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Community structure of a southern Chihuahuan Desert grassland under different grazing pressures

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Abstract

The effect of different grazing intensities on the semiarid grasslands of the southern Chihuahuan Desert was studied using a fence-line contrast between a moderately grazed cattle ranch, from which goats and sheep had been excluded for forty-five years, and an ejido, heavily overgrazed for at least the last century. Each plant species density and cover was quantified in three distinctive microhabitats on the ranch and on the adjacent common-use rangelands. The results indicated that three grass species were important in the dynamics of this rangeland. *Hilaria belangeri*, a stoloniferous, mat-forming grass species, was dominant on the heavily grazed ejido but is in the process of being replaced by two taller grasses, *Bouteloua gracilis* and *Bouteloua curtipendula*, on the more moderately grazed ranch. These data suggest that the dynamics of this system in the semiarid grasslands of the southern Chihuahuan Desert are based primarily on two functional groups of species. Members of the first functional group are stoloniferous and clonal. Their growth form slows the rate of surface water movement, thereby controlling erosion while building up the soil by entrapping debris. In contrast, the second functional group is comprised of non-stoloniferous grasses that are described variously as bunch, tufted or tussock grasses in the literature. These species have the capacity to invade, overtop and replace individuals of the first functional group. They are limited in their lateral growth by their rhizomatous growth habit, which is much less efficient in co-opting space. Finally, there is, at least, a third functional group of much taller grasses present that are limited in these rangelands to refuges by the heavy grazing. These species are usually obligate seed producers. Such species have the potential to replace members of the earlier functional groups by overtopping them. They are limited by their inability to reproduce vegetatively, once established by their seed bank. This research suggests that restoration of the heavily eroded, semiarid grasslands of the southern Chihuahuan Desert must begin with the re-establishment of members of the first functional group. These species have the ability to facilitate the entry of the later functional groups and, in turn, be replaced competitively by them.

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1. Introduction

The dynamics of multi-species communities of grasses and their associates are often difficult to interpret. This is because large differences between the density, cover and the individual plant sizes of their component species occur that are dependent upon their previous history in ecological and evolutionary time, their responses to macro- and micro-environmental gradients, inter-specific competition and, each species' palatability and

tolerance of grazing. The dynamics of simple communities of perennial grasses (2–5 species), such as those forming on the sides of sand dunes in the Namib Desert of southwestern Africa, are relatively easy to explain because the gradients are not complex and are characterized by increasing rainfall events from west to east across the dune fields, which increase vegetative cover. As a consequence, the increased plant cover along this geographical gradient reduces the rates of sand movement on individual dune-slopes from west to east, enabling more grass species to successfully establish on their sides (Yeaton, 1988). In more complex communities, such as those found in the savannas of northeastern South Africa, grass

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species also respond to simple environmental gradients, such as the series of soil types that occur from the edge of a riverside flood plain upslope to the top of the ridge (Yeaton et al., 1986). However, these grass species also experience and respond to a complex of other environmental factors, in addition to the moisture gradient from the river to the upper slopes. These factors include a sun-shade gradient caused by the presence of trees in the savanna grassland (i.e. open sites, partially shaded sites to the north of the tree, more heavily shaded areas to the south of the tree's canopy), areas disturbed by the burrowing of large communal animals (e.g. the warthog, *Phacochoerus aethiopicus*, where the size of their excavation around their den provides a relative measure of the length of time the site has been occupied), and the frequency of fire (e.g. protected sites, annual burns, or five-year burns imposed by management) that an area experiences (Yeaton et al., 1986, 1988).

The problems with studying the dynamics of grasslands in the southern Chihuahuan Desert are more difficult. There, the previous land-use history of an area is largely unknown, due mainly to the region having been exploited as common-use rangelands (hereafter referred to as “ejidos”) by the descendants of the original workers on the haciendas (i.e. ranches) for the last ninety-five years after the Mexican Revolution (García-Ugarte, 1992; Silva-Herzog, 1998). These rangelands have been severely overgrazed by domestic livestock (La Baume and Dahl, 1986) and currently have a large component of invasive shrubs, cacti and trees. Initially, this grazing would have been in the form of selective foraging, which in many cases can affect the spatial distribution of the vegetation (Adler et al., 2001) and the distributional patterns of species (Fowler, 2002). In addition, the grass species composition of the region is complex, consisting of a mixture of grasses, from various geographical sources (i.e. southwestern, southeastern and northwestern North America; Brown and Gersmehl, 1985; Brown, 1993). Many of these grass species may be functionally equivalent in their ecological roles in the development of the structure and function of grassland. One such example would be the short, stoloniferous grasses; *Cyclostachya stolonifera*, *Buchlōe dactyloides*, *Hilaria belangeri*, which form clones that appear to stabilize the soil and provide sites for the establishment of taller clump-grass species, such as *Bouteloua gracilis* in the southern end of the Chihuahuan Desert. In order to begin to understand the dynamics of these grasslands and the role that functional groups of species play, a fence-line contrast approach was used. The density, cover and relative abundance for each plant species present in three distinctive sub-habitats within an area, moderately grazed by cattle for the last 45 years, were compared with those of the adjacent common-use rangelands, which had been heavily grazed by goats, sheep, horses and cattle over the same period.

2. Study area and methods

The study areas are located on a 2 km-long, southeast-facing, 3–4° slope at approximately 2200–2300 m elevation on the privately-owned ranch, Laguna Seca, and on the adjacent ejido, Vicente Guerrero. These sites are approximately 35 km north of

Charcas, San Luis Potosi (23° 07'N; 101° 07'W). Temperatures at the nearest long-term recording weather station in Charcas (2020 m), averaged over the period 1962–1997 were for annual maximum, 23.3 °C, and for annual minimum, 8.6 °C, (García, 1973; Garcia, unpublished data). The highest monthly average temperature recorded during this period was 39 °C in March of 1967 and the lowest monthly average temperature was –9 °C in January of the same year (García, 1973). Average annual relative humidity during the period is not available. Rainfall in this area averages 411 mm (±203 mm) per year, with annual extremes 165 mm (1982) and 897 mm (1976) (García, 1973). The peak rainfall months are June (70 mm) and September (71 mm). The soils are derived from Cretaceous limestone rocks. They are shallow (80–100 cm deep), have a silt/loam texture, and are ochre in color due to the acidic soil moisture regime. Under the FAO–UNESCO system of soil classification, they are classified as xerosols or cambisols (INEGI, 2002). The climate and the soils support a semi-arid, short-grass prairie with scattered, small (<6-m tall) individuals of *Yucca filifera* and *Acacia schaffneri* (Rzedowski, 1994).

Historically, the site on the ranch, Laguna Seca, has been separated since 1960 from the ejido, Vicente Guerrero, by a fence that excludes grazing by goats, sheep and other livestock (H.N. Silva G., pers. comm.). After an initial period of experimentation with various cattle breeds (Creole from 1960–1970, Swiss/Cebu cross from 1970–1985), Beefmasters' have grazed Laguna Seca. The stocking rate during the 45 years of exclusion of goats and sheep has been maintained at 0.63 cattle per hectare on the 8000 ha ranch. The grazing history of the ejido is unknown but, since the Mexican Revolution of 1910 until the fencing of the ranch in 1960, the area was common-use rangelands, with annually varying but high numbers of goats and sheep, mixed with lesser numbers of cattle and horses. The Vicente Guerrero study site is 5000 ha in size and is grazed currently by two tended, transient herds of approximately 200–300 goats and 10–20 sheep. In addition, two-to-four groups of free-ranging cattle and horses regularly use the ejido study site (group sizes 2–6 animals).

The goat- and sheep-proof fence, separating Laguna Seca from Vicente Guerrero, passes almost directly down-slope between the two areas. Three sets of sub-habitats were studied on each side of the fence along this slope-angle gradient. These sub-habitats consisted of open areas on the lower slope, open areas on the upper slope, and partially shaded, north-facing sites under the canopies of *A. schaffneri* on the lower and middle sections of the slope. All areas sampled were on sections of the slope-angle gradient where no gullies, running transversely to the fence, were present to interrupt surface drainage down the slope. Finally, to minimize fence-line grazing and trampling effects, all transects were located at least 20 m from the fence. The sub-habitats were selected because they represented different microenvironments within which plant species' responses could be evaluated. Open sites on the lower slope receive relatively more effective rainfall than open areas on the upper slope due to run-on and subsurface drainage from the upper slope. Sites under the north side of the canopy of *A. schaffneri* represented a more complex situation due to run-on from the upper slopes as well as shading, which would lower evapo-

transpiration in comparison to open sites. In addition, their soils may be higher in nutrients due to leaf-fall and nitrogen fixation under their canopies and, thus more productive (Knoop and Walker, 1985; Polley et al., 1997; Rossi and Villagra, 2003; Schade and Hobbie, 2005). Sample sizes for each open site consisted of ten randomly chosen, 5 m-long line transects. The number of samples for transects under the trees remained the same but, due to the diameters of the tree canopies and to maximize the effect of shading by the canopy, were 3 m in length, measured from the base of the trunk.

The identity of each plant intersected by a line transect was recorded and its length along its long axis (L) and its greatest width at right angles to the length (W) measured. Cover of each individual was calculated according to the formula for an ellipse, $\pi LW/4$. For the stoloniferous grass species, *B. dactyloides* and *H. belangeri*, plants not connected by ramets were measured as individuals. For those plants with interconnecting ramets, the size of the entire clone was measured. Species densities and cover were calculated using a plot-less vegetation sampling technique, the ellipse-intercept method (Stokes and Yeaton, 1994). In contrast to line- and point-intercept methods, the additional information provided by this technique (i.e. species densities and size distributions) is useful for interpreting vegetation differences and dynamics, which are not detectable by measures of species' covers alone. Inclusion of a species in the data analysis for each of the three pairs of sites sampled was determined as follows. The total densities and covers, measured at a site, were summed from the contributions made by each species present in the ten samples taken. Each species' total density and cover at a site was divided by these totals to obtain their relative density and cover. Following Yeaton and Esler (1990), a species was included as a member of the grassland community if it contributed 5% or more to the relative density or cover present in, at least one of either the Laguna Seca or Vicente Guerrero sub-habitats.

Means, standard errors and relative frequencies of plant densities and covers were calculated for each member of a community for the three pairs of matched sites. Two-sample t -tests were used to determine differences in plant densities and covers of the paired sites on Laguna Seca and Vicente Guerrero (Steel and Torrie, 1960). In addition, two-sample t -tests or one-way analysis of variance were used to determine differences between the different grazing regimes present on Laguna Seca or on Vicente Guerrero.

Finally, sizes of individuals of the two commonest grasses in the study, *H. belangeri* and *B. gracilis* were compared using χ^2 tests for 2×2 contingency tables, using Yates' correction (Siegel and Castellan, 1988) for the three pairs of sites. The size data for these two species were grouped as individuals $< 10 \text{ cm}^2$ and individuals $> 10 \text{ cm}^2$ in area, assuming that smaller individuals are, with some exceptions, generally seedlings and larger individuals represent older plants.

3. Results

3.1. Species composition

The numbers of species recorded, with at least 5% occurrence in density or cover, differed between open sites on

the lower slope (maximum of six species), open sites on the upper slope (maximum of fourteen species) and under the canopies of *A. schaffneri* (maximum of twenty-one species) (Table 1). Five species, four grasses and a succulent, were recorded on the lower, open sites on both the ranch and the ejido. On the open sites of the upper slope, nine species were present including six grasses, a sedge, a succulent and a woody shrub were present on both sides of the fence. The greatest differences in plant community composition occurred under the canopies of *A. schaffneri*. A maximum of eleven species were recorded on the ranch and on the ejido, respectively. These included eight grass species, a succulent (present at both sites), and two woody shrubs. The differences between the sites in grass composition in these shaded sites were the absence of *B. dactyloides* and *Leptochloa dubia* on the ranch and the absence of *Bouteloua hirsuta* on the ejido. There were no differences in the woody shrub species recorded on the two sites.

3.2. Plant density and cover

3.2.1. Comparison of sites under the same grazing regime

Only one species, *H. belangeri*, was recorded in all three habitat types on the ranch, Laguna Seca and the ejido, Vicente Guerrero (Table 1). This species decreased in density on the ranch from the lower open sites to the under-canopy sites of *A. schaffneri* and reached its lowest density on the upper open sites ($F_{2,27}=40.6$, $p<0.001$). The same pattern occurred on the ejido ($F_{2,27}=78.1$, $p<0.001$). The coverage of this species also followed the same pattern, decreasing from the lower open sites to the under-canopy to the upper open slopes for both the ranch and the ejido. On the ranch, plant cover for this species decreased continuously. The lower open sites were significantly higher than the upper open sites but neither open site was statistically different from the under-canopy sites ($F_{2,27}=7.7$, $p<0.005$). On the ejido, plant cover of *H. belangeri* was significantly higher on the lower open sites than on the other two sub-habitats studied there ($F_{2,27}=15.9$, $p<0.001$). However, no difference in plant cover for this species occurred between the under-canopy sites and the upper open sites on the ejido.

B. gracilis, the second most abundant species in the lower open transects on the ranch, was also a common species under the canopies of *A. schaffneri* on the ranch and was also recorded in the same two habitat types on the ejido. This grass species was significantly denser and had greater cover in the open habitat than in the shaded sites on the ranch ($t=6.6$, $p<0.001$ for density; $t=6.1$, $p<0.001$ for cover). The reverse was true for the ejido, where *B. gracilis* density and cover were greater in the shade than in the lower open sites ($t=2.2$, $p<0.05$ for density; $t=2.1$, $p<0.05$ for cover). Finally, another minor grass species, *Microchloa kunthii*, had a higher density in the lower open transects than in the shade of *Acacia* on the ejido ($t=3.4$, $p<0.005$).

3.2.2. Comparison of paired sites under different grazing regimes

Significant differences between the paired sites in density and cover were measured (Table 1). Densities for *H. belangeri*,

Table 1

Densities, cover and relative abundance of grasses and herbaceous species in three micro-sites of the moderately grazed ranch, Laguna Seca, and the heavily grazed adjacent ejido, Vicente Guerrero.

Lower-slope open sites						
Density (m ²)	Laguna Seca			Vicente Guerrero		
	Mean	S.E.	Relative abundance (%)	Mean	S.E.	Relative abundance (%)
Grasses and sedges						
<i>Hilaria belangeri</i>	25.40	1.80	51.8	42.50	2.59	71.7
<i>Bouteloua gracilis</i>	20.30	1.93	41.4	0.90	0.59	1.5
<i>Microchloa kunthii</i>	2.80	0.49	5.7	8.00	1.63	13.5
<i>Buchlœe dactyloides</i>	0.10	0.10	0.3	7.50	3.66	12.6
Non-grasses						
<i>Mammillaria</i> sp.	0.40	0.22	0.8	0.40	0.22	0.7
Cover (cm ² /0.1 m ²)	Mean	S.E.	Relative cover (%)	Mean	S.E.	Relative cover (%)
Grasses and sedges						
<i>Hilaria belangeri</i>	153.01	30.70	57.8	71.51	8.60	72.4
<i>Bouteloua gracilis</i>	105.14	11.04	39.7	1.96	1.29	2.0
<i>Microchloa kunthii</i>	2.73	0.80	1.0	5.04	1.38	5.1
<i>Buchlœe dactyloides</i>	0.31	0.31	0.1	14.93	7.07	15.1
Non-grasses						
<i>Mammillaria</i> sp.	3.53	1.97	1.4	5.37	3.08	5.4
Upper-slope open sites						
Density (m ²)	Laguna Seca			Vicente Guerrero		
	Mean	S.E.	Relative abundance (%)	Mean	S.E.	Relative abundance (%)
Grasses and sedges						
<i>Hilaria belangeri</i>	4.50	1.84	19.2	7.20	0.98	23.0
<i>Bouteloua curtipendula</i>	6.50	1.10	27.8	15.10	1.34	48.2
<i>Bouteloua scorpiodes</i>	0.70	0.33	3.0	2.40	0.85	7.7
<i>Aristida schideana</i>	4.50	1.24	19.2	0.80	0.61	2.6
<i>Lycurus phleoides</i>	2.30	0.84	9.8	1.20	0.42	3.8
<i>Bothriochloa barbinodis</i>	1.30	0.40	5.5	2.80	1.46	8.9
<i>Carex potosina</i>	1.80	0.85	7.7	0.80	0.33	2.6
Non-grasses						
<i>Mammillaria</i> sp.	0.20	0.20	1.9	0.20	0.13	0.6
<i>Comolina</i> sp.	1.60	0.76	6.8	0.80	0.33	2.6
Cover (cm ² /0.1 m ²)	Mean	S.E.	Relative cover (%)	Mean	S.E.	Relative cover (%)
Grasses and sedges						
<i>Hilaria belangeri</i>	32.36	16.98	10.8	21.10	4.75	17.5
<i>Bouteloua curtipendula</i>	75.64	16.73	25.3	68.06	10.38	56.5
<i>Bouteloua scorpiodes</i>	3.91	2.24	1.3	6.31	2.84	5.2
<i>Aristida schideana</i>	96.34	34.14	32.2	2.15	1.98	1.8
<i>Lycurus phleoides</i>	20.61	9.66	6.9	2.68	0.88	2.2
<i>Bothriochloa barbinodis</i>	21.76	8.75	7.3	8.68	4.26	7.2
<i>Carex potosina</i>	15.92	7.89	5.3	2.04	0.69	1.7
Non-grasses						
<i>Mammillaria</i> sp.	11.57	11.57	3.9	8.23	8.23	6.8
<i>Comolina</i> sp.	20.68	9.75	7.0	1.16	0.55	1.1
Under <i>Acacia</i> sites						
Density (m ²)	Laguna Seca			Vicente Guerrero		
	Mean	S.E.	Relative abundance (%)	Mean	S.E.	Relative abundance (%)
Grasses and sedges						
<i>Hilaria belangeri</i>	13.50	1.23	46.4	15.10	2.35	53.0
<i>Bouteloua gracilis</i>	5.40	1.17	18.5	3.80	1.20	13.3
<i>Bouteloua hirsuta</i>	2.25	0.72	7.7	–	–	–
<i>Microchloa kunthii</i>	2.10	0.74	7.2	1.90	0.69	6.7
<i>Buchlœe dactyloides</i>	–	–	–	2.80	1.72	9.8
<i>Lycurus phleoides</i>	3.10	1.07	10.6	0.30	0.21	1.1
<i>Dichondra argentea</i>	0.20	0.20	0.7	0.50	0.22	1.8

(continued on next page)

Table 1 (continued)

Under <i>Acacia</i> sites							
Density (m ²)	Laguna Seca			Vicente Guerrero			
	Mean	S.E.	Relative abundance (%)	Mean	S.E.	Relative abundance (%)	
<i>Muhlenbergia repens</i>	0.30	0.21	1.1	1.90	1.27	6.7	
Non-grasses							
<i>Arenaria lycopodioides</i>	1.70	0.54	5.8	1.80	0.92	6.3	
<i>Happlopappus spirulescens</i>	0.30	0.15	1.0	–	–	–	
<i>Mammillaria</i> sp.	0.30	0.15	1.0	0.40	0.22	1.3	
Cover (cm ² /0.1 m ²)	Mean	S.E.	Relative cover (%)	Mean	S.E.	Relative cover (%)	
Grasses and sedges							
<i>Hilaria belangeri</i>	144.68	23.54	32.8	62.33	8.92	45.6	
<i>Bouteloua gracilis</i>	48.09	9.66	10.9	16.77	5.97	12.3	
<i>Bouteloua hirsuta</i>	54.92	25.11	12.5	–	–	–	
<i>Microchloa kunthii</i>	6.94	2.55	1.6	3.06	1.24	2.2	
<i>Buchlœe dactyloides</i>	–	–	–	18.58	11.75	13.6	
<i>Lycurus phleoides</i>	33.10	11.53	7.5	0.57	0.47	0.4	
<i>Dichondra argentea</i>	12.98	10.49	2.9	8.24	4.08	6.0	
<i>Muhlenbergia repens</i>	12.30	8.11	2.8	9.00	6.00	6.6	
Non-grasses							
<i>Arenaria lycopodioides</i>	89.23	41.78	20.2	16.80	8.51	12.3	
<i>Happlopappus spirulescens</i>	33.10	20.12	7.5	–	–	–	
<i>Mammillaria</i> sp.	5.60	2.95	1.3	1.39	1.04	1.0	

the most common species on the lower-slope, open site, were lower on the lightly grazed ranch than on the more heavily grazed ejido ($t=5.4$, $p<0.001$) while its cover was greater on the ejido ($t=2.6$, $p<0.05$). The second most abundant species in this zone on the ranch was *B. gracilis*, which had both higher density ($t=9.6$, $p<0.001$) and covers ($t=9.3$, $p<0.001$) on the ranch than on the ejido. A third species, *Microchloa kunthii*, had a significantly higher density on the ejido than on the ranch ($t=3.05$, $p<0.05$) but represented only a small percentage of the individuals present in the community. On the open upper-slope sites, a relatively common perennial grass species, *Aristida schideana*, had significantly higher densities ($t=2.7$, $p<0.05$) and cover ($t=2.7$, $p<0.05$) on the ranch than on the adjacent ejido. *Bouteloua curtipendula*, the commonest species there in both relative abundance and cover, had significantly lower densities on the ranch than on the ejido ($t=5.0$, $p<0.001$) but was not different in its cover. No significant differences in density for the commonest grass species, *H. belangeri* or *B. gracilis*, were found under the canopies of the *Acacias* but both species had significantly higher covers on the ranch than on the more heavily grazed ejido ($t=3.3$, $p<0.01$ for *H. belangeri*; $t=2.8$, $p<0.05$ for *B. gracilis*). Also, a less abundant grass, *Lycurus phleoides*, had a significantly higher density ($t=2.6$, $p<0.05$) and covers ($t=2.9$, $p<0.05$) in the shade of *A. schaffneri* on the ranch than on the ejido.

3.3. Plant sizes

H. belangeri has significantly greater numbers of individuals smaller than 10 cm² in area on the ejido than were sampled on the ranch ($\chi^2=190.97$, $p<0.001$ on the lower open sites; $\chi^2=6.35$, $p<0.02$ for upper open sites; $\chi^2=59.43$, $p<0.001$ for under *Acacia* sites (Table 2). In contrast, *B. gracilis* has significantly greater numbers of larger individuals in the

samples taken from the ranch than were measured on the ejido in the two microsites where it was common ($\chi^2=12.0$, $p<0.001$ on the lower open sites; $\chi^2=21.57$, $p<0.001$ for under *Acacia* sites (Table 2). No similar analysis of the *B. curtipendula* data was undertaken as grazing pressure was very similar on both sites (see discussion below).

4. Discussion

At the time of the study, three grass species (*H. belangeri*, *B. gracilis* and *B. curtipendula*) were important in the structure and dynamics of this rangeland. All three species were recorded at high relative frequencies in both density and cover on the

Table 2

Comparison of the numbers of small individuals (<10 cm²) versus larger individuals of *Hilaria belangeri* and *Bouteloua gracilis* in the three microsites studied on Laguna Seca and Vicente Guerrero.

<i>Hilaria belangeri</i>		
Lower open sites	Laguna Seca	Vicente Guerrero
<10 cm ²	44	309
>10 cm ²	211	159
Upper open sites		
<10 cm ²	10	34
>10 cm ²	35	38
Under <i>Acacias</i>		
<10 cm ²	11	77
>10 cm ²	124	74
<i>Bouteloua gracilis</i>		
Lower open sites	Laguna Seca	Vicente Guerrero
<10 cm ²	32	6
>10 cm ²	172	3
Under <i>Acacia</i>		
<10 cm ²	4	20
>10 cm ²	50	18

lightly-grazed ranch, Laguna Seca, and the heavily-grazed ejido, Vicente Guerrero. A comparison of their responses to the different grazing pressures suggests that *H. belangeri*, the only species present in all three sub-habitats on both the ranch and the ejido, is in the process of being replaced on the ranch by the bunchgrasses (*B. gracilis* and *B. curtipendula*). This stoloniferous grass reached its greatest density and cover on the open, lower slopes. Its density on the lower open slopes of the heavily grazed ejido is nearly twice as great as that of the ranch. In contrast the total cover for this species on the ejido is about one-half that on the ranch, where its clonal units are more than twice as large. These size differences are the result of the impact of the different grazing regimes, which affect average plant size as well as the recruitment of new ramets (e.g. Canfield, 1957; Launchbaugh, 1955; Fuhlendorf and Smeins, 1996).

In contrast, the two bunchgrasses occupied distinctive habitat types over the slope on both the ejido and the ranch. *B. gracilis* was only recorded in the open area and under *Acacias* on the relatively wetter lower slopes. It was not found upslope on the drier open sites where the bunchgrass form of *B. curtipendula* (var. *caespitosa*) occurs. More importantly, *B. gracilis* has higher density, greater total cover and much larger individuals on the more lightly grazed ranch. These results suggest that, on the ranch, *B. gracilis* is in the process of replacing the stoloniferous *H. belangeri*. A similar process of replacement of *H. belangeri* by the caespitose form of *B. curtipendula* on the drier, upper-open slopes may also be occurring. However, this replacement pattern is not as clear on the upper slopes where the abundance and productivity of the grasses is lower due to increased water stress. Also, grazing pressure is reduced on the upper slopes of the ejido as the herd is rarely taken upslope to graze (authors, pers. obs.).

Clones of stoloniferous grass species, such as *B. dactyloides* and *H. belangeri* can act as a soil stabilizer, forming mats which reduce surface flow of water and entrap soil (e.g. Koler et al., 2008). Over time and with reduced grazing pressure, bunchgrasses may establish from seed within openings in these mats or occasionally by rhizomes invading at their edges, eventually overtopping and replacing them. Replacement of stoloniferous, mat-forming grasses such as *H. belangeri*, *Bouteloua eriopoda* or *B. dactyloides* by *B. gracilis* and/or *B. curtipendula* as a result of reducing grazing pressure or resting rangelands have been reported by many investigators in North American arid and semi-arid rangelands (e.g. Havard, 1888; Whitfield and Anderson, 1938; Bock and Bock, 1993; Coffin and Laurenroth, 1996; among others). In the southern Chihuahuan Desert, two additional species of stoloniferous grasses (*Cyclostachya stoloniferous* and *B. dactyloides*) occur commonly, both of which are present on the ranch and the ejido and function similarly to *H. belangeri*. Of these two species, only *B. dactyloides* was recorded, albeit sporadically, on the open lower sites on the ranch and the ejido as well as in the shade of *Acacia* on the ejido. Both species are more common at lower elevations in the vicinity of the study site.

Based on the data obtained in this study, dominance of the first functional group appears to last about 40–50 years, after which the second functional group begins to dominate. Also,

Peters (2002), in a study of the biology of two congeneric species (the stoloniferous *B. eriopoda* and *B. gracilis*, a species that has the potential for rhizomatous growth) in an arid-semiarid transition zone in southern New Mexico cites longevities of 35–40 and 400 years for these species, respectively.

The patterns, in which mat-forming, stoloniferous or rhizomatous grasses persist in heavily grazed rangelands while associated tufted, tussock or bunchgrass forms decline in abundance occur in other arid and semi-arid regions of the world. As examples, there are several species of stoloniferous grasses that occur along a rainfall and grazing intensity gradient in South Africa, whose ranges begin in the mesic savannas in the northeast of the country and continue southwest-wards through mesic and xeric grasslands to the semi-deserts of the Great and Little Karoo (Acocks, 1988; Gibbs-Russell et al., 1990). Among these mat-forming species are *Cynodon dactylon*, *C. incompletus* and *Sporobolus ioclades*. More palatable, tufted (bunchgrass) species, such as *Digitaria argyrograpta*, *Eragrotis curvula* and *Stipagrostis ciliata*, occur along this gradient and, with reduced grazing pressure, can overtop the prostrate forms and replace them. These tufted grasses decrease more rapidly in abundance than the stoloniferous species towards the southwest in response to lower rainfall coupled with heavy grazing pressure from sheep (Acocks, 1988). Similar patterns occur in the more mesic savannas of eastern Africa between the mat-forming *Andropogon greenwayi* and the tufted *Chloris picnothrix* (Belsky, 1986) and between *Digitaria macroblephara* (stoloniferous) and the caespitose *Themeda triandra* (Anderson et al., 2006).

The stages of mat-forming and bunchgrass species are only the first two functional groups in a potential successional sequence of grasses in southern end of the Chihuahuan Desert and elsewhere. In the past, there was at least a third functional group involved in the dynamics of these grasslands. Where overgrazing occurs, these species are now only found in protected sites or on the upper parts of rocky ridges. For example, Guervitch (1986) reports that the C₃ grass, *Stipa neomexicana*, is more common on the ridges of her study site in southeastern Arizona and suggests that competition with the C₄ grass, *Aristida glauca*, is limiting its presence downslope. In the southern Chihuahuan Desert, such refuges are in dense patches ($\approx 3\text{--}10\text{ m}^2$) of decumbent platyopuntias (authors, pers. obs.) but, on a larger scale, they can be found throughout the semiarid desert regions of North America as relict populations in areas inaccessible to livestock (Ambos et al., 2000; Milchunas and Noy-Meir, 2004). Members of this group are grass species that can grow approximately 0.7–2.0 m in height. To overtop the bunch or tufted grass growth forms, these species expend resources in the development of coarse stems to support their leaves and inflorescences, thereby reducing their forage value seasonally when mature. The commonest species in the region of this study are *Bothriochloa barbinodis*, *Muhlenbergia rigida* and *Stipa eminens*, all of which are coarse grasses with reduced nutritive values when mature (e.g. USDA, 1937; Koshi et al., 1977; Powell, 1994; Adler and Morales, 1999). Members of this third functional group may also have other problems that affect their abundance and reproduction, making them prone to

extinction on a local scale. They are almost always obligate seed producers (i.e. do not grow vegetatively), producing low numbers of large seeds that have limited dispersal ability and are subjected to high levels of predation (O'Connor, 1991; Everson, 1994). As a consequence, re-establishment of grasses comprising this later functional group in an area is slow. For example, O'Connor (1991) cites as examples a North American grass species, *Andropogon scoparius*, as not having recovered forty years after abandonment of a cultivated field in Kansas and a South African grass species, *Themeda triandra*, requiring more than seventy years to recover in a similar situation in the savannas of northeastern South Africa. The latter species occurs as a relict on rocky outcrops throughout the arid and semiarid Karoo region and may have been more common in the region before the onset of heavy grazing. It can be established successfully when its seedlings are transplanted onto the open plains in sites where grazing pressure is reduced (Smith and Yeaton, 2005), suggesting that lack of a soil seed bank is one reason for its present absence there.

Two different ecological processes, facilitation and competition are considered to be important in the restoration of degraded environments (e.g. Callaway and Walker, 1997; Holmgren et al., 1997). Facilitation, involving the use of nurse plants can minimize the effects of harsh environmental conditions enabling later successional species to establish and replace them (e.g. Padilla and Pugnaire, 2006; Halpern et al., 2007). It is clear that the restoration of grasslands in the southern part of the Chihuahuan Desert has to begin with members of the first functional group, the stoloniferous, mat-forming grasses of which *B. dactyloides*, *Cyclostachya stoloniferous* and *H. belangeri* are the most apparent. These species have the potential to establish in the large, denuded areas of the former grassland, with the effect of slowing the rate of surface water flow and entrapping soil and organic debris. These species can potentially ameliorate the environmental conditions, enabling the second and later functional groups of grasses to establish and replace them through competition over time. The key question involving the first functional group of species is whether they are ecologically equivalent in their successional role. If the answer to this question is no, then there is a dynamic among these species in which one or more of these species is necessary for the establishment of other members within this functional group. As an example, if *C. stoloniferous* is necessary for the other members of this functional group to establish, what is its actual role? Are the other two members of this functional group necessary for the later functional groups to establish or can one simply proceed from the *C. stoloniferous* stage directly to the establishment of the second functional group, which in this region is dominated by *B. gracilis* or *B. curtipendula*? These aspects of interspecific competition between the members of the first functional group, as well as others involving the effectiveness of each member's ability to build up the soil, are currently in the process of being investigated. Future work will involve the competitive relationship that the second functional group has with the mat-forming species, what determines the co-existence of *Bouteloua* species in these rangelands, as well as developing potential options for the conservation of members of later

functional groups which are strongly dependent on a minimum viable population size for their survivorship regionally.

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