



Long-term influences of shrub removal and lagomorph exclusion on Chihuahuan Desert vegetation dynamics

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Cover of perennial species in long-term experimental plots in a creosotebush (*Larrea tridentata* Sess. & Moc. Ex DC.) dominated community in the Chihuahuan Desert was monitored for 56 years. Sixteen 21.3 × 21.3 m plots were established in 1938–39 to evaluate the effects of lagomorph exclusion and shrub removal. Major dominant shrubs were individually severed at ground level and removed by hand in 1939, and this process was repeated after measuring plant cover in 1947, 1956, 1960, 1967, 1989, and 1995. Lagomorphs were excluded with poultry wire fencing. Shrub removal increased ($p \leq 0.05$) the basal cover of two major desert grass species, black grama (*Bouteloua eriopoda* Torr.) and spike dropseed (*Sporobolus contractus* A.S. Hitch.) between 1939 and 1995, but differences were not evident until 50 years after initial treatment. Temporal effects of lagomorph exclusion were less pronounced than shrub removal. Clearly, shrub dominance has an extremely important and lasting role in determining vegetation community structure in this arid environment, even when above-ground shrub structures are periodically removed.

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Introduction

Creosotebush (*Larrea tridentata* Sess & Moc. Ex DC) is a species that characterizes desert scrub vegetation in the Chihuahuan Desert. Creosotebush has been a dominant species for millennia in this region (Van Devender, 1990), and its historic presence within the Chihuahuan Desert has probably been underestimated (Stein & Ludwig, 1979). However, the encroachment of this species into former desert grasslands has been well documented (Buffington & Herbel, 1965; Grover & Musick, 1990). Though temporal fluctuations in vegetation composition can be pronounced in arid environments, particularly in regard to annuals (Guo & Brown, 1996), creosotebush can be expected to remain a dominant species for decades without catastrophic disturbance. Nearly 60 years ago Muller (1940) described the creosotebush desert scrub in the south-western U.S. as a vegetation type lacking seral stages and deserving of the label “super-climax” because of its stability within this arid region.

Vegetation dynamics are frequently unpredictable, particularly for grazing lands in arid environments (Friedel, 1991). Conceptual models of rangeland vegetation dynamics are currently debated (Westoby *et al.*, 1989). Even within a particular region, there can be controversy regarding mechanisms controlling vegetation dynamics within specific community types (Archer *et al.*, 1995). It has been observed that seriously degraded rangelands will support stable communities which bear little resemblance to prior states (Milton *et al.*, 1994). Though degraded conditions may be as productive as prior states (Huenneke, 1996) they typically are more susceptible to erosion and less able to support certain functions, especially livestock production. Simple rest from livestock grazing may not be a solution for remediation of degraded conditions, and more intensive improvement practices are often neither ecologically nor economically sustainable (Fredrickson *et al.*, 1996).

In 1938, an experiment was established on the Jornada Experimental Range in south-central New Mexico to evaluate effects of shrub removal and lagomorph exclusion on perennial vegetation dynamics of a degraded site dominated by creosotebush (*Larrea tridentata* Sess. & Moc Ex DC.). The original null hypothesis was that there would be no response by perennial grass species to reduced shrub competition or reduced herbivory. The alternative hypothesis was that bush muhly (*Muhlenbergia porteri* Scribn), a perennial grass that grows in association with creosotebush, would decrease in basal cover, and other perennial grass species would increase with the reduced competition resulting from shrub removal. These treatments have been maintained over the ensuing years, and vegetation cover as a response variable was measured for perennial species following the 1995 growing season. Our objective was to quantify perennial vegetation dynamics in response to these treatments in order to test the original hypothesis proposed in 1938.

Materials and methods

The study was established on the Jornada Experimental Range, 37 km north of Las Cruces, New Mexico. The study area is located on a bajada slope where typical Paleorthid soils have formed on an old alluvial fan. Annual precipitation averages approximately 250 mm with 55% occurring from July through September. Annual precipitation can fluctuate widely, and yearly totals for the entire study period are shown in Fig. 1. A detailed site description is provided in Gibbens *et al.* (1993).

Vegetation is dominated by creosotebush, with honey mesquite (*Prosopis glandulosa* Torrey) and tarbush (*Flourensia cernua* DC) also present. Suffrutescents, including mariola (*Parthenium incanum* H.B.K.), broom snakeweed (*Gutierrezia sarothrae* Pursh), and desert zinnia (*Zinnia acerosa* DC), are abundant. Principal perennial grasses are black grama (*Bouteloua eriopoda* Torr.), spike dropseed (*Sporobolus contractus* A.S. Hitch.), bush muhly, and fluffgrass (*Dasyochloa pulchella* Kunth).

Sixteen plots (21.3 m × 21.3 m) were established in 1938 in four rows of four plots per row with a buffer zone of 7.6 m between plots. All plots were sampled prior to treatment applications. Each plot was divided into east and west halves and 14 randomly located 10.65 m line intercept transects were sampled for shrub canopy cover and perennial grass basal cover in each half-plot. These plots were resampled in the same fashion in 1947, 1956, 1960, 1967, 1989, and 1995, using a separate set of randomly located transects in each sampling year.

Treatments were factorially applied, yielding a control plot, single factor plots, and plots with varying degrees of combinations of factors. Original treatments applied to these 16 plots were clearing (hand removal of shrubs severed at ground surface), furrowing (shallow, hand raked furrows designed to trap surface water), seeding (broadcast application of seeds of native perennials), and lagomorph exclusion (Table 1). Poultry netting with a 2.5 cm mesh buried about 15 cm in the ground and extending

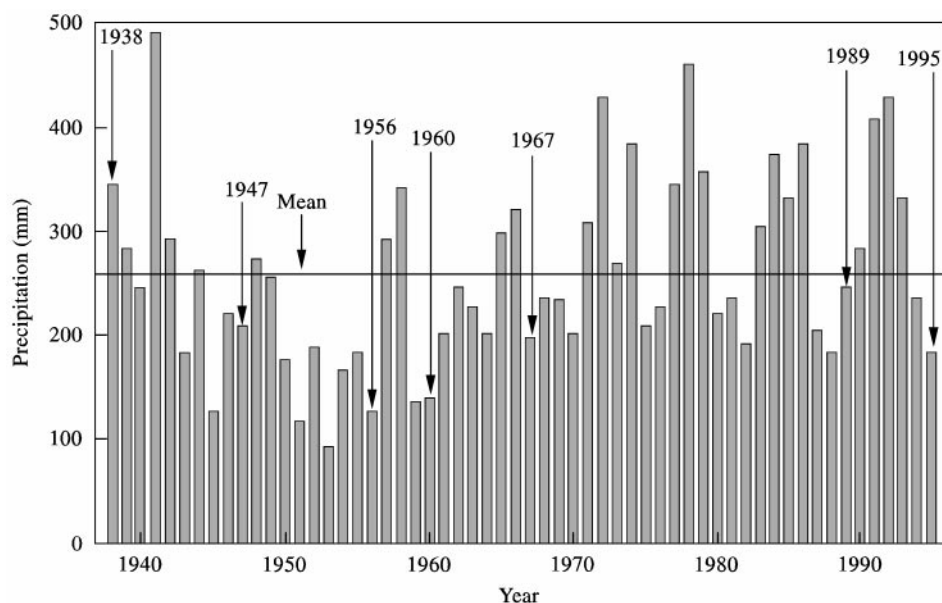


Figure 1. Annual precipitation from 1938 to 1995. Mean annual precipitation for this period was 260 mm. Years when plots were sampled are indicated.

above-ground about 75 cm was used to exclude lagomorphs. Shrubs (not including suffrutescents) have been removed from the cleared plots immediately following all resampling periods listed above. Seeded species were black grama, spike dropseed, mesa

Table 1. *Treatments as applied to individual plots in 1938–39. Seeded and furrowed treatments did not persist, and 1995 data were analysed as a 2 × 2 factorial using the whole plot factors of shrub removal and lagomorph exclusion*

Plot No.	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			

dropseed (*Sporobolus flexuosus* Thurb. ex Vasey), and fourwing saltbush (*Atriplex canescens* Pursh). All treatments were applied after the initial vegetation measurements were recorded in 1938, except that the lagomorph exclusion fences were constructed in 1939. Livestock were excluded from the study area in 1938, and the site has not been grazed by livestock at any time during the study period.

Effects of furrowing and seeding treatments were either short-lived or non-existent, and analyses of these treatments following the 1989 measurements indicated that measured responses were inconsequential (Gibbens *et al.*, 1993). Our analyses examined only the two factors (lagomorph exclusion and shrub removal) which have persisted over the 56-years period of this experiment.

Statistical analyses

For each of the individual perennial species cover data were analysed by analysis of variance as a split-plot in time with a 2×2 factorial treatment structure in a completely randomized design. The two whole-plot factors were lagomorph exclusion and shrub removal. *F*-tests in the analysis of variance and means for main effects and interactions were calculated using PROC GLM (SAS Institute Staff, 1996). Normal probability plots and Wilk-Shapiro test statistics from PROC UNIVARIATE (SAS Institute Staff, 1996) were used to examine the normality of the residuals.

For bush muhly, mariola, the sum total of all grasses, and total grasses minus bush muhly, an additional seven degree of freedom set of contrast statements was included to examine differences in per cent cover within a factor within years. These species or class totals demonstrated normality of residuals and further contrasts were justified. For normally distributed variables with significant *F*-tests, mean separations within a single year were performed.

A repeated measures analysis, with year as the repeated response variable, was also used to assess the effect of possible differential correlation between years on analysis of variance tests. The observed significance levels of tests involving the year main effect and interactions were adjusted by the Greenhouse-Geisser and Huynh-Feldt epsilons. In general, the observed significance levels from the split-plot analysis of variance and adjusted repeated measures were not dramatically different. Therefore, it was assumed that the correlation structure between all pairs of years was equivalent and that the split-plot analysis was appropriate.

A final set of analyses was performed to assess the effect of treatments on per cent cover for 1995 only. These data were analysed using PROC GLM as a two-way analysis of variance. Normal probability plots and Wilk-Shapiro test statistics from PROC UNIVARIATE were again utilized to assess the normality of the residual values. For several grasses and shrubs, non-normality was detected. PROC RANK (SAS Institute Staff, 1996) was used to perform a rank transformation of the response variables. Analysis of variance was then repeated with ranked responses and normality of the residuals was re-examined. The distributions of residuals from the rank transformation data, for all grasses and shrubs except black grama and fluffgrass, were not different from normal ($p \leq 0.05$).

Results

Main effects were evident 56 years after the study was initiated. Individual species showed differential responses to either lagomorph exclusion or periodic shrub removal (Table 2). Shrub cover increased ($p \leq 0.05$) with lagomorph exclusion. In particular, mariola, creosotebush, mesquite, and tarbush increased by at least 45% with long-term exclusion of lagomorphs. However, miscellaneous shrubs (primarily cacti

Table 2. Percentage canopy cover of shrubs and suffrutescents and percentage basal area of grasses for lagomorph exclusion and shrub removal treatments 56 years after initial treatment

Species	Lagomorphs		Shrubs	
	excluded	unexcluded	low cover	high cover*
Shrubs and suffrutescents				
creosotebush	9.9 ^{a†}	6.8 ^b	2.9 ^a	13.8 ^b
honey mesquite	4.0 ^a	2.2 ^b	1.3 ^a	5.0 ^b
tarbush	1.4 ^a	0.5 ^b	0 ^a	1.9 ^b
mariola	5.6 ^a	2.1 ^b	5.5 ^a	2.3 ^b
miscellaneous	0.7 ^a	3.3 ^b	2.7 ^a	1.2 ^b
Total	21.6 ^a	15.0 ^b	12.4 ^a	24.2 ^b
Grasses				
black grama	0.6 ^a	0.6 ^a	1.2 ^a	0
bush muhly	2.0 ^a	2.1 ^a	1.2 ^a	2.9 ^b
spike dropseed	0.9 ^a	0.1 ^b	0.8 ^a	0.1 ^b
miscellaneous	0 ^a	0.1 ^b	0.1 ^c	0.0 ^b
Total	3.5 ^a	2.9 ^b	3.3 ^a	3.0 ^a

* The three major shrub species (creosotebush, honey mesquite, and tarbush) were severed at ground level and removed from low cover plots in 1938, 1947, 1956, 1960, 1967, 1989 and 1995 following vegetation measurements. The low cover treatment represents a 0 to 6% range in shrub canopy cover during intervals of plant removal and remeasurement. The high cover treatment represents a 15–25% range in shrub canopy for these three species.

† Means within a row and treatment with different letters differ ($p \leq 0.05$).

(*Opuntia* spp.) and desert zinnia) declined with lagomorph exclusion. Increased cover of the four dominant shrub species may have limited establishment of these miscellaneous shrub species.

The major grass response to lagomorph exclusion was increased cover of spike dropseed. The dropseed genera are highly preferred forages by black-tailed jackrabbits (*Lepus californicus*) in this region (Dabo *et al.*, 1982). A slight increase in other grasses accompanied lagomorph herbivory.

Periodical shrub removal (resulting in a range of shrub cover from 0 to 6% over the 56-year period) increased ($p \leq 0.05$) basal cover of black grama and spike dropseed. In fact, black grama did not occur on any intact shrub sites irrespective of lagomorph presence or absence. Conversely, bush muhly cover was higher ($p \leq 0.05$) on plots with high shrub cover. Differential responses among these three perennial grass species within the shrub-removed treatment resulted in no difference ($p \leq 0.05$) in total grass cover between shrub intact and shrub-removed plots.

The data collected in 1995 would support rejection of the original null hypothesis. Bush muhly was less evident on the shrub-removed plots, and other perennial grasses were more prevalent. However, these results were not consistent over the course of the study (Figs 2 and 3).

Variable responses in basal cover of bush muhly and total grass cover were evident over the course of the study for both the shrub removed (Fig. 2) and lagomorph exclusion factors (Fig. 3). Bush muhly is commonly found in association with creosotebush, and cover of this grass species was greater for the shrub intact treatment when measured in 1989 and 1995. Data for other individual grass species were difficult to analyse statistically due to frequent complete absence from plots during some years of measurement. These absences resulted in non-normally distributed data. However, total

grass species cover minus bush muhly (normally distributed data) increased ($p \leq 0.05$) in response to shrub removal in the 40 years after the 1950–56 drought (Fig. 2). This collective response is due to increases in the cover of black grama and spike dropseed.

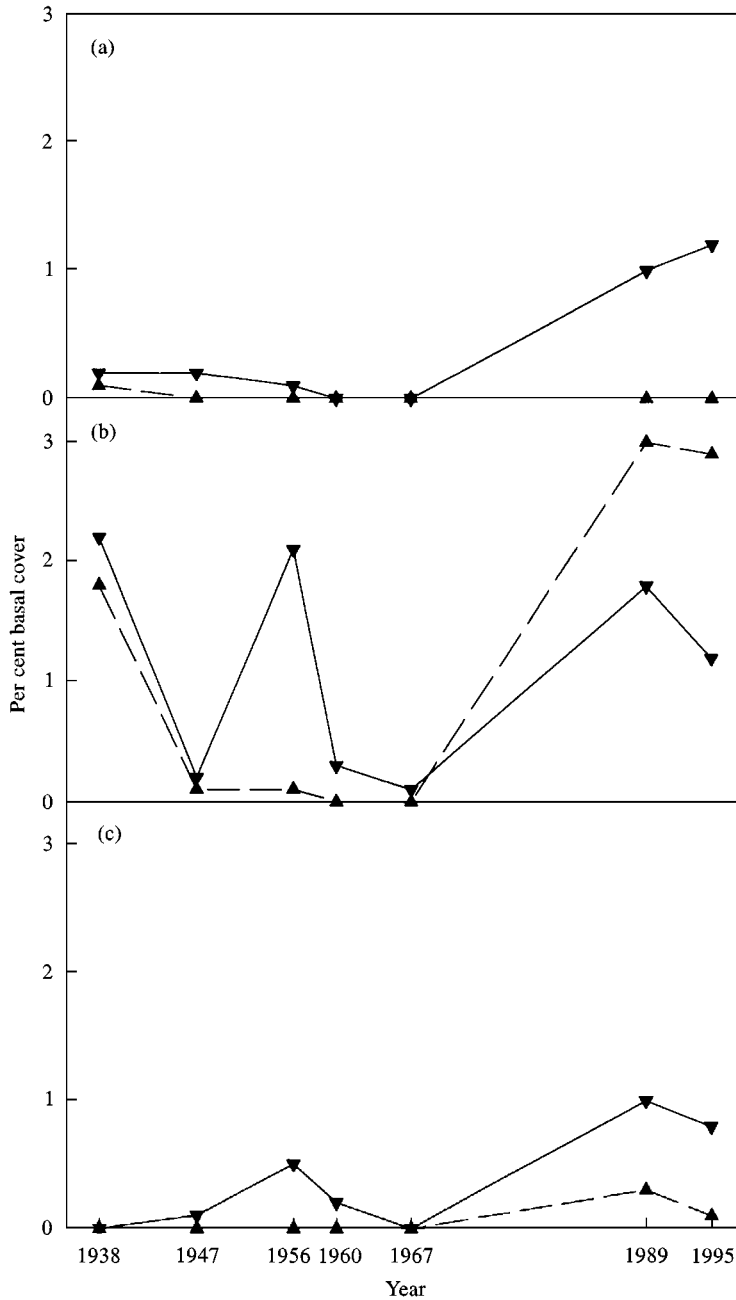


Figure 2. Basal cover of (a) black grama, (b) bush muhly, (c) spike dropseed, (d) total grasses, and (e) total grasses minus bush muhly on shrub cleared (▼) and uncleared (▲) treatments in 1938, 1947, 1956, 1960, 1967, 1989, and 1995. Treatment means within years with different letters differ ($p \leq 0.05$); treatment means within years without letters do not differ ($p \leq 0.05$).

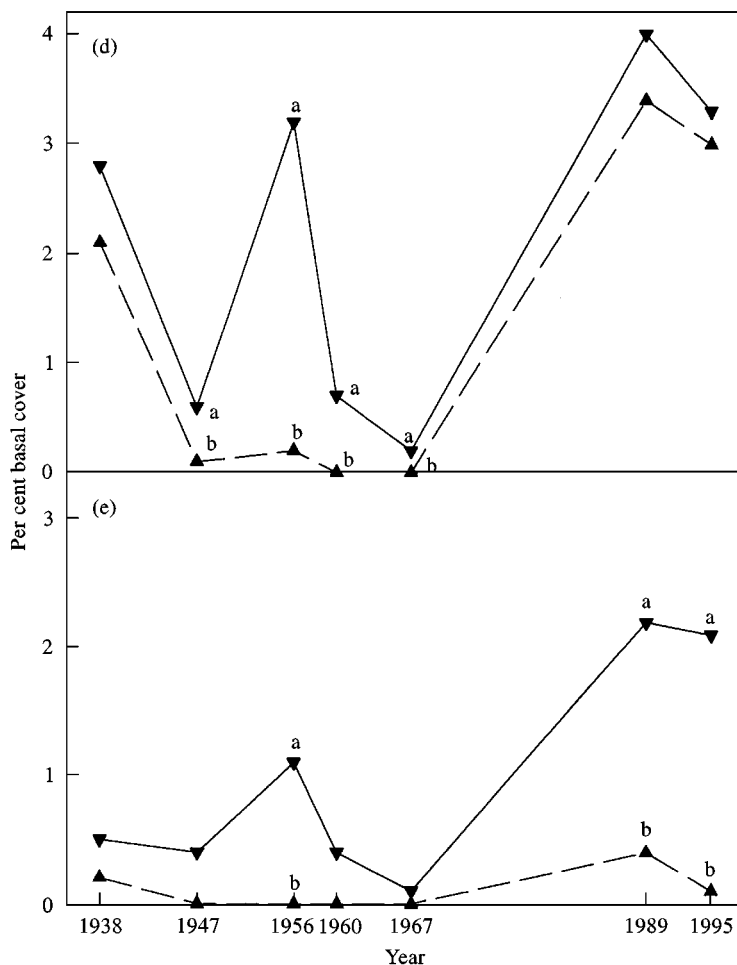


Figure 2. (Continued.)

Temporal effects of lagomorph exclusion were less pronounced than for shrub removal. Basal cover by species exhibited a similar response to treatments during the first 30 years of the study (1938–1967). However, since the 1967 measurements, effects of lagomorph preferences for both spike dropseed and mariola were apparent. Both of these preferred forages had lower cover within the unexcluded (grazed) treatment. Other perennial grasses were not affected by lagomorph exclusion even after 56 years (Fig. 3).

Analyses of perennial grass cover correlations with antecedent rainfall have indicated some influence of rainfall over the previous 10 months on grass basal cover measured in the late summer (Gibbens *et al.*, 1993). However, the seven sampling times within the 56-year period of this study limit the statistical rigor of this type of analysis. Our examinations of precipitation as a covariate (including the 1995 sampling period) did not change the above discussed results.

Discussion

Vegetation responses to release from shrub competition were delayed in our study. This observation supports the hypothesis that shrubs influence, through biological and

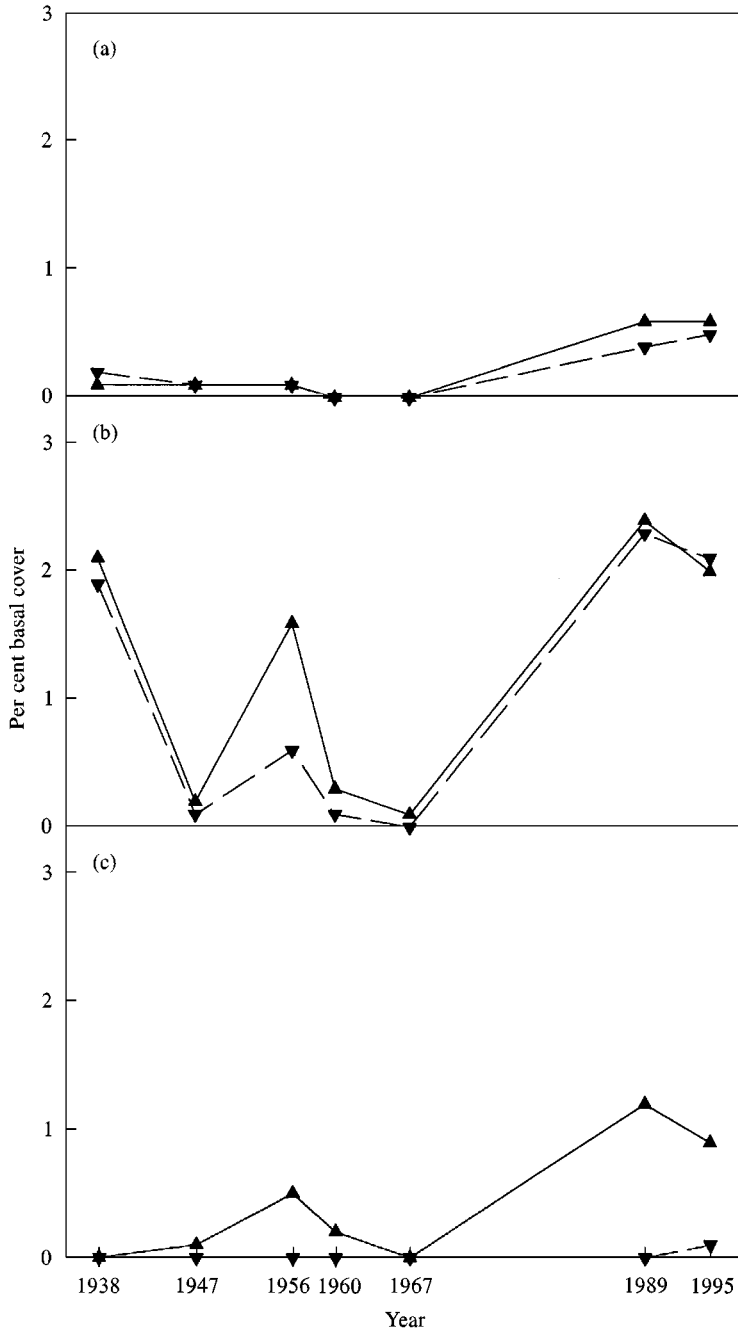


Figure 3. Basal cover of (a) black grama, (b) bush muhly, (c) spike dropseed, (d) total grasses, and (e) canopy cover of mariola on lagomorph excluded (▲) and unexcluded (▼) treatments in 1938, 1947, 1956, 1960, 1967, 1989, and 1995. Treatment means within years with different letters differ ($p \leq 0.05$); treatment means within years without letters do not differ ($p \leq 0.05$).

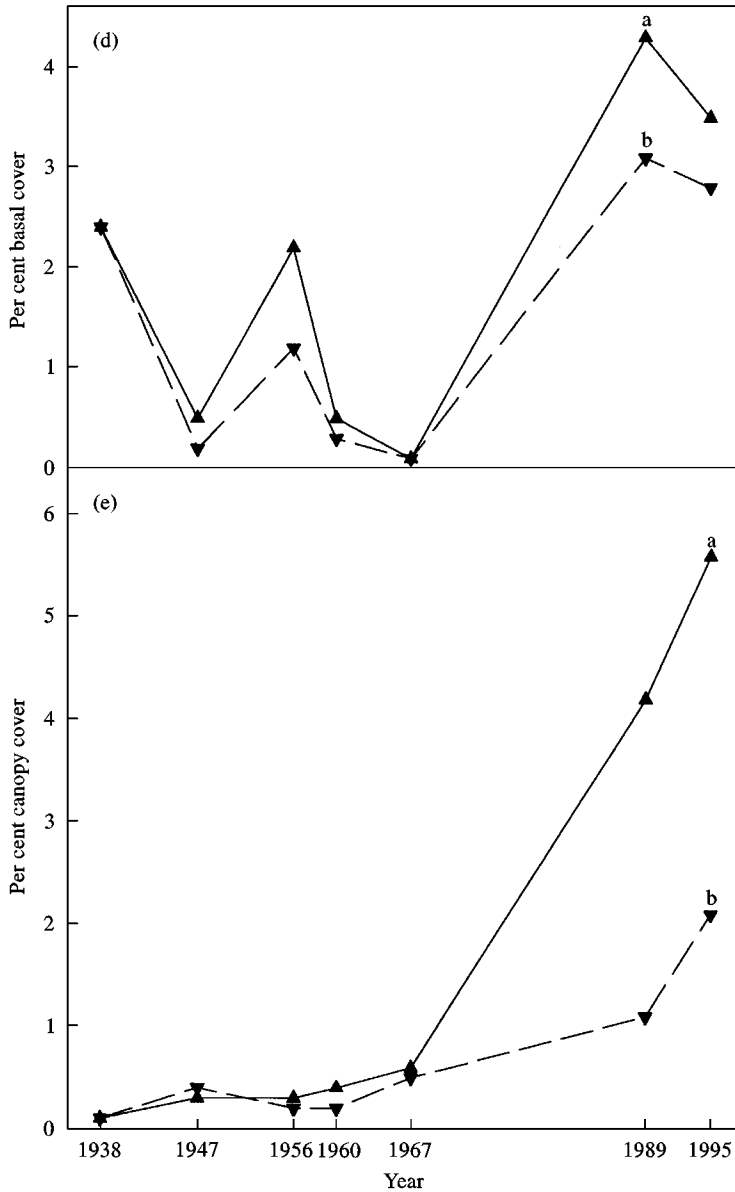


Figure 3. (Continued.)

physical processes, the redistribution of moisture and nutrients (Garcia-Moya & McKell, 1970; Schlesinger *et al.*, 1990). However, biological forces in arid environments do not quickly redistribute critical resources to prior spatial patterns following shrub removal. No responses to shrub removal were evident 30 years (1938–1967) after creosotebush, mesquite, and tarbush were initially removed. This observation is supported by other studies in the Chihuahuan Desert that reported few significant vegetation responses to protection from livestock grazing even after relatively long protection periods (Chew, 1982; Kelt & Valone, 1995; Wondzell & Ludwig, 1995).

It is recognized that this system is nutrient-regulated, though moisture limited (Gutierrez & Whitford, 1987). Spatial redistribution of these limited nutrients, especially N, will significantly affect community structure and functions (Schlesinger *et al.*, 1990). In mesquite communities this nutrient legacy has been shown to persist for decades after natural mortality of the shrub species (Barnes & Archer, 1996). Preliminary data on soil C and N at our study site indicated C and N were highest (481 and 33 g m⁻² on a gravel-free basis, respectively) for the shrub cleared and lagomorph excluded treatment combination (Herrick *et al.*, 1997a). The C and N levels were similar (444 and 29 g m⁻², respectively) for the other three treatment combinations. Overall, these values are slightly higher than expected for this type of rangeland. However, soils in these plots were sampled only to a depth of 5 cm, compared to up to 30 cm sampling depth in other studies. The concentration of soil organic matter in the top 5 to 10 cm might explain these higher values. It could be inferred that livestock grazing management (or removal of livestock) in arid, shrub-dominated landscapes (> 8% canopy cover) will not have significant positive effects on soil C and N content. These preliminary observations require further detailed experimentation.

The exclusion of lagomorph grazing did not entirely eliminate mammalian herbivory from these plots. The significance of rodents as keystone species in the Chihuahuan Desert is well recognized (Brown & Heske, 1990). However, harvest rates by native mammals are relatively low (< 15% of above-ground biomass annually) (Pieper *et al.*, 1983). Black-tailed jackrabbits are the principle mammalian herbivore, and plant responses to lagomorph exclusion reflect foraging preferences of jackrabbits for young shrub seedlings, mariola, and graminoids other than bush muhly. These preferences have been documented by jackrabbit dietary studies in this area (Dabo *et al.*, 1982; Wansi *et al.*, 1992), and are reflected in analyses of data from an earlier stage of this experiment (Gibbens *et al.*, 1993). Minor species show a positive response, though slight, to grazing by lagomorphs. It is likely this response is due to the reduced competition for resources from the more preferred species.

Some studies have reported a positive graminoid response following exclusion of livestock (Bock & Bock, 1993), but these have generally been in desert grasslands with minimal (< 8%) shrub cover (Smith & Schmutz, 1975). In addition, recovery of black grama is notoriously slow and highly sensitive to severe disturbances of prolonged drought and overgrazing (Gosz & Gosz, 1996).

Non-linear vegetation dynamics have been identified in the Chihuahuan Desert (Friedel, 1991), and stable, shrub-dominated non-climax states have been described for arid rangelands (Westoby *et al.*, 1989). Three central postulates that have emerged from this state-and-transition model are that the ecological character of these communities is strongly influenced by a single species, that this dominance is long lived, and that there are transitional thresholds to these states.

The significance of shrub dominance in long-term control of community structure has been demonstrated in mesquite communities (Barnes & Archer, 1996) and is apparent from our data. Shrub canopy cover, generally between 15% and 25%, strongly affects the composition of non-woody species. Only when gaps were created in the canopy cover by removing shrubs were there any responses by species other than bush muhly. Gap dynamics, even on relatively small spatial scales, have been viewed as important influences on vegetation patterns on rangelands (Coffin & Lauenroth, 1990). Other data from this region (Smith & Schmutz, 1975; Holechek *et al.*, 1994) would suggest that shrub canopy cover below 6 to 8% will allow graminoid species to increase in response to improved management practices or favorable moisture periods. A measurable transitional level of 6–8% shrub cover may exist between grass- and shrub-dominated states in this arid environment (average long-term annual precipitation less than 250 mm).

Conclusion

Plant community structure in this arid environment is strongly shaped by disturbance regimes, especially prolonged drought (Herbel & Gibbens, 1996). Disturbance regimes can be chronic or acute, and natural or anthropogenic in origin. It is not unusual in arid environments for the effects of these regimes to be manifested by only a few plant species (Noy-Meir, 1979/80). The recent history of disturbance regimes in the Chihuahuan Desert has resulted in shrub-dominated landscapes. Future trajectories of vegetation structure will also be strongly shaped by disturbances. It is likely that natural disturbances will result in non-deterministic trajectories given that numerous elements of this environment now differ from historical conditions. These differences from prior conditions include deteriorated soil quality, presence of alien plant and animal species, reduction of predator species diversity, and altered atmospheric conditions. Remediation efforts within this vegetation type will require interventions, but we lack a sufficient understanding of system trajectories to be able to trigger specific desired responses. We do understand, though, that remediation strategies will require low input technologies (Herrick *et al.*, 1997*b*). For creosotebush communities, remediation programs will need to address the overwhelming effect of shrub competition in controlling vegetation dynamics of these rangelands.

References

- Archer, S., Schimel, D.S. & Holland, E.A. (1995). Mechanisms of shrubland expansion: land use, climate or CO₂? *Climate Change*, **29**: 91–99.
- Barnes, P.W. & Archer, S. (1996). Influence of an overstory tree (*Prosopis glandulosa*) on associated shrubs in a savanna parkland: implications for patch dynamics. *Oecologia*, **105**: 493–500.
- Bock, C.E. & Bock, J.H. (1993). Cover of perennial grasses in Southeastern Arizona in relation to livestock grazing. *Conservation Biology*, **7**: 371–377.
- Brown, J.H. & Heske, E.J. (1990). Control of a desert-grassland transition by a keystone rodent guild. *Science*, **250**: 1705–1707.
- Buffington, L.C. & Herbel, C.H. (1965). Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs*, **35**: 139–164.
- Chew, R.M. (1982). Changes in herbaceous and suffrutescent perennials in grazed and ungrazed desertified grassland in Southeastern Arizona, 1958–1978. *American Midland Naturalist*, **108**: 159–169.
- Coffin, D.P. & Lauenroth, W.K. (1990). A gap dynamics simulation model of succession in a semiarid grassland. *Ecological Modelling*, **49**: 229–266.
- Dabo, S.M., Pieper, R.D., Beck, R.F. & Southward, G.M. (1982). *Summer and fall diets of black-tailed jackrabbits on semidesert rangeland*. New Mexico Agricultural Experiment Station Research Report 476. 20 pp.
- Fredrickson, E.L., Barrow, J.R., Herrick, J.E., Havstad, K.M. & Longland, B. (1996). Low cost seeding practices for desert environments. *Restoration Management Notes*, **14**: 72–73.
- Friedel, M.H. (1991). Range condition assessment and the concept of thresholds: a viewpoint. *Journal of Range Management*, **44**: 422–426.
- Garcia-Moya, E. & McKell, C.M. (1970). Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology*, **51**: 81–88.
- Gibbens, R.P., Havstad, K.M., Billheimer, D.D. & Herbel, C.H. (1993). Creosotebush vegetation after 50 years of lagomorph exclusion. *Oecologia*, **94**: 210–217.
- Gosz, R.J. & Gosz, J.R. (1996). Species interactions on the biome transition zone in New Mexico: response of blue grama (*Bouteloua gracilis*) and black grama (*Bouteloua eripoda*) to fire and herbivory. *Journal of Arid Environments*, **34**: 101–114.
- Grover, H.D. & Musick, H.B. (1990). Shrubland encroachment in Southern New Mexico, U.S.A.: an analysis of desertification processes in the American Southwest. *Climate Change*, **17**: 305–330.

- Guo, Q. & Brown, J.H. (1996). Temporal fluctuations and experimental effects in desert plant communities. *Oecologia*, **107**: 568–577.
- Gutierrez, J.R. & Whitford, W.G. (1987). Chihuahuan Desert annuals: importance of water and nitrogen. *Ecology*, **68**: 2032–2045.
- Herbel, C.H. & Gibbens, R.P. (1996). *Post-drought vegetation dynamics on arid rangelands in Southern New Mexico*. New Mexico Agricultural Experiment Station Bulletin 776, 102 pp.
- Herrick, J.E., Havstad, K.M. & Gibbens, R.P. (1997a). Changes in soil factors following 56 years of shrub removal and lagomorph exclusion. *Bulletin of the Ecological Society of America*, (Suppl.) **78**: 258.
- Herrick, J.E., Havstad, K.M. & Coffin, D.P. (1997b). Rethinking remediation technologies for desertified landscapes. *Journal of Soil and Water Conservation*, **52**: 220–225.
- Holeczek, J.L., Tembo, A., Daniel, A., Fusco, M. & Cardenas, M. (1994). Long-term grazing influences on Chihuahuan Desert rangeland. *Southwestern Naturalist*, **39**: 342–349.
- Huenneke, L.F. (1996). Temporal patterns of primary productivity in Chihuahuan Desert ecosystems of the Jornada LTER site. *Bulletin of the Ecological Society of America*, **77**: 205.
- Kelt, D.A. & Valone T.J. (1995). Effects of grazing on the abundance and diversity of annual plants in Chihuahuan scrub habitat. *Oecologia*, **103**: 191–195.
- Milton, S.J., Dean, W.R.J., du Plessis, M.A. & Siegfried, W.R. (1994). A conceptual model of arid rangeland degradation: the escalating cost of declining productivity. *BioScience*, **44**: 70–76.
- Muller, C. H. (1940). Plant succession in the *Larrea-Flourensia* climax. *Ecology*, **21**: 206–212.
- Noy-Meir, I. (1979/80). Structure and function of desert ecosystems. *Israel Journal of Botany*, **28**: 1–19.
- Pieper, R.D., Anway, J.C., Ellstrom, M.A., Herbel, C.H., Packard, R.L., Pimm, S.L., Raitt, R.J., Staffeldt, E.E. & Watts, J.G. (1983). *Structure and function of North American desert grassland ecosystems*. New Mexico Agricultural Experiment Station Special Report 39, 298 pp.
- SAS Institute Staff (1996). *SAS User's Guide, Version 6.11*, Cary NC: SAS Institute Inc. 1072 pp.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. & Whitford, W.G. (1990). Biological feedbacks in global desertification. *Science*, **247**: 1043–1048.
- Smith, D.A. & Schmutz, E.M. (1975). Vegetative changes on protected versus grazed desert grassland ranges in Arizona. *Journal of Range Management*, **28**: 453–458.
- Stein, R.A. & Ludwig, J.A. (1979). Vegetation and soil patterns on a Chihuahuan Desert bajada. *American Midland Naturalist*, **101**: 28–37.
- Van Devender, T.R. (1990). Late quaternary vegetation and climate of the Chihuahuan Desert, United States and Mexico. In: Betancourt, J.L., Van Devender, T.R. & Martin, P.S. (Eds), *Packrat Middens: the last 40,000 years of biotic change*, pp. 104–133. Tucson, AZ: The University of Arizona Press. 467 pp.
- Wansi, T., Pieper, R.D., Beck, R.F. & Murray, L.W. (1992). Botanical content of black-tailed jackrabbit diets on semidesert rangeland. *Great Basin Naturalist*, **52**: 300–308.
- Westoby, M., Walker, B. & Noy-Meir, I. (1989). Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, **43**: 266–274.
- Wondzell, S. & Ludwig, J.A. (1995). Community dynamics of desert grasslands: influences of climate, landforms and soils. *Journal of Vegetation Science*, **6**: 377–390.