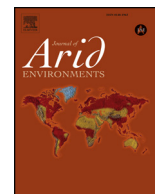




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## The effect of small mammal exclusion on grassland recovery from disturbance in the Chihuahuan Desert



Lauren N. Svejcar<sup>a,\*</sup>, Brandon T. Bestelmeyer<sup>b</sup>, Darren K. James<sup>b</sup>, Debra P.C. Peters<sup>b</sup>

<sup>a</sup> Department of Plant and Environmental Sciences, New Mexico State University, Las Cruces, New Mexico, 88003, USA

<sup>b</sup> United States Department of Agriculture-Agricultural Research Service Jornada Experimental Range, Jornada Basin Long Term Ecological Research Program, New Mexico State University, Las Cruces, New Mexico, 88003, USA

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### ABSTRACT

In many arid ecosystems, shrub encroachment is coupled to the loss of perennial grasses and associated ecosystem services. Increased native herbivore abundance associated with shrub encroachment can have negative effects on grass restoration. In the Chihuahuan Desert, native herbivore abundance can be two times greater in shrubland states dominated by *Prosopis glandulosa* (honey mesquite) than in historical *Bouteloua eriopoda* (black grama) grasslands. We compared the recovery of *B. eriopoda* patches following disturbance in plots that were exposed to or protected from native herbivores in shrub-dominated, grass-dominated and ecotone (grass and shrub co-dominated) states. We created a disturbance in the center of *B. eriopoda* grass patches in each treatment quadrat in 2001. The disturbed areas were measured for recruitment and re-establishment of *B. eriopoda* in 2002, 2005 and 2008. Although mean rodent abundance was generally greater in shrub-dominated states than other states over the study period, reproductive potential of *B. eriopoda* was similar in shrub and grass dominated states. Additionally, there was no revegetation by *B. eriopoda* in any state in response to rodent exclusion. Because increased herbivore abundance in shrub-dominated states did not constrain grass revegetation, other factors are likely to be more important constraints on perennial grass recovery in the Chihuahuan Desert.

### 1. Introduction

Woody plant encroachment and associated decline of perennial grasses is a key management and restoration challenge in rangelands worldwide (Parizek et al., 2002; Ratajczak et al., 2012; Roques et al., 2001; Van Auken, 2009). The persistent loss of perennial grasses is usually ascribed to competitive preemption of water and other resources by shrubs and to soil erosion feedbacks due to the absence of ground cover (Archer et al., 2017; Peters et al., 2013; Pierce et al., 2018). Another possible and little understood effect in these systems involves the impact of native mammalian herbivores, specifically rodents and lagomorphs, on perennial grass recovery following shrub encroachment and grass loss (Bestelmeyer et al., 2007).

In the northern Chihuahuan Desert, historical grasslands dominated by the perennial grass *Bouteloua eriopoda* (black grama) have undergone state transitions to shrublands dominated by *Prosopis glandulosa* (mesquite) over the last century (Peters et al., 2006). Attempts to

restore *B. eriopoda* in areas where it has been completely lost have met with minimal success (Herrick et al., 2006). Lack of *B. eriopoda* grassland regeneration and restoration success is attributed to abiotic factors in these cases (Peters, 2000). Where *B. eriopoda* remnants exist, however, gradual recovery is possible (Bestelmeyer et al., 2013). Native herbivores, however, can limit the ability of grasses to recolonize from remnant plants through consumption of seeds and tillers (Bestelmeyer et al., 2007; Brown and Heske, 1990). This effect may be exacerbated by the presence of shrubs. Shrubs often serve as habitat and a water source for many rodent and lagomorph species (Jaksic, 1986; Jaksic and Sorriquer, 1981; Kerley, 1992), and certain rodent and lagomorph species may increase in abundance and/or activity with increasing shrub cover (Daniel et al., 1993; Reynolds, 1950; Schooley et al., 2018; Whitford, 1993). While evidence exists for small herbivore impacts on native grasses, our understanding of herbivore impacts on plant dynamics under a range of biotic and abiotic conditions is lacking (Maron and Crone, 2006). Furthermore, there is scant evidence for the

\* Corresponding author.

E-mail addresses: [lauren.svejcar@dbca.wa.gov.au](mailto:lauren.svejcar@dbca.wa.gov.au) (L.N. Svejcar), [Brandon.Bestelmeyer@ars.usda.gov](mailto:Brandon.Bestelmeyer@ars.usda.gov) (B.T. Bestelmeyer), [Darren.James@ars.usda.gov](mailto:Darren.James@ars.usda.gov) (D.K. James), [debra.peters@ars.usda.gov](mailto:debra.peters@ars.usda.gov) (D.P.C. Peters).

<sup>1</sup> Present address: School of Veterinary and Life Sciences, Murdoch University; Murdoch Western Australia 6150 Australia; and Biodiversity Conservation Centre; Kattidj Close, Kings Park, Western Australia, 6005, Australia.

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interaction of increases in shrub cover and impacts of herbivores. In one study along a gradient between *P. glandulosa* and *B. eriopoda* dominated states, herbivory on seedlings was greatest in *P. glandulosa*-dominated states, but small mammal abundance measured in that study was not higher in those states—likely indicating increases in foraging effort by small mammals within these shrub-dominated areas (Bestelmeyer et al., 2007).

*Bouteloua eriopoda* spreads predominantly through asexual reproduction by stolons and ramets (Nelson, 1934; Smith et al., 2004). Although seeds are produced in years with sufficient rainfall (Nelson, 1934), their viability is often low (< 50%) as a result of genetic (Hanson, 1972) and insect-related (Watts, 1965) factors. Based on model simulations and field studies, Peters (2000) suggested that the frequency of optimal conditions for viable seed set and seedling establishment of *B. eriopoda* is low, and successful seedling establishment events are rarely observed in this region (Neilson, 1986). Thus, disturbed areas within *B. eriopoda* grasslands are likely to be recolonized primarily through the establishment of ramets; herbivory on stolons and ramets would limit grass recovery.

We conducted an experiment to examine the impact of native small herbivores on recovery of disturbed *B. eriopoda* patches through vegetative spread (stolons, non-rooted ramets) and recruitment (rooted ramets, seedlings). We simulated a disturbance by removing sections of *B. eriopoda* patches and observed recovery over seven years. We hypothesized that exposure to rodent and lagomorph activity would constrain grass recovery in disturbed patches. We also hypothesized that the magnitude of this constraint would increase along local grassland to shrubland gradients due either to greater rodent numbers or increased small mammal foraging activity in shrublands.

## 2. Methods

### 2.1. Study area

The study was established on the Jornada Experimental Range (JER) and the Chihuahuan Desert Rangeland Research Center (CDRRC), 37 km north of Las Cruces, New Mexico, USA (32° 35' N, 106° 51' W; 1334 m a.s.l.). The study sites are currently or formerly dominated by *Bouteloua eriopoda* grasslands that have been invaded to varying degrees by *Prosopis glandulosa* shrubs. This desert grassland ecosystem type historically extended across the U.S. states of Arizona, New Mexico, and Texas, as well as northern Mexico (McClaran, 1995). Soils at all study plots have sedimentary parent materials derived from the Ancestral Rio Grande (Monger, 2006). Surface textures are sandy to sandy loam and are usually underlain by a horizon cemented by calcium carbonate (petrocalcic) at depths of 30–100 cm. Mean annual precipitation (80 y) is 240 mm with > 60% occurring during the summer monsoon, and mean monthly temperatures range from 3.78 °C in January to 26.03 °C in July (Wainwright, 2006). During the time of this study (2001–2008), annual precipitation was generally below average for the period between 2002 and 2005 and above average from 2006 to 2008 (Fig. 1).

### 2.2. Experimental design

The study was initiated in 2001 with two treatments: (1) wire mesh enclosures that excluded all mammalian herbivores from a 4 m<sup>2</sup> area; and (2) non-caged controls. Enclosures were 1-m tall, 2.5 cm-mesh cages curved outward at the top to prevent small mammals climbing in and an additional 20 cm was buried to prevent rodents from entering underneath the cages. Enclosures were periodically monitored for activity of small mammals and structural integrity. Small mammal activity was not observed in any enclosure, and wire and caging were intact for all enclosures for the duration of the study. Cattle stocking rates and native ungulate densities were low to nil in the study pastures during the study period, so rodents and lagomorphs are the primary

mammalian herbivores excluded by the full enclosures.

For each treatment type (enclosure and non-caged controls) we established five replicate plots (1.44 m<sup>2</sup> area) within *B. eriopoda* patches in each of three states representing a gradient between grassland and shrubland (*B. eriopoda*-dominated [Grass], *B. eriopoda* and *P. glandulosa* co-dominated [Ecotone], *P. glandulosa*-dominated [Shrub], Fig. 2.). Grass states had at least 50% cover of *B. eriopoda*, Ecotone states had 25% cover of each *B. eriopoda* and *Prosopis glandulosa*, and Shrub states had at least 50% cover of *P. glandulosa* and included some *B. eriopoda* patches. Shrub states were not located in dune systems and were edaphically similar to Grass and Ecotone states. Three blocks were identified within which all three states occurred. States were located in relatively close proximity to each other, from 50 to 300 m apart. Blocks were from 5 to 10 km apart. There were a total of 90 plots (3 blocks × 3 states × 2 treatments × 5 plots).

All plots were located in patches dominated by *B. eriopoda* with 75–100% vegetative cover in the plot. A disturbance of 40 cm × 40 cm was created and permanently marked in the center of each plot in 2001. All above ground biomass (on average 78 g) was removed once to examine recovery into the disturbed area by adjacent *B. eriopoda* plants via stolons or seeds. These disturbed areas were resampled for recruitment and regrowth of *B. eriopoda* three times (October 2002, July 2005 and August–October 2008). Counts were conducted on *B. eriopoda* reproductive parts: stolons, non-rooted ramets with potential to root (i.e. mature), rooted ramets, and seedlings. Reproductive parts were only counted if at least 2/3rds of the part occurred within the disturbed area. In addition, ocular estimates of total canopy cover of *B. eriopoda* in the disturbed area were made to the nearest 1% (Elzinga et al., 1998).

Rodent abundance was measured in each state over the course of the study. Rodent populations were sampled once per year in late summer using live traps (model XLK, H.B. Sherman Inc., Tallahassee, FL, USA) with grain bait. Lagomorph populations were measured along roads throughout the grassland to shrubland gradient using spotlighting techniques four times a year. This technique cannot be used to estimate abundance differences among states, and is used here only to evaluate change in abundance in the study area over time. Number of lagomorphs per hectare was similar throughout the study period (average 29 individuals/ha). Three genera of rodents (*Dipodomys*, *Neotoma*, and *Sigmodon*) and two species of lagomorphs (*Lepus californicus* and *Sylvilagus audobonii*) were present throughout the sites.

## 3. Analysis

SAS Version 9.4 (SAS Institute, Cary NC) was used for data manipulation and analyses. Rodent abundance per year was modeled with a Poisson generalized linear mixed model (PROC GLIMMIX) with the Laplace method for likelihood approximation. Habitat, year, and their interaction were modeled as fixed effects. A G-side random effect for habitat\*wet/dry period was included to account for interannual variability and overdispersion.

*Bouteloua eriopoda* canopy cover and counts of stolons, non-rooted ramets, total rooted ramets, and total ramets were analyzed separately for three time periods with gain scores. The three time periods are: (1) 2002–2005 [dry], (2) 2006–2008 [wet], and (3) 2002–2008 [all]. The time periods were distinguished based on rainfall data collected at the sites (Fig. 1). For each plot, gain scores were calculated as the later measurement minus the earlier measurement so that the direction of the difference corresponded to the direction of change over the time period.

For each of the 5 variables in each of the 3 time periods, gain scores were analyzed with mixed linear effects models (PROC MIXED) with treatment, vegetation state and their interaction as fixed effects. Vegetation state nested within block was modeled as a random effect. Mean comparisons were conducted with Fisher's least significant difference (LSD) but were only carried out on fixed effects whose Type III tests were significant at  $\alpha = 0.10$ .

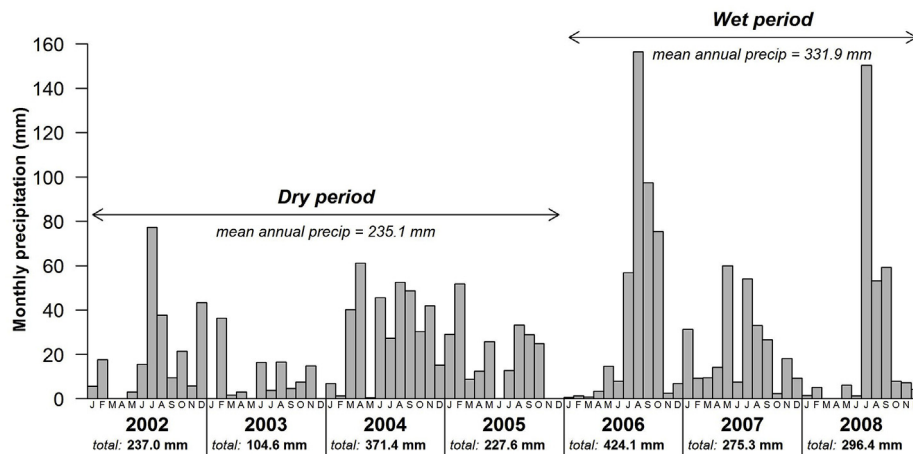


Fig. 1. Monthly and yearly precipitation totals as recorded by a meteorological station in the study area. Two periods were distinguished (dry, wet) based on the annual precipitation compared with the long-term mean. Mean annual precipitation over the whole study period was 276.6 mm.

#### 4. Results

The main effects of year and state on rodent abundance were highly significant ( $p < 0.0001$  and  $p = 0.0001$  respectively) but there was no evidence of a year\*state interaction ( $p = 0.9699$ ) (Fig. 3). Across states rodent numbers increased from 2004 to 2005 ( $p = 0.0386$ ) and 2006 to 2007 ( $p = 0.0017$ ) before declining between 2007 and 2008 ( $p = 0.0002$ ) to a level no different than 2004 ( $p = 0.4678$ ). Compared to Grass states, rodent abundance was  $3.87 \pm 1.72$  rodents/ha higher in the Ecotone state ( $p = 0.0336$ ) and  $6.76 \pm 1.72$  rodents/ha higher in the Shrub state ( $p = 0.0006$ ). However, there was no significant difference in rodent abundance between Ecotone and Shrub states ( $p = 0.1057$ ). All small mammals recorded were granivores/herbivores.

Overall, plant recruitment (total rooted ramets) and canopy cover of *B. eriopoda* was not significantly different between caged and non-caged areas ( $p > 0.8$  in both cases). However, other variables related to reproductive potential were influenced by the cage treatments in the wet period and over all time periods measured (non-rooted ramets 2005–2008:  $p = 0.0083$ ; non-rooted ramets 2002–2008:  $p = 0.0424$ ; total ramets 2005–2008:  $p = 0.0522$ ; total ramets 2002–2008:  $p = 0.0753$ ). No seedlings of *B. eriopoda* were recorded for any plots.

There were no significant state-treatment interactions in indicators of plant recruitment (canopy cover and rooted ramets) (Fig. 4). Nonetheless, we detected interactions in variables related to reproductive potential, including an increase in non-rooted ramet production in caged plots observed in Grass and Shrub states. Collectively, these results suggest that there was an effect of herbivory on reproductive structures, but that it was not strong enough to create a recruitment limitation. No treatment differences on reproductive structures were observed in the dry period of the study, but some differences were apparent in the wet period, indicating that climate can influence the magnitude of herbivore impacts (Fig. 4).

#### 5. Discussion

##### 5.1. Impact of herbivory on *B. eriopoda*

We hypothesized that reproductive effort and success of *B. eriopoda* in rodent-excluded plots would be greater than non-excluded plots for all states. Rodent and lagomorph exclusion in Grass, Ecotone, and Shrub states did not have a significant effect on the recolonization of disturbed *B. eriopoda* patches over 7 years. Our results are not consistent with research findings that documented an increased impact of herbivores on herbaceous vegetation in shrub-dominated versus grass-dominated states (Bestelmeyer et al., 2007; Kerley and Whitford, 2009; Kerley et al., 1997). Evidence presented in one Chihuahuan Desert

study suggests that bunchgrasses that regularly reproduce by seed have increased growth of leaves and tillers, and production of inflorescences, when protected from herbivory (Kerley and Whitford, 2009). No such evidence exists for the impacts of herbivores on the clonally reproductive organs of the stoloniferous grass *B. eriopoda*. It is possible that the native herbivore foraging on perennial bunchgrass and annual grass reproductive structures limits the populations of those species (Brown and Heske, 1990; Heske et al., 1993; Thibault et al., 2010), whereas *B. eriopoda* reproductive structures (stolons, ramets) are not targeted by herbivores and therefore herbivory does not affect *B. eriopoda* spread.

Shrub canopies provide protection against predators (Brown and Lieberman, 1973; Kotler and Brown, 1988; Whitford, 1997) leading to higher abundances of herbivores in shrub encroached states. Our results agree with these findings and demonstrate that herbivore abundance is greater with a higher cover of shrubs. Fewer guilds of rodents were present at our site than previous studies in the northern Chihuahuan Desert (Thibault et al., 2010) and we recorded lower densities of rodents than studies in other Chihuahuan Desert regions conducted over the same time period (Christensen et al., 2018). However, rodents and lagomorphs were common during the study, and population densities in 2007 were among the highest in the long-term record for this area (Schooley et al., 2018). Variability of mammalian herbivory may have been driven by spatiotemporal variation in the perception of predation risk or predator activity (DaVanon et al., 2016), although predator data was not available for this study period. Compositional differences in herbivore species, specifically greater abundance of *Sylvilagus audubonii* in the western Chihuahuan Desert (Abercrombie et al., 2019), may also contribute to regional differences in vegetation responses.

Other studies at the Jornada site, however, indicate that our results may not be anomalous. In a 56 year study, Havstad et al. (1999) found lagomorph exclusion did not significantly affect *B. eriopoda* growth. Other long-term studies in the Chihuahuan Desert region found that rodent exclusion promoted grass growth, but the species documented as increasing were annuals and an invasive perennial grass species, not *B. eriopoda* (Brown and Heske, 1990; Heske et al., 1993; Thibault et al., 2010).

Experimental disturbances were implemented in 2001 and between 2001 and 2003 all plots were subjected to severe drought conditions as noted by Wainwright (2006). We would expect minimal re-establishment of *B. eriopoda* during this period and a delayed growth response from plants recovering from drought (Herbel et al., 1972; Nelson, 1934). Results from our study, however, show no significant difference in measured plant variables between 2002 and 2005. Average and above average precipitation from 2006 to 2008 did accentuate the effects of small mammal exclusion on some variables. Nonetheless, the

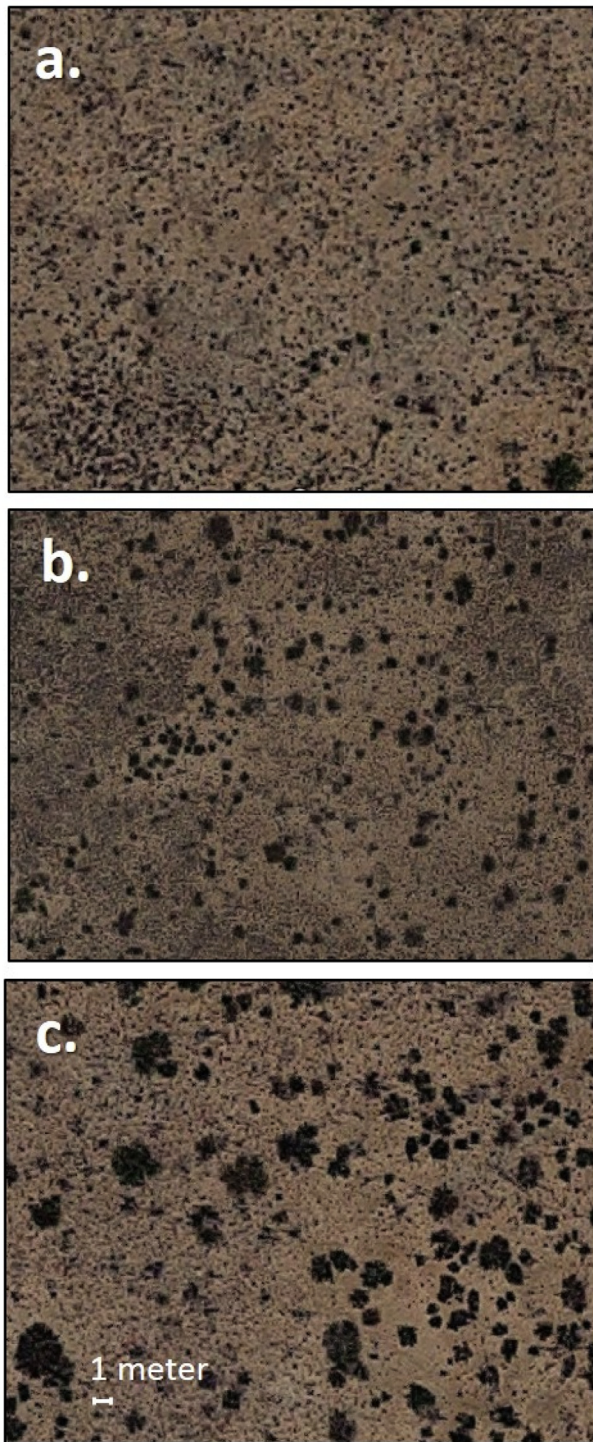


Fig. 2. Aerial photos of three states within one of the three blocks in 2016: a) Grass, b) Ecotone, and c) Shrub states.

lack of treatment effects on establishment and cover in both wet and dry periods during our study suggests that climate does not mediate mammalian impacts on *B. eriopoda* recruitment.

Herbivory by arthropods was not explicitly controlled for in this study due to logistical constraints (e.g. structures excluding arthropods could substantially alter microsites of *B. eriopoda* patches over a seven year period). Several species of phytophagous insects are important in the Chihuahuan Desert (Forbes et al., 2005; Logarzo et al., 2012), but there is little reason to suspect that shrub encroachment accelerates insect herbivory on perennial grasses. Further research on the habits

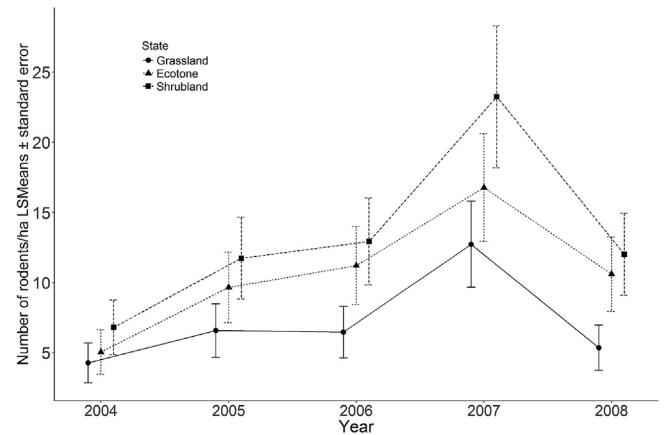


Fig. 3. Year\*state least squares means with standard error bars of rodent abundance from Poisson generalized linear mixed model. Rodent data was unavailable for 2002 and 2003.

and preferences of insect herbivores is needed to understand the extent of their impacts.

## 5.2. Impacts of state on establishment

Vegetation state had no apparent effect on recovery of *B. eriopoda* into disturbed areas, in contrast to the expectation that recruitment would be limited in shrub-dominated states via abiotic and/or biotic mechanisms (Moreno-de las Heras et al., 2016; Peters, 2000). Competitive effects of mesquite on perennial grasses should be most apparent during wet periods (Pierce et al., 2018). However, any important differences in competitive effects should have been apparent in both wet and dry periods.

Patch size affects the reproductive output and success of *B. eriopoda* in this ecosystem (Svejcar et al., 2015). Patches selected for our study were large (over 60 cm in diameter) in order to evaluate the impact of disturbance on clonal reproduction. Plants in large patch interiors have lower reproductive effort than large patch edges or medium (40–60 cm diameter) patches, which is likely the result of resource competition (Svejcar et al., 2015). We assumed removal of biomass from the patch center would alleviate competition for resources and create conditions similar to patch edges. However, resource competition in large patches might have limited reproductive success in disturbed areas, irrespective of herbivory and the presence of shrubs.

## 6. Conclusions

Models of vegetation dynamics in desert grassland ecosystems predict accelerating loss of perennial grasses due to altered biogeochemical and erosion processes resulting from shrub encroachment and climate change (Schlesinger et al., 1990). Shrub encroachment could induce grass loss by facilitating increases in rodent and lagomorph populations with subsequent impacts on grasses via herbivory and disturbance to root systems (Bestelmeyer et al., 2007). Multiple studies suggest that either greater abundance of mammalian herbivore species in shrub dominated states (which was confirmed in our study) and/or greater foraging activity should negatively affect perennial grass persistence and recruitment (Bestelmeyer et al., 2007; Kerley and Whitford, 2009). In contrast, our experimental study suggests that re-establishment of a dominant grass species, *B. eriopoda*, is not limited by mammalian herbivores across grassland-shrubland gradients. However, reproductive potential of *B. eriopoda* did increase as a result of mammalian exclusion in grass-dominated and shrub-dominated states. Recruitment failure of *B. eriopoda* is poorly understood, and more a detailed examination of bottlenecks for sexual and asexual reproduction of this species is needed

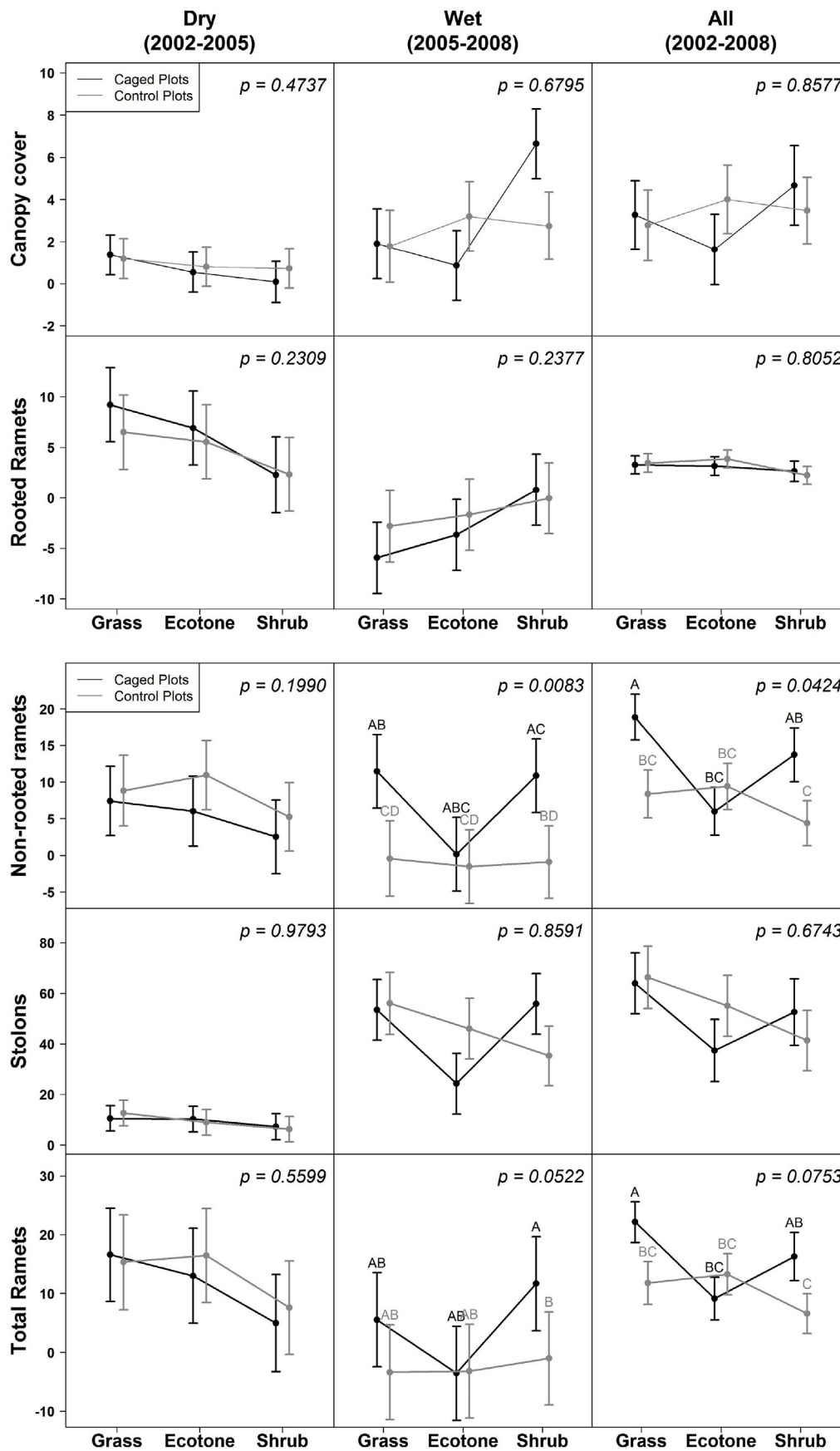


Fig. 4. Response of *Bouteloua eriopoda* (Canopy cover, Stolons, Non-rooted ramets, Rooted ramets, Total ramets) in three states for two time periods (dry, wet) and combined. Means with the same letter are not different at  $\alpha = 0.10$ . P-values are from Type III tests of the treatment effect.

in order to identify drivers of recruitment success (e.g. Larson et al., 2015).

### Author contributions

BTB, DPCP conceived of the study and designed the research; BTB, LNS, DKJ conducted the research; BTB, DKJ analyzed the data; LNS, BTB, DKJ wrote the manuscript; LNS, BTB, DKJ, DPCP edited the manuscript. All authors approve the final article.

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