Journal of Applied Ecology (1987) **24,** 305–313

EFFECTS OF SUBSTRATE DISTURBANCE ON SECONDARY PLANT SUCCESSION; MOJAVE DESERT, CALIFORNIA

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SUMMARY

(1) The effects of substrate disturbance on perennial plant succession in the Mojave Desert were assessed at three military camps abandoned for 40 years.

(2) Soil compaction, removal of the top layer of soil, and alteration of drainage channel density caused significant changes in perennial plant cover, density, and relative species composition.

(3) Long-lived species, predominantly *Larrea tridentata*, were dominant in all control areas but percentage cover and density were greatly reduced in areas where substrate alterations were significant.

(4) Pioneer species such as *Ambrosia dumosa* and *Hymenoclea salsola* had percentage cover values similar to or greater than controls in most areas where substrate alterations were significant, and these species were dominant in the majority of disturbed areas.

(5) Where substrate alterations were insignificant in disturbed areas at one camp, *Larrea* was the dominant species as in the control.

INTRODUCTION

Human activities that disturb vegetation commonly also modify the soil substrate. Substrate disturbances reported in studies of secondary plant succession in the Mojave Desert include soil trampling, trench backfilling, and road grading during power and pipe-line construction (Vasek 1975a, b; Lathrop & Archbold 1980a, b); excavation of borrow pits for road-building materials (Vasek 1979/80); soil trampling in town sites of abandoned mining communities (Webb & Wilshire 1980; Webb, Wilshire & Henry 1983; Webb, Steiger & Turner 1987); tillage of agricultural fields (Carpenter, Barbour & Bahre 1986; Romney, Wallace & Hunter 1979); and soil trampling and loading by soldiers and vehicles in military manoeuvre areas and base-camps (Lathrop 1983). These disturbances commonly produced substrate alterations that persisted for decades after disturbance, such as soil compaction, destruction of the soil profile, and/or soil loss by direct removal or by erosion. Since these alterations are detrimental to vegetation growth (reviews of this topic include Rosenberg 1964), most studies listed above conclude that substrate alterations slow the rate of plant succession. However, few of these studies quantitatively assess substrate alterations in disturbed areas. Webb & Wilshire (1980) and Webb, Steiger & Turner (1987) measured soil compaction in mining towns abandoned for 50–75 years and found that minimally-compacted areas supported vegetation assemblages similar to those in undisturbed areas, whereas plant cover and species composition were significantly changed in highly compacted areas.

The purpose of this study was to assess the effects of different degrees of substrate disturbance on perennial plant succession in *Larrea tridentata* (Sesse & Moc. ex DC)–*Ambrosia dumosa* (Gray) communities in the eastern Mojave Desert. This area was designated the Desert Training Center in 1942 and was used for military training exercises for 2 years (Meller 1946). Three abandoned base-camps offered a number of study areas that were disturbed in varying degrees. Natural substrate and vegetation properties varied between camps, allowing comparison of successional trends between slightly different micro-environments in the Mojave Desert.

STUDY AREA

The three abandoned military camps—Ibis, Clipper, and Iron Mountain—were located in the eastern Mojave Desert of California, in a sparsely-populated area between the towns of Ludlow, Calif., Needles, Calif., and Parker, Arizona (see Prose (1986) for exact locations). The elevation of Camp Ibis was 525 m, Clipper 575 m, and Iron Mountain 350 m. Each camp encompassed 1000–2600 ha, and consisted of a network of graded dirt roads and cleared areas used for tent sites, vehicle parking lots, and other purposes. The regional climate is arid, with annual rainfall during the period 1940–84 averaging 11·2 cm at Needles (located within 61 km of camps Ibis and Clipper), and 7·9 cm at Iron Mountain. Average January and July temperatures at Needles during this period were 11·1°C and 35·5°C, respectively (National Climatic Center, written communication, 1985).

The camps were established on gently sloping, coalescing alluvial fans (bajadas). The fan surfaces at Ibis and Iron Mountain were incised by numerous shallow drainage channels. Clipper was astride a more stable surface with large, widely-spaced wash channels. Average soil textures in the 0–30 cm depth range were gravelly sand at Ibis and Iron Mountain and loamy sand at Clipper. The plant community at all camps was creosote bush scrub (Munz 1974). *Larrea tridentata* was the dominant species in undisturbed areas with *Ambrosia dumosa* subdominant. There was some variation in community characteristics between camps (see Table 1).

MATERIALS AND METHODS

Exact locations of the camps and their layouts were obtained from National Archives records in Washington, D.C. and from aerial and ground-level photographs taken when the camps were active. Soil and vegetation measurements were made in minimally-disturbed control areas and adjacent tent sites, parking lots, and roads. The controls were traversed by some vehicles during training exercises, but many vehicle tracks remain and thus significantly-disturbed areas could be avoided when sampling. Records indicate that the tent sites were cleared of vegetation by soldiers using hand-tools and subjected to foot trampling. Vehicle parking lots were also manually cleared of vegetation but were subjected to intensive use by a wide variety of armoured vehicles and lighter jeeps and trucks. Roads were constructed by removing the upper 10–20 cm of soil by grading and were heavily used by both vehicles and personnel. Camp Clipper was active for a shorter time than the other two camps; operations were transferred from an adjacent camp that was subject to flooding. The camps were abandoned with no apparent attempt to reclaim them, and no signs of recent disturbance were present in sampled areas because of the remoteness of the area; the roads are the only areas likely to have been recently disturbed by vehicles.

TABLE 1. Density (plants ha^{-1}) (D) and percentage cover (C) of perennial vegetation at three abandoned military base-camps; Mojave Desert. *Significantly different ($P \leq 0{\cdot}05$) from control.

	Camp Ibis								Camp Clipper								Camp Iron Mountain							
	Control		Tent site		Parking lot		Road		Control		Tent site		Parking lot		Road		Control		Tent site		Parking lot		Road	
Long-lived	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C
Krameria parvifolia	790	2·0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Larrea tridentata	584	7·4	127	1·7	84	0·5	43	0·4	726	11·3	299	5·4	175	3·0	100	1·3	200	5·5	167	2·2	84	0·9	—	—
Opuntia echinocarpa	—	—	—	—	—	—	—	—	75	0·1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Opuntia ramosissima	83	0·1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Yucca schidigera	124	0·1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total long-lived	1581	9·6	127	1·7	84	0·5	43	0·4	801	11·4	299	5·4	175	3·0	100	1·3	200	5·5	167	2·2	84	0·9	—	—
Long-lived opportunistic																								
Ambrosia dumosa	2959	7·4	3043	8·6	3449	9·3	791	3·3	1274	1·9	1501	4·6	650	2·0	700	4·3	233	1·0	2150	3·9	750	1·8	100	0·3
Short-lived																								
Bebbia juncea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17	0·1	—	—	—	—	—	—
Dyssodia porophylloides	83	0·1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Encelia farinosa	—	—	—	—	52	0·2	—	—	—	—	—	—	—	—	—	—	—	—	17	0·1	18	0·1	67	0·5
Encelia frutescens	331	0·4	457	0·4	1501	2·7	832	1·8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hymenoclea salsola	—	—	249	0·9	42	0·3	—	—	—	—	—	—	—	—	—	—	—	—	100	0·4	1267	6·4	—	—
Lepidium fremontii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	33	0·1	50	0·1	—	—
Porophyllum gracile	—	—	167	0·1	42	0·1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Stephanomeria pauciflora	207	0·2	41	0·1	84	0·1	43	0·1	—	—	—	—	—	—	—	—	32	0·2	132	0·5	91	0·3	—	—
Total short-lived	621	0·6	914	1·5	1721	3·4	875	1·9	—	—	—	—	—	—	—	—	49	0·3	282	1·1	1426	6·9	67	0·5
Totals	5161	17·6	4084	11·8	5254	13·2	1709*	5·6*	2075	13·3	1800	10·0	825*	5·0*	800*	5·6*	467	6·8	2599*	7·2	2260*	9·6*	167*	0·8*

Soils and surface hydrology studies

Soil compaction was assessed by the bulk density method (Blake 1965). Recording penetrometer measurements were not used because severely disturbed areas were compacted beyond the working range of the instrument (Prose & Metzger 1985). Bulk density was calculated from oven-dried soil samples that were collected with a piston-driven cylinder (volume: 224 cm^3). Thirty samples were collected from soils between shrubs and drainage channels at depths of 0–10 cm, 10–20 cm, and 20–30 cm in each study area. Particle-size distribution was determined on additional samples by the hydrometer method (Day 1965). Bulk density values were averaged for the 0–30 cm depth range in each control, and disturbed area and differences between means were analysed statistically at a confidence level of 95% with an appropriate t-test.

Drainage channel density was analysed at Camps Ibis and Iron Mountain because vegetation was concentrated along wash channels and alteration of surface drainage characteristics can significantly affect vegetation (Schlesinger & Jones 1984). The number of drainage channels was recorded on traverses perpendicular to the dominant drainage direction in each study area. Density of channels in each area was calculated as number of channels per 100 m, and control and disturbed pairs were analysed with a t-test. Measurements were not made at Camp Clipper because dissection of the surface was minimal in the study areas.

Vegetation studies

Perennial shrubs were sampled in 20 m^2 rectangular plots at Camp Ibis and in 50 or 100 m long $\times$ 2 m wide belt transects at Camps Clipper and Iron Mountain. The plots and transects were aligned perpendicular to the dominant drainage direction to minimize errors caused by concentration of vegetation along wash channels. A stratified, random sampling technique was used (Greig-Smith 1983) and the number of plots or transects required for a representative sample was determined from spacing and species area curves (Brower & Zar 1977) of the dominant species, *Larrea* and *Ambrosia*, in the controls. Sample areas in the controls and disturbed areas were 240 m^2 ($n=12$) at Camp Ibis, 400 m^2 ($n=20$) Camp Clipper, and 600 m^2 ($n=30$) at Camp Iron Mountain.

Larrea plants occurring in clumps were considered individuals if the main stems of visually-distinct shrubs were separated by a distance of at least 1 m. Density (number of individuals ha^{-1}) and percentage cover of each shrub species were determined for each study area. Distributions of cover values were normalized by angular transformation (Campbell 1974) and differences in total percentage cover between controls and disturbed areas were tested for significance ($P \leq 0{\cdot}05$) with a t-test. Total density values for each study area were also analysed statistically.

To analyse the adaptability of species with particular life-histories to substrate alterations, species were categorized as either long-lived, long-lived opportunistic, or short-lived (Vasek 1983; R. H. Webb, personal communication 1986).

RESULTS

Soils and surface hydrology

Bulk density measurements were highly variable but indicated that disturbed areas were significantly compacted between 0 and 30 cm depth, except at Camp Clipper, where

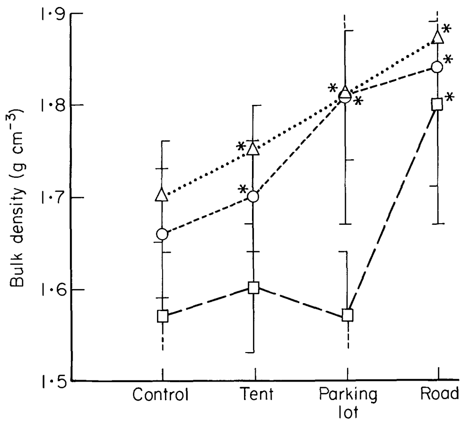

FIG. 1. Soil bulk density at three abandoned military camps, Mojave Desert. (○) Camp Ibis; (□) Clipper; (△) Iron Mountain. Vertical bars represent standard deviation. *Significantly different from control ($P \leq 0{\cdot}05$).

only the road had significantly higher density values than the control (Fig. 1). The deep, fine-grained soils at Clipper had the lowest overall bulk density of all camps.

Drainage channel densities at Camp Ibis were not statistically different in the control and disturbed areas (Table 2). At Iron Mountain, channel densities were similar in the control and tent site, but were significantly lower in the parking lot and road than in the control. Surfaces between channels in the parking lot contained fluvial deposits of silt and sand.

Vegetation

Total plant density and cover in all roads and the parking lot at Clipper were significantly lower than in the controls (Table 1). At Iron Mountain, total density was significantly higher in the tent site than in the control because of an abundance of *Ambrosia* seedlings. The parking lot at this camp had a significantly higher total density and cover than the control because of an abundance of *Hymenoclea salsola* (T & G). All other disturbed areas had total density and cover values similar to those in respective controls.

Long-lived species were greatly reduced in disturbed areas compared to controls. *Larrea tridentata* was negatively correlated with disturbance at all camps, and was very

TABLE 2. Drainage channel density at three abandoned military camps; Mojave Desert. Channel density = number of streams per 100 m. n = number of traverses. *Significantly different from control ($P \leq 0{\cdot}05$)

	Ibis			Iron Mountain		
	n	Mean	Standard deviation	n	Mean	Standard deviation
Control	3	8·5	1·21	3	11·6	0·91
Tent site	3	12·0	0·99	2	10·8	0·35
Parking lot	3	12·0	1·51	2	5·7*	1·06
Road	2	10·1	0·49	2	6·4*	1·13

sparse or not present in the parking lots and roads. The dominant species in the controls, *Larrea* was subdominant in all disturbed areas except the tent site and parking lot at Camp Clipper. Other long-lived species occurred in the controls at Ibis and Clipper but were not present in disturbed areas.

Ambrosia dumosa, the sole long-lived opportunistic species, had higher cover values in disturbed areas than in controls except in the roads at Ibis and Iron Mountain. This species was dominant in over half of the disturbed areas.

Short-lived species were present in undisturbed areas at all camps, but were encountered in measured areas only at Ibis and Iron Mountain. Disturbance generally caused an increase in these species, particularly of *Encelia frutescens* (Gray) at Camp Ibis and *Hymenoclea salsola* at Iron Mountain.

Relation of soil bulk density and perennial shrub cover

Percentage cover of perennials was chosen for comparison with changes in soil bulk density rather than density because cover is considered to be of greater ecological significance (Daubenmire 1968). Total cover was significantly reduced in the extremely-compacted roads compared to controls at all camps (Fig. 2). Cover of long-lived species, predominantly *Larrea*, decreased with increased soil density. *Ambrosia dumosa*, the long-lived opportunistic species, and short-lived species, had higher cover values in compacted areas than in controls except in the extremely compacted roads at Camps Ibis and Iron Mountain. Thus, relative species composition shifts from *Larrea*-dominant assemblages in non-compacted areas to assemblages dominated by short-lived species and/or *Ambrosia* in significantly compacted areas.

DISCUSSION

Soil compaction was significant in most disturbed areas 40 years after the military camps were abandoned. Webb & Wilshire (1980), Prose (1985), and Webb, Steiger & Wilshire (1986) reported that various desert soils remained compacted as a result of human disturbances for similar or longer periods of time, probably because animal burrowing and plant root growth are the primary agents of soil-loosening in low desert valleys but animals and plants have difficulty displacing highly-compacted soils. Soil compaction has been shown to inhibit plant growth in many laboratory studies (for example, Rosenberg & Willits 1962), and compaction caused significant decreases in cover of desert vegetation in disturbed areas (Rowlands 1980; Webb & Wilshire 1980). In this study, *Larrea tridentata* was found to be highly sensitive to soil compaction. These observations of recently disturbed areas indicate that established individuals can survive moderate disturbances, but *Larrea* has a very low rate of germination and seedling survivorship even under ideal laboratory conditions (Barbour 1968). Because the tent sites and parking lots at the camps were evidently only cleared of above-ground vegetation before use, some *Larrea* root-crowns may have survived and produced new foliage after the camps were abandoned. The virtual absence of *Larrea* in the camp roads may be due to extreme soil compaction, combined with the effects of road construction when grading probably destroyed most root-crowns. In addition, nutrients essential for plant growth may have been stripped by grading which removed 10–20 cm of soil. Charley & Cowling (1968) found that removal of the surface 5–10 cm of soil significantly depleted nutrient reserves and caused a significant reduction of perennial cover after 13 years of succession in a desert saltbush community in Australia.

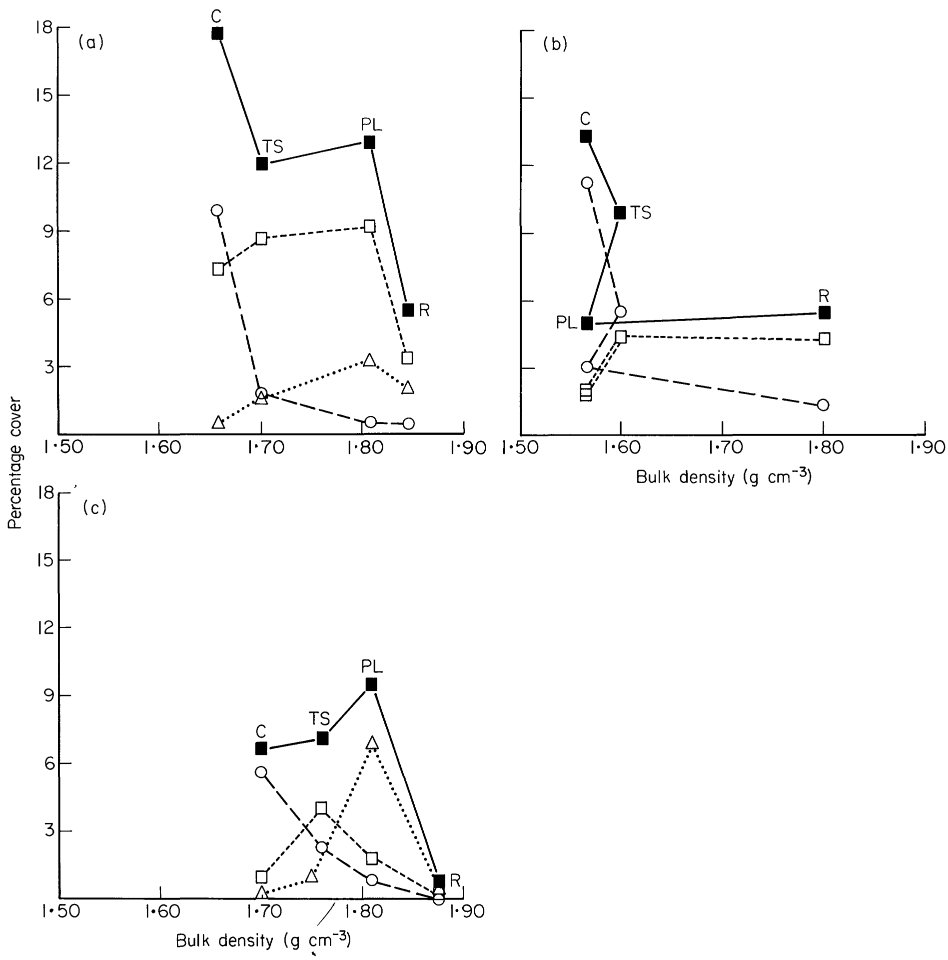

FIG. 2. Relation of soil bulk density and vegetation cover at three abandoned military camps, Mojave Desert: (a) Camp Ibis; (b) Clipper; (c) Iron Mountain. (■) Total percentage cover; (○) long-lived perennials; (□) long-lived opportunistic; (△) short-lived. C, control; TS, tent site; PL, parking lot; R, road.

Cover of *Ambrosia dumosa* in most disturbed areas was similar to or higher than that in the controls. This species is a common pioneer in disturbed areas in the Mojave Desert (Vasek 1979/1980; Lathrop & Rowlands 1983) apparently because of its ability to reproduce both asexually and by efficient dispersal of abundant seeds. Reductions of *Larrea* in disturbed areas may have further enabled *Ambrosia* to re-establish quickly by reducing interspecies interference. Such interference was observed in a western Mojave Desert *Larrea–Ambrosia* community by Fonteyn & Mahall (1981).

Short-lived species such as *Encelia frutescens* and *Hymenoclea salsola* were more abundant in most disturbed areas than in controls at Camps Ibis and Iron Mountain. These species were early colonizers of disturbed areas elsewhere in the Mojave Desert (Vasek 1979/1980; Webb, Wilshire & Henry 1983), partly because they inhabit naturally 'disturbed' areas such as drainage channels. *Hymenoclea* was greatly increased in the parking lot at Iron Mountain. In this area, alteration of surface drainage characteristics may have created favourable growing conditions for this species. Runoff capacity frequently exceeds that of the reduced number of drainage channels as indicated by fluvial deposits on inter-channel surfaces. A similar, frequently-disturbed environment exists in large drainage channels where *Hymenoclea* occurs naturally.

At Camp Clipper, *Larrea* was the dominant species in the tent site and parking lot. These were the only disturbed areas examined where substrate alterations were not significant, and where pioneer species did not dominate vegetation assemblages. Thus, it appears that disturbed *Larrea–Ambrosia* communities can re-establish climax conditions quickly in terms of relative species composition if substrate alteration is minimal. If disturbance causes significant substrate alteration, pioneer species assume dominance because they are adaptive to a wide range of disturbance while substrate alterations inhibit re-establishment of *Larrea* and other long-lived species. Substantial amelioration of substrate conditions must take place in highly-disturbed areas before *Larrea* re-assumes dominance in accordance with classical succession theory.

ACKNOWLEDGMENTS

We thank Denise Polk for her assistance in the field. Frank Vasek and Robert Webb provided very helpful reviews of the manuscript. This project was supported by a grant from the U.S. Army Research Office; contract No. 104–84.

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(Received 11 November 1985; revision received 15 October 1986)