0·798	4·232	0·442
3: track	0·894	0·138	27·635	1·457	– 13·576	2·561	2·732	0·414
3: control	0·559	0·068	31·803	1·530	– 8·407	3·427	3·802	0·903
4: bladed	0·689	0·082	25·303	0·943	– 0·614	1·072	11·850	1·856
4: control	0·595	0·088	26·606	0·323	2·004	0·889	8·350	0·661
5: bladed	0·783	0·113	28·579	1·429	2·041	2·687	3·292	0·731
5: control	0·706	0·085	26·210	2·167	3·081	2·244	4·271	0·671
6: track	0·889	0·195	25·967	1·332	3·092	1·841	3·326	0·705
6: control	0·646	0·070	24·088	0·432	– 1·028	1·186	2·866	0·353
7: track	0·667	0·093	25·125	1·301	– 14·028	3·709	2·040	0·585
7: control	0·704	0·063	25·500	1·717	– 8·890	4·576	5·668	0·946
8: bladed	0·729	0·111	30·734	0·607	– 15·994	0·977	6·746	0·515
8: control	0·514	0·008	27·913	0·348	– 13·509	0·874	4·569	0·351

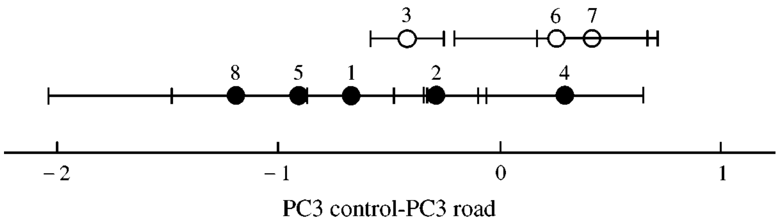

Figure 4. PCA plot for plant cover values. PC3 was the only factor to show significant differences among application types. Numbers above symbols indicate road numbers. Bladed roads (○); Track roads (●).

roads were separated in a pattern similar to the plot of soil PCA differences (Fig. 2; e.g., Road 4 had greatest similarity to Roads 6 and 7). Univariate analysis of the plant cover data showed that perennial shrub cover was significantly greater on controls than on road plots ($p < 0{\cdot}0001$), largely due to greater cover of *Larrea* ($p < 0{\cdot}0001$) on control plots (Fig. 5). Cover of *Krameria* was also significantly greater on control than on road plots ($p = 0.0024$; Fig. 5). The cover of *Ambrosia*, *Encelia*, and *Hymenoclea* did not differ between road and control plots overall. Cover of all 15 species of perennial shrubs varied greatly among control plots (e.g. *Ambrosia*: 1–18% cover: *Larrea*: 16–36% cover) and road plots (e.g., *Ambrosia*: 0–8% cover; *Larrea* 2–24% cover; Fig. 5). Road 7 plots had nearly as much cover as their controls (Fig. 5), due largely to the presence of large *Larrea* shrubs.

Despite the lack of significant differences in vegetation along the road series (PCA/MANCOVA results), some patterns are suggested from Figure 5. *Encelia* had the highest cover on Roads 1–3, *Ambrosia* on intermediate aged Roads 4 and 5, and *Larrea* on the oldest roads (Roads 6–7). Road 8 was an exception, with greater cover of *Ambrosia* than *Larrea*. *Hymenoclea* appeared often on the sandy roads but only once on controls, and *Krameria* was only found on Roads 5, 6, and 7, but was in all control areas (Fig. 5), albeit at low values

Overall shrub density did not differ significantly between road and control plots, but density did differ greatly among control plots (e.g. *Ambrosia*: 0·02–0·29 plants m^{-2}; *Larrea*: 0·06–0·19 plants m^{-2}) and road plots (e.g. *Ambrosia*: 0·0–0·20 plants m^{-2}; *Larrea*: 0·004–0·27 plants m^{-2}) (Fig. 6). No trends along the road series were noted in plant densities. Individual comparisons between road and control plots showed significantly greater plant density on control plots for Roads 1 and 4 only (Fig. 6).

Species richness ranged from two to seven species per road and four to seven species per control area. Roads 5 and 7 had as many species as their paired control plots, but all others had lower species richness than their paired controls (data not shown). Overall only a total of seven perennial species were found on roads, whereas controls contained all 15 species noted in the study. Control plots had significantly higher overall shrub volume than road plots ($p < 0{\cdot}001$; data not shown), but high spatial heterogeneity in the vegetation obscured any pattern along the road series.

Application differences were apparent for plant parameters. Bladed roads had significantly lower total plant cover than controls, and significantly lower *Larrea* cover than either tracks or controls (Fig. 7(a, b)). Track roads had significantly lower total cover, *Larrea* cover and *Ambrosia* cover than control areas (Fig. 7 (a, b, c)). Bladed roads tended to have more early successional species (*Encelia*, *Hymenoclea*; Fig. 7 (d, e)) than track roads, and track roads tended to have more *Krameria* (Fig. 7 (f)) than bladed roads.

To examine broad patterns of *Larrea* size across roads, *Larrea* shrubs were grouped into five size classes (Fig. 8). Because of its growth form, *Larrea* age is particularly hard

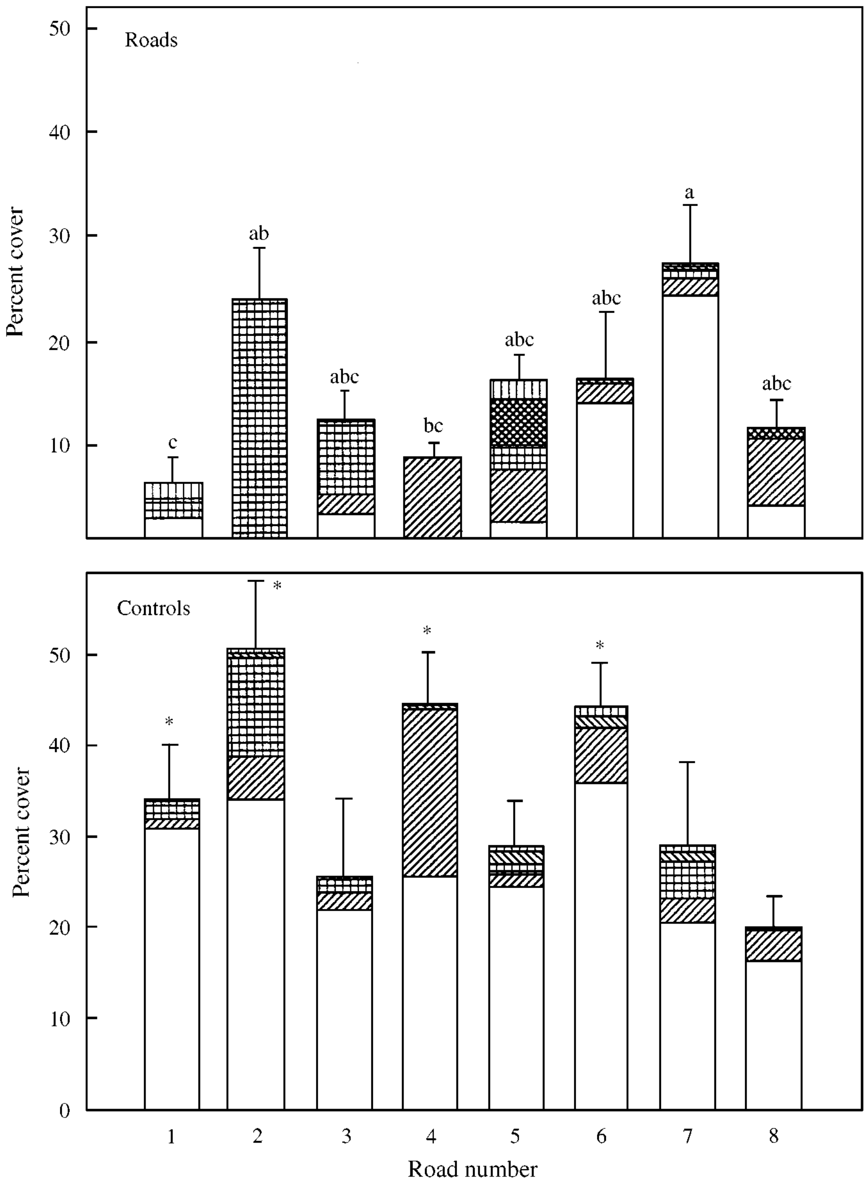

Figure 5. Percent cover for perennial shrubs. Values are means ± S.E. of 10 plots. Error bars and statistical analyses based on total cover for all species. Different letters indicate significant pairwise differences between roads ($p < 0{\cdot}05$). Asterisks indicate significant treatment differences (control *vs*. roads; $p < 0{\cdot}05$). No significant pairwise differences among control plots were found: □ *Larrea tridentata*; ▨ *Ambrosia dumosa*; ⊞ *Encelia farinosa*; ⊠ *Hymenoclea salsola*; ▧ *Krameria parviflora*; ▥ other.

to measure (Vasek, 1980); therefore we used size as an approximation of age. *Larrea* alone was examined because it is a dominant species in this community and occurs in a broad range of sizes. None of the other major species presented such a broad range of sizes or were as indicative of long-term recovery as *Larrea*. Most roads had many small

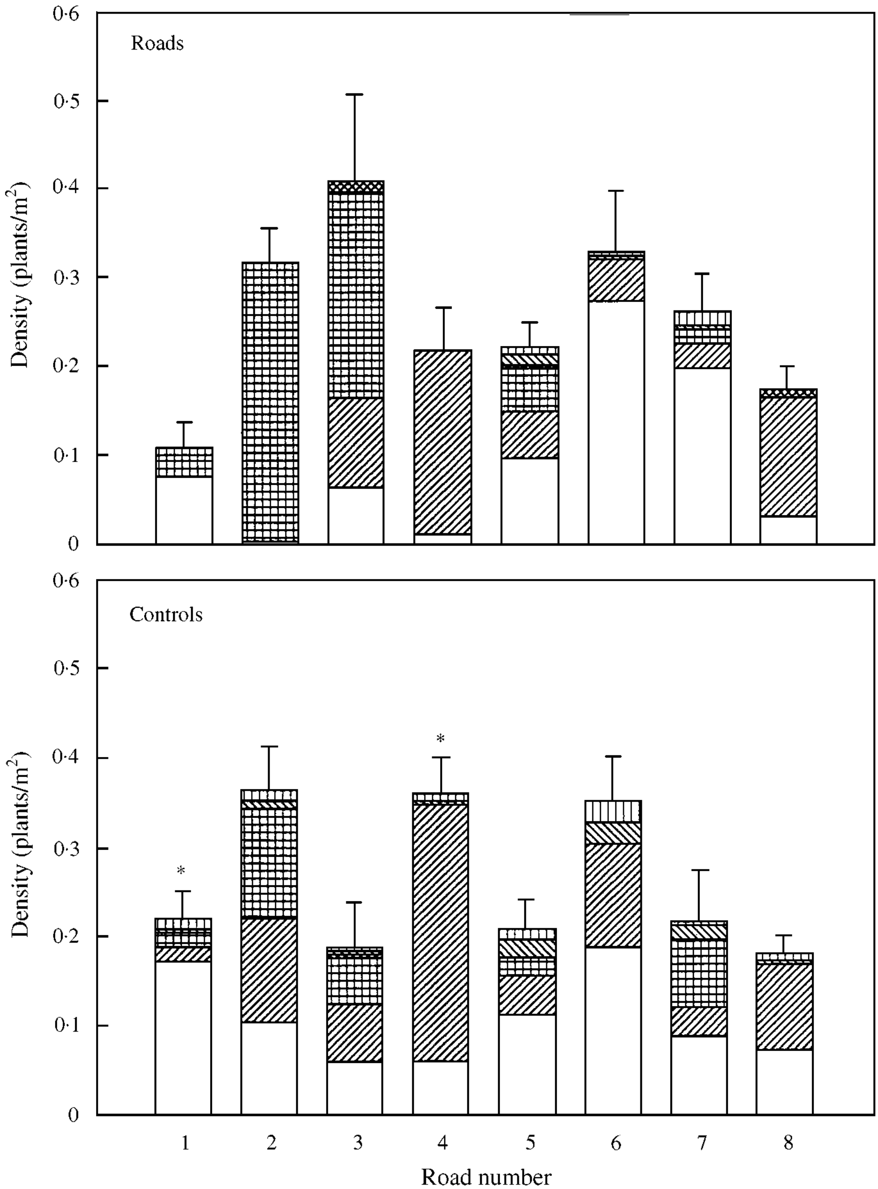

Figure 6. Density of perennial shrubs. Values are mean $\pm$ S.E. of 10 plots. Error bars and statistical analyses based on total density for all species. Asterisks indicate significant treatment differences (controls *vs.* roads; $p < 0{\cdot}05$). No significant pairwise differences (at $p < 0{\cdot}05$) among road plots or among control plots were found: □ *Larrea tridentata*; ▨ *Ambrosia dumosa*; ⊞ *Encelia farinosa*; ⊠ *Hymenoclea salsola*; ▧ *Krameria parviflora*; Ⅲ other.

individuals ($< 0{\cdot}15$ m^3 volume) of *Larrea*, with few or no larger plants. In contrast, control plots tended to show the opposite pattern, with a larger number of more voluminous plants and few small ones (Fig. 8). Road 1 showed the same number of small *Larrea* on roads and controls, possibly indicating a recent reproduction event. Levels of *Larrea* recruitment on this road, however, did not correlate with any of the measured soil variables ($r = 0{\cdot}006$–$0{\cdot}486$; data not shown). Germination and growth are

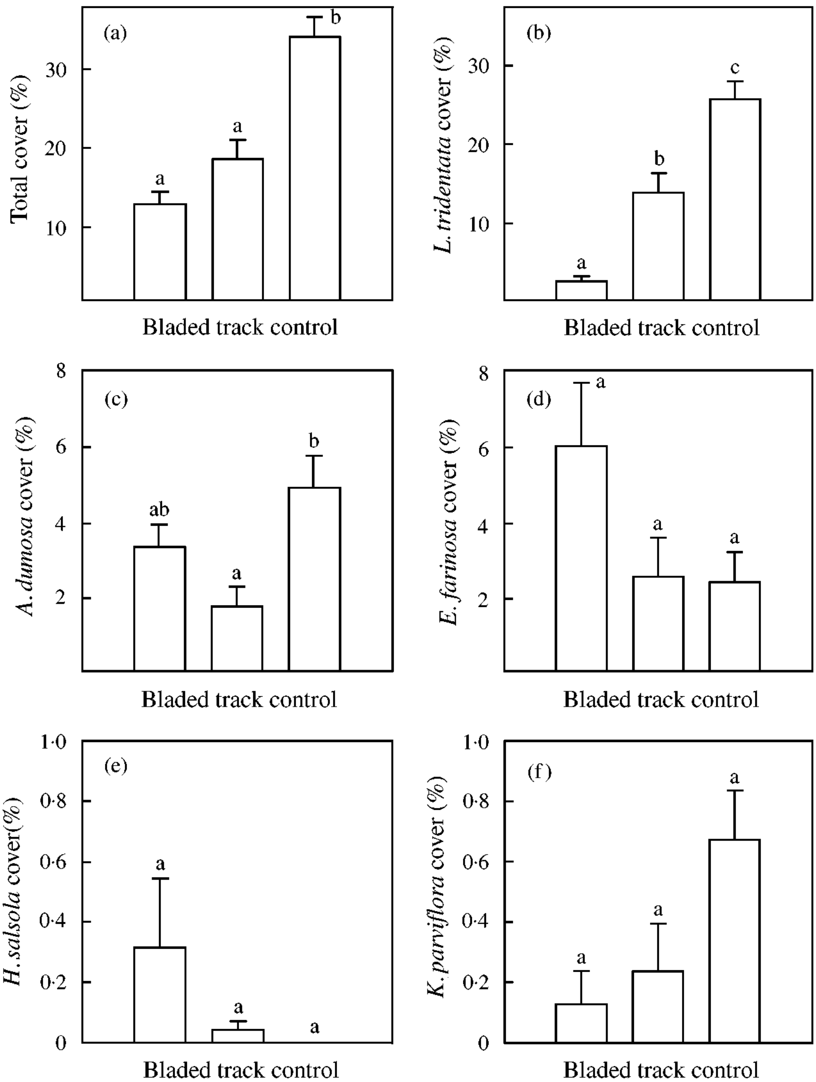

Figure 7. Plant cover comparisons between the different applications. Values are means $\pm$ S.E. of 10 plots. $n = 50$ for bladed roads, 30 for tracks, and 80 for controls. Different letters above the bars indicate significant differences among means ($p < 0{\cdot}05$). Note axis differences.

probably more strongly controlled by short-term climatic events than by edaphic factors. Track Roads 3, 6, and 7 showed strong recruitment of small *Larrea*, while bladed Roads 2, 4, and 8 showed little or no *Larrea* recruitment, similar to their paired controls. Roads 1, 5 and 6 were in close proximity to each other (approximately 3 km), and showed similar patterns for *Larrea* size in control areas (Fig. 8).

Discussion

Despite efforts to reduce broad and small scale spatial heterogeneity among roads (geographic restriction to one valley, composites of five soil subsamples per plot, road

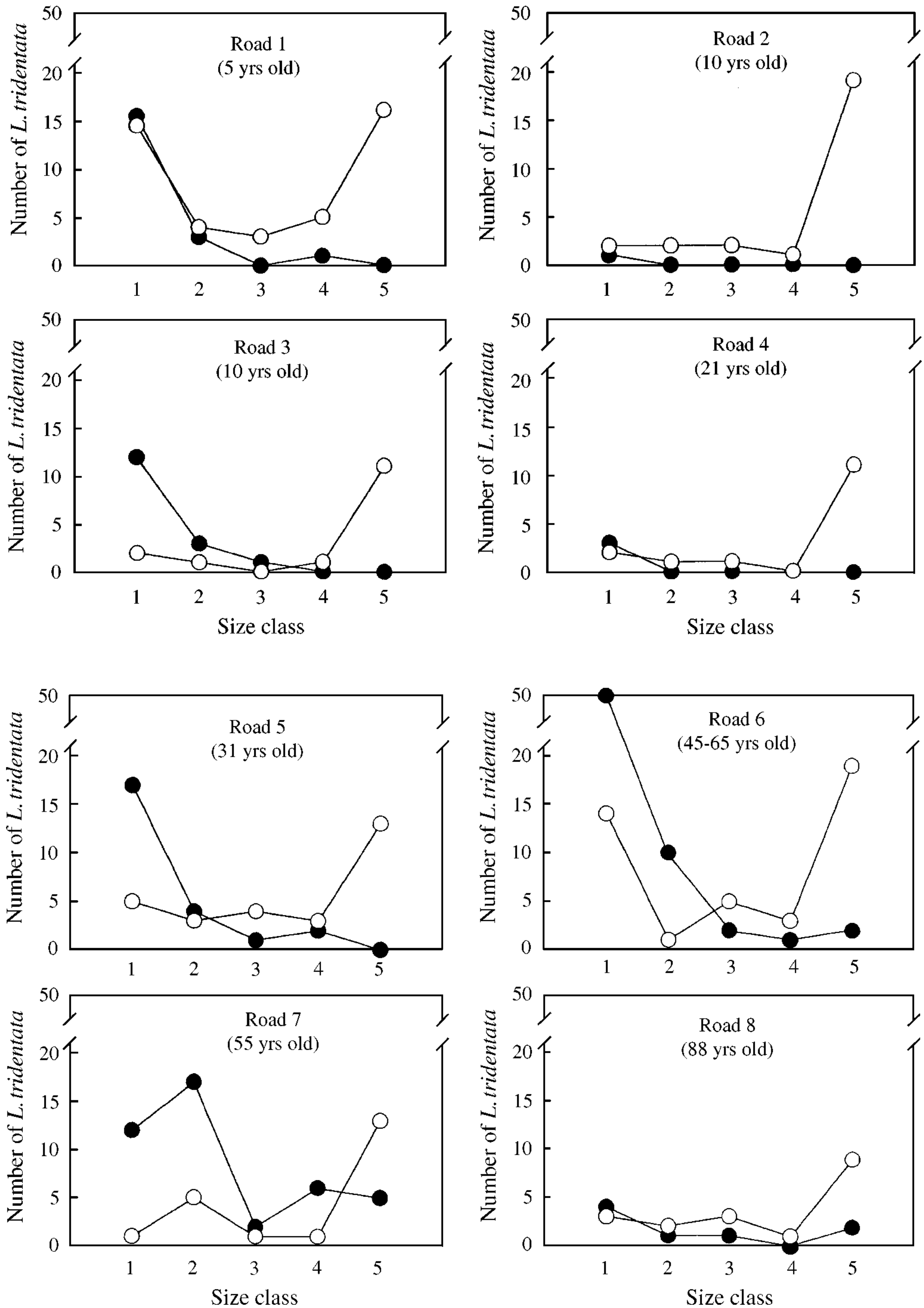

Figure 8. Number of *Larrea tridentata* shrubs by size (volume) classes. Size classes: 1 = < 0·15 m^3; 2 = 0·15–0·30 m^3; 3 = 0·30–0·45 m^3; 4 = 0·45–0·60 m^3; 5 = > 60 m^3. All shrubs > 10 cm height were included; all plots for each road were combined. Control plots (○); Road plots (●).

and plot acceptance criteria: avoidance of sections of roads with deep erosion channels or on steep slopes), no significant changes were found in soil parameters as a direct result of time since road abandonment. Successional changes in soil factors in this system could be happening on the scale of centuries or millennia instead of the 5–87 year time frame examined here. Alternatively, any temporal changes may be obscured by some overlooked aspect of spatial heterogeneity among roads. Accumulations of nutrients and organic materials, as almost universally noted in succession in other systems, were not seen here. To identify successional patterns and determine mechanisms, chronosequences of 500–4000 yr. may be necessary (McAuliffe, 1991, 1994). All further discussion will focus on the contrasts in plant and soil parameters between application types.

Track roads may have been more susceptible to soil compaction because they had a more even mix of soil components (i.e. significantly higher clay than bladed roads). This was true even though plots were located in centre berm areas that were presumably less impacted than tire track areas. Soils with a wide variety of particle sizes are highly susceptible to density increases (Webb, 1983). Track roads also had higher levels of organic matter than bladed roads at 7·5–15 cm because surface soil layers, where most biological activity is concentrated (Wallace et al., 1978, Skujins, 1981), were not removed during the initial disturbance. Raised centre berms may have also facilitated the aeolian deposition of organic materials (as described by Allen, 1988), although organic matter was only slightly higher for these roads at 0–7·5 cm. The organic materials may have resulted in pH levels remaining near the control conditions on track roads. Levels of available P, available N and total N, however, were reduced on track roads (compared to bladed roads and controls), possibly due to increased nutrient uptake by plant roots that were not destroyed with disturbance. Additionally, soil surface compaction likely reduced decomposer (i.e. bacteria, fungi and nematode) activity in the soil (Belnap, 1995), which can have an impact on nutrient cycles. The effect of central berms might have had a significant impact on soil water relations and nutrients, as microtopography can have a strong impact on water infiltration and runoff in the Mojave Desert (Schlesinger & Jones, 1984).

Soils on bladed roads were more similar to soils from control plots than to track road soils. Soil pH at 7·5–15 cm on bladed roads was the only parameter to differ significantly from control soils. Higher pH on bladed versus control surfaces may have been caused by the removal of surface organic materials. Levels of labile inorganic P, though similar to control plots, may not have been a true representation of P availability in these soils, as P availability decreases in soil as pH values rise between 7·0 and 8·5 (Brady, 1974). Contrary to the supposition that removal of surface soils reduces the levels of N and P (Charley & Cowling, 1968), bladed roads showed higher levels of these two nutrients than track roads. The similarity between controls and bladed roads of other soil factors (e.g., compaction, organic matter, nutrients) is evidence that these factors were not as important to determining the makeup of plant communities as we orginally thought. Generally, even the youngest sites had similar soil characteristics in disturbed and control plots suggesting that roadbuilding disturbance did not cause a large change in many soil factors.

Although total plant cover showed no discernible pattern across all of the sites combined, the relative contributions by the dominant species did change through time (Fig. 5(a)). As *Encelia* is thought to be early successional and *Larrea* late successional, these data suggest a logical progression in community development along the road series, as shown in previous studies of desert succession (Wells, 1961; Vasek *et al.*, 1975; Webb & Wilshire, 1980; Carpenter *et al.*, 1986; Prose *et al.*, 1987). Edaphic factors appear to play only a minor role in initiating and controlling the rate and direction of this plant community development. In other successional studies, it has been presumed that pioneer shrub species cause changes in soil conditions (Vasek, 1979/1980), which have an influence on later successional species by stabilizing soil and increasing soil organic matter. Mineralized forms of organic nutrients then become available to later successional species (Vitousek et al., 1989). In this study, however, temporal trends in organic matter and nutrient levels in soils from roads were not seen, probably partially due to the sampling being restricted to open spaces and not including areas beneath shrub canopies where organic matter accumulates in desert systems (see Bolling, 1996; Bolling & Walker, in press).

Differences between application types in terms of plant parameters are likely a result of a complex combination of soil and environmental factors. The even principal component loadings in the soil PCA are evidence of this (absolute value of most PC loadings between 0·21 and 0·45; Table 3). However, plant species composition appears to change in conjunction with some of the differences in soil conditions between applications. Bladed roads, which were lower in *Larrea* cover, also had lower soil clay (both depths), compaction (surface) and organic matter (7·5–15 cm) and higher available nutrients (both depths) than track roads. *Larrea* could be excluded from bladed roads by interference competition (Fonteyn & Mahall, 1981), or by phosphorus toxicity (Musick, 1978). Similar to the findings of Webb *et al.* (1987), the rate and direction of vegetation change seen in this study is a function of the type of initial disturbance. Given that only one road of each age class was included in the study, species abundance data should be interpreted with caution.

Encelia, an early successional species, may have been able to take advantage of a nutrient pulse which commonly occurs immediately after disturbance (Vitousek et al., 1989). *Encelia* inhabits moderately disturbed areas such as arroyos and other natural disturbances (Vasek, 1979/1980). Road 2 in this study was dominated by *Encelia* and is located in a broad arroyo where water availability was presumably high. A nutrient pulse early in succession may have impacted *Encelia* occurrence in this area. *Ambrosia* cover and density were sporadic across all sites. This species may have been adversely impacted by feral burros, which prefer it as a food source (O'Farrell, 1978). *Krameria* appeared on most control plots, but had low sociability (widely dispersed, growing singly). It was very rare on road plots, appearing only on Roads 6 and 7, two of the older roads.

The only two roads that had a higher mean plant density than paired controls were both track roads (Roads 3 and 7). The other track road (Road 6) had nearly as many plants as its paired controls (0·33 *vs.* 0·35 plants m^{-2}; Fig. 6). In addition to cover and density, on Roads 6 and 7 there were more *Larrea* (mainly in small and intermediate size classes) on the roads than off (Fig. 8). These patterns of plant establishment, survival and growth on track roads may have been partly due to local edaphic conditions which made these sites more favourable for establishment of seedlings than bladed road conditions.

Variation in the magnitude of disturbance is evident in Figure 8. Two recently abandoned bladed roads (Roads 2 and 4) had very few *Larrea* on them, whereas Road 1 (also bladed) had many small individuals. As the control plots for Road 1 had the same number of small individuals (contrary to the overall pattern on control plots), this could be evidence of a recent mass recruitment event in the area. Additionally, when disturbed, this road may not have received full blading, as the bulldozer probably passed through part of the area with its blade raised (J. Riley, pers. comm.). Although recruitment of *Larrea* was high on Road 1 control and treatment plots (Fig. 8), a simple correlation analysis showed that no measured soil variable changed in conjunction with *Larrea* occurrence (data not shown). Recruitment, occurring on roads of both application types (Roads 1, 3, 5, 6, and 7), was probably due to either chance events or other climatic or soil factors that were not examined here. These might include microbial biomass and the presence of mycorrhizal inoculum. Another important factor could be resprouting from root crowns that remained alive during the active road use period. This has been invoked as a possible mechanism by other authors (Jaynes & Harper, 1978; Webb & Wilshire, 1980; Prose *et al.*, 1987). The fact that a large number of individuals on Road 7 were in larger size classes than other roads (track road; Fig. 8) is evidence suggesting root crown sprouting.

If the presence of large mature *Larrea* individuals is indicative of recovery from disturbance, then Road 7 (55 years old) was the only site close to achieving this (Fig. 8). Very old clones of *Larrea* were not encountered on any control plots in this study. Maximum shrub radii were approximately 130 cm, putting ring size-age extrapolations at 200–300 years (Vasek, 1980), although variations in growth rates may make them somewhat younger. The largest individuals were seen on control plots for Road 2, in a broad arroyo where higher water availability would have allowed faster growth rates. Additionally, outward ring growth of *Larrea* may be restricted by the coarseness of the alluvium in the region (McAuliffe & McDonald, 1995).

The importance of patterns of heterogeneity in vegetation and soils is critical to explaining community structure along the series of roads examined in this study. A recent study by Schlesinger *et al.*, (1996), showing autocorrelation of soil N at distances equaling the mean *Larrea* size, exemplifies this spatial dependence. In a twelve year study of succession in the sagebrush steppe, McLendon & Redente (1990) found that the type of disturbance affected the direction of succession. They suggested that over a longer time frame successional pathways might converge upon a single community type. This convergence may take place over long time spans in the Mojave Desert, as suggested by the results of this study, where after 87 years of abandonment full vegetation and soil recovery and time series effects were not seen. Long-term change was noted by McAuliffe (1991) on Sonoran Desert bajadas formed between 500 and 4000 year ago. The results of this study suggest that the clarity of successional patterns in Mojave Desert plant communities would improve over a 500–1000 year time frame.

Efforts to restore natural communities in this ecosystem are difficult at best (Wallace *et al.*, 1980). Early attempts showed little success in propagating perennial shrub species or ameliorating soil damage (Marble, 1985). We believe that decompaction of roads and amelioration of microtopographic differences would increase the probability of a more natural community development trajectory. This labor intensive process would involve flattening out of lateral and centre berms. Once erosional gullies form on unstable ground, they are difficult to redirect. Restoration of soil horizons is also important to the re-establishment of microbial communities. Addition of much would lower surface soil pH and increase soil organic matter levels. Inoculation of soils with native microbes and mycorrhizae would likely have a restorative effect as well. Long-term monitoring including analysis of microbial populations would ensure that soils are on the path to recovery. Transplantation efforts would then have a better chance at success. The creation of artificial patchiness in nutrients might help to restore fertile islands to bladed roads where patterns of soil heterogeneity were eliminated. Without restoration efforts, successional trajectories will be permanently altered after disturbance (Marble, 1985).

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