

## **Creosotebush vegetation after 50 years of lagomorph exclusion**

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Received: 8 February 1993 / Accepted: 17 February 1993

**Abstract.** In 1939, an experiment was established on the Jornada Experimental Range to evaluate the effects of shrub removal, rabbit exclusion, furrowing, and seeding in creosotebush [*Larrea tridentata* (DC.) Cov] vegetation. Sixteen plots (21.3 × 21.3 m) were laid out in four rows of four plots per row with a buffer zone of 7.6 m between plots and rows. A barbed wire fence excluded cattle and poultry wire fencing excluded lagomorphs. Treatments were factorially applied at two levels. Plant cover in the plots was sampled in 1938 (before treatment), 1947, 1956, 1960, 1967 and 1989 with randomly located, line-intercept transects. Data from all sampling dates were analyzed as a split plot in time and main effects for 1989 tested by analysis of variance for a 2 × 4 factorial experiment. There were significant ( $P < 0.10$ ) year × treatment interactions. Seeding and furrowing treatments were ineffective but lagomorph exclusion and shrub clearing treatments resulted in significant treatment differences for several species. In 1989, basal area of spike dropseed (*Sporobolus contractus* A.S. Hitchc.) was 30-fold greater on the lagomorph excluded than on the lagomorph unexcluded treatment. Canopy cover of honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*), tarbush (*Flourensia cernua* DC.) and mariola (*Parthenium incanum* H.B.K.) were affected by lagomorph exclusion. None of the responses were viewed as successional in nature. They principally represented individual species sensitivities to either absence of a primary herbivore or removal of aboveground shrub biomass. Though the physical treatments could be regarded as relatively severe disturbances of the system, the impacts on community vegetation dynamics were relatively insignificant.

**Key words:** Black-tailed jackrabbit – *Larrea tridentata* – *Sporobolus contractus* – Spike dropseed – *Parthenium incanum*

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Lagomorphs are among the most widely distributed native herbivores in North America and the black-tailed jackrabbit (*Lepus californicus*) is found throughout western rangelands (Hall and Kelson 1959; Hansen and Flinders 1969). The diets of black-tailed and other jackrabbits have been studied extensively, in part because of their potential competition with domestic livestock for forage resources. Jackrabbits eat a wide variety of plants, primarily grasses and forbs in spring and summer and woody plants in fall and winter (Vorhies and Taylor 1933; Riegel 1942; Brown 1947; Bear and Hansen 1966; Currie and Goodwin 1966; Hayden 1966; Fagerstone et al. 1980; Westoby 1980; Dabo et al. 1982). Several studies have shown considerable dietary overlap of livestock and jackrabbits (Hansen and Flinders 1969; Sparks 1968; Schneberger 1990). Jackrabbit diets are determined largely by what is available in their feeding areas but they do graze selectively and utilize plants in proportions widely different from their relative availability (Uresk 1978; Sparks 1968; Johnson and Anderson 1984). The combined herbivory of jackrabbits and rodents can effectively prevent improvement of deteriorated arid rangelands (Norris 1950).

In 1938 and 1939, an experiment was established by U.S. Forest Service personnel on the Jornada Experimental Range to evaluate the effects of shrub removal, lagomorph exclusion, furrowing, and seeding in areas dominated by creosotebush [*Larrea tridentata* (DC.) Cov]. At one of three replicates the lagomorph exclusion fences withstood the vicissitudes of time and provided a unique opportunity to evaluate the long-term effects of lagomorph exclusion, principally black-tailed jackrabbits, although desert cottontails (*Sylvilagus audubonii*) may have foraged in the area as well.

## Materials and methods

This study was conducted on the Jornada Experimental Range 37 km north of Las Cruces, New Mexico (Lat. 32°37' N, Long. 106°40' W). The study area is located on a bajada slope of the San

Table 1. Treatments applied to individual plots in 1938-39

Plot No.	Treatment				
	Seeded	Furrowed	Shrub removal (cleared)	Lagomorph exclusion (fenced)	None
1				X	
2			X		
3	X	X	X	X	
4	X	X			
5	X	X	X		
6	X				
7	X		X		
8			X	X	
9	X		X	X	
10		X	X	X	
11	X	X		X	
12	X			X	
13		X	X		
14		X		X	
15					X
16		X			

Andres Mountains at an elevation of 1,608 m. Study plots are located on a ridgetop where loamy-skeletal, carbonatic, thermic, shallow, Typic Paleorthid soils (Tencee series) have formed on an old alluvial fan (Neher and Bailey 1976). Long-term annual precipitation (1922-1990) at the nearest rain gauge (1.7 km distant at an elevation of 1,585 m) is 257 mm. Summer precipitation is mostly from high intensity, short duration, convective storms covering small areas and 55% of total precipitation occurs in July, August and September. Winter precipitation comes from low intensity frontal storms covering broad areas. Snow is infrequent. The frost-free period averages 200 days, but the effective growing season, when soil water and temperature are favorable, is often 90 days or less (Paulsen and Ares 1962).

The vegetation is dominated by creosotebush with honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) and tarbush (*Flourensia cernua* DC.) also present. Suffrutescents, including mariola (*Parthenium incanum* H.B.K.), broom snakeweed [*Gutierrezia sarothrae* (Pursh) Britt & Rusby], and desert zinnia [*Zinnia acerosa* (DC.) Gray], are abundant. Principal perennial grasses are bush muhly (*Muhlenbergia porteri* Scribn.), spike dropseed (*Sporobolus contractus* A.S.Hitchc.), fluffgrass [*Erioneuron pulchellum* (H.B.K.) Tatoka], and black grama [*Bouteloua eriopoda* (Torr.) Torr.].

In 1938, sixteen plots (21.3 × 21.3 m) were established in four rows of four plots with a buffer zone of 7.6 m between plots. Treatments (clearing, lagomorph exclusion, furrowing, and seeding) were factorially applied, yielding a check plot, four single factor plots, and 11 plots with varying degrees of interaction (Table 1). The clearing, furrowing, and seeding treatments were applied in 1938 but the lagomorph exclusion fences were not constructed until 1939. Poultry netting with a 2.5 cm mesh buried about 15 cm in the ground and extending above ground about 75 cm was used to exclude lagomorphs. The furrowing treatment consisted of shallow, handraked furrows designed to trap surface runoff water. A barbed-wire fence excluded cattle from all plots. All the plots were sampled in 1938 before the treatments were applied. Each plot was divided into east and west halves and 14, randomly located 10.65 m line-intercept transects sampled for shrub canopy cover and grass basal area in each half-plot. Following the same procedures, with a new set of random line locations each time, the plots were resampled in 1947, 1956, 1960, 1967, and 1989. Shrubs (not including suffrutescents) were removed from the cleared plots following the 1947, 1956, 1960, and 1967 samplings. Some creosotebush plants may have been left on the cleared plots in 1960 and 1967 for age-growth

studies. In 1938, the seeding treatment plots were seeded with a mixture of black grama, spike dropseed, mesa dropseed [*Sporobolus flexuosus* (Thurb.) Rydb.], and four-wing saltbush [*Atriplex canescens* (Pursh) Nutt.] Some of the seeding treatment plots were reseeded in 1947.

Effects of lagomorph exclusion, shrub removal, seeding and furrowing on canopy cover of shrubs and basal area of grasses were tested by Analysis of Variance (SAS 1990) for a split plot in time experimental design. The mixed model included fixed main effects and year as a random split effect. Main effects and two-way interactions were tested using pooled higher level interactions. Year effects and year × main effect interactions were tested using year × higher-level interactions. Main effects fifty-one years post-treatment were tested by Analysis of Variance (SAS 1990) for a 2 × 4 factorial experiment. Main effects and two-way interactions were tested using pooled high level interactions. Means within a significant treatment were separated using least significant difference ( $P < 0.10$ ). All analyses were performed with the data in number of basic measurement units (3 mm) and then means converted to percentages.

Relationships between rainfall and total shrub canopy cover and total grass basal area were determined. Correlation coefficients were calculated for canopy cover and basal area and rainfall for the month preceding sampling, for the first plus the second month preceding sampling, etc., until 24 months of antecedent rainfall had been accumulated.

## Results

Annual precipitation during the 51-year period was extremely variable (Fig. 1). During the 1937 to 1989 period, 32 years had below average annual precipitation and 28 years below average July, August and September precipitation. Correlations of shrub canopy cover and grass basal area with accumulated antecedent rainfall revealed that correlations fell sharply after 10 antecedent months (Fig. 2). Grasses had higher  $r$  values than shrubs during the year of sampling but shrubs maintained higher  $r$  values than grasses with increasing antecedent periods. Because only six sample points out of 52 are available, these data must be viewed with caution.

The analysis of variance for a split plot in time revealed that several shrub and grass species had significant ( $P < 0.10$ ) year × treatment interactions for the lagomorph exclusion and shrub clearing treatments. Only two shrub species had significant year × treatment interactions for the seeding and furrowing treatments and data for these treatments will not be presented. Results were similar to those of Korzdorfer (1968) who analyzed the 1938, 1947, 1956, 1960 and 1967 data using a mixed model, with years random and treatments fixed.

In 1938, the pre-treatment shrub canopy cover averaged 24% with a range among plots of 15-30%. Creosotebush predominated, with canopy cover ranging from 9 to 24% among plots and an average of 18% over all plots. Mesquite and tarbush occurred on all plots with canopy cover ranging from 0.1 to 5% and 0.7 to 5%, respectively.

There were no differences between creosotebush canopy cover on the lagomorph excluded and unexcluded treatments in 1938 (Fig. 3A). However, by 1947 creosotebush canopy cover was significantly greater on the excluded than on the unexcluded treatment and canopy

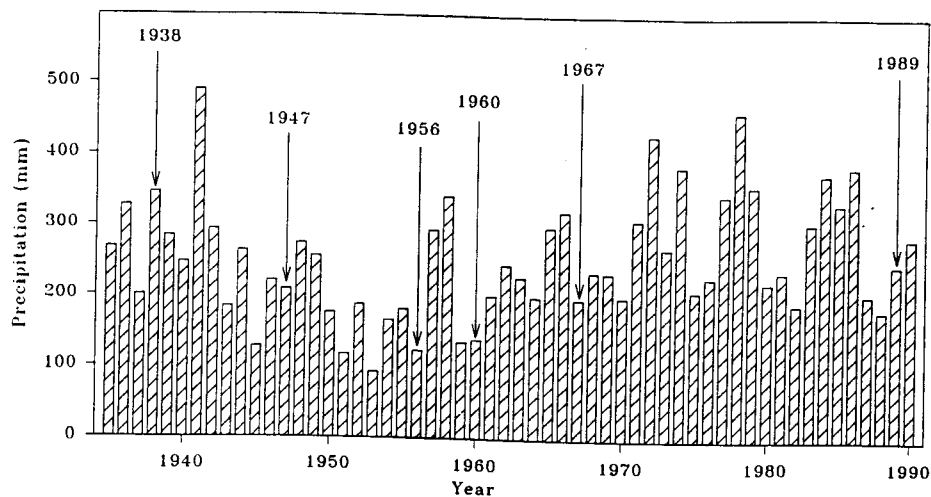


Fig. 1. Annual precipitation from 1935 to 1990. Years when plots were sampled are indicated

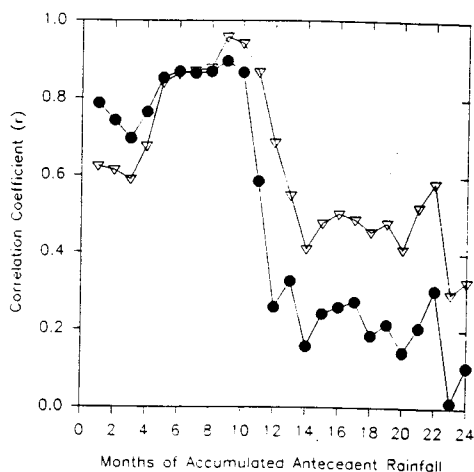


Fig. 2. Correlation coefficients ( $r$ ) for total grass (●) basal area and total shrub (▽) canopy cover with months of accumulated antecedent precipitation

cover remained higher on the excluded treatment at each later sampling date (Fig. 3A). There was a significant decline in creosotebush canopy cover from 1938 to 1989 with the excluded and unexcluded treatments showing a similar pattern (Fig. 3A). As expected, there were significant differences in creosote bush canopy cover between the cleared and uncleared treatments from 1947 to 1989. Across year differences of creosotebush canopy cover for the uncleared treatment varied somewhat from that of the lagomorph treatments but 1989 canopy cover was significantly less than in 1938 (Fig. 3A). Creosotebush reestablished as the dominant shrub after each clearing of the plots, making up 57, 66, 74 and 56% of total shrub cover in 1947, 1956, 1960 and 1967, respectively. In 1989, when suffrutescents were more abundant than in prior years, creosotebush made up 35% of total shrub cover on the cleared plots.

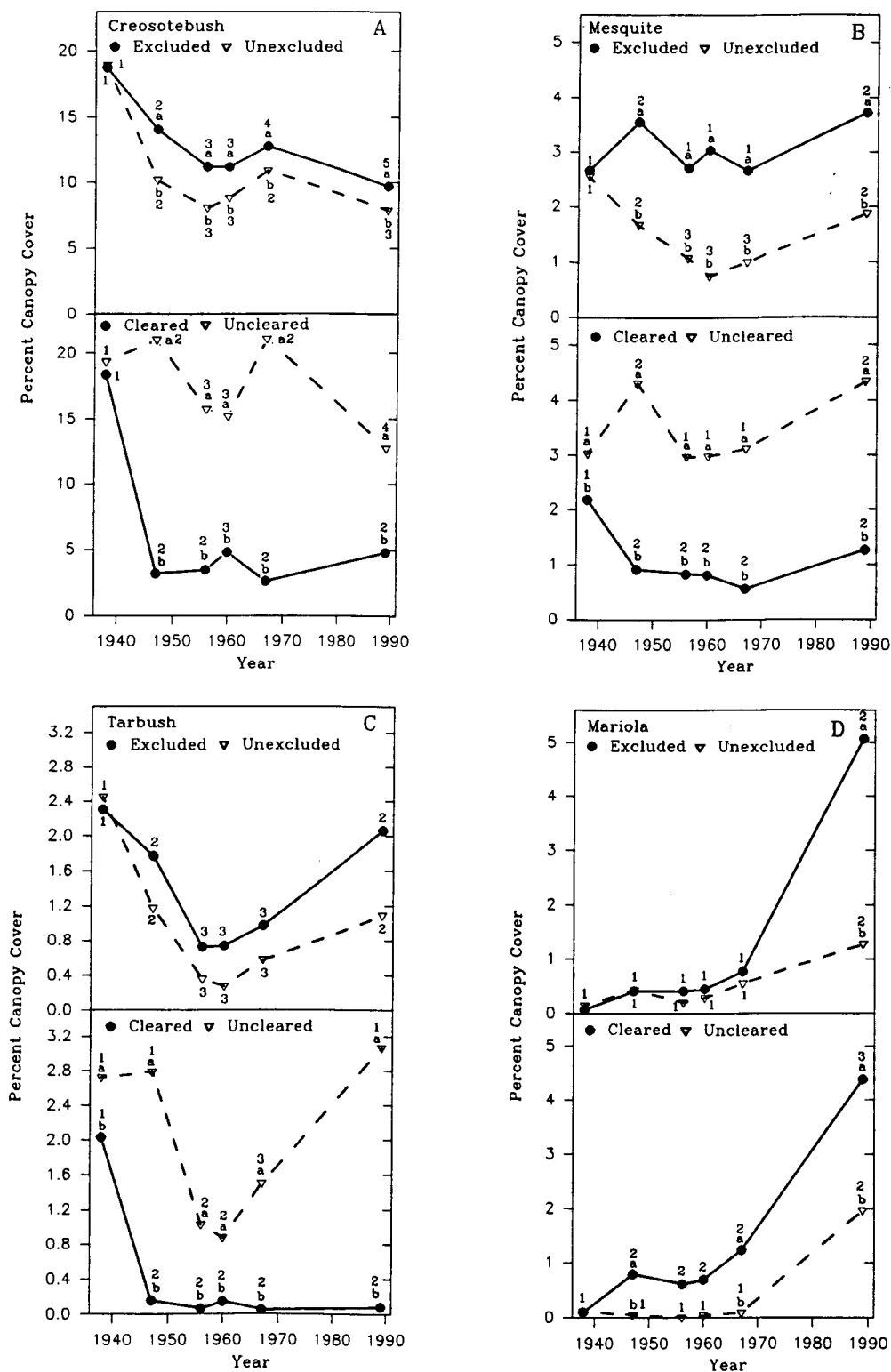
Mesquite canopy cover was significantly higher on the lagomorph excluded than on the unexcluded treatment in 1947 and later sampling years (Fig. 3B) Mesquite

canopy cover was significantly higher in 1947 and 1989 than in 1938 on the lagomorph excluded treatment (Fig. 3B). However, on the lagomorph unexcluded treatment, mesquite canopy cover was significantly lower than in 1938 at all sampling dates. Mesquite canopy cover was significantly less on the cleared than on the uncleared treatment in 1938 and the clearing treatment increased this difference. The gravelly soil and alluvial fan characteristics of the study site provide scattered suitable microsites for mesquite (and tarbush). Differences in canopy cover for plots in 1938, prior to treatment, reflect this site heterogeneity. Among-year differences for the uncleared treatment were very similar to the lagomorph excluded treatment with mesquite canopy cover in 1947 and 1989 being significantly higher than in 1938 (Fig. 3B).

There were no significant differences between the excluded and unexcluded lagomorph treatments for tarbush canopy cover (Fig. 3C). Among year differences were significant for the lagomorph treatments with a sharp decline in cover from 1938 to 1960 and only partial recovery by 1989. There was a significant difference in tarbush canopy cover in 1938 on the shrub clearing treatments and shrub clearing reduced tarbush canopy cover to very low levels in later years (Fig. 3C). Differences in tarbush canopy cover among years for the uncleared treatment followed the same pattern as in the lagomorph treatments.

Mariola had very low canopy cover in 1938 and a significant difference was not found between lagomorph excluded and unexcluded treatments until 1989 (Fig. 3D). Mariola was not cleared from the plots but significant differences in cover on cleared and uncleared treatments occurred in 1947, 1967 and 1989. Both cleared and uncleared treatments had a large increase in mariola canopy cover from 1967 to 1989 (Fig. 3D).

In 1938, perennial grass basal area averaged 2.9% over all plots. Bush muhly was most abundant, with an overall average basal area of 2.3% and a range among plots of 0.5 to 5.2%. Fluffgrass occurred on all plots but maximum basal area was only 0.7%. Black grama was present on 14 of the 16 plots with a maximum basal area of 0.8%.



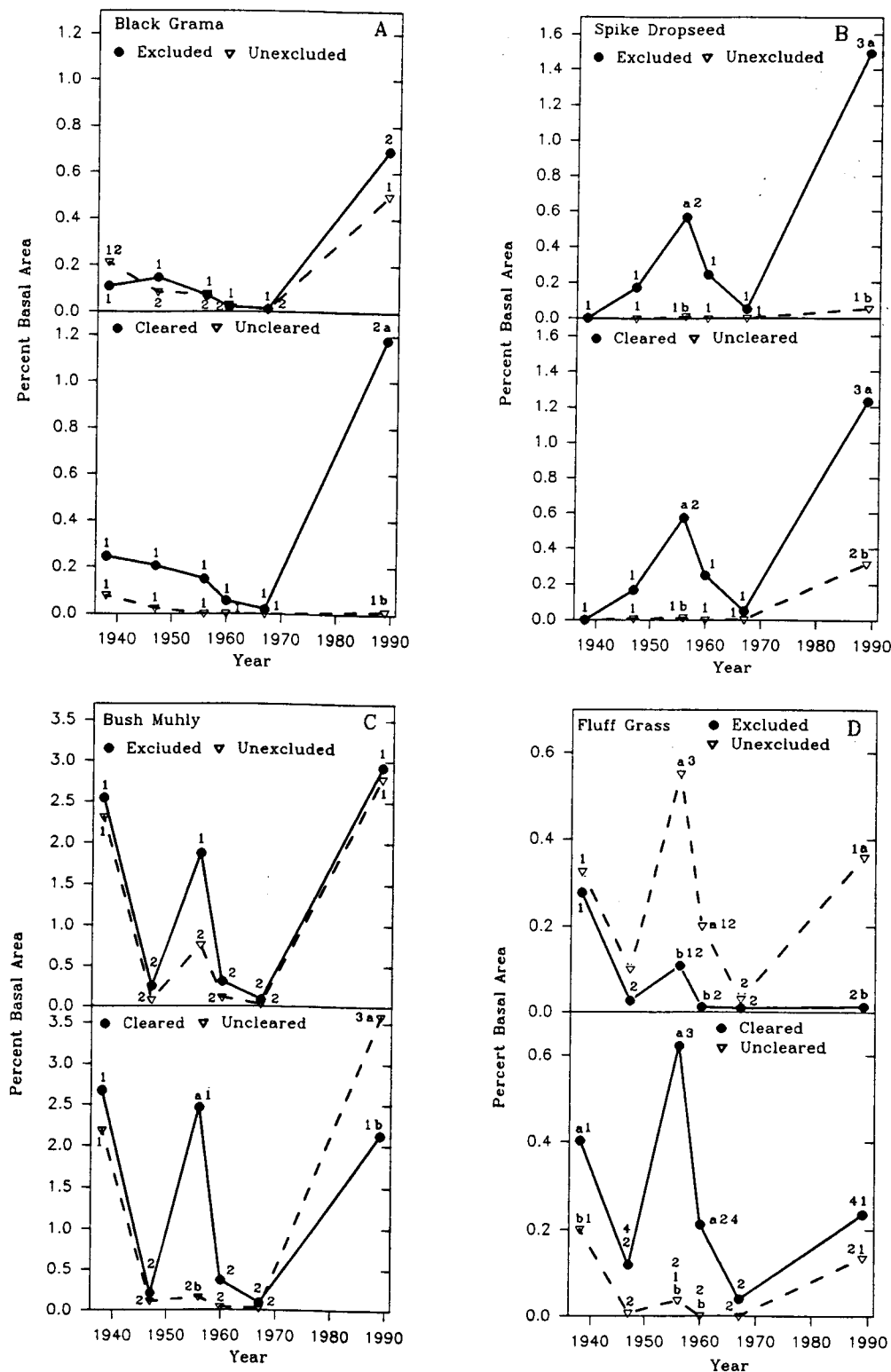
**Fig. 3A–D.** Canopy cover of creosotebush, mesquite, tarbush and mariola on lagomorph excluded and unexcluded and shrub cleared and uncleared treatments in 1938, 1947, 1956, 1960, 1967 and 1989. Treatment means with different letters differ ( $P < 0.10$ ). Within treatments, years with different numbers differ ( $P < 0.10$ ).

Spike dropseed was not recorded on the transects in 1938.

There were no significant differences in black grama basal area between lagomorph excluded and unexcluded treatments at any sampling date (Fig. 4A). On the shrub cleared and uncleared treatments there was a significant difference in black grama basal area only in 1989. Only

the lagomorph excluded and shrubs cleared treatments showed a significant increase in black grama basal area in 1989 when compared to previous years.

Spike dropseed was present on all treatments in 1947 and later sampling years. By 1956 spike dropseed basal area was significantly greater on the lagomorph excluded than on the unexcluded treatment and significantly



**Fig. 4A–D.** Basal area of black grama, spike dropseed, bush muhly and fluffgrass on lagomorph excluded and unexcluded and shrub cleared and uncleared treatments in 1938, 1947, 1956, 1960, 1967 and 1989. Treatment means with different letters differ ( $P < 0.10$ ). Within treatments, years with different letters differ ( $P < 0.10$ ).

greater on shrub cleared than on uncleared treatment (Fig. 4B). Basal area declined in 1960 and 1967 on both lagomorph excluded and shrub clearing treatments but by 1989 there were again significant differences between treatments. In 1989, spike dropseed basal area was significantly greater than at any previous sampling (Fig. 4B). Bush muhly, the most abundant grass, did not

have any significant differences between lagomorph excluded and unexcluded treatments (Fig. 4C). On the clearing treatments significant differences in bush muhly basal area were found only in 1957 and 1989. Bush muhly basal area varied widely among years on both lagomorph and shrub clearing treatments with lows in 1947, 1960 and 1967 and highs in 1938, 1957 and 1989. Fluffgrass

**Table 2.** Percentage canopy cover of shrubs and suffrutescents and percentage basal area of grasses for lagomorph excluded, shrubs removed, seeded, and furrowed treatments evaluated fifty-one years after treatment

Species	Lagomorphs		Shrubs		Seeding		Furrowing	
	Excluded	Unexcluded	Cleared <sup>2</sup>	Uncleared	Seeded	Unseeded	Furrowed	Unfurrowed
Shrubs and Suffrutescents	- % Canopy Cover -							
Creosotebush	9.7	7.9	4.8 <sup>a1</sup>	12.7 <sup>b</sup>	7.9	9.6	9.0	8.5
Mesquite	3.7 <sup>a</sup>	1.9 <sup>b</sup>	1.3 <sup>a</sup>	4.3 <sup>b</sup>	2.3 <sup>a</sup>	3.3 <sup>b</sup>	2.2 <sup>a</sup>	3.4 <sup>b</sup>
Tarbrush	2.1 <sup>a</sup>	1.1 <sup>b</sup>	0.1 <sup>a</sup>	3.1 <sup>b</sup>	1.1 <sup>a</sup>	2.0 <sup>b</sup>	1.7	1.4
Mariola	5.1 <sup>a</sup>	1.3 <sup>b</sup>	4.4 <sup>a</sup>	2.0 <sup>b</sup>	3.1	3.3	3.5	2.8
Miscellaneous	0.7	2.5	2.2	1.0	1.1	2.1	2.1	1.2
Total	20.9 <sup>a3</sup>	14.6 <sup>b</sup>	12.7 <sup>a</sup>	22.8 <sup>b</sup>	15.6 <sup>a</sup>	19.9 <sup>b</sup>	18.5	17.0
Grasses <sup>4</sup>	- % Basal Area -							
Black grama	0.7	0.5	1.2 <sup>a</sup>	<0.1 <sup>b</sup>	0.5	0.7	0.4	0.8
Bush muhly	2.9	2.8	2.1	3.6	3.6	2.1	3.1	2.6
Fluffgrass	<0.1 <sup>a</sup>	0.4 <sup>a</sup>	0.2	0.1	0.3 <sup>a</sup>	0.1 <sup>b</sup>	0.1	0.2
Spike dropseed	1.5 <sup>a</sup>	0.1 <sup>b</sup>	1.2 <sup>a</sup>	0.3 <sup>b</sup>	0.7	0.9	0.6	1.0
Total	5.1 <sup>a</sup>	3.7 <sup>b</sup>	4.8	4.1	5.1	3.7	4.3	4.6

<sup>1</sup> Means within a row and treatment with different letters differ ( $P < 0.10$ )

<sup>2</sup> Shrub removal treatment was reapplied to plots in 1947, 1956, 1960, and 1967

<sup>3</sup> Percentages are derived from least-square means and totals deviate slightly from simple arithmetic sums

<sup>4</sup> Basal area of grasses other than those listed are less than 0.1% for any treatment and are not reported

had significantly greater basal area on the lagomorph unexcluded treatment than on the excluded treatment in 1957, 1960 and 1989 (Fig. 4D). Fluffgrass basal area was significantly greater on the shrub cleared than on the uncleared treatment in 1938 and remained higher on the cleared treatment with differences being significant in 1957 and 1960. Among year fluctuations of fluffgrass and bush muhly are similar (Fig. 4C, 4D).

Factorial analysis of the 1989 data revealed very few significant treatment interactions. Among shrubs only mesquite (cleared  $\times$  furrowed, seeded  $\times$  furrowed) and tarbrush (cleared  $\times$  seeded) had significant treatment interactions (Table 2). Among grasses only spike dropseed (excluded  $\times$  cleared) and fluffgrass (excluded  $\times$  seeded) had significant treatment interactions. Except for the excluded cleared interaction for spike dropseed it is difficult to accept the interactions as due to actual treatment effects. More likely they result from inherent differences in species cover among the plots.

Mesquite, tarbrush, and mariola had significant differences in canopy cover between the lagomorph excluded and unexcluded treatments (Table 2). Among grasses, only spike dropseed and fluffgrass showed significant differences for the lagomorph treatments. Canopy cover for the shrubs periodically cleared, creosotebush, mesquite and tarbrush, differed between cleared and non-cleared treatments. However, mariola, which was not cleared, had a significantly higher canopy cover on the cleared than on the uncleared treatment (Table 2). This indicates mariola may have benefited from reduced shrub competition. Black grama and spike dropseed had significantly higher basal area on the cleared than on the uncleared treatment. Only mesquite, tarbrush and fluffgrass had significant differences between the seeded and unseeded treatments and these differences are not believed to reflect a treatment effect (Table 2). The same is

true for the difference between furrowed and unfurrowed treatments for mesquite canopy cover.

Desert zinnia was present in 1989 but had not been recorded in previous years. It occurred on 13 of the 16 plots and had an average canopy cover of 1%. There was some question whether it would have been recorded in samples taken before 1989. However, it did not appear in any of an extensive series of photographs of each plot taken in 1967.

Perennial grass basal area was higher in 1989 than during previous sample years. However, there was evidence in the form of recently dead crowns of spike dropseed, black grama, bush muhly, and fluffgrass that the low rainfall in 1977 and 1978 had affected perennial grass populations. It was estimated that about 90% of the fluffgrass plants encountered when sampling in 1989 were dead.

## Discussion

Rangelands of the northern Chihuahuan Desert changed substantially during the previous 120 years. A primary transition has been replacement of perennial warm season grasslands by shrub dominated states. These vegetative transitions have been driven by a combination of natural and anthropomorphic disturbances (Buffington and Herbel 1965). The result is a desert that is characterized by increasingly heterogenous distribution of limited resources. Schlesinger et al. (1990) described this phenomena as desertification that resulted in areas of resource accumulations best characterized as islands of fertility. It has been proposed that processes which spatially concentrate resources, particularly of limiting nutrients such as nitrogen, are self-augmenting (Westoby et al. 1989). Current shrubland states, including those

dominated by creosotebush, are viewed as permanent without considerable intervention (Friedel 1991). Our study was initiated in 1938 on a site that had already been converted to a self-augmenting shrubland state. Our interpretations of these data support hypotheses of stable shrubland states as a function of heterogeneous resource distribution.

Interpretation of these data is difficult because of the number of important but uncontrolled variables, particularly precipitation and lagomorph population densities. Precipitation patterns are crucial to the expression of community structure in arid environments (Noy-Meir 1973; Laycock 1991). This study, with only six, widely separated yearly sampling points does not permit a definitive evaluation of precipitation influences. Probably the low levels of shrub canopy cover and perennial grass basal area in 1957 and 1960 result from the severe drought of the early 1950's which had a great impact on vegetation in the Jornada Basin (Herbel et al. 1972). It is also likely the high cover values found in 1989 reflect the mostly above average precipitation of the 1980's. The appearance of desert zinnia on the plots between 1967 and 1989 is probably due to weather patterns favorable for this species. The recently dead crowns of perennial grasses found in 1989 apparently reflect the 50% below average precipitation received in July, August and September of 1988.

It is well recognized that lagomorph populations exhibit large annual variation and densities from 0.25/ha (Steinberger and Whitford 1983) to 2.33/ha (Norris 1950) have been reported in the Jornada Basin. Specific vegetation responses may be confounded by the inherent variation in rabbit densities and foraging pressures.

Neither seeding nor furrowing treatments had substantive longterm vegetative impacts. These results were not surprising. Reseeding treatments in this environment are typically unsuccessful due to insufficient or ineffectual moisture for either seed germination or seedling survival. Furrowing treatments do not persist due to the susceptibility of bajada slopes to surface erosion during high-intensity rainstorms.

Perennial grasses showed only limited increases in basal cover for thirty years following removal of above-ground shrub biomass. The shrub clearing treatment would not directly redistribute nutrients from their concentration beneath shrub canopies. Beck and Tober (1985) also found that removal of shrubs did not always result in an increase of herbaceous species.

The lagomorph treatment, however, demonstrated definite impacts on plant community structure and composition. It is recognized that lagomorphs, like the rodent guilds studied by Brown and Heske (1990), can have profound impacts on desert shrub habitats and on ecosystem processes, e.g., litter inputs (Steinberger and Whitford 1983).

Jackrabbits utilize creosotebush twigs with high moisture content during winter and early spring (Steinberger and Whitford 1983). If this occurred on the plots the level of use did not create a significant difference between lagomorph excluded and unexcluded treatments. The differences between mesquite and tarbush canopy cover

on the lagomorph treatments may reflect a true jackrabbit influence. Mesquite is an important part of jackrabbit diets (up to 30%) in the Jornada Basin, particularly in fall and winter (Dabo et al. 1982; Fatehi 1986). In a tarbush vegetation type, tarbush constituted up to 14% of jackrabbit diets (Wansi 1989). While browsing of canopy components may account for the difference between treatments, it is also likely that consumption of seedlings played an important role. The greater canopy cover of mariola on the lagomorph excluded treatment in 1989 indicates that this species is heavily browsed by lagomorphs. In Arizona, Chew and Chew (1970) found that jackrabbits and wood rats (*Neotoma* spp.) pruned from 56 to 65% of the volume of mariola plants but consumed only about half of the material. Our study indicates that jackrabbits can affect canopy cover of mariola. However, at a site in southwestern New Mexico mariola had 1.5- to 2.6-fold more individuals on plots open to rabbits than on plots where rabbits had been excluded for 22 years (Beck and Tober 1985).

The 30-fold greater basal area of spike dropseed on the lagomorphs excluded than on the unexcluded treatments indicates a real treatment response. Dropseeds are preferred forages (up to 40% of diets) for jackrabbits (Dabo et al. 1982). The large treatment difference shows that spike dropseed is susceptible to grazing pressure. Fluffgrass, which was more abundant on the lagomorph unexcluded treatment, may be occupying niches which would otherwise be occupied by spike dropseed. Fluffgrass is a component of jackrabbit diets (Fatehi 1986; Wansi 1989), but is probably not a preferred item in this particular species mix. The many dead plants found in 1989 indicate that this short-lived species is controlled more by water availability than by grazing pressure. Neither black grama or bush muhly showed a response to the lagomorph treatments. Bush muhly was recorded as an item of jackrabbit diets in several studies in the Jornada Basin (Fatehi 1986, Wansi 1989; Schneberger 1990) but did not exceed 6% composition, indicating a low preference by jackrabbits. However, black grama is preferred by jackrabbits and contributes up to 54% of diets in summer months (Fatehi 1986). The lack of an exclusion response by black grama at the study site may result from reproductive strategy that is almost entirely vegetative in this weather regime (Nelson 1934).

Shrubs, including creosotebush, characteristically produce secondary terpene metabolites as an anti-herbivory strategy in carbon-rich, nutrient-poor desert environments (Meyer and Karasov 1991). Herbivore uses of non-chemically defended plants are proportionately high. Though the ratio of shrub canopy cover to grass basal cover was similar (4:1) between excluded and unexcluded treatments, there was an approximately 40% increase in both shrub canopy and grass basal cover with lagomorph exclusion. Exclusion of a principle herbivore from this system not only minimized differential defoliation between herbaceous species and the dominant shrub species, but probably also lessened the competitive advantages of species with chemical-based herbivore defenses. It is well-understood that excessive herbivory can be a transitional force in this environment. However,



grazing by even native herbivores within shrub-dominated states may be a mechanism of self-augmentation.

## Conclusions

With the great concern over the impacts of livestock grazing upon native vegetation, the impact of small native herbivores is often overlooked. Our study shows: 1) Preferential grazing by lagomorphs can influence the species composition of shrub, suffrutescent and perennial grass cover, and 2) Creosotebush dominated communities are resistant to substantial vegetative change by seeding, disturbance of the soil surface, or periodic removal of above-ground shrub biomass. These results were cumulative over time and persisted through the wet and dry weather cycles typical of arid ecosystems. There is still much to be learned about the influence of small native herbivores; however, it is apparent that they can and do play an important role in shaping the composition of desert plant communities. Inputs which fail to directly affect redistribution of limited nutrients should not be expected to disrupt self-augmentation of shrub-dominated states.

## References

- Bear GD, Hansen RM (1966) Food habits, growth and reproduction of white-tailed jackrabbits in southern Colorado. Colorado State Univ Agr Exp Sta Tech Bull 90, Ft Collins
- Beck RF, Tober DA (1985) Vegetation changes on creosotebush sites after removal of shrubs, cattle and rabbits. New Mexico State Univ Agr Exp Sta Bull 717
- Brown HL (1947) Coaction of jackrabbits, cottontails, and vegetation in mixed prairie. Trans Kans Acad Sci 50:28-44
- Brown JH, Heske EJ (1990) Control of a desert-grassland transition by a keystone rodent guild. Science 250:1705-1707
- Buffington LC, Herbel CH (1965) Vegetational changes on a semidesert grassland range from 1858 to 1963. Ecol Monogr 35:139-164
- Chew RM, Chew AE (1970) Energy relationships of the mammals of a desert shrub (*Larrea tridentata*) community. Ecol Monogr 40:1-21
- Currie PO, Goodwin DL (1966) Consumption of forage by black-tailed jackrabbits on salt-desert ranges of Utah. J Wildl Manage 30:304-311
- Dabo SM, Pieper RD, Beck RF, Southward GM (1982) Summer and fall diets of blacktailed jackrabbits on semidesert rangeland. New Mexico State Univ, Agr Exp Sta. Res Report 476
- Fagerstone KA, Lavoie FK, Griffith RE Jr (1980) Black-tailed jackrabbit diet and density on rangeland and near agricultural crops. J Range Manage 33:229-233
- Fatehi M (1986) Comparative seasonal food habits of black-tailed jackrabbits and cattle on semi-desert rangeland. PhD Diss New Mexico State Univ, Las Cruces
- Friedel MH (1991) Range condition assessment and the concept of thresholds: a viewpoint. J Range Manage 44:422-426
- Hall ER, Kelson KR (1959) The mammals of North America. Ronald Press Co, New York, vol 1
- Hansen RM, Flinders JT (1969) Food habits of North American hares. Science Series No 1 Range Science Dept, Colorado State Univ, Ft Collins
- Hayden P (1966) Food habits of black-tailed jackrabbits in southern Nevada. J Mammal 47:42-46
- Herbel CH, Ares FN, Wright RA (1972) Drought effects on a semidesert grassland range. Ecology 53:1084-1093
- Johnson RD, Anderson JE (1984) Diets of black-tailed jackrabbits in relation to population density and vegetation. J Range Manage 37:79-83
- Korzdorfer EJ (1968) Seeding, furrowing, brush removal, and rabbit exclusion effects on creosotebush-infested sites. MS Thesis New Mexico State Univ, Las Cruces
- Laycock WA (1991) Stable states and thresholds of range conditions on North American rangelands. J Range Manage 44:427-433
- Meyer MW, Karasov WH (1991) Chemical aspects of herbivory in arid and semiarid habitats. In: Palo RT, Robbins CT (eds) Plant defenses against mammalian herbivory. CRC Press, Inc. Boston
- Neher RE, Bailey OF (1976) Soil survey of White Sands Missile Range, New Mexico. USDA Soil Conservation Service, US Dept Army, and New Mexico Agr Exp Sta
- Nelson EW (1934) The influence of precipitation and grazing upon black grama. New Mexico Agr Expt Sta Press Bul 409
- Norris JJ (1950) Effect of rodents, rabbits, and cattle on two vegetation types in semidesert range land. New Mexico State Univ Agr Exp Sta Bull 353
- Noy-Meir I (1973) Desert ecosystems: environment and producers. Ann Rev Ecol Syst 4:25-51
- Paulsen HAJr, Ares FN (1962) Grazing values and management of black grama and tobosa grasslands and associated shrub ranges of the Southwest. USDA Forest Service Tech Bull no 1270
- Riegel A (1942) Some observations of the food coactions of rabbits in western Kansas during periods of stress. Trans Kans Acad Sci 45:369-375
- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. Science 247:1043-1048
- Schneberger A (1990) Botanical diets and dietary overlap of black-tailed jackrabbits and cattle on black grama grassland. MS Thesis New Mexico State Univ, Las Cruces
- Sparks DR (1968) Diets of black-tailed jackrabbits on sandhill rangeland in Colorado. J Range Manage 21:203-208
- Statistical Analysis System (1990) SAS User's Guide SAS Institute Inc Cary, NC
- Steinberger Y, Whitford WG (1983) The contribution of shrub pruning by jackrabbits to litter input in a Chihuahuan Desert ecosystem. J Arid Environ 6:183-187
- Uresk DW (1978) Diets of the black-tailed hare in steppe vegetation. J Range Manage 31:439-442
- Vorhies CT, Taylor WP (1933) The life histories and ecology of jackrabbits, *Lepus alleni* and *Lepus californicus* ssp. in relation to grazing in Arizona. Arizona State Univ Agr Exp Sta Tech Bull 49:471-587
- Wansi T (1989) Botanical content of blacktailed jackrabbit diets on semi-desert rangeland. MS Thesis New Mexico State Univ, Las Cruces
- Westoby M (1980) Black-tailed jackrabbit diets in Curlew Valley, northern Utah. J Wildl Manage 44:942-948
- Westoby M, Walker B, Noy-Meir I (1989) Opportunistic management for rangelands not at equilibrium. J Range Manage 43:266-274