



Establishment and effects of establishment of creosotebush, *Larrea tridentata*, on a Chihuahuan Desert watershed

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(Received 13 December 1999, accepted 4 August 2000)

Creosotebush (*Larrea tridentata*) seedlings were planted in plots that were irrigated, plots that were irrigated and fertilized with ammonium nitrate, and plots that were not amended in three plant communities on a Chihuahuan Desert watershed: ungrazed black grama (*Bouteloua eriopoda*) grassland, creosotebush shrubland, and overgrazed grassland. No seedlings were planted in one-half of the area of each plot. No seedlings survived in the black grama grassland or the creosotebush shrubland 2 years after planting. Growth of established creosotebush shrubs was highest in plots with the lowest grass cover. Fifteen years after the seedlings were planted in the overgrazed grassland, the area under the shrubs was nearly devoid of perennial grasses and forbs. The aggregate stability of the soils under the established creosotebush shrubs was significantly lower than the soils in the unplanted split-half of the plots. Electrical conductivity, calcium, and nitrate were significantly lower in soils under shrubs than soils in the unplanted split-half of the plots. There were also significant reductions in densities of annual plants growing under the shrubs than in the unplanted split-half of the plots. Successful establishment of creosotebush in desert grasslands is dependent upon the presence of large patches of soil with no perennial plant cover. Intense grazing by domestic livestock creates microsites and landscape characteristics favourable for seed dispersal, germination and establishment of creosotebush. Soil changes resulting from shrub establishment reduce the probability of re-establishing perennial grasses in creosotebush-dominated shrubland.

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Keywords: aggregate stability; annual plants; creosotebush; *Larrea tridentata*; overgrazing; soil chemistry; survivorship

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Introduction

Creosotebush (*Larrea tridentata*) is known to have spread into many areas of the Chihuahuan Desert during the past 150 years (Gardner, 1951; Branscomb, 1958; Buffington & Herbel, 1965). Despite the importance of this process in the degradation of rangelands, there are no empirical studies that examine the establishment of this shrub and the immediate post-establishment changes in soil and structure of the community. Early studies of the vegetation of the northern Chihuahuan Desert suggested that creosotebush establishment was limited to areas of overgrazed grassland. Gardner (1951), in a study of vegetation of the Rio Grande valley of New Mexico, stated 'throughout the area, in those places where bodies of creosotebush adjoin grassland with a history of heavy grazing, the bush is advancing into the grassland'. The evidence for this pattern of establishment of creosotebush was the appearance of young bushes in the open spaces of the grassland 'well out beyond the edge of the main body'. Gardner (1951) also observed that on the conservatively grazed grassland of the New Mexico Agricultural College Ranch, isolated creosotebush individuals in the good grassland were not forming colonies. Based on these published observations, it is logical to hypothesize that creosotebush will exhibit higher rates of establishment in heavily grazed grassland than in ungrazed, good condition grassland.

Once established, creosotebush plants appear to live for extremely long periods. There is little or no establishment of young plants within mature stands (Bowers *et al.*, 1995). Bowers *et al.* (1995) reported that, based on repeat photography, 84 of 85 individual creosotebush shrubs survived 'over the past 100 years'. The failure of creosotebush seedlings to survive in mature stands was confirmed by an experimental study (Boyd & Brum, 1983). They reported that creosotebush seedlings that were not protected from jackrabbits exhibited higher mortality during the first 2 months after seedlings were transplanted, but less than 2% of the seedlings in either treatment were alive 90 days after transplantation. An earlier study by Sheps (1973) found that creosotebush seedling mortality was highest for seedlings nearest mature shrubs. Sheps (1973) suggested that this was an allelopathic effect of mature shrubs on seedlings. However, Barbour *et al.* (1977) reported no conclusive laboratory evidence of allelopathic effects of mature creosotebush shrubs on the seedlings.

In order to examine the factors that affect successful seedling establishment and survival, we established a creosotebush seedling transplant study in three plant communities on a northern Chihuahuan Desert watershed. It was hypothesized that creosotebush seedling survival would be highest in a grassland with a history of grazing and lowest in a mature stand of creosotebush and in an ungrazed, black-grama, *Bouteloua eriopoda*, grassland. The growth of mature creosotebush is dependent upon soil nitrogen availability as well as water (Fisher *et al.*, 1988). In order to examine the mechanisms affecting establishment of creosotebush, some plots were irrigated for the first year after seedlings were planted and some plots were fertilized with nitrogen. It was hypothesized that both water amendment and fertilization would result in higher rates of seedling growth and greater survivorship than seedlings lacking treatment. Here, the results of that study are reported.

After establishment, creosotebush acts as a community dominant. As a dominant in the community, it affects soil resources by creating fertile islands in low-fertility soil, and by changing soil water storage patterns (Martinez-Meza & Whitford, 1996; Whitford *et al.*, 1995, 1997). These effects on the soil resources appear to be time dependent (de Soyza *et al.*, 1997). Here, the effects of creosotebush of documented age on soil properties and other species in the plant community are also examined.

Methods and materials

Plots for water and nitrogen amendments were established within three plant communities on a desert watershed: an upper-slope piedmont desert-grassland dominated by black-grama grass (*Bouteloua eriopoda*), a mid-slope piedmont creosotebush shrubland, and a lower slope piedmont desert-grassland dominated by several bunch grasses. Domestic livestock had not grazed the upper two areas for more than 25 years. The lower slope piedmont was fenced to exclude cattle in 1982 but had been intensively grazed by domestic livestock for more than 75 years prior to that. Within these three communities, six 8 × 8 m plots were fenced with chicken mesh (2.6-cm diameter) to exclude rabbits. Two 8 × 8 m plots were enclosed by a single fence with a sheet metal barrier splitting the 8 × 16 m area into two plots. Water was added by overhead sprinklers to plots that were assigned to irrigation at 2-week intervals from May 1983 to December 1984 at a rate that approximately doubled the long-term average (i.e. approximately 10 mm per application). This added approximately 250 mm to the natural rainfall regime during the growing season of the first year that seedlings were planted. Nitrogen was added as a one-time application in May 1983 at a rate of 10 g m⁻² to the nitrogen fertilized plots and to the irrigated, nitrogen fertilized plots.

Creosotebush seeds were collected from mature plants on the watershed on 6 January 1983. The seeds were planted in desert soil in flats in a greenhouse on 15 March 1983. Germination of creosotebush was nearly complete by the first week of April. Seedlings were maintained in the greenhouse until 17 August 1983. Twenty seedlings were transplanted into one-half of the area of each plot: the control, irrigated, and irrigated plus N-fertilized plots in each of the three areas producing a split plot design for each area. Ten seedlings were planted in open areas between grass clumps or between shrubs. Ten seedlings were planted adjacent to grass clumps or under shrub canopies in the creosotebush community. When the seedlings were transplanted into the field, they were single stem with between 4 and 12 leaves. Canopy diameters and heights of seedlings were measured in March and May 1984, and in May 1986.

During August 1998 to March 1999, we made a series of measurements on the plots with surviving creosotebush. We made paired measurements of cover and composition of perennial and annual plants in the establishment half and control half of the plots using a 0.5-m² Daubenmire frame (Bonham, 1989). Three soil cores (6.0-cm diameter, 15-cm deep) were collected from each plot with creosotebush, and three soil cores were collected from the reference half of each plot. Soil chemical analysis was performed at the New Mexico Soil and Water Testing Laboratory using standard tests (Page *et al.*, 1982). An indirect measure of soil aggregate stability (a modified slake test) was used to compare soils under creosotebushes and in the reference plots (Herrick *et al.*, in press). Ten samples of surface crust and 10 samples of soil at 5-cm depth were collected in each location (creosotebush and reference plots). Samples were rated on a scale from one to six based on a combination of visual slaking during the first 5 min following immersion in distilled water, and the per cent remaining on a 1.5-mm sieve after five dipping cycles at the end of the 5 min period (Herrick *et al.*, in press).

Post-establishment data from the plots with creosotebush and the controls were analysed by split-plot ANOVA if the data passed the normality test. For data that did not meet the normality test, Kruskal-Wallis ANOVA on ranks was used. Survivorship and growth of seedlings were analysed by Kruskal-Wallis ANOVA because the data were not normally distributed.

Results and discussion

In 1984, 9 months after planting, there was no mortality of seedlings planted in the water plus nitrogen-fertilized plots, and there was a loss of only 1 or 2 seedlings in the

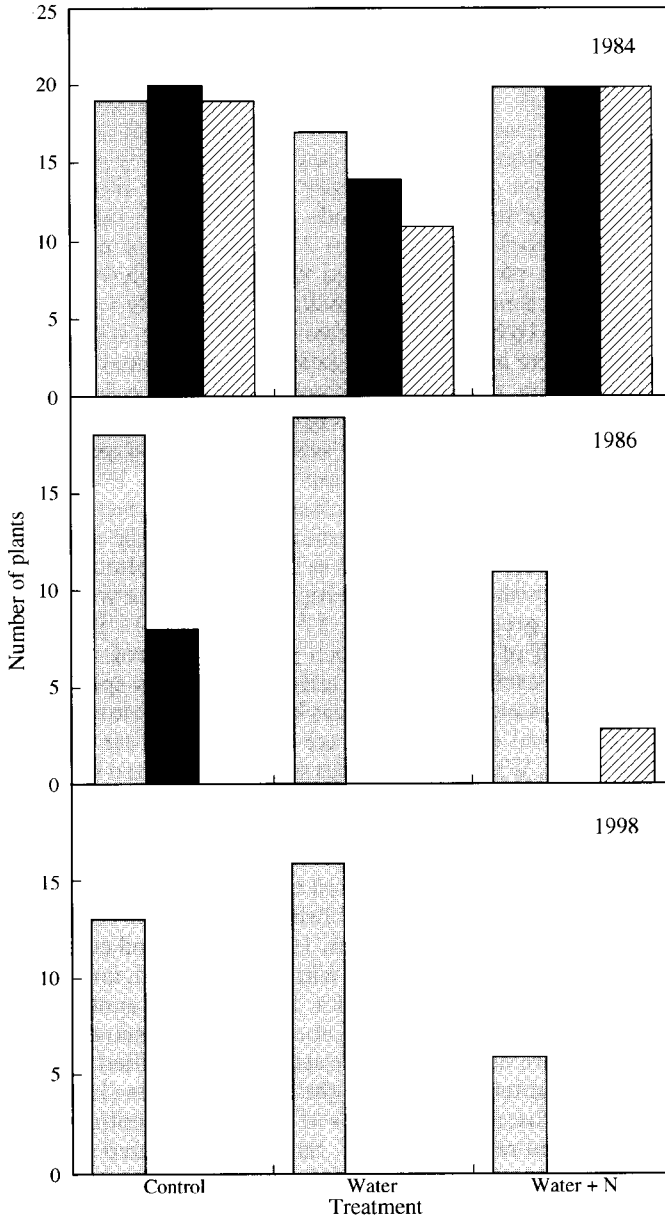


Figure 1. Number of surviving creosotebush seedlings planted in three different plant communities (▨ = upper bajada—ungrazed black-grama (*Bouteloua eriopoda*) grassland; ■ = middle bajada—mature creosotebush (*Larrea tridentata*) community; ▩ = lower bajada—overgrazed black-grama grassland) in August 1983. Number of surviving creosotebush seedlings in 1984 water (irrigated) treatment was significantly lower than other treatments (Kruskall-Wallis ANOVA, $p < 0.05$).

unfertilized, unwatered plots (Fig. 1). Nearly one-third to one-half of the seedlings in the irrigated plots died within the first year (Fig. 1). The causes of that mortality appeared to be mostly due to some kind of damping-off with shrivelling of the stem just above the ground. One or two of the seedlings appeared to have been bitten off. Rodents

had access to the establishment plots because they burrowed under the fence and could also crawl through the mesh (unpublished data) which probably accounts for the loss of seedlings by herbivory. Because irrigation was terminated in December 1984, the effect of water supplementation could only be evaluated for the first year of the study. There was significantly higher mortality in the irrigated plots than in the control and irrigated-fertilized plots ($p < 0.05$) (Fig. 1). At the end of the first year, the seedlings in the irrigated plots were significantly smaller than the seedlings in the other treatment and the control plot ($p < 0.05$) (Fig. 2). Irrigation probably affected the availability of nitrogen to the growing seedlings by leaching and increasing the rate of nitrogen mineralization from soil organic matter (Fisher *et al.*, 1987).

By 1986, there were no surviving seedlings in the control and or in the irrigated plots on the black-grama grassland on the upper bajada, and only three seedlings survived in the water plus N-fertilization plots at that location (Fig. 1). The only surviving creosotebush seedlings within the mature creosotebush stand were in the unfertilized plot that was not irrigated (Fig. 1). On the lower bajada, (overgrazed grassland), there was no mortality in the control and irrigated plots but half of the shrub seedlings in the water plus nitrogen plot had died and disappeared. When the plots were examined in August 1987, there were no surviving seedlings in the upper and middle bajada locations and no measurements were made on the surviving shrubs on the lower bajada.

Gardiner (1951) reviewed the historical evidence for the spread of creosotebush into the desert grasslands of southern New Mexico. He reported that creosotebush spread from dense creosotebush communities into overgrazed grassland but that there was essentially no establishment in lightly grazed grassland. The high mortality rates of creosotebush seedlings in the ungrazed black-grama grassland and in the creosotebush community were similar to those reported by Valentine & Gerard (1968). However, Valentine & Gerard (1968) did not record high numbers of seedlings surviving in grazed grassland pastures. They reported high levels of mortality resulting from damping-off but concluded that drought was the primary cause of mortality. If dry soil conditions are the primary cause of death in creosotebush seedlings, surviving seedlings in the irrigated plots should have been recorded regardless of landscape position or plant community. The pattern of surviving creosotebush in this study suggests that the close spacing of grass plants in the ungrazed grassland and the high root densities in the creosotebush shrubland (Brisson & Reynolds, 1994) prevented acquisition of water and nutrients by seedling shrubs. This competition occurred even when there were excess amounts of these resources in the irrigated, fertilized plots. In 1984, when the creosotebush seedlings were planted, the grazed grassland plots were characterized by variable-sized bare patches interspersed with grass clumps. Comparison of grass cover on the control plots in 1999 revealed that grass cover ($33.7 \pm 17.0\%$) was higher on the split half with only six surviving shrubs. On the control halves of the plots, with 16 and 13 surviving shrubs, the mean grass cover was $3.7 \pm 3.1\%$. Creosotebush survival was lowest in the plot with the highest grass cover. These data suggest that grass cover and sizes of bare patches may have had a greater effect on long-term survivorship than nitrogen fertilization. The spatial distribution and density of grass clumps would affect the supply of both water and soil nutrients to shrub seedlings.

Our study confirms the earlier observations of Boyd & Brum (1983) on the failure of creosotebush seedlings to establish within mature stands of *L. tridentata*. The studies of Boyd & Brum (1983) showed that browsing by jackrabbits accounted for most of the mortality of the unprotected seedlings. Although the seedlings were protected from jackrabbit browsing in our study, rodents had access to the plots and accounted for more than 90% of the seedlings that had died by the 1984 census.

The smallest shrubs were in the plot with the lowest density of shrubs (Figs. 1 & 2). There were significant differences ($p < 0.05$) in mean height of creosotebush in the water plus nitrogen plot (52.3 ± 23.7 cm) and the other two plots (83.6 ± 22.2 cm and 85.5 ± 34.0 cm). The split-half of this plot also had the highest grass and perennial forb

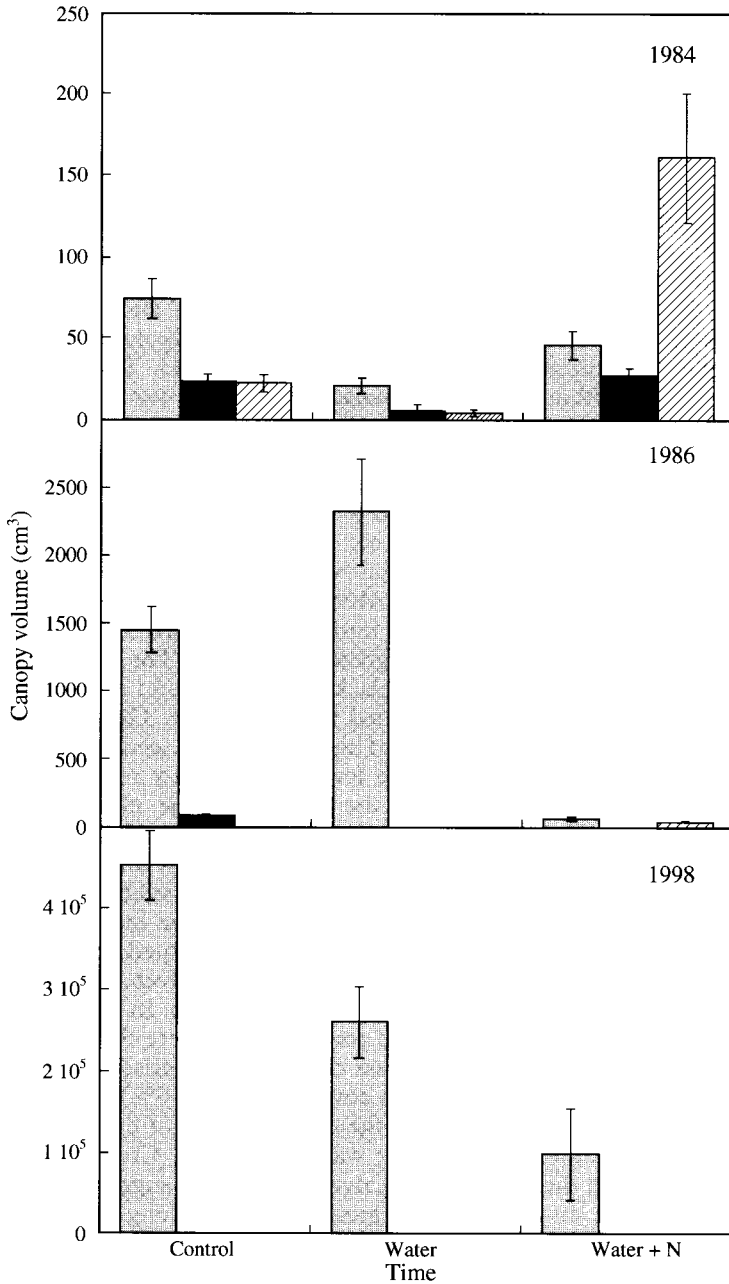


Figure 2. Mean canopy volumes of surviving creosotebush seedlings planted in three different plant communities (▨ = upper bajada—ungrazed black-grama (*Bouteloua eriopoda*) grassland; ■ = middle bajada—mature creosotebush (*Larrea tridentata*) community; ▤ = lower bajada—overgrazed black-grama grassland) in August 1983. Canopy volumes of the 1984 water (irrigated) treatment seedlings were significantly smaller than canopy volumes of seedlings in other plots (Kruskall-Wallis ANOVA, $p < 0.05$).

cover (33.7%) compared to the split-halves of the other plots (4.5% and 17.7%). The canopies of surviving creosotebush overlapped on the other two plots resulting in complete canopy cover of the soil surface within the patch of surviving creosotebush.

The water plus nitrogen treatment had a significant effect on the growth of the creosotebush seedlings in the upper bajada black-grama grassland during the first year after planting ($p < 0.05$) (Fig. 2). However, this difference disappeared during the following year (Fig. 2). The shrubs in the water plus nitrogen plot in 1999 were growing with clumps of black grama (*B. eriopoda*) and fluff grass (*Dasyochloa (Erioneuron) pulchella*) accounting for an average of 2.1% cover, interspersed among the surviving plants. There was less than 0.1% cover of perennials on the other two plots. The dominant perennial grass on all split plots was black grama (*Bouteloua eriopoda*) with a low cover of fluff grass (*D. pulchella*). Other species of grasses (*Aristida purpurea*, *Aristida ternipes*, and *Sporobolus* spp.) were found only on the split plots without shrubs. Other perennial plants were also restricted to the plots without shrubs (snakeweed, *Gutierrezia sarothrae*, soap tree yucca, *Yucca elata*, and a composite, *Zinnia grandiflora*). Competition with perennial grasses and forbs probably accounts for the small canopy volumes of the surviving shrubs in the water plus nitrogen plot. Competition with perennial grasses and cacti has been shown to reduce growth of creosotebush (Briones *et al.*, 1998).

The establishment of creosotebush had a significant effect on the soil aggregate stability of the surface soil ($p < 0.04$) and soil at 5 cm depth ($p < 0.05$) as measured by the modified slake test. The mean value for surface soil under creosotebush was 2.2 ± 0.17 compared to the mean value of 3.1 ± 0.53 in the plots without creosotebush. The corresponding values for soil from 5 cm depth were 2.0 ± 1.1 and 3.2 ± 1.3 , respectively. Soil aggregates are formed by the activities of the soil microflora (Tisdall, 1996) and affect numerous soil processes such as infiltration, water storage, and carbon storage. The reduction in aggregate stability in soils under establishing creosotebush suggests that leachates from the shrubs may be having an adverse effect on the soil microflora.

The establishment of creosotebush had a significant effect on some soil chemical parameters (Table 1). Electrical conductivity, calcium, and nitrate were significantly lower in soils under the shrubs than in the grassland soils without shrubs. The reduction in nitrate concentration in soils under shrubs is consistent with a pattern of reduced microbial biomass and/or activity, as was suggested for the soil aggregate stability patterns. This is probably related to effects of leachates on the microflora. The significant differences in electrical conductivity and calcium are related. A reduction in a dominant cation would also reduce electrical conductivity. The loss of cations from the soil under creosotebush suggests that microbial processes that result in the retention of cations are compromised by the presence of the shrubs. This is additional indirect evidence that establishing creosotebush impacts soil processes by directly impacting the soil microflora.

There were significantly lower values of cover of perennial grasses and spring annual plants on the plots with creosotebush shrubs than in the adjacent grassland plots (Table 2). There were also fewer annual plants and reduced species richness in the plots with creosotebush than in the plots with no creosotebush. This pattern is expected with shrubs that produce allelopathic compounds (Rice, 1984). However, this is the reverse of the pattern seen in mature creosotebush shrublands where the highest cover of perennial grasses is frequently that of bush muhly (*Muhlenbergia porteri*) growing under the canopies of creosotebush (Whitford *et al.*, 1978). The highest cover and densities of annuals are also under shrub canopies in mature creosotebush stands (Muller, 1953; Patten, 1978; Parker *et al.*, 1982). All of the shrubs in the establishment plots had exterior stem angles of $>45^\circ$. Creosotebush shrubs with inverted cone morphology do not retain litter below the canopy nor do they support high densities of annual plants (de Soyza *et al.*, 1997). Shrubs with large external stem angles are more efficient in transferring stemflow water to root channels than are the hemispherical shrubs. Thus, the morphology of establishing creosotebush may be the cause of decreased grass cover and the reduction in cover and the density of ephemeral plants.

Table 1. Mean and median values of soil parameters of soil samples from under creosotebush canopies (*Larrea*) ($n = 9$) and of soil samples from the grassland half of the plots ($n = 9$). Mean values are reported for comparisons that met normality tests for ANOVA and median values are reported for comparisons that failed normality tests and were analysed by Kruskal-Wallis ANOVA on ranks

Soil parameter	ANOVA (means)		Kruskal-Wallis (median)		
	<i>Larrea</i>	Control	<i>Larrea</i>	Control	<i>p</i>
PH (mmhos cm^{-1})	7.07	7.18	—	—	> 0.58
EC (meq l^{-1})	—	—	0.28	0.34	< 0.05
Mg (meq l^{-1})	—	—	0.87	0.74	> 0.13
Ca (meq l^{-1})	2.11	3.29	—	—	< 0.06
Na (meq l^{-1})	0.23	0.27	—	—	> 0.59
OM (%)	0.65	0.71	—	—	> 0.25
NO ₃ (ppm)	—	—	2.1	2.7	< 0.05
P (ppm)	9.5	10.2	—	—	> 0.61
K (ppm)	29.3	33.7	—	—	> 0.21

This study suggests some important attributes of desert grasslands in which creosotebush establishment is possible. The early observations of Gardner (1951), that creosotebush establishment was limited to areas of overgrazed grassland, were supported by this study. The most important difference between the ungrazed grassland and heavily grazed grassland in this study was the difference in size of bare patches. The size of unvegetated patches is the best indicator of a degrading rangeland (Whitford *et al.*, 1998). Large bare patches provide a large soil volume that is not exploited by the established perennials in the community. A shrub seedling establishing in a large bare patch can grow deep roots without competition by roots of neighboring grasses. Once deep roots are developed, the stemflow and root channelization of water and nutrients circumvents competition with neighbouring grasses (Martinez-Meza & Whitford, 1996; de Soyza *et al.*, 1997). Large bare patches in heavily grazed desert grasslands also contribute to the dispersal of creosotebush seeds. Creosotebush seeds are transported readily by wind (de Soyza *et al.*, 1997) and water. Perennial vegetation provides obstruction to overland flow and traps wind-transported material. The relatively high cover of lightly grazed and ungrazed desert grassland effectively prevents the dispersal of seeds of creosotebush to potential germination-establishment microsites within the grassland.

Other aspects of this study that have important implications for rangeland management and rangeland restoration efforts are the importance of available nitrogen and sufficient water for survival and growth of creosotebush seedlings, and the gradual

Table 2. Comparison of vegetation characteristics under creosotebush (*Larrea tridentata*) plants established in a Chihuahuan Desert grassland for 15 years and the grassland split plots without creosotebush. Vegetation measurements are mean \pm standard deviations

	<i>Larrea</i>	Grassland	<i>p</i>
Perennial grass cover %	0.23 \pm 0.4	14.8 \pm 12.0	< 0.002
Annual plant cover %	2.0 \pm 1.5	13.3 \pm 4.8	< 0.02
Density of annual plants (No. per 0.5 m ⁻²)	7.3 \pm 6.4	33.4 \pm 13.5	< 0.04
Species richness of annual plants	3.2 \pm 1.8	6.6 \pm 0.65	< 0.03

changes in soil properties resulting from growth of newly established plants. The water and nitrogen requirements demonstrate that it is probable that not all large bare patches are equally suitable as germination-establishment sites. Patches with animal-disturbed soils are more likely to meet the requirements for germination and establishment because these soils are more likely to have higher infiltration rates and higher levels of available nitrogen (Whitford, 1999). The reduction in perennial herbaceous and grass cover under newly established creosotebush and the reduction in aggregate stability inevitably lead to soil loss by wind and water. Loss of topsoil will probably reduce the likelihood of the return of grass cover in the event of a shift in climate that is favourable to grasses. The development of shrub resource islands results from trapped sub-soil that is eroded from intershrub spaces in well-established creosotebush stands (Whitford *et al.*, 1995). Thus, ecosystem changes that occur during the early establishment and growth phase of creosotebush shrubland communities set the stage for the development of a resistant and resilient stable state that is an alternate of desert grassland (Whitford *et al.*, 1995).

Graham Kerley assisted with some of the field work. This research was partially funded by the U.S. Environmental Protection Agency through its Office of Research and Development and has been subjected to the Agency's administrative review process and approved for publication.

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