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Community response to removals of plant functional groups and species from a Chihuahuan Desert shrubland

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Arid and semi-arid ecosystems often exhibit diverse plant growth forms in water-limited environments, but it is unclear whether resource competition (interference) is actually important in structuring communities. We chose a diverse Chihuahuan desert shrubland to examine the response of the plant community to experimental removals of selected perennial plant species or groups of species. Four treatments involved the removal of all individuals of all species of a single functional group (functional group removals: shrub removal, succulent removal, subshrub removal, perennial grass removal). Three other treatments involved removing species within functional groups. These seven treatments plus a control (no plants removed) were replicated six times each in 25 × 25 m experimental plots, in summer 1995. Permanent belt transects were surveyed for number and sizes of all vascular plants in spring and fall in 1997, 1999, 2000, and 2001. Those plots from which the dominant shrub, *Larrea tridentata*, was removed had not recovered in total plant cover or volume by 2001, but cover and volume in all other treatments were similar to those in control plots. Relatively few species demonstrated a positive response to the removal of other species or functional groups. The perennial grass group and forbs were the most responsive; perennial grass cover increased in the shrub removal treatment relative to the control but treatment differences diminished after dry growing seasons in 2000 and 2001. Results over the first five years suggest that either environmental conditions or intrinsic biological characteristics limit the ability of most plant species to respond to the removal of substantial fractions of community biomass and composition in the short term. Such slow response by both dominant and less abundant components of the community has implications for the recovery of semi-arid systems after human disturbance or other events leading to the reduction of biological diversity.

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Most ecological systems appear to be experiencing an erosion of biological diversity (Vitousek 1994, Chapin et al. 2001), and arid and semi-arid regions are no exception. Over-grazing by domestic livestock, harvesting of woody or succulent species, elimination of burrowing and predatory animals, and other human activities are eliminating species or groups of species from many semi-arid regions (Huenneke and Noble 1996). Arid lands represent an important opportunity to study plant diversity, particularly the importance of diversity of growth forms within a community. Arid and semi-arid ecosystems are not so diverse as to be intractable for experimentation, yet many deserts contain an intriguing diversity in terms of plant

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morphology, life history, and physiology. In the harsh environment and low resource availability of desert ecosystems, one might expect both strong negative interactions (e.g. competition for water) and strong amelioration effects (e.g. facilitation by shading: Pugnaire et al. 1996). This suggests the possibility of dramatic responses to the removal of some species by the remaining biota. On the other hand, it is often assumed that in desert systems most species are constrained by extreme environmental limitations, rather than by biotic interactions (Louw and Seely 1982, Noy-Meir 1979/80). Previous work in semi-arid systems has shown that in some cases the members of one functional 'group' (e.g. perennial grasses) may indeed be influenced by members of another 'group' (e.g. shrubs; Sala et al. 1989, Aguiar and Sala 1994).

It is important to understand the capacity of ecosystems to respond to the reduction of biodiversity or the elimination of some components of a community. Do remaining community members (e.g. species) respond by increasing their absolute abundance or rate of activity? Do all remaining species respond positively, or only certain subsets or groups of species? Or conversely, do removals trigger further species losses? Can the identity of responding species be predicted based on the characteristics of those species removed from a system? Finally, does the reduction of biological diversity in a system increase the likelihood of establishment of new species?

The northern Chihuahuan Desert region of New Mexico, USA, has sustained a dramatic shift in the relative abundance of plant growth forms over the past century, with desert shrub species invading and displacing extensive perennial grasslands (Buffington and Herbel 1965). The region still contains a diverse set of plants and plant assemblages; however, surprisingly little is known about how plants of different growth forms differ in resource use or how they interact with one another. In an attempt to understand community structure in these ecosystems, we initiated a species removal experiment in a diverse desert shrubland at the Jornada Basin Long-Term Ecological Research (LTER) site in southern New Mexico. Our approach was to identify plant functional 'groups' according to growth form and physiology, and to remove all or some of the species representing each functional group from large, replicated field plots. Our objective here is to test the hypothesis that resource competition is an important structuring force in the system, and that removals of some species will result in increased access to resources and increased growth by some or all of the remaining species. Specifically, the experiment should test whether species respond most strongly to the removal of similar species – that is, wheth biotic interactions are strongest within functional groups.

Our experimental removals may address the larger question of the future of semi-arid systems in the face of continued reduction of diversity. In the longer term, if the remaining species recover so that treatments have equivalent total cover or biomass, then we will be able to address questions of compositional or diversity effects on ecosystem function (Díaz et al. 2003). In this paper, though, we address only the short-term response to the manipulations. We describe the behavior of the remaining plant functional groups and individual species in response to both: 1) functional group removals and, 2) manipulations of plant richness within a functional group, during the first five years after removals. We also discuss the implications of these results for understanding the potential response of desert systems to perturbation.

Material and methods

Study site

The Jornada Basin LTER site was established in the early 1980s to build a research program focused on desertification, using two existing long-term facilities. The Chihuahuan Desert Rangeland Center (CDRRC) of New Mexico State University, and the adjacent USDA-ARS Jornada Experimental Range (JER) are located approximately 37 km northeast of Las Cruces, NM, USA. Potential sites at the CDRRC and the adjacent JER were investigated and evaluated for relatively high diversity of plant cover, minimal evidence of recent human disturbance, protection from grazing livestock, and convenient access by vehicle. The study site selected is located in a Chihuahuan desert creosote bush (*Larrea tridentata*) shrubland near the southern boundary of the CDRRC. The southeastern portion of the CDRRC has been fenced to exclude cattle and has been administered by the Jornada Basin LTER program since 1982. The site slopes to the east from a road and power line corridor. Soils are mapped as Casito-Terino with a gravel surface layer. Historical information documents that this bajada (alluvial slope) east of the Doña Ana Mountains has been dominated by *L. tridentata* throughout the history of the CDRRC, in contrast to more recently "desertified" areas in the region where shrubs have encroached on former perennial grassland (Buffington and Herbel 1965). Perennial vegetation is more diverse than in many *L. tridentata*-dominated areas. This region of the Chihuahuan desert averages 210 mm of rainfall each year, with most of the precipitation falling in late summer. A tipping bucket rain gauge installed on site recorded precipitation in mm for each rainfall event.

Experimental design

Four functional groups were identified for manipulation in the research area based on coarse similarities of growth form and physiological characteristics, rather than a careful assessment of similarities in resource use or in response to agents of disturbance: shrubs, succulents, subshrubs and perennial grasses. The shrub community is dominated by *L. tridentata* and *Prosopis glandulosa*, or mesquite. Subordinate shrubs are numerous; *Flourensia cernua* or tarbush and *Parthenium incanum* are the most abundant of these. Succulents are dominated by *Yucca* and *Opuntia* species with a small number of subordinates, including *Echinocereus* spp. Subshrubs are dominated by *Zinnia acerosa*, *Gutierrezia microcephala* and *Melampodium leucanthum*. The perennial grass functional group is perhaps the least diverse at the site. *Muhlenbergia porteri* and *Dasyochloa pulchella* dominate with other species encountered in some seasons.

A 250 × 150 m area was located on the slope and gridded into 25 × 25 m plots. Plots containing conspicuous drainage channels were eliminated from use in the experiment. Remaining plots were evaluated by the use of two diagonal line – intercept transects run through each, along which the cover of specific shrub and succulent species (and of bare ground or openings) was recorded to the nearest cm. These preliminary data did not reveal any gradient from west to east (along the slope) in total vegetative cover or in the relative abundance of particular woody species. However, a gradient from south to north in *P. glandulosa* abundance was detected. Due to this spatial pattern in vegetative composition, and probable environmental gradients from upslope to down, we chose to use a randomized complete block design with 48 plots (8 treatments × 6 blocks; Fig. 1).

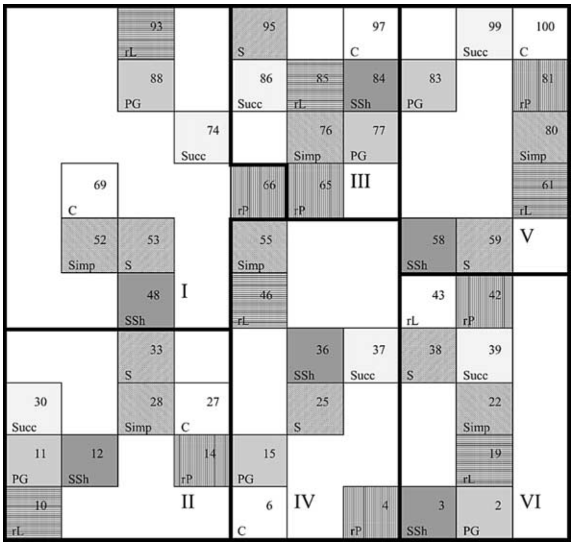


Fig. 1. Experimental design of plant removals incorporating 8 treatments, replicated 6 times. Treatment abbreviations as in Table 1. Roman numerals denote blocks.

Design of this field experiment involved several compromises. Plot size is not large relative to the sparseness and scale of pattern in semi-arid or arid ecosystems (Huenneke et al. 2001). However, larger plots would have presented impossible challenges in terms of time required for maintenance and sampling. The issue of scale is also relevant to our use of blocks within the design, and to the adequacy of replication. Though few of the vegetation characters assessed in preliminary sampling varied in a statistically detectable way across the study site, we judged that environmental gradients were likely in this sloped site and we apportioned plots into blocks accordingly. Having six blocks was again a compromise; more would be desirable in the face of considerable environmental and community variation, but would have made maintenance and sampling impossible in terms of labor. Given the considerable environmental 'noise' and variation, and the compromises deviating from an ideal or very-well-replicated design, we chose to be very conservative in analysis of results (Raffaelli and Moller 2000, Díaz et al. 2003).

Treatments were established by the selective removal of plant species or of all species of a functional group within a plot. There are eight treatments: a control (C, no removals); four functional group removal treatments (PG, perennial grass removed; S, shrubs removed; SSh, subshrubs removed; Succ, succulents removed), and three treatments where richness within a functional group was manipulated (Table 1). The latter include the simplified treatment (Simp, where only the single most abundant species of each growth form remains, while all other species of those growth forms are removed), the reduced-*Larrea* treatment (rL, where the dominant of each growth form is removed, and minority components remain), and a second form of the reduced

Table 1. Experimental functional group and functional group richness removal treatments.

Functional group manipulations

Treatment	*Functional group removed*
C–Control	No removals
PG–perennial grass	Perennial grass
S–shrub	Shrub
SSh–subshrub	Subshrub
Succ–succulent	Succulent

Functional group richness manipulations

Treatment	*Species removed*	*Richness level*
C–Control	No removals	High
rL–reduced minus *Larrea*	All dominants–*Larrea*, *Yucca*, *Zinnia*, *Muhlenbergia*	Intermediate
rP–reduced minus *Prosopis*	All dominants–*Prosopis*, *Yucca*, *Zinnia*, *Muhlenbergia*	Intermediate
Simp–simplified	All subordinates	Low

treatment (rP, where *Prosopis* rather than *Larrea* is removed as the shrub dominant).

We established treatments in summer/fall 1995. Plants were removed by cutting at the soil surface (no soil disturbance or herbicide application). Within each treatment, all plants removed from at least one plot were both field weighed and oven dried to constant weight. These data were used to construct regressions of dry weight versus live biomass weight. In the remaining plots of each treatment, removed plants were weighed in the field by species. Cumulative live mass totals for each species in each plot were used in the regressions to calculate the amount of dry mass removed. Dead material from shrubs and subshrubs was removed and weighed separately; this material was regarded as dry matter and no regression was used.

For most species, removal methodology has been effective; recruits of perennial plants are removed and regrowth of perennials is clipped back from the appropriate plots twice per year. After five years, only one perennial grass and two shrubs require substantial effort for plot maintenance.

Within the central 15 × 15 m of each of the 48 plots, we established three permanent belt transects, 15 × 1 m. In 1997, 1999, 2000 and 2001 plants were measured in the spring and fall (spring only in 2001). We measured every plant rooted in the transects by measuring the longest diameter and the longest diameter perpendicular to the first for each individual; height was measured from the tallest point of the plant to the ground directly below that point. Plants were recorded by specific quadrat (1 m^2) to permit tracking of individual survivorship and growth. Nomenclature follows Allred (1993) and the Jornada Basin LTER plant species list (http://jornada-www.nmsu.edu). Cover was calculated from diameters as the area of an oval; cylindrical volume was calculated with diameters and height.

Statistical analyses

Total plant cover and volume were calculated for each plot; in addition, totals were calculated for each functional group, and for the dominant and subordinate species. Individual forb species were selected for analysis based on response to disturbance and seasonal abundance. Cover and volume totals were analyzed using a mixed linear model in the MIXED procedure of SAS® (SAS Institute, 1999), with treatment as the fixed factor and block as the random factor. To examine whether a particular functional group responded to the removal of other functional groups, the following preplanned (one degree of freedom) comparisons were used: control versus each functional group removal treatment (PG, S, SSh and Succ) and PG versus S. To examine whether a particular functional group responded to richness manipulations within groups, the following comparisons (one degree of freedom) were used: C versus each richness manipulation treatment (Simp, rL and rP), C versus all three, Simp versus the two reductions, and rL versus rP. When the overall test was significant (alpha = 0.05) the a priori comparisons, described above, were made. Visual inspection of residual plots showed only minimal deviation from normality and equality of variance. Forb richness (number of forb species present) was analyzed with the same tests used for total cover and volume with all a priori comparisons used.

All preplanned comparisons were used as described to analyze the overall (across all functional groups) cover and volume totals, but had to be modified to analyze cover and volume totals within functional groups or species. Where response values for a functional group or species were zeroes due to the treatment manipulation itself, the comparisons of this treatment with others was removed from analysis. For example, in the shrub cover and volume analyses, comparisons were not performed against the S treatment. However, comparisons to rL remained in the analysis; while we might not expect shrub volume to have completely recovered from *L. tridentata* removals in the reduced-*Larrea* treatment only five years after treatment removals, we left the reduced-*Larrea* treatment in the analysis in order to test whether the remaining shrub community did respond. Contrasts between simplified and reduced treatments provide a broad test of community response to magnitude of disturbance; both involve removals of substantial amounts of biomass, but very different species remain to respond to that disturbance. Hence they may demonstrate the relative importance of species-level differences, as opposed to differences among functional groups.

Results

Magnitude of plant removals

The amount of live biomass removed for the four key functional groups varied by plot and treatment (Fig. 2). The greatest amount of biomass, 311 $g\,m^{-2}$ and 286 $g\,m^{-2}$, was removed from the shrub removal and the *Larrea* reduction plots, respectively. The perennial grass and subshrub removal treatments had the least biomass removed, only 4 to 15 percent of the total amount removed from the shrub treatments. Because the dominants in each functional group comprise so large a proportion of total community biomass, the amount of biomass removed for the simplified treatment was lower overall than that of the reduction treatments even though all subordinate species were removed from the former. The range in biomass removed for an individual treatment was greatest in the succulent removal due to large differences in the amount of *Yucca baccata* originally present (and then removed) in the six plots.

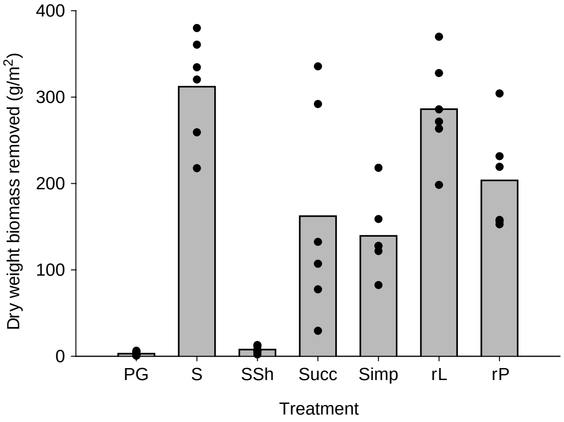


Fig. 2. Dry weight biomass originally removed by treatment. Bars represent treatment means, circles represent plot totals. Treatment abbreviations as in Table 1.

Community response

Plant cover in this desert shrub ecosystem ranged between 19 and 50% when the experiment was initiated (based on pre-treatment data). Cover in the plots fluctuated greatly depending on seasonal growing conditions, as forbs and annual grasses can contribute significant amounts of cover and biomass in some growing seasons. There has been no consistent trend in total mean plant cover or volume over the five years since treatment imposition in 1995 (Fig. 3). Total biomass in most treatments decreased from spring 1997 to spring 1999 and then increased substantially during fall 1999. Since fall 1999, total cover/volume for all treatments has decreased. In all seasons total cover and volume significantly differed among treatments (except in spring 2000 and spring 2001 for cover: Table 2). However, the range in cover and volume from

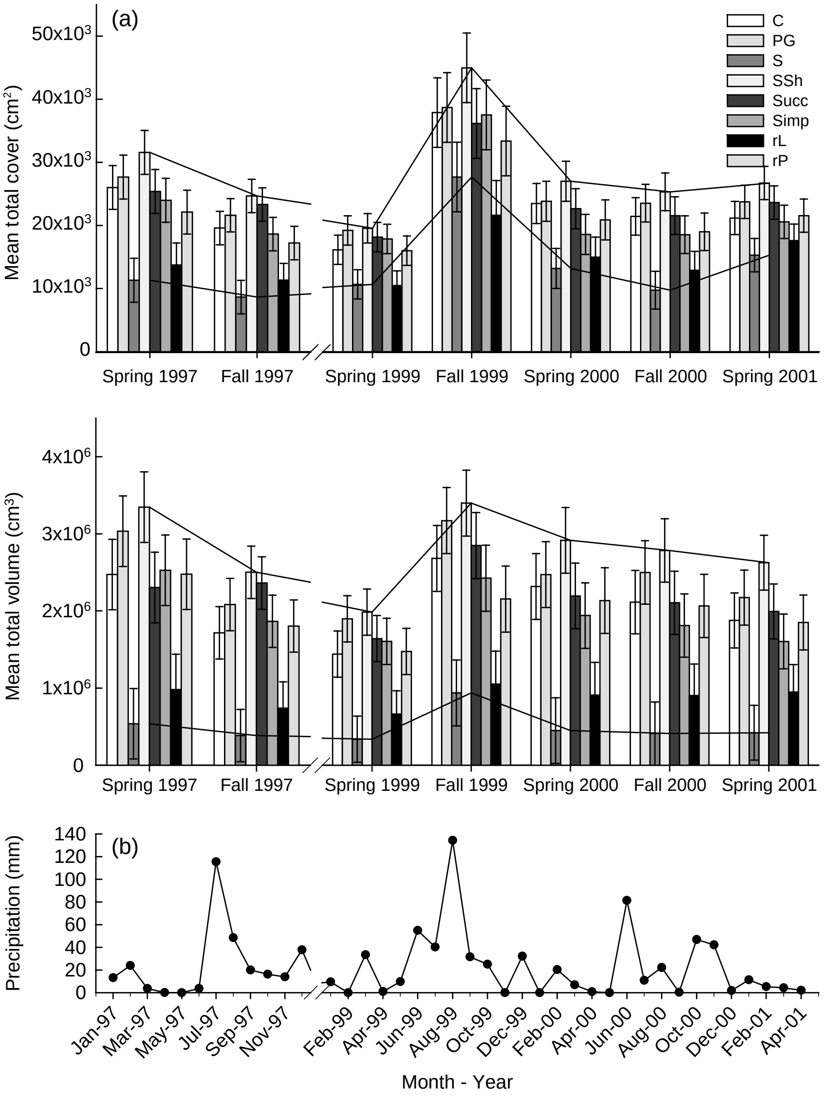


Fig. 3. (a) Mean total cover and volume (±se) by treatment across time; lines show trend in cover over time for the subshrub (highest cover) and shrub removal (lowest cover) treatments. Treatment abbreviations as in Table 1; (b) precipitation in mm measured by a tipping bucket rain gauge located on site.

Table 2. Mixed linear model analysis results for total plant cover, functional groups and species by season/year. F statistics and p-values are presented with those treatments removed from analysis noted. DAPU = *Dasyochloa pulchella*, BAAB = *Bahia absinthifolia*, DEPI = *Descurainia pinnata*, ERDI = *Eriastrum diffusum* * $P < 0.05$, ** $P < 0.007$, *** $P < 0.0001$. Periods denote season in which analysis was not run due to low sample size.

Response variable		Season/Year							Trt removed from analysis
		Spring 97	Fall 97	Spring 99	Fall 99	Spring 00	Fall 00	Spring 01	
Total cover	P	0.0136*	0.001**	0.0378*	0.0242*	0.0604	0.0123*	0.0933	none
	$F_{7,35}$	3.02	4.57	2.44	2.69	2.18	3.08	1.93	
Volume	P	0.0013***	0.0007***	0.0038**	0.0011**	0.0039**	0.0038**	0.0032**	none
	$F_{7,35}$	4.41	4.86	3.77	4.56	3.75	3.77	3.87	
Shrub cover	P	0.0478*	0.038*	0.1734	0.0362*	0.1249	0.1408	0.1333	S
	$F_{6,30}$	2.45	2.6	1.63	2.63	1.84	1.76	1.8	
Volume	P	0.0659	0.0399*	0.1482	0.0544	0.1392	0.1359	0.1166	S
	$F_{6,30}$	2.24	2.56	1.73	2.37	1.77	1.79	1.88	
Succulent cover	P	0.1633	0.1778	0.0963	0.0586	0.1557	0.0825	1077	succ
	$F_{6,30}$	1.67	1.61	2	2.32	1.7	2.1	1.93	
Volume	P	0.1563	0.1943	0.1069	0.0593	0.1256	0.0753	0.1146	succ
	$F_{6,30}$	1.7	1.56	1.94	2.31	1.84	2.16	1.89	
Subshrub cover	P	0.1859	0.3808	0.0984	0.0582	0.1421	0.0868	0.0236*	SSh
	$F_{6,30}$	1.58	1.11	1.99	2.32	1.76	2.07	2.9	
Volume	P	0.2446	0.414	0.1502	0.0434*	0.2403	0.0982	0.0376*	SSh
	$F_{6,30}$	1.41	1.05	1.72	2.51	1.42	1.99	2.6	
Per. grass cover	P	0.1816	0.0733	0.0912	0.0011**	0.0014**	0.0073**	0.0154*	PG
	$F_{6,30}$	1.67	2.18	2.04	5.04	4.89	3.68	3.19	
Volume	P	0.0284*	0.0153*	0.0726	0.0009***	0.1131	0.0015**	0.007**	PG
	$F_{6,30}$	2.78	3.19	2.18	5.23	1.9	4.82	3.72	
Forb cover	P	0.066	0.324	<.0001***	0.4076	0.231	0.5543	0.0065**	none
	$F_{7,35}$	2.13	1.21	6.35	1.06	1.41	0.85	3.45	
Volume	P	0.0091**	0.2028	0.0001***	0.5886	0.4313	0.3645	0.0109*	none
	$F_{7,35}$	3.25	1.49	5.97	0.81	1.03	1.13	3.15	
DAPU cover	P	0.0002***	<0.0001***	<0.0001***	<0.0001***	<0.0001***	<0.0001***	0.0003***	PG, simp
	$F_{5,25}$	7.81	12.02	10.22	20.91	22.62	11.43	7.13	
Volume	P	<0.0001***	<0.0001***	<0.0001***	<0.0001***	<0.0001***	<0.0001***	0.0025**	PG, simp
	$F_{5,25}$	9.4	8.52	9.49	18.73	17.54	10.35	5.05	
BAAB cover	P	.	0.0016**	0.0003***	0.0017**	.	.	.	none
	$F_{7,35}$	.	4.3	5.34	4.26	.	.	.	
Volume	P	.	0.0011**	0.0002***	0.0031**	.	.	.	none
	$F_{7,35}$	.	4.52	5.63	3.9	.	.	.	
DEPI cover	P	.	.	<0.0001***	.	.	.	0.0011**	none
	$F_{7,35}$	.	.	10.69	.	.	.	4.53	
Volume	P	.	.	<0.0001***	.	.	.	0.0028**	none
	$F_{7,35}$	.	.	9.16	.	.	.	3.95	
ERDI cover	P	.	.	<0.0001***	.	.	.	.	none
	$F_{7,35}$	.	.	8.67	.	.	.	.	
Volume	P	.	.	<0.0001***	.	.	.	.	none
	$F_{7,35}$	.	.	8.88	.	.	.	.	

season to season is greater than many differences among treatments within a season. Because large woody plants dominate community response, total mean perennial plant cover and volume show trends similar to total plant cover and volume, but peaks are lower in the most productive seasons when high annual forb abundance adds considerable cover and volume.

Those treatments involving the removal of the dominant shrub had not recovered (in biomass) from initial disturbance after five years. Plant volume remained significantly lower for the shrub removal ($p = 0.0067$) and *Larrea* reduction treatments ($p = 0.0108$) than the control in fall 1999, the year of maximum plant cover and volume (Fig. 4). Cover, however, had recovered to a greater extent even in the more extreme removal treatments. Increased forb and grass cover had partially compensated for the loss of perennial species. Variability of the control plots, as well as some of the treatments, was high.

Species richness (the number of species present per plot) varied by season and by treatment within a given season. Richness of the perennial species followed expected differences given the treatment manipulations (although this was not tested statistically as it is an artifact of the treatment manipulations). That is, the simplified treatment plots had the lowest total perennial richness with only four species present and control plots had the highest richness with approximately 10 perennial species (Fig. 5a). Herbaceous richness (including forbs and annual grasses) was similar in all treatments except in spring 2000. Differences were not detected even in fall 1999 when forb cover and volume was at its peak and forb richness averaged 14 species per treatment (Fig. 5b). In spring 2000, forb richness was significantly lower in the control and perennial grass removal with only 2 species present in each of those treatments, than in the shrub removal ($p < 0.0001$) where 6 species were encountered.

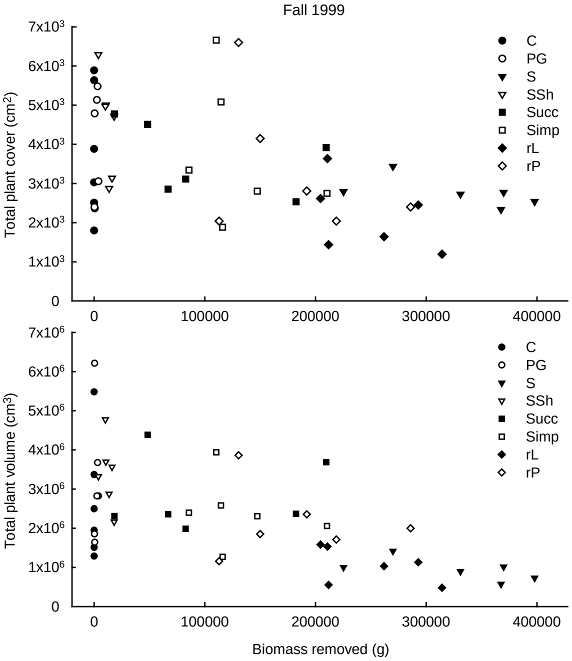


Fig. 4. Total plant cover and volume by plot and treatment plotted against biomass removed. Treatment abbreviations as in Table 1.

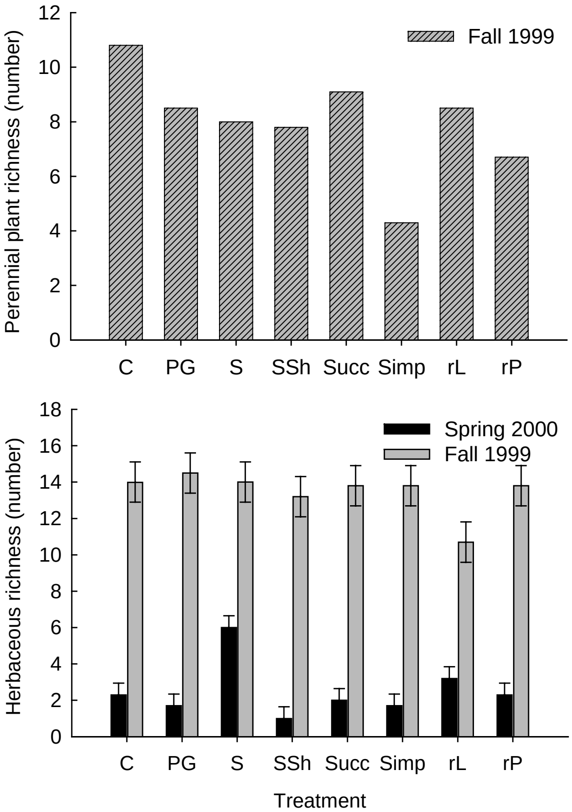


Fig. 5. (a) Perennial plant richness by treatment in fall 1999 and (b) mean forb richness (±se) by treatment in fall 1999 and spring 2000. Treatment abbreviations as in Table 1.

Functional group response

Functional groups and the species within functional groups varied in their response to treatments (Table 2). Cover and volume responses were similar in most cases. By fall 1999, shrub cover and volume were similar in all treatments except the *Larrea* reduction, and in all subsequent seasons there were no differences evident among any of the treatments (Table 2, Fig. 6a). Shrub volume is presented rather than cover because volume for such a tall growth form is more highly correlated with biomass than cover. *Prosopis* was the second most abundant shrub in all treatments where it was not removed; there were no significant differences in *P.*

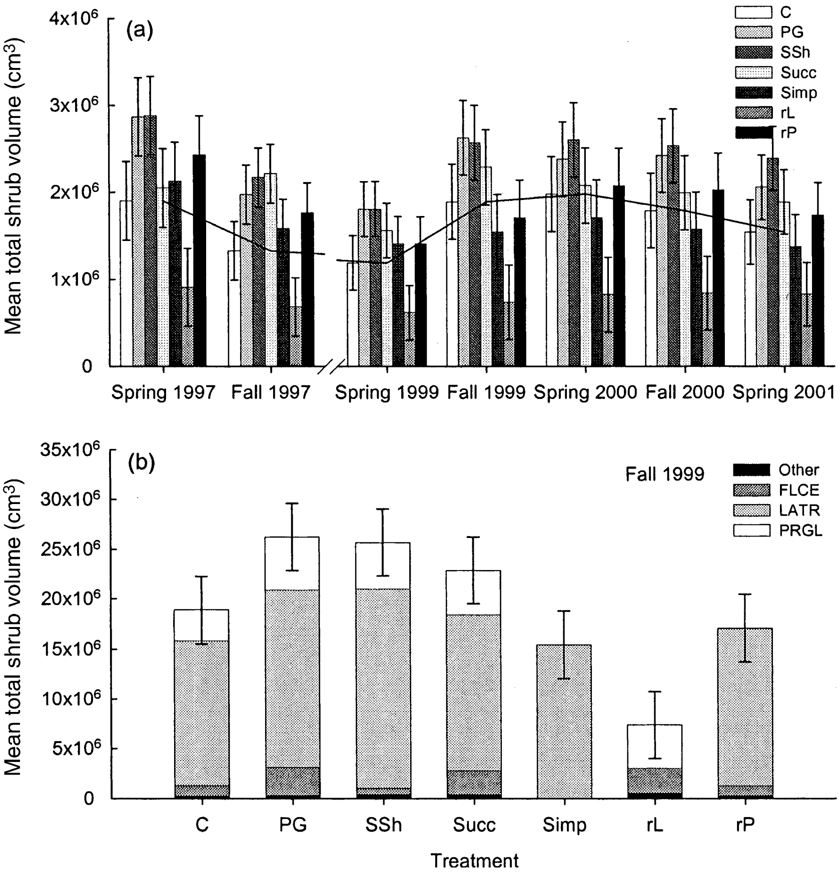


Fig. 6. (a) Mean total shrub volume (±se) by treatment across time; line shows trend in volume over time for control, and (b) mean total shrub volume (±se) by treatment displayed by species in fall 1999. FLCE = *Flourensia cernua*, LATR = *Larrea tridentata*, PRGL = *Prosopis glandulosa*. Treatment abbreviations as in Table 1.

glandulosa volume among treatments, meaning that it had not responded positively to plant removals (Fig. 6b).

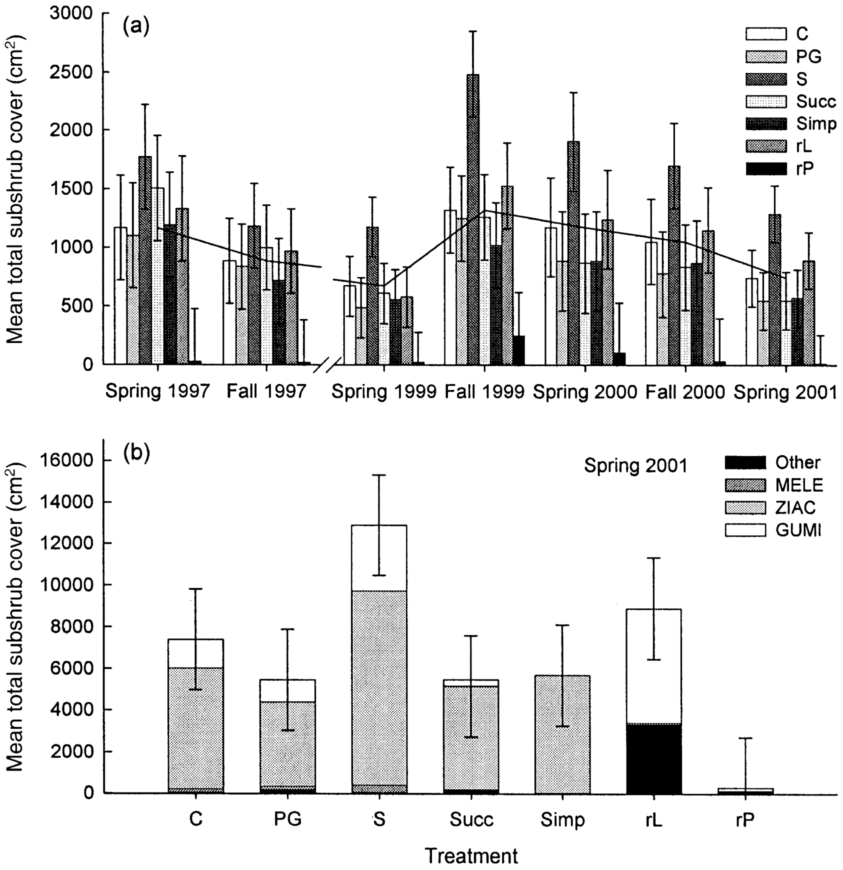
Succulent cover and volume were similar in all treatments in every season (Table 2). *Opuntia violacea* (more recently recognized to include both *O. macrocentra* and *O. santa-rita*), the second most abundant succulent, did not respond to the removal of the dominant succulent, *Yucca baccata.*

Differences among treatments in subshrub volume first appeared in fall 1999 (Table 2) with significantly more subshrubs in the shrub removal treatment compared with the perennial grass removal ($p = 0.0261$, Fig. 7a). By spring 2001, differences in both subshrub cover and volume were greater with virtually no subshrubs present in the *Prosopis* reduction (rP) and continued high abundance of subshrubs, primarily the dominant *Zinnia acerosa*, in the shrub removal treatment (Fig. 7b). Subshrub cover was significantly higher in both the *Larrea* reduction (even though a subset of the original subshrub cover was removed from this treatment) and control treatments than in the *Prosopis* reduction ($p = 0.0109$ and $p = 0.0321$ respectively).

While *Gutierrezia microcephala* cover and volume did not differ significantly among the treatments (except in spring 2001), there was virtually none present in the *Prosopis* reduction plots even though this subshrub was not targeted for removals. In spring 1997 cover and volume of *Gutierrezia* in *Prosopis* reductions equaled zero and had increased and decreased again over time to only one tenth the amount present in the controls by 2001. In contrast, in spring 2001 there was significantly more *Gutierrezia* in the *Larrea* reduction treatment than in the control ($p = 0.0188$).

Perennial grasses were the most responsive functional group to treatment removals (Table 2). Grass cover and grass volume differed in pattern of response (Fig. 8, 9). By fall 1999 (through to fall 2000), perennial grass cover was significantly higher in the shrub removal plots than in the controls ($p = 0.0012$, Fig. 8a). Perennial grass cover was significantly higher in the reduction treatments than in the simplified treatment in fall 2000 ($p = 0.0307$). However, perennial grass volume was greater in the simplified treatment than in the reductions ($p < 0.0001$), though only a single perennial grass species, *Muhlenbergia porteri*, was present in that treatment (Fig. 9a). Perennial grass volume was also greater in the control than the reduction treatments ($p = 0.0454$ and $p = 0.0207$, Fig. 9b); thus the intermediate functional group richness treatments (rL and rP) had lower perennial grass volume than both the high functional

Fig. 7. (a) Mean subshrub cover (±se) by treatment across time; line shows trend in cover over time for the control, and (b) mean total subshrub cover (±se) by treatment displayed by species in spring 2001. MELE = *Melampodium leucanthum*, ZIAC = *Zinnia acerosa*, GUMI = *Gutierrezia microcephala.* Treatment abbreviations as in Table 1.



group richness (C) and low functional group richness (Simp) treatments. The pattern began to change by spring 2001 with perennial grass cover/volume declining in all treatments, although differences were still significant.

Analysis by species (Fig. 8b) shows that *Dasychloa pulchella*, a low growing short-lived perennial grass, was the most responsive grass to treatment removals, increasing substantially in the shrub removal and *Larrea* reduction plots. The increase in cover for *Dasychloa* was not reflected proportionally in volume because of the small stature of this species (Fig. 9b). The dominant grass, *M. porteri*, a bushy perennial grass often growing up through shrubs, did not respond to removals in any treatment or season. Interestingly, no grasses other than *D. pulchella* were observed in the *Prosopis* reductions even though *M. porteri* was the only grass removed during treatment imposition and seven other species were present in other treatments.

Forb abundance is highly dependent on climatic conditions; the adequacy of our sampling for forbs also depended on climatic conditions, as the 45 m^2 sampled in each plot might be too little for accurate sampling of sparse annual vegetation. Nonetheless, it appeared that forb response to removals varied by treatment and by year. In four individual seasons, conditions were sufficiently favorable to measure forb response to treatment removals (Table 2). In spring 1997, forb volume in the shrub removals was significantly greater than in control ($p = 0.0038$) and perennial grass removals ($p = 0.0227$). In spring 1999 (Fig. 10a) and 2001, forb cover/volume was again greater in the shrub removal treatment than in control and perennial grass removals ($p < 0.0001$). However, in fall 1999 when plant cover and volume reached a peak, no differences were observed between treatments. In addition, spring 1999 and spring 2001 forb data indicate the treatment with the greatest diversity of functional groups, the control, had the lowest forb cover and volume, while the treatment with the lowest species richness, the simplified, had the highest forb volume (and cover in spring 1999).

Response of individual forb species was also highly variable. Individual forb species were selected for analysis based on known responsiveness to disturbance or relative dominance among the forb species represented. *Descurainia pinnata*, an annual spring forb, is known to favor disturbed ground (Correll and Johnston 1970, Allred 2000). *Descurainia* cover/volume increased significantly in the shrub removal and simplified treatments in spring 1999 ($p < 0.0001$) and again in the shrub removal in spring 2001 ($p = 0.0063$; Fig. 10c). *Descurainia* cover was also greater in the shrub removals than

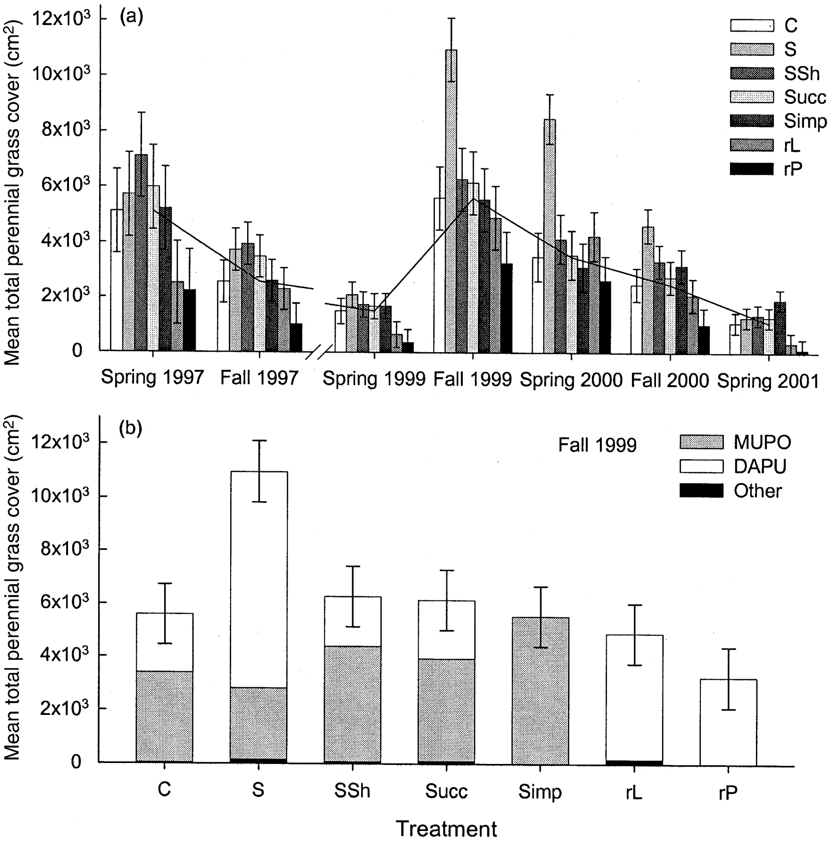


Fig. 8. (a) mean perennial grass cover (±se) by treatment across time; line shows trend in cover over time for the control, and (b) mean perennial grass cover (±se) by treatment displayed by species for fall 1999. MUPO = *Muhlenbergia porteri*, DAPU = *Dasyochloa pulchella.* Treatment abbreviations as in Table 1.

in the perennial grass removals in both years ($p = 0.0007$). *Eriastrum diffusum*, a small but abundant annual forb, showed the same trends as *Descurainia* in spring 1999 and 2000 ($p < 0.0001$). *Bahia absinthifolia*, an often dominant perennial forb, also showed similar responses. *Bahia* increased in the shrub removal and simplified treatments in fall 1997 and spring and fall 1999 and in the *Larrea* reduction in spring 1999 (Fig. 10b). As seen with total forb cover, *Bahia* and *Descurainia* cover were lower in the control than in treatments with lower functional group richness (rL, rP, and Simp). Despite the large number of forbs present in many seasons, no other forbs selected for analysis consistently responded to treatment removals.

Summary of responses to removals

Functional groups and/or species did not respond to the removal of perennial grass species after five years. The removal of shrubs, however, resulted in numerous responses, although responses were not always consistent across sampling seasons (Table 2). Forb cover, volume, and richness increased with the removal of shrubs. Individual forb species, such as *D. pinnata*, *B. absinthifolia* and *E. diffusum*, increased both cover and volume in response to removals. Perennial grass cover, in particular *Dasychloa pulchella*, also increased in response to the removal of shrub species. While these responses were strong, total cover and volume had not recovered from the initial removal of shrub biomass in this removal treatment. We did not observe any response to either subshrub or succulent removals.

Response to our highly simplified community with only one species present in each of the four major functional groups (Simp) was seen only with forbs. Forb cover/volume increased in response to the simplified treatment; in particular *Descurainia* and *Bahia* responded favorably. Response to our reduced communities, where dominants were removed from each functional group (rL and rP), was generally similar. Forb cover and volume, particularly of *Descurainia*, increased in the reduced-*Prosopis* reduction. Cover/volume of the forb *Bahia* and the perennial grass *Dasychloa* increased in the reduced-*Larrea* reduction. As with the shrub removals, the reduced-*Larrea* treatment had not recovered from the initial removal of the *L. tridentata* biomass. In most respects, the reduced-*Prosopis* treatment behaved much like the Simplified treatment (e.g. in total plant volume, shrub volume, or perennial grass cover). However, the difference in subshrub response between these two treatments, and between the two reduced treatments, was striking. The

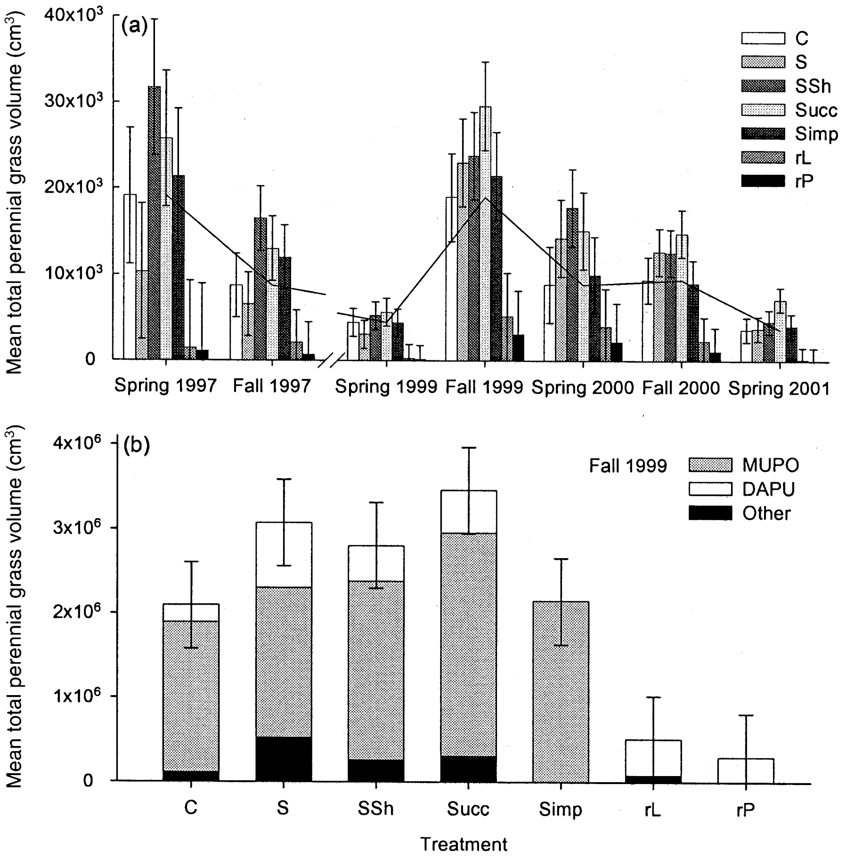


Fig. 9. (a) mean perennial grass volume (±se) by treatment across time; line shows trend in cover for control, and (b) mean perennial grass volume by treatment displayed by species for fall 1999. MUPO = *Muhlenbergia porteri*, DAPU = *Dasyochloa pulchella*. Treatment abbreviations follow Table 1.

reduced-*Larrea* treatment had subshrub cover (and volume) as great as that in the control and in the simplified treatment, though of course the species composition was different. However, the reduced-*Prosopis* treatment plots had very low subshrub cover and volume, even though the same species were present initially as in reduced-*Larrea.* It is not the presence of *Larrea* that prevents a positive response by *Gutierrezia* or other subshrubs; further examination of species-specific interactions with *Prosopis* would seem to be in order.

Even over five years, there were very few cases of a perennial species establishing within a plot where it had previously been absent. This was true even for perennial grasses with abundant populations elsewhere in the experimental area.

Discussion

In semi-arid ecosystems around the globe, there are processes acting to reduce diversity or to eliminate species (Huenneke and Noble 1996, Chapin et al. 2001). We have chosen a management-oriented definition of functional group, based on architectural types rather than resource use or environmental responses, and many of our treatments replicate common rangeland management approaches. Removal of shrubs to stimulate grass production, removal of the "weedy" subshrub *Gutierrezia*, and succulent harvesting, are all management approaches to range rehabilitation, and all result in the loss of species and often functional groups (Holechek et al. 1998). In these relatively species-poor systems (Shmida 1985), further reduction of species number could be a threat to system function and stability. A more immediate and tangible issue, though, is that of response. When there are relatively few biotic components in the system, which (if any) have the potential to respond positively? Do management-oriented removals (e.g. brush removal in rangelands) actually free up resources to be used by the remaining vegetation?

If so, we would expect an increase in cover or volume of the remaining functional groups relative to the controls. Yet, in general, few such positive responses were observed. Despite substantial removal of plant material, we observed no new species entering treatments. Only a few herbaceous and/or short-lived species appeared to exhibit any positive recruitment response. Shrubs and succulents have been virtually incapable of responding during a five year period. Chihuahuan desert shrublands are dominated by long-lived perennial species, and therefore recovery from disturbances often

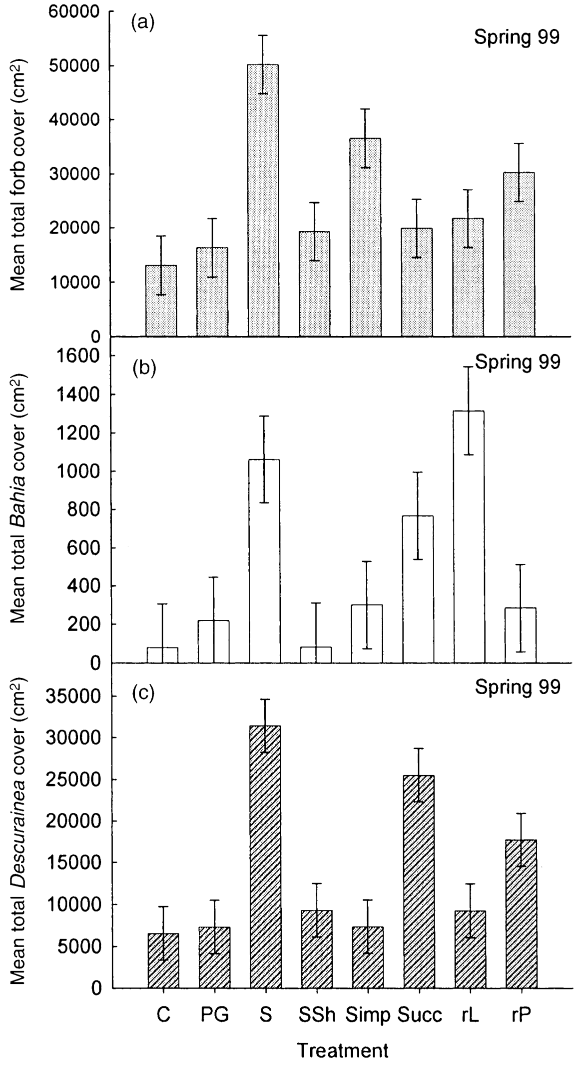


Fig. 10. (a) Mean total forb cover (±se) by treatment in spring 1999, (b) mean total *Bahia absinthifolia* cover (±se) by treatment in spring 1999, and (c) mean total *Descurainia pinnata* cover (±se) by treatment in spring 1999. Treatment abbreviations follow Table 1.

takes decades. Community response to even intense removals from this system might take just as long to develop. In particular, removal of the dominant shrub, *Larrea*, represents the most extreme of our treatment manipulations and the remaining plant community had not yet fully recovered from such an extensive loss of biomass. Recruitment processes are slow and increased growth may be limited by environmental conditions. Goldberg and Turner (1986) found a very slow turnover of long-lived populations of individual woody and succulent plants over a 72 year study in the Sonoran desert and limited ability to recover from disturbance due to infrequent recruitment years. Miller and Huenneke (2000) likewise found that *L. tridentata* did not respond to a thinning study where neighboring *L. tridentata* individuals were removed and hypothesized that extending the time-frame of the study might lead to different results. A long term study in the vicinity of the current study in the Jornada Basin (Havstad et al. 1999), looking at the influences of shrub removal and lagomorph exclusion on vegetation dynamics, found no plant community responses to shrub removal after 30 years.

Rather than indicating that the physical environment is constraining these species, however, we believe the lack of initial response in our experiment shows that woodiness, long life-span, and slow growth rates are negatively correlated with the ability to respond to plant removal or other perturbations. We might predict similar constraints in community response to disturbance in other ecosystems where the same plant traits dominate (e.g. low-fertility habitats). MacGillivray et al. (1995) did a careful assessment of a number of physiological traits, and documented that a suite of plant traits correlated with nutrient stress tolerance was negatively associated with the rate of recovery (resilience) after major disturbance events. Similar characteristics of growth rate, nutrient use physiology, and so forth may be limiting the ability of the woody and succulent species in our experiment to respond to community perturbation.

In contrast, short-lived perennials and annual forbs have been able to respond to losses of functional groups and functional group richness in the relatively short time-frame since initiation of the experimental treatments. Subshrubs, to a limited extent, and perennial grasses have been able to respond to removals. Results indicate that subshrubs responded to the removal of *Larrea*. Grasses responded to the removal of all shrubs, but this trend was driven by the response of one grass in particular, *Dasychloa*. The species is capable of high recruitment by seed in favorable years and thus could take advantage of increased soil moisture in the uppermost soil layers and/or increased amounts of bare soil (open space). Havstad et al. (1999) also found species-specific grass response to shrub removals in a long-term study in the Chihuahuan desert; however, responses were not detected until 50 years after initial removals. In contrast, in the Patagonian Steppe, Sala et al. (1989) found that grasses did not respond to shrub removals, suggesting reliance on different resources (particularly water) by the different functional groups. While some grasses did respond in our system, we did not see a reciprocal response by the shrubs; shrubs did not respond to grass removal. If shrub removal resulted in increased water availability in shallow soil layers accessible to the grasses, it is difficult to understand how grass removal would fail to increase water availability to shrubs. Alternatively, short-lived grasses and forbs may be responding to increased soil disturbance in the shrub removal treatment or to increased nutrients available from decaying root material, rather than responding to a release from competition for soil water or nutrients. This explanation is more consistent with the non-symmetric and species-specific responses we observed.

Responses to the richness-within-functional group manipulations were similar, with only short-lived species capable of responding after five years. Forbs responded most to the lowest within-functional group richness treatment (Simp) and least to the highest within-functional group richness treatment. However, forbs and *Dasychloa* did not respond to the two intermediate richness treatments (rL and rP) in the same way. Our results were idiosyncratic with no clear response patterns to diversity level.

In the first five years we have not observed any significant examples of removals triggering further species losses in this system. There are some indications that subshrub cover has decreased in the *Prosopis* reduction treatments, particularly *Gutierrezia*. However, a longer sampling period is required to determine whether this trend continues. On the other hand, removals have not facilitated any invasions by new species, either native or introduced. Even these large perturbations do not appear to open 'windows' for rapid compositional change.

In addition, interannual variation in climate functions as an important influence and constraint to recovery in this system. We found that differences between years were greater than differences between treatments in some comparisons. Perennial grasses were able to take advantage of favorable growing conditions during the first few years after treatment manipulations and high levels of recruitment were witnessed for some species. In less favorable conditions, results may have differed. Morton and Melgoza (1991) found that grasses were able to respond to differing shrub removal treatments only in years with above-average precipitation; in below-average precipitation years, grasses were negatively affected by shrub removal treatments. Briones et al. (1998) found that competition could be absent or reduced in low precipitation years and high in years with abundant precipitation. In our study, low rainfall years resulted in low forb numbers; in seasons with large forb numbers, differences between treatments were not detected. Species and community composition responses varied, but our experiment may not have been running long enough to encounter the full range of climatic variation possible, and therefore we have not completely eliminated the possibility that either competition or facilitation are, at times, important drivers in this system.

Decadal-scale variation in climate is substantial in the semi-arid southwest, and we have not yet observed the response of our experimental systems to all typical conditions. Slow or subtle responses, episodic recruitment events, or occasional die-off events might all be important (Watson et al. 1997); yet all require long observational periods to detect. In the short term, though, neither competition nor facilitative interactions among functional groups (or among species within functional groups) appear to drive rapid responses in this system.

In conclusion, we observed very limited responses of plant community components to our removals in this semi-desert shrubland – no establishment of new species, few positive responses of remaining species, and few negative responses. Those positive responses observed are more consistent with a hypothesis of disturbance than resource competition among functional groups. Plant traits (woodiness, growth rate, lifespan) appear to be important limits on the system's response to disturbance. This Chihuahuan Desert shrubland demonstrates considerable resistance in the face of substantial perturbation, but resistance also represents severe constraints on the rate of system recovery.

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References

Aguiar, M. and Sala, O. E. 1994. Competition, facilitation, seed distribution, and the origin of patches in a Patagonian Steppe. – Oikos 70: 26–34.

Allred, K. W. 1993. A field guide to the grasses of New Mexico, Dept of Agric. Communications. – New Mexico State Univ.

Briones, O., Mantana, C. and Ezcurra, E. 1998. Competition intensity as a function of resource availability in a semiarid ecosystem. – Oecologia 116: 365–372.

Buffington, L. C. and Herbel, C. H. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. – Ecol. Monogr. 35: 139–164.

Chapin III, F. S., Sala, O. E. and Huber-Sannwald, E. 2001. Global biodiversity in a changing environment: scenarios for the 21st century. – Springer-Verlag.

Correll, D. S. and Johnston, M. C. 1970. Manual of the vascular flora of Texas. – Texas Research Foundation.

Díaz, S., Symstad, A., Chapin III, F. S. et al. 2003. Functional diversity revealed by removal experiments". – Trends Ecol. Evol. 18: 140–146.

Goldberg, D. E. and Turner, R. M. 1986. Vegetation change and plant demography in permanent plots in the Sonoran desert. – Ecology 67: 697–712.

Havstad, K. M., Gibbens, R. P., Knorr, C. A. et al. 1999. Long-term influences of shrub removal and lagomorph exclusion on Chihuahuan Desert vegetation dynamics. – J. Arid Environ. 42: 155–166.

Holechek, J. L., Pieper, R. D. and Herbel, C. H. 1998. Range management: principles and practices. – Prentice Hall.

Huenneke, L. F. and Noble, I. R. 1996. Ecosystem function of biodiverslty in arid ecosystems. – In: Mooney, H. A., Cushman, E. M., Sala, O. E. et al. (eds), Functional roles of biodiversity: a global perspective. Wiley and Sons, pp. 99–128.

Huenneke, L. F., Clason, D. and Muldavin, E. 2001. Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. – J. Arid Environ. 47: 257–270.

Louw, G. N. and Seely, M. K. 1982. Ecology of desert organisms. – Longman.

MacGillivray, C. W., Grime, J. P. and the Integrated Screening Programme (ISP) Team. 1995. Testing predictions of resistance and resilience of vegetation subjected to extreme events, Funct. Ecol. 9: 640–649.

Miller, R. E. and Huenneke, L. F. 2000. Demographic variation in a desert shrub, *Larrea tridentata*, in response to a thinning treatment. – J. Arid Environ. 45: 315–323.

Morton, H. L. and Melgoza, A. 1991. Vegetation changes following brush control in creosotebush communities. – J. Range Manage. 44: 133–139.

Noy-Meir, I. 1979. 80. Structure and function of desert ecosystems. – Isr. J. Bot. 28: 1–19.

Pugnaire, F. I., Haase, P. and Puigdefabregas, J. 1996. Facilitation between higher plant species in a semiarid environment. – Ecology 77: 1420–1426.

Raffaelli, D. and Moller, H. 2000. Manipulative field experiments in animal ecology: do they promise more than they can deliver? – Adv. Ecol. Res. 30: 299–338.

Sala, O. E., Golluscio, R. A., Lauenroth, W. K. et al. 1989. Resource partitioning between shrubs and grasses in the Patagonian Steppe. – Oecologia 81: 501–505.

SAS Institute Inc. 1989. SAS/STAT users guide. – SAS Institute Inc.

Shmida, A. 1985. Biogeography of the desert flora. – In: Evenari, M., Noy-Meir, I. and Goodall, D. W. (eds), Hot deserts and shrublands. Elsevier Science Publishers B. V, pp. 23–72.

Vitousek, P. M. 1994. Beyond global warming: ecology and global change. – Ecology 75: 1861–1876.

Watson, I. W., Westoby, M. and McR. Holm, A. 1997. Continuous and episodic demographic change in arid zone shrubs: models of two *Eremophila* species from western Australia compared with published data on the species. – J. Ecol. 85: 833–846.

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