

Grass-Shrub Competition in Arid Lands: An Overlooked Driver in Grassland–Shrubland State Transition?

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ABSTRACT

Traditional models of state transition in arid lands emphasize changes in disturbance regimes and abiotic feedbacks that promote the degradation of grassland into shrubland, whereas biotic interactions like competition and facilitation are often overlooked. Here, we conducted an experiment to determine whether shrubs have a positive, neutral, or negative effect on grasses and if these interactions may play a role in grassland–shrubland state transition. *Prosopis glandulosa* shrub neighbors within 5 m of *Bouteloua eriopoda* grass patches were left intact (controls) or killed with foliar herbicide, and metrics of grass performance were evaluated over 5 years. We saw no evidence of shrub facilitation of grasses. Instead, grass ANPP responded positively to shrub removal in all years, but more so

in years with above-average rainfall. Grass allocation to vegetative reproduction and grass patch size also increased when shrub neighbors were removed. These results demonstrate that biotic interference by shrubs upon grasses reinforce and magnify grazing- and drought-induced abiotic feedbacks during grassland–shrubland transitions. Shrub effects on grass should therefore be considered a key process in desert grassland state transitions.

Key words: *Bouteloua eriopoda*; Chihuahuan desert; Competition; Grassland; *Prosopis glandulosa*; Shrubland; State transition; Woody plant encroachment.

HIGHLIGHTS

- Grasses with shrub neighbors have lower productivity than grasses without shrub neighbors.
- The competitive effect of shrubs on grasses was also evident in allocation to reproductive structures and grass patch size/continuity.

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- Shrub-on-grass competition can reinforce and amplify abiotic feedbacks during grassland–shrubland state transition.

INTRODUCTION

Arid and semiarid grasslands worldwide have undergone state transitions from grassland to shrubland dominated by xerophytic, unpalatable shrubs and bare ground. This transition can represent landscape degradation with regard to primary production (Knapp and others 2008), erosion and nutrient loss (Li and others 2008), biodiversity (Ratajczak and others 2012), and forage production (Fredrickson and others 1998), although specific patterns and interpretations vary globally (Eldridge and others 2011). Grassland-to-shrubland state transitions in drylands are the result of changes in disturbance regimes amplified or mitigated by abiotic factors related to climate and soil (Archer and others 2017). For example, livestock grazing coupled with drought reduces fine fuel mass and continuity, thus reducing the probability of fire—a disturbance that historically kept woody plants in check (Higgins and others 2007). In the absence of fire, shrubs can establish and progress to more advanced life-history stages (Higgins and others 2000). At the same time, rates of erosion typically increase with declines in grass cover in arid grasslands, depleting soil resources and concentrating them below developing shrub canopies, as well as increasing disturbance to grasses by burial and abrasion, which constitutes a positive abiotic feedback that impedes future grass recovery while promoting shrub survival (Schlesinger and others 1996; Okin and others 2009). Inherent in these scenarios is the implicit assumption that grass-shrub interactions in arid grasslands are of little or no significance after shrubs have established. However, this assumption has not been widely tested or rigorously evaluated.

Grass-shrub interactions may be dismissed as a driver of state change in arid lands under the presumption that selection pressures favor adaptations for stress tolerance over competitive ability (Grime 1977; Brooker and Callaghan 1998). Accordingly, a growing body of research supports the notion that facilitation takes precedence over competition with increasing environmental stress (Maestre and others 2009; Dohn and others 2013). This framework helps explain the coexistence of grasses and woody plants in some systems, whereby woody plants facilitate understory grasses via ameliorating harsh environmental conditions (Ludwig and others

2004b) or by providing refugia from grazers (Howard and others 2012). However, in grassland–shrubland transitions, shrub-on-grass facilitation must be eclipsed by other factors detrimental to grass survival, including shrub-on-grass competition. The predominance of facilitation versus competition might also change along a continuum of woody plant abundance, that is, competition increases with increasing shrub size and density (Scholes 2003; Vander-Yacht and others 2017).

The predominance of competition versus facilitation in grass-shrub interactions may also vary at fine spatial scales. Certain xerophytic shrub species have extensive shallow lateral roots (Gibbens and Lenz 2001) and may therefore interact with grasses occurring well beyond their canopies. Such shrubs could facilitate grasses via hydraulic redistribution (Priyadarshini and others 2016). However, shrub lateral roots could also have a negative effect on grasses by utilizing soil resources that grasses would otherwise obtain (Ludwig and others 2004a). In situations where grass and shrub rooting niches are segregated spatially (Walker and others 1981; Ward and others 2013), or where phenology separates their activity patterns temporally, shrubs may have no influence on neighboring grasses (Golluscio and others 1998; Ludwig and others 2001). Net neutral interactions could also occur if competitive and facilitative processes are in balance (Maestre and others 2009). Neutral interactions would support the prevailing assumption that grass loss and shrub proliferation in the course of grassland–shrubland transition are driven primarily by interrelationships among climate, disturbance (grazing, fire), and soil erosion.

Here, we report the outcome of a 6-year field experiment aimed at quantifying grass-shrub interactions to ascertain if shrubs have a positive (facilitation), neutral, or negative (competition) effect on grass production beyond their canopies. We hypothesized that the production of grasses occurring in the vicinity of shrubs with extensive, shallow lateral root systems would be reduced owing to the predominance of competitive interactions. Knowledge of the direction and strength of the influences of shrubs on grasses growing beyond their canopies would help us predict grass patch capacity to recover from disturbance and the extent to which shrub interactions with grasses might either dampen or reinforce abiotic feedbacks during grassland–shrubland state transitions. Support of the hypothesis that shrubs have no discernible effect or a positive effect on grasses would corroborate the prevailing view that competitive grass-shrub interactions are of little consequence compared to facilitation or abiotic drivers. We offer three alternative predictions in testing these

hypotheses regarding shrub effects on grasses: (1) no effect, which would suggest abiotic processes triggered by grazing-induced grass losses and subsequent soil erosion are responsible for grassland–shrubland transitions (Okin and others 2006); (2) a positive effect due to hydraulic lift, from which we would infer grasses might be more persistent in the face of grazing and drought stress; and (3) competition, wherein the presence of shrubs would amplify stresses on grasses imposed by grazing and drought.

METHODS

Study Area

The field experiment was conducted on the USDA Agricultural Research Service Jornada Experimental Range (JER), which hosts the Jornada Basin Long-Term Ecological Research (LTER) site, approximately 37 km north of Las Cruces, NM, in the northern Chihuahuan Desert (UTM 13S 336659 3610160; 1325 m a.s.l.; <https://jornada.nmsu.edu/lter>). The climate is arid (Köppen Climate Classification BWk), with long-term (1926–2015) mean annual precipitation (PPT) of 241 mm (SE $\pm$ 9.6, CV = 36%), approximately 65% of which occurs in July–October. June is the warmest month (mean minimum of 17°C and mean maximum 36°C); January is the coldest month (mean minimum and maximum of -6 and 4°C, respectively).

The study was conducted along a grassland-to-shrubland gradient, reflecting the ongoing spread of shrubs and consequent spatial variations in the rate of state transitions (Bestelmeyer and others 2011). One end of the 3 km $\times$ 1 km study area (UTM 13S 334878, 3601198) was grassland dominated by the C₄ perennial grass *Bouteloua eriopoda* (Torr.) Torr. (26% foliar cover), which is a stoloniferous bunchgrass that proliferates via axillary tillers from the genet, as well as stoloniferous ramets. The grassland end was also populated with small, scattered C₃ *Prosopis glandulosa* (Torr.) shrubs (2% canopy cover). The opposing end (UTM 13S 333764, 3604817) was shrubland, with *B. eriopoda* foliar cover of 4% and *P. glandulosa* canopy cover of 18%. Soils are fine-loamy, mixed, thermic Typic Haplargids and Typic Petrocalcids underlain by a petrocalcic horizon 64 to 76 cm beneath the surface (Havstad and Schlesinger 2006).

Experimental Design

Ninety plots were established in 2010 in a stratified random fashion at locations along the grassland–shrubland continuum, ensuring 30 plots within the

grassland, the ecotone, and the shrubland portions of the gradient. Plots with a fixed radius of 5 m were centered upon 1 $\times$ 1 m subplots containing a *B. eriopoda* patch. Only grass patches with at least one *P. glandulosa* shrub within the 5 m plot radius were chosen. Target grass patches therefore had a broad range of shrub neighborhood configurations, that is, few, small shrub neighbors in the grass-dominated segments of the transect and numerous, larger shrub neighbors in the shrub-dominated segment. Grass patch size and shape was quantified within a grid of 25–20 $\times$ 20 cm cells in the 1 $\times$ 1 m subplots at the end of the 2010 growing season (October, near peak production) by counting the number of cells occupied by *B. eriopoda*. Clonal reproductive output (number of ramets) was also quantified at this time. Grasses in the entire subplot were then clipped to a height of 10 cm, and current year's biomass was dried and weighed to estimate aboveground annual net primary productivity (ANPP). These measurements were repeated in October of 2011–2013 and 2015 (measurements were not taken in 2014).

The volume of all *P. glandulosa* shrubs within the 5 m radius of each plot was determined in the spring of 2011 by measuring canopy diameter along the longest axis and the diameter perpendicular to the midpoint of the longest axis, as well as plant height. Aboveground ANPP was then determined using a site- and species-specific allometric regression ($R^2 = 0.89$, Gherardi and Sala 2015).

All *P. glandulosa* shrubs located within 45 randomly selected plots were killed in June 2011, prior to the summer rainy season, using a foliar herbicide solution (0.5% triclopyr, 0.5% clopyralid, and 5% diesel fuel) applied in a fine mist. The herbicide mixture was effective at defoliating shrubs within 2 weeks of spraying, and no new growth was observed for the remainder of the growing season. Targeted spot-spraying was conducted as needed to suppress new basal shoots (which typically emerged from only the largest of shrubs) in 2012 and 2013, after which no regrowth occurred.

Data Analysis

Overall treatment effects on *B. eriopoda* aboveground ANPP were analyzed using repeated-measures linear-mixed effects models (PROC MIXED; SAS V9.4; SAS Institute, Cary, NC, USA). Shrub removal, year, and their interaction were fixed effects; year was also a repeated effect with plot as the subject. A heterogeneous Topelitz temporal covariance model was used based on Akaike's

Information Criterion (AIC_c). The Kenward–Roger method was used to adjust denominator degrees of freedom to account for bias associated with estimating the fixed effects after the repeated effect. All fixed effects were highly significant; because of the highly significant shrub removal $\times$ year interaction, interpretations of the main effects are qualified by year.

We also examined the relationship between *B. eriopoda* ANPP and PPT by regressing annual, growing season (July–October) and dormant season (November–June) PPT (independent variable) against *B. eriopoda* ANPP (dependent variable) and calculating the treatment $\times$ PPT interaction coefficients (JMP, Version 13. SAS Institute, Cary, NC, USA). As antecedent precipitation can be a better predictor of current year's ANPP (Sala and others 2012), we also conducted this analysis for previous year's PPT.

ANOVA was used to compare the number of non-stoloniferous and un-rooted stoloniferous ramets on plots with intact and killed shrubs; Tukey's HSD was used to test for significant differences among treatments and years.

Finally, we sought to determine if differences in ramet production translated into changes in grass patch size and continuity over the course of the experiment. We approached this using repeated-measures linear-mixed effects models as described above, but using a heterogeneous compound symmetry covariance structure, which was the best fit based on AIC_c. The response variable was the number of 20 cm $\times$ 20 cm cells within the 1 m² subplot that was occupied by *B. eriopoda*. An increase in the number of cells occupied over time would reflect net ramet recruitment and genet patch infilling and/or expansion; a decrease in cell occupation would be indicative of patch fragmentation and/or contraction.

RESULTS

Precipitation patterns varied considerably over the course of the experiment (Figure 1). Drought occurred during the first 2 years of the study with annual PPT 54% (2011) and 50% (2012) below the long-term (1926–2015) mean. Similarly, growing season (July–October) PPT was 33% below average in 2011 and 55% below average in 2012. Annual PPT in 2013 and 2014 approximated the long-term average, but growing season PPT was 41 and 37% higher than the long-term mean, respectively. Annual PPT in 2015 was 15% higher than the long-term average, while growing season PPT was near average.

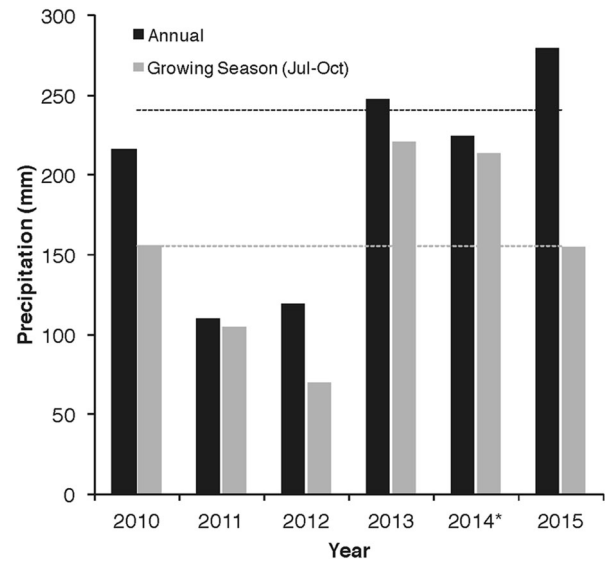


Figure 1. Annual (black) and growing season (July–October, gray) precipitation (PPT) over the course of the experiment. The dashed black and gray lines represent long-term (1926–2015) annual and growing season mean PPT, respectively. (*Plot data was not collected in 2014).

B. eriopoda aboveground ANPP in 2010 on control plots and plots slated for shrub removal was nearly identical (Figure 2). Subsequent to shrub

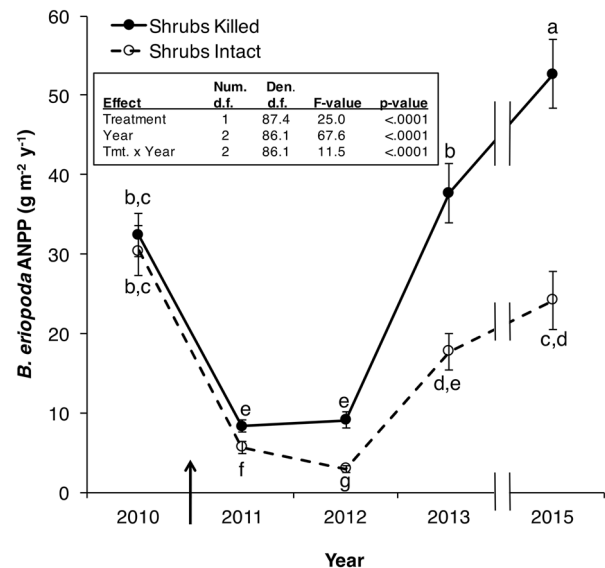


Figure 2. *Bouteloua eriopoda* aboveground ANPP in plots with neighboring shrubs intact (open circles) or killed (closed circles). Different letters denote significant ($P < 0.05$) differences among treatments and dates. Inset: ANOVA summary table of main effects. The arrow between 2010 and 2011 designates when shrub neighbors were killed in treatment plots. Data were not collected in 2014.

removal, grass ANPP varied by an order of magnitude in both control and treated plots over the course of the 6-year experiment in response to inter-annual variation in PPT (Figure 1). For example, mean ($\pm$ SE; $\text{g m}^{-2} \text{y}^{-1}$) ANPP in control plots was 2.9 (0.7) during the dry year of 2012 and increased to 24.2 (3.9) in the above-average PPT year of 2015.

The presence of shrub neighbors mediated grass ANPP response to precipitation (Figure 2). During the dry period (2011–2012), control plots with shrub neighbors intact had significantly reduced *B. eriopoda* ANPP compared to treatment plots with shrub neighbors killed. Upon return to average and to above-average PPT conditions in 2013 and 2015, differences in grass ANPP between treatment and control plots were amplified: mean *B. eriopoda* ($\pm$ SE; $\text{g m}^{-2} \text{y}^{-1}$) ANPP was 19.9 (4.4) and 28.1 (5.6) higher in plots with shrubs killed than in plots with shrubs intact in 2013 and 2015, respectively.

B. eriopoda ANPP was directly related to PPT in both control and treatment plots. However, *B. eriopoda* ANPP was more responsive to PPT in plots with shrub neighbors killed than in control plots with shrub neighbors intact. This was true for annual PPT, growing season PPT, and dormant season PPT (Figure 3). There was no significant relationship between *B. eriopoda* ANPP and previous year's annual PPT in either the control or treatment plots ($F = 2.07$; $df = 1$; $P = 0.152$; data not shown).

Allocation to clonal reproduction, measured by the number of ramets produced per plot, was near zero in the dry years of 2011–2012 on control and treated plots. During the wet years of 2013 and 2015 ramet production increased, but more so on plots where shrubs had been killed than on plots where shrubs were intact (Figure 4). Vegetative production of axillary tillers also differed in 2013, where the mean number of tillers was significantly higher in plots with shrub neighbors killed than in plots with shrub neighbors intact (Table 1). Despite this difference in tiller number, average ANPP per tiller did not differ between control and treatment plots ($P = 0.37$).

Ramet production, in concert with axillary tiller proliferation, translated into changes in grass patch size over the course of the experiment (Figure 5). Where shrubs were present, the mean number of $20 \text{ cm} \times 20 \text{ cm}$ cells within the 1 m^2 subplot occupied by *B. eriopoda* decreased from 2011 to 2012, was stable through 2013 and then returned to 2011 levels by 2015. Conversely, where shrubs had been killed, *B. eriopoda* cell occupancy was maintained through the 2011–2012 dry period and

subsequently increased to reach levels 65% higher in 2015.

DISCUSSION

Our results support the hypothesis that competitive effects of shrubs on perennial grasses play an important role in the progression of grassland–shrubland transitions. Shrubs in this Chihuahuan Desert system were relatively short-statured (mean height = 0.6 m, mean canopy diameter = 1.5 m), and focal grass patches occurred well beyond their canopies. Consequently, aboveground interactions related to light competition or temperature amelioration were not likely to have been important. Rather, competitive interactions between grasses and shrubs must have occurred for belowground resources. The presumption of competition for soil water is reflected in the fact that the presence of shrubs significantly reduced grass production during dry periods (2011, 2012) and moderately (2013) to substantially (2015) constrained grass responses to increased rainfall (Figure 2).

Further evidence of belowground competition is demonstrated in the relationship between grass ANPP and PPT. The grass ANPP response to precipitation was positive on plots with and without shrubs; however, this trend was more pronounced for grasses without shrub neighbors than for grasses with shrub neighbors (Figure 3). The contrasting slopes of the ANPP versus PPT lines suggest the competitive influence of *P. glandulosa* shrubs on *B. eriopoda* grasses strengthens with increasing PPT over the rainfall ranges encountered in this study. We hypothesize that intensification of shrub competition with increased PPT may reflect the plastic response of shrub roots to variations in soil moisture availability. *P. glandulosa* plants at the study site have dimorphic root systems, with deep tap roots and lateral roots that extend many times their canopy diameters at depths overlapping grass root systems (Gibbens and Lenz 2001). These shallow coarse lateral roots may opportunistically proliferate fine roots when soil moisture is abundant and curtail this fine root production and lose fine root mass under dry conditions. Competition between grasses and shrubs could thus be more intense when water and other soil resources are more abundant. Such trait-mediated interactions (Callaway and others 2003) have been observed for other dryland plant species (Schwinning and others 2002).

Collectively, the vegetation in our 6-year experiment experienced a dry year with average antecedent conditions (2011); a dry year with dry

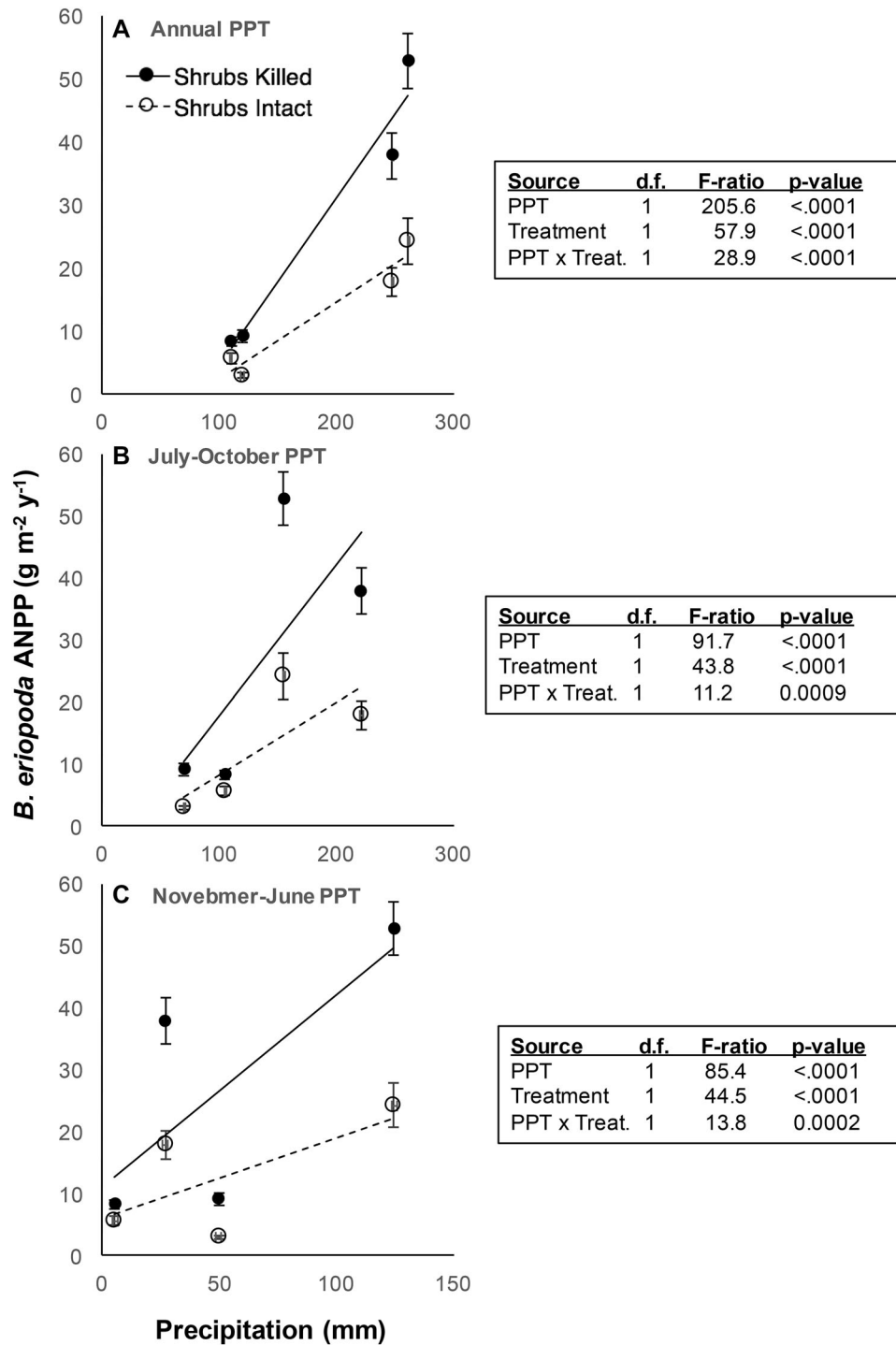


Figure 3. Relationship between precipitation (PPT) and *Bouteloua eriopoda* aboveground ANPP on plots where neighboring shrubs were intact (open circles) or killed (filled circles). **A** Annual PPT; **B** growing season (July–October) PPT; **C** dormant season (November–June) PPT. Analysis of variance summaries are shown beside each panel.

antecedent conditions (2012); a wet year with dry antecedent conditions (2013); and wet years with wet antecedent conditions (2014–2015). Strong seasonality signals also occurred: growing season PPT predominated 2013–2014, whereas rainfall in

2015 was mostly during the cool season when grasses were largely dormant. Our results support those of other research that shows how the intensity of grass-shrub interactions fluctuates as a function of variability in PPT quantity and season-

ality. Grasses tend to respond to precipitation more quickly than shrubs (Jobaggy and Sala 2000), which may portend a competitive advantage for grasses under the highly variable precipitation regimes characteristic of drylands (Soriano and Sala 1984). However, recent studies demonstrate the importance of previous years' precipitation in determining current year's grass productivity, wherein wet antecedent conditions lead to higher production than expected based on current year's precipitation alone, and antecedent dry conditions have the opposite effect (Sala and others 2012). Although consecutive wet years are thus a boon for grass productivity, this timescale would also allow for a positive shrub response to the wet conditions. Our data suggest that shrub competition intensifies in multiple, consecutive wet years to constrain increases in grass ANPP that might otherwise occur. Accordingly, we saw no effect of previous year's PPT on current year's grass ANPP. Winter/spring

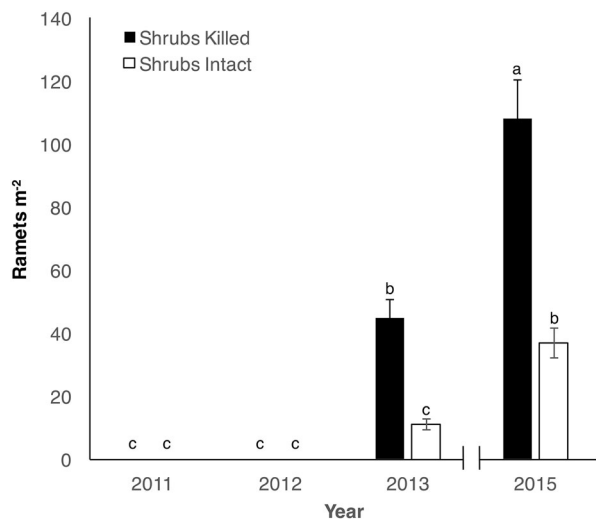


Figure 4. Number of ramets per m^2 in plots with neighboring shrubs intact (open bars) or killed (filled bars); different letters indicate significant ($P < 0.05$) differences among treatments and years (Tukey's HSD). Years with below-average PPT (2011, 2012) had zero ramet production, but were included in the analysis.

PPT could amplify this effect if a significant proportion of rain falls while grasses are dormant, allowing moisture to percolate to deeper soil layers where it is ostensibly less accessible to grasses when their growth resumes and more accessible to shrubs (Walker and Noy-Meir 1982; Ward and others 2013). Moreover, leaf-level carbon and water relations indicate that *P. glandulosa*, a deciduous shrub, physiologically outperforms *B. eriopoda* under conditions of both low and high soil moisture availability, and for a longer portion of the year (Throop and others 2012), providing a possible mechanism by which shrubs outcompete grasses in this study. This is in direct contrast to interactions between *B. eriopoda* and *Larrea tridentata*, an evergreen shrub species featured in studies of grass-shrub interactions in the Chihuahuan Desert. In these studies, *B. eriopoda* had higher leaf-level photosynthetic rates than the shrub following small rainfall events that characterize dryland systems (Pockman and Small 2010), yet *B. eriopoda* cover declines under long-term drought while *L. tridentata* cover remains consistent (Baez and others 2013). Furthermore, precipitation variability along with changes in aridity can favor one grass species over another (Rudgers and others 2018). This suggests that the relative importance of stress tolerance versus competitive ability as a driver of grassland-to-shrubland transitions may vary with grass and shrub species or functional types.

The competitive influence of shrubs on grasses was also apparent via changes in grass patch structural attributes. When shrub neighbors were present, grass patches contracted and became fragmented, and did not rebound to their initial configuration until after three consecutive years of above-average PPT (Figure 5). Plots without shrub neighbors, on the other hand, did not contract/fragment during the dry period, and dramatically expanded/infilled during the wet period. Grass patch size and bare soil connectivity can be used as leading indicators of state transitions in arid systems (Kefi and others 2007; Dakos and others

Table 1. Mean ($\pm$ SE) Values for *B. eriopoda* Patch-Scale Aboveground ANPP ($\text{g m}^{-2} \text{y}^{-1}$), Number of Tillers per m^{-2} , and One-Way ANOVA Results for Differences Between Control and Treatment Plots in 2013

Variable	Treatment		F ratio	P value
	Shrubs intact	Shrubs killed		
ANPP	17.3 (3.1)	37.7 (3.1)	21.4	< 0.0001
Number tillers	145.0 (19.2)	268.1 (19.0)	20.7	< 0.0001

Tiller production was near zero in the dry years of 2011–2012.

2011), and abiotic soil erosion processes are considered the primary drivers of grass patch contraction (Okin and others 2009). Our results demonstrate that biotic interference can also influence grass patch size and level of fragmentation and hence bare soil connectivity and susceptibility to erosion forces.

Grass ANPP is a combined function of the total number of tillers and the mass per tiller, that is, similar productivity could be achieved with fewer large tillers or with a greater number of small tillers. Our results suggest that grass ANPP at the Jornada site was more dependent on the number of tillers. Although the number of 20 cm × 20 cm cells occupied by *B. eriopoda* was similar between control and treatment plots in 2013 (Figure 5), axillary tiller number was higher in plots with shrubs removed than in plots with shrub neighbors intact (Table 1). This could help explain the increasing ANPP difference between control and treatment plots following consecutive years of wet conditions, as current year ANPP is related to previous year tiller density (Reichmann and others 2013).

Some evidence suggests shrub effects on grasses shift from net negative to net positive along gradients of increasing environmental stress (Maestre and others 2009). Annual precipitation at our site during this experiment (216–279 mm) was well below the threshold (479 mm) that has been pro-

posed for this shift (Dohn and others 2013), so our findings of competitive suppression in this arid grass-shrub system do not support this idea. Instead, our results are more in line with predictions that have been reported for grass-woody plant interactions in mesic savanna systems. Shrubs do, however, appear to facilitate some grass species at this Chihuahuan Desert site. Whereas our study focused on *B. eriopoda* patches in areas beyond shrub canopies, *Muhlenbergia porteri* has been observed growing within and seemingly confined to *P. glandulosa* and *Larrea tridentata* canopies (Welsh and Beck 1976). It is unclear if this is because shrubs ameliorate microclimate conditions, enhance nutrient availability, or provide refugia from grazers. This study supported the stress gradient hypothesis in that shrub-on-grass competition intensified with increasing precipitation. However, we detected no facilitative influence of shrubs on grasses. Due to the small stature of *P. glandulosa* shrubs and the occurrence of *B. eriopoda* grass patches beyond their canopies, aboveground shrub facilitation of grasses via environmental amelioration is irrelevant between these species. If *P. glandulosa* at our site carried out beyond-canopy hydraulic redistribution (Bleby and others 2010) as has been shown in other systems (Zou and others 2005), the redistributed water was not utilized by grasses to a degree that overcame soil water competition with shrubs (Barron-Gafford and others 2017).

Land-management practices have long sought to restore herbaceous cover and production in shrub-invaded grasslands using herbicides, mechanical treatments, or prescribed fire. Such treatments often do not produce the expected results, however, and reasons for this are not clear (Archer and Predick 2014). Under the assumption that abiotic factors are largely driving system dynamics, shrub removal at broad scales could be expected to exacerbate grass loss because of increased erosion potential. Similarly, if hydraulic lift was important, removing shrubs could render grasses more susceptible to stresses imposed by grazing and drought. Our results, however, confirm that shrub removal in this Chihuahuan Desert system has the potential to be an effective restoration tool in that grass patches expanded in size, connectivity, and productivity when shrub neighbors were removed. Although not addressed in this study, reducing shrub cover could also reduce the density and/or activity of mammalian herbivores to the benefit of grasses, particularly in dry years when C_3 forbs with large seeds are less available (Daniel and

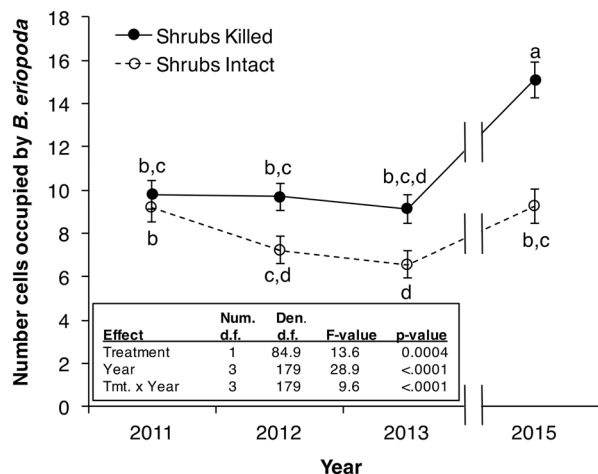


Figure 5. Number of 20 × 20 cm cells per 1 m² plot containing rooted *Bouteloua eriopoda* genets or ramets in control (open circles) and treatment (closed circles) plots; an increase in number of cells occupied represents grass patch expansion/infilling, whereas a decrease represents grass patch size constriction/fragmentation. Different letters denote significant ($P < 0.05$) differences among treatments and dates. Inset: ANOVA summary table of main effects.

others 1993; Whitford 1993; Kerley and Whitford 2009).

Traditional models of grassland–shrubland transition in drylands emphasize changes in disturbance regimes and abiotic feedbacks that promote the degradation of grassland into shrubland (Schlesinger and others 1990, 1996). In this study, we demonstrate that shrub-on-grass biotic interference has the potential to reinforce grazing- and drought-induced stresses on mesophytic grasses that would amplify positive abiotic feedbacks driving grassland–shrubland transition. Accordingly, competitive ability may be as, or more, important than stress tolerance in shaping community structure and function in this arid grassland. Shrub-driven declines in grass cover and production also help explain observations of shrub encroachment into arid grasslands where disturbances related to livestock grazing (Browning and Archer 2011) and fire (O'Connor and others 2014) have been eliminated. Further development of dryland state-and-transition models (for example, Bestelmeyer and others 2011) should incorporate biotic interactions as a mechanistic driver of state change.

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