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ARTICLE

Special Feature: Dynamic Deserts

Extreme drought induces rapid declines in co-occurring native *Bouteloua eriopoda* and invasive *Eragrostis lehmanniana*

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Abstract

Global climate change is expected to result in increased temperatures and variation in precipitation. In the Desert Southwest region of the United States, climate change may result in drier conditions. *Eragrostis lehmanniana* (Lehmann lovegrass) is an invasive species that has extensively colonized the southwestern United States, including *Bouteloua eriopoda* (black grama) grasslands. While both *E. lehmanniana* and *B. eriopoda* evolved in arid conditions, drier conditions may influence this invader–native system in unforeseen ways. Using a combination of precipitation pivot point (PPP) and drought sensitivity (DS) analysis, we compared responses of *B. eriopoda* and *E. lehmanniana* to altered precipitation regimes including long-term drought treatments in the northern Chihuahuan Desert, New Mexico. We defined PPP as the critical point in precipitation amount below which plant percent cover decreased and above which it increased. We used DS, defined as the square millimeters of cover lost when precipitation decreased by 1 mm, to elucidate the direct response of biomass to drought on either side of the PPP. We estimated mean monsoon PPPs of 62.5 and 63.7 mm for *B. eriopoda* and *E. lehmanniana*, respectively. We estimated mean annual (1 October–30 September) PPPs of 108.6 and 108.5 mm for *B. eriopoda* and *E. lehmanniana*, respectively. *Bouteloua eriopoda* mean DS was 4.71 mm^2/mm. *Eragrostis lehmanniana* mean DS was 1.56 mm^2/mm. Results suggest that it is unlikely that extended drought will benefit *E. lehmanniana* over *B. eriopoda* and both species may decline under extreme drought.

KEYWORDS
black grama, Chihuahuan Desert, drought sensitivity, Lehmann lovegrass, plant invasion, precipitation pivot point, Special Feature: Dynamic Deserts

INTRODUCTION

Anthropogenic climate change is forecasted to lead to increasingly warmer temperatures and variable precipitation, with more extreme rain events and longer periods of drought (Intergovernmental Panel on Climate Change [IPCC], 2014). Within arid lands, ecosystem services are predicted to decline due to increased variability in precipitation (Fischlin et al., 2007). As the climate becomes warmer and drier, the effect on plant community composition will be determined by species' relative abilities to adapt to changing environmental conditions (Munson et al., 2011). Introduced plant species that are potentially preadapted to warmer and drier conditions may realize an advantage under novel climate conditions, and such species may contribute to the loss of ecosystem services including loss of arid land native plant species, rangeland grazing, and genetic sources for adaptation (Fischlin et al., 2007).

Changing climate, overgrazing, and soil loss have contributed to arid land degradation in the southwestern United States (Fredrickson et al., 1998). In the 21st century, the aridity of lands in the southwestern United States is projected to normalize at a level equal to the drought of the 1950s (Seager et al., 2007), which was more severe than any other in 350 years (Fredrickson et al., 1998). During this period of drought, the area received 53%–57% of the long-term average annual precipitation (Herbel et al., 1972). Like many other arid and semiarid lands, the northern Chihuahuan Desert experienced a dramatic loss of grasslands (McGlone & Huenneke, 2004).

The ability of plants, whether native or invasive, to rapidly respond to increased drought conditions may govern the impact of invasive plant species in plant communities. Invasive plant species may expand ranges or increase in abundance if the environmental changes are within species tolerance. Conversely, an invasive plant species may decrease in range or population size if it is unable to survive under new conditions. Drought can increase or decrease the native community resistance to invader establishment (Diez et al., 2012). The response of native and invasive plants to global climate change is complex and, especially for invaders, unpredictable (Bradley et al., 2010). Shifts in plant–plant interactions under climatic extremes are species-specific and dependent upon the community composition (Grant et al., 2014), and it is necessary to assess the differential responses of the invader and native species to environmental changes.

Changes in extreme precipitation patterns due to climate change may facilitate or inhibit the spread of invasive *Eragrostis lehmanniana* in native *Bouteloua eriopoda* grasslands. Understanding the interaction between climate change and plant invasion is necessary for the development of policies and programs for natural resource management (Thuiller et al., 2008) and the development of invasive plant management policies and programs (Bradley et al., 2010), especially in arid lands. Furthermore, at small spatial scales, biodiversity is strongly influenced by invasive species, but this effect is variable (Powell et al., 2011), indicating a need for site-specific research into the interaction between climate change and invaded plant communities. Both evolved under arid conditions, albeit on different continents and under different environmental and biological conditions. Understanding how *E. lehmanniana* and *B. eriopoda* may respond to drought is especially important in the Chihuahuan Desert ecosystem, which is susceptible to land degradation (Munson et al., 2013).

The goal of this study was to evaluate the responses of *B. eriopoda* and *E. lehmanniana* to experimentally induced extended drought conditions in the northern Chihuahuan Desert, New Mexico. We predicted that the drought treatments would decrease *B. eriopoda* cover, possibly through mortality. Further, we predicted that under the drought conditions, *E. lehmanniana* would survive and maintain its cover.

MATERIALS AND METHODS

Study site

The study site (latitude 32.516 N, longitude −106.802 W) is at New Mexico State University's Chihuahuan Desert Rangeland Research Center (CDRRC), Doña Ana County, New Mexico (Figure 1). The CDRRC is contiguous with the USDA Jornada Experimental Range, which together comprises the area covered by the Jornada Basin Long Term Ecological Research (JB-LTER) program. Located approximately 37 km northeast of Las Cruces, NM, the climate is arid with a mean annual precipitation of 230 mm, 60% of which occurs as high-intensity, short-duration events in the monsoon season of July, August, and September (Wainwright, 2006). The mean maximum annual temperature is approximately 35°C.

The site is 1375–1379 m above sea level, located at the base of Mt. Summerford on the northern end of the Doña Ana Mountains. This upland grassland is located on the eastern slope of the alluvial fan collar (Monger, 2006) created from the deposition of alluvial particles eroded from the granitic pediment of Mt. Summerford (Wondzell et al., 1996). The soil is coarse-textured with a high percentage of sand and coarse (>2 mm) particles, leading to a high rate of precipitation infiltration (Schlesinger et al., 2000) and percolation to the deeper layers (Duniway et al., 2018). Grazing has been excluded in this

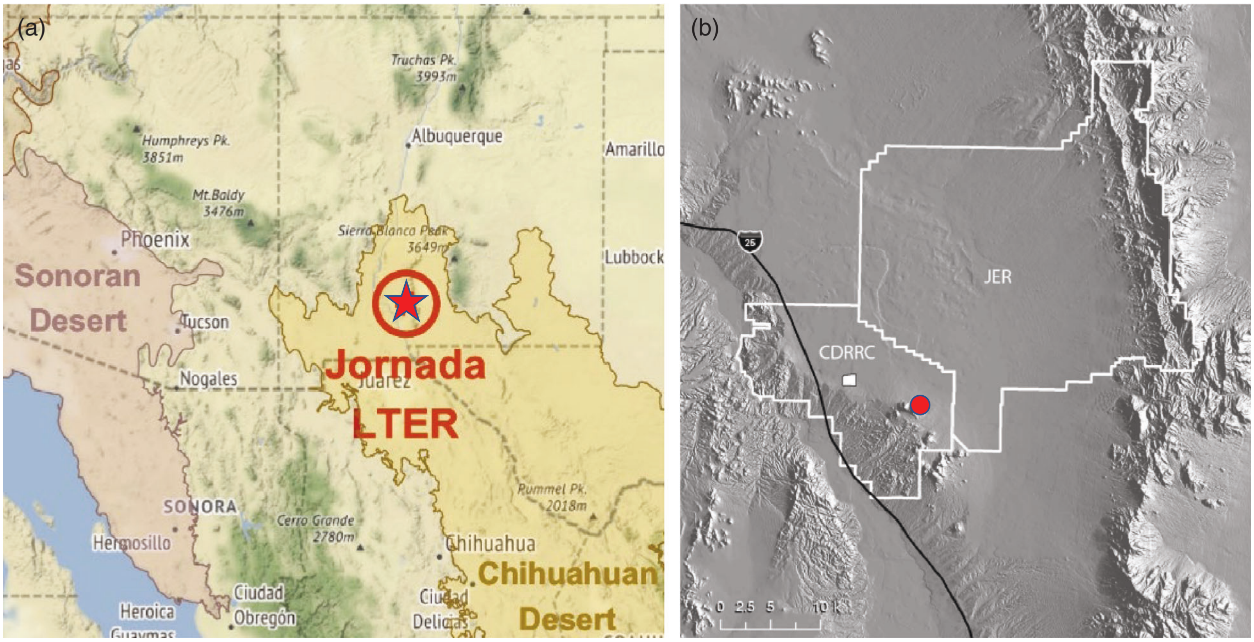

FIGURE 1 (a) Location of the Jornada Basin Long Term Ecological Research (JB-LTER) program (star). (b) Eighteen 4-m^2 experimental plots were established at the New Mexico State University's Chihuahuan Desert Rangeland Research Center (CDRRC), Doña Ana County, New Mexico, 37 km northeast of Las Cruces, NM (circle). The CDRRC is contiguous with the USDA Jornada Experimental Range, which together comprises the area covered by the JB-LTER

site since before 1936, when brush grubbing was used to remove *Larrea tridentata* (creosote bush) and *Flourensia cernua* (tarbush) (Rango et al., 2002). Vegetation is typical of semidegraded lands of the JB-LTER and included both *E. lehmanniana* and *B. eriopoda*, as well as other perennial grasses including *Aristida purpurea* (purple three-awn) and *Sporobolus cryptandrus* (sand dropseed), the shrubs *L. tridentata* (creosote bush), *F. cernua* (tarbush), *Opuntia polyacantha* (plains prickly pear), and *Yucca elata* Engelm. (soaptree yucca), and the forbs *Croton potsii* (leatherweed), *Baileya multiradiata* (desert marigold), and *Amaranthus palmeri* (Palmer amaranth).

Plant species

Bouteloua eriopoda (black grama), a C4 grass that occupies sandy and gravelly dry mesas in the northern Chihuahuan Desert of southern New Mexico, once dominated more than 36 million ha in the southwestern United States (Wright & Streetman, 1958). Overgrazing, shrub encroachment, and drought greatly decreased *B. eriopoda* abundance on the Jornada Experimental Range, with basal area declining by 77% between 1915 and 1979 (Gibbens & Beck, 1988). Bare soil areas, created as native grasslands receded, provided an opportunity for invasive plant establishment (Huenneke et al., 2002) throughout the southwestern United States.

Eragrostis lehmanniana is a South African native C4 bunchgrass that is invasive in the United States. Beginning in 1937, it was introduced into the southwestern United States and northern Mexico to restore degraded rangelands (Cox & Ruyle, 1986). It has formed monospecific stands in many areas of Arizona and New Mexico. In areas surrounding the Jornada Experimental Range, the densest populations are currently found predominantly on alluvial slopes of the Dona Aña Mountains and the nearby mountain ranges, which receive precipitation runoff, potentially indicating it may have reached the extent of its environmental tolerance for low precipitation.

Experimental design and data collection

In June 2016, permanent 2 m × 2 m plots were installed to evaluate change in percent cover of *B. eriopoda* and *E. lehmanniana* in response to precipitation manipulation treatments of +80% (irrigated), −80% (drought), and ambient (control) precipitation. We used a randomized complete block design with six replicates per treatment, with blocks parallel to the slope, for a total of 18 plots. Plot locations were adjusted to exclude ant nests and non-target plant species other than annuals. The cover of other plant species was <1% at the beginning of the study and may not have influenced the cover or responses of the target species. This cover included *Aristida turnipes* (0.13%), *Panicum hallii* (0.20%), and *Sporobolus* spp. (0.15%). At the upslope border of each plot, we installed galvanized flashing to a depth of approximately 11.4 cm to block the surface flow of water onto plots. Metal rebar stakes were driven into the ground at each corner of each plot as permanent markers. A large nail embedded in the center of each plot was used to standardize the placement of data collection frames.

Rainout shelters, constructed according to the design by Yahdjian and Sala (2002), extended 0.5 m beyond the boundaries of the plots. Rainout shelters manipulated precipitation received so that irrigated plots received 180% ambient precipitation, drought plots received 20% of ambient precipitation, and control plots received 100% ambient precipitation. Due to repeated malfunctions including pipe leaks and electronic component failures, the maintenance of the irrigation systems became untenable after 2017. Therefore, irrigation plots were excluded and only control and drought data were included in 2018 and 2019 analyses.

Data were collected in August and September of each year from 2016 to 2019 because this is the peak of growth for these species in this monsoon-driven system. The live green foliar cover for each species was mapped for each plot using four 1-m^2 data collection frames each divided into 16 sections each measuring 0.0625 m^2. These frames were anchored on the nail in the center of the plot for standardized placement.

Precipitation data

Precipitation in the Chihuahuan Desert is very heterogeneous across the landscape (Havstad et al., 2000). Therefore, precipitation data used in this study (Figure 2) were collected from the closest weather station. This weather station, located within 1 km, provided coverage of our study site (Anderson, 2020). Cumulative annual and monsoon precipitation was calculated by summing monthly precipitation between data collection times for 2016–2017, 2017–2018, and 2018–2019. Annual precipitation from. 1 October through 30 September reflected the precipitation available to the plant from the end of one growing season to the end of the next and between data collections. Monsoon precipitation from 1 July through 30 September reflected precipitation available to the plant during the growing season.

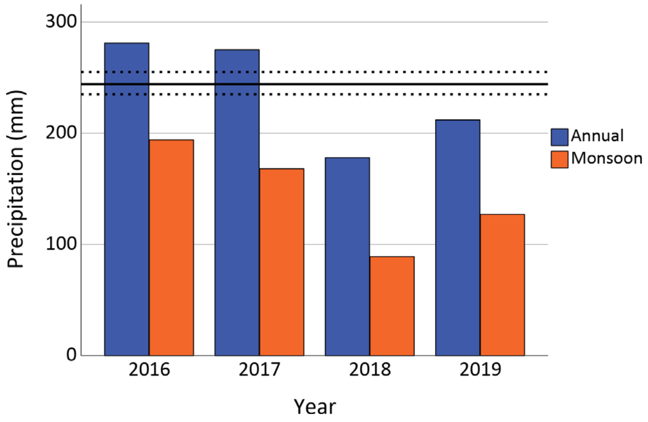

FIGURE 2 Cumulative annual and monsoon precipitation recorded at the Jornada Basin Long Term Ecological Research Wireless Meteorological Station, New Mexico State University Chihuahuan Desert Rangeland Research Center, Las Cruces, NM, USA. Monsoon precipitation was recorded from 1 June to 30 September. Annual precipitation was measured from 1 October to 30 September. Mean annual precipitation from 1915 to 2018 is represented by horizontal lines for the mean (solid) and mean ± SE (dashed)

Data analysis

The live cover data did not meet the ANOVA assumption of normality and were transformed using the log transformation $\ln(x + 1)$ to improve the distribution. Normality of data was assessed pre- and post-transformation with a Shapiro–Wilk test of normality (Shapiro & Wilk, 1965). Levene's test (Levene, 1960) was used to assess the homogeneity of variance before and after transformation, which improved the distribution. These statistics were completed with SPSS Statistics 25 (IBM, 2017).

We used full-factorial repeated-measures mixed model analysis of covariance (SPSS Statistics 25, IBM, 2017) to evaluate annual changes in percent cover for *B. eriopoda* and *E. lehmanniana* in response to precipitation treatments with species, treatment, and year as fixed factors, block as a random factor, and cover values of the other species as a covariate. Data were paired with the precipitation measurements for the same year as cover measurements. Because covariance between *B. eriopoda* and *E. lehmanniana* cover was not significant ($p > 0.05$), we reduced the model for each species to a full-factorial repeated-measures mixed-model ANOVA. Data were subset by species for subsequent analysis because ANOVA results revealed a significant ($p < 0.05$) interaction between species and treatment, indicating species' responses to treatments differed. Significant differences between years were identified using Tukey's honestly significant difference (HSD) post hoc analyses.

Percent change in plant cover was calculated as:

$$\%\Delta = \left(\frac{\text{cover}_2 - \text{cover}_1}{\text{cover}_1}\right), \tag{1}$$

where cover_1 is the plant cover in year 1, and cover_2 is the plant cover in year 2.

All models included cover data from both the drought and control treatments for three sets of years (2016–2017, 2017–2018, and 2018–2019), and six precipitation values paired for the corresponding years. Consequently, six data points of percent change in plant cover were modeled for each precipitation value. Initially, logarithmic regression of these data was used based upon similar work on *B. eriopoda* (Munson et al., 2013). In addition, we used orthogonal polynomial regression with first- to fourth-order polynomials to explore the effects of linear versus curvature terms (Appendix S1: Table S1). For each species, regression models were compared based upon the Akaike information criterion to determine the best-fitting model that did not overfit the data. Regression analysis was carried out in RStudio Cloud (R version 3.6.3; RStudio Team, 2020).

Drought response may be measured directly, described with climate pivot point (CPP) analysis (Munson, 2013; Munson et al., 2015), quantified by drought sensitivity (DS; Cherwin & Knapp, 2012), or a combination of these methods. The CPP is defined as the critical point in environmental conditions below which a plant species decreases, and above which it increases, in abundance (Munson, 2013) or biomass. Analysis of CPP has been used to predict the effect of elevated temperatures and drought on plant communities and plant species in the Chihuahuan (Munson et al., 2013), Sonoran (Munson et al., 2012), and Mojave (Munson et al., 2015) Deserts. We only used the precipitation component of the CPP method to calculate the precipitation pivot point (PPP), which identifies the critical point in precipitation below which a plant species decreases in cover and above which it increases. Drought sensitivity analysis is a subset of climate variability models, which have been used at varying spatial and community scales to determine plant response to increasingly arid conditions (Kleinhesselink & Adler, 2018; Knapp et al., 2015). We defined DS as the square millimeters of cover lost when precipitation decreased by 1 mm. Both PPP and DS are valuable indices to compare plant drought responses and to predict potential drought outcomes in native–invader plant communities.

To provide a point estimate of the direct response of biomass, DS (Equation (2)) was calculated from the control–drought pair within each block. Drought sensitivity equals the square millimeters of cover lost when precipitation decreases by 1 mm and was calculated as:

$$\text{DS} = \left[\frac{\left(\text{cover}_{\text{control}} - \text{cover}_{\text{drought}}\right)}{\left(\text{precipitation} \times 1.0\right) - \left(\text{precipitation} \times 0.80\right)}\right] \times 100, \tag{2}$$

where $\text{cover}_{\text{control}}$ and $\text{cover}_{\text{drought}}$ are the cover values in square millimeters produced in the control and drought treatments within one block, respectively; precipitation is the amount (in millimeters) received in a given year under ambient conditions; and precipitation × 0.80 is the amount of precipitation removed from the ambient precipitation by the rainout shelter. Difference in mean DS was analyzed with a one-way ANOVA (SPSS 25; IBM, 2017). Data were $\log_{10}$ transformed prior to analysis to meet normality ($\text{Shapiro–Wilk}_{24} = 0.934$, $p = 0.120$) and homoscedasticity (Levene's $\text{statistic}_{[1,22]} = 0.594$, $p = 0.449$) assumptions.

RESULTS

Precipitation

Annual precipitation at the site (Figure 2) was below average in 2018 and 2019. During 2018, the low amount of precipitation created a localized drought (Anderson, 2020).

Plant cover

There were no differences in percent cover between control, drought, and irrigated treatments for *B. eriopoda* from 2016 to 2017 ($p = 0.555$). Differences between the control and drought treatments became apparent in 2018 ($p < 0.001$, $F_{2,20} = 14.372$) and continued in 2019 (Figure 3). Under the drought treatment, *B. eriopoda* cover decreased from 10.4% to 1.7% between 2017 and 2018. In 2018, standing dead or dormant biomass remained in plots with zero live green cover. In 2019, the live green cover was produced in patches that were recorded in 2018 as containing only standing dead or dormant biomass.

There were no differences between control, drought, and irrigated treatments in percent cover for *E. lehmanniana* from 2016 to 2018 ($p = 0.644$), but differences between the control and drought treatments became apparent in 2019 ($p = 0.012$, Figure 3). Under drought treatment, *E. lehmanniana* live green cover

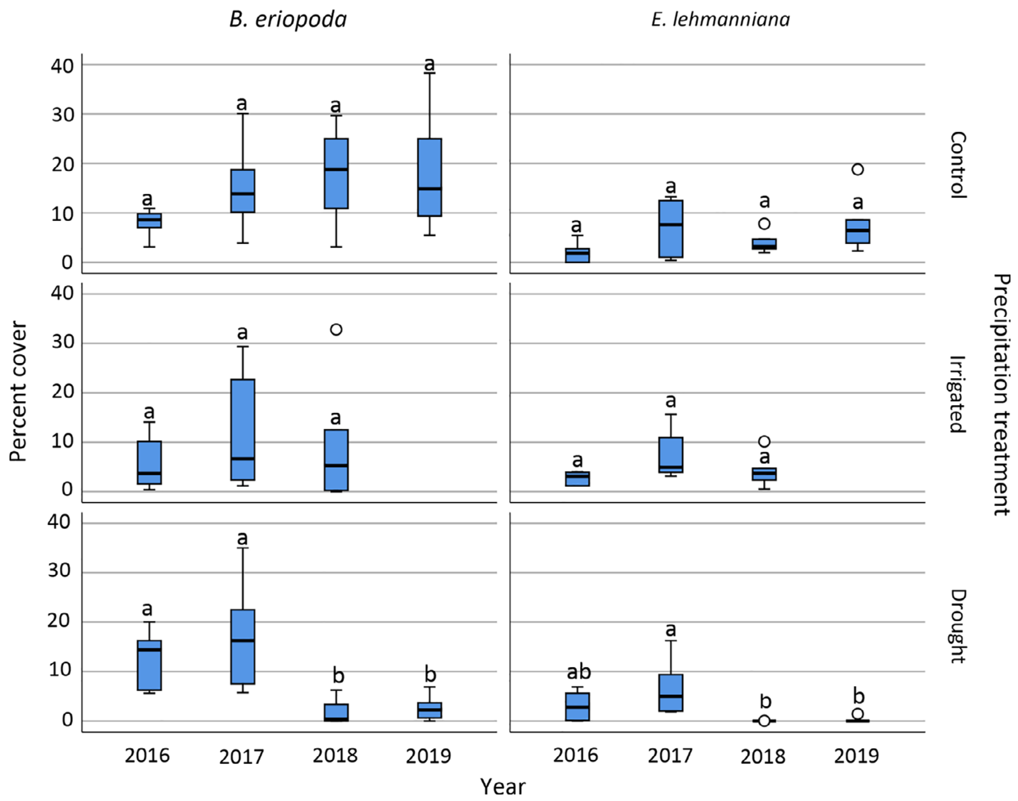

FIGURE 3 Percent cover of *Bouteloua eriopoda* and *Eragrostis lehmanniana* under control, irrigated, and drought treatments across 4 years. Different letters indicate the difference in percent cover ($p < 0.05$) within species and treatment, as determined by Tukey's HSD. $n = 6$ per treatment. Irrigated treatments were discontinued after 2018

decreased from 2.5% to 0% in 2018 and did not produce any live foliage in 2019.

Precipitation pivot point

Logarithmic regression indicated that there was a significant positive relationship between precipitation and change in plant cover (Appendix S1: Figure S1). However, it was not clear that the curvature in the model provided the best fit. Orthogonal polynomial regression analysis indicated that the response of both species to precipitation was linear (Figure 4). None of the higher order polynomial terms was significant or upon visual inspection appeared to overfit the data. Thus, the linear model was used for subsequent analyses. Slopes were not significantly different for annual and monsoon precipitation or between species. *Bouteloua eriopoda*'s mean PPP (monsoon = 62.5 mm, range: 10.1–89.2 mm; annual = 108.6 mm, range: 13.2–157.2 mm) was similar to *E. lehmanniana*'s mean PPP (monsoon = 63.7 mm, range: 18.9–86.5 mm; annual = 108.5 mm, range: 25.3–150.9 mm) for both monsoon and annual precipitation, but within species, PPP values differed between monsoon and annual precipitation (Table 1). These models explained 22%–32% of the variation observed.

Drought sensitivity

Bouteloua eriopoda mean DS was 4.71 (SD = 3.37) mm^2/mm, and *E. lehmanniana* mean DS was 1.56 (SD = 1.04) mm^2/mm (Figure 5). Drought sensitivity differed between species ($p = 0.005$, $F_{1,22} = 9.586$).

DISCUSSION

Our research evaluated the potential implications of increased aridity due to climate change in an *E. lehmanniana*-invaded *B. eriopoda* grassland community located on an alluvial fan collar. We evaluated plant cover changes of *B. eriopoda* and *E. lehmanniana* under altered precipitation regimes including extreme drought conditions created with rainout shelters from 2016 through 2019 in the northern Chihuahuan Desert, New Mexico. Based on cover data, we quantified the cover response of each species to simulated drought. Our

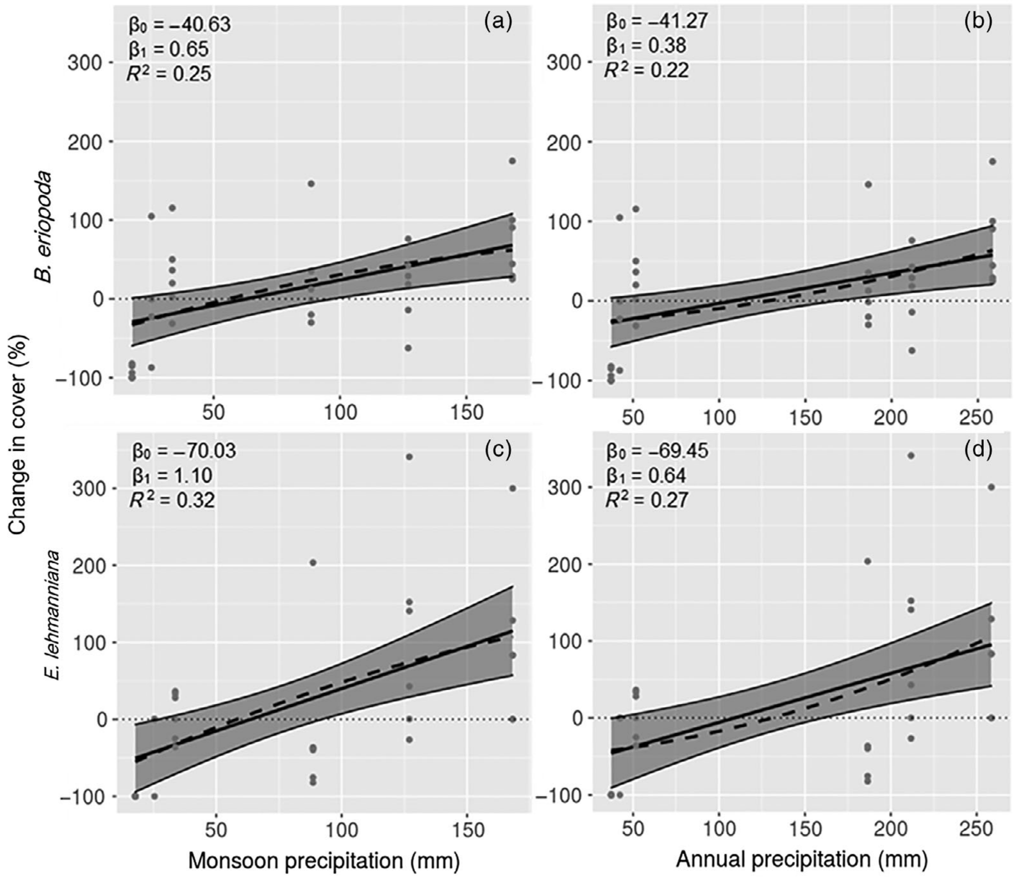

FIGURE 4 Responses of *Bouteloua eriopoda* (a, b) and *Eragrostis lehmanniana* (c, d) cover to annual (a, c) and monsoon (b, d) precipitation. Solid lines represent linear models, dashed lines represent the second-order polynomial models, and dotted lines indicate zero percent change in cover. Data for each panel are change in cover in drought ($n = 6$) and control ($n = 6$) plots over 3 year-pairs, 2016–2017, 2017–2018, and 2018–2019, for a total of 36 points. Parameter estimates are for linear models

TABLE 1 Coefficients of the predictors for linear models of percent change of cover for *E. lehmanniana* and *B. eriopoda*, with intercept and slope SE in parentheses, coefficients of determination, precipitation pivot points (PPPs), and lower and upper limits of PPP 95% CI

						PPP range	
Species	**Precipitation**	**β_0 (SE)**	**β_1 (SE)**	**R^2**	**PPP (mm)**	**Lower**	**Upper**
Eragrostis lehmanniana	Annual	−69.45 (27.16)	0.64 (0.17)	0.27	108.5	25.3	151.0
	Monsoon	−70.03 (25.14)	1.10 (0.26)	0.32	63.7	18.9	86.5
Bouteloua eriopoda	Annual	−41.27 (18.48)	0.38 (0.12)	0.22	108.6	13.3	157.2
	Monsoon	−40.63 (17.37)	0.65 (0.18)	0.25	62.5	10.1	89.2

expectations were that the drought treatments would decrease *B. eriopoda* cover, possibly through mortality, while *E. lehmanniana* would survive and maintain its cover. Instead, we found that both *B. eriopoda* and *E. lehmanniana* suffered decreased cover and mortality. Though PPPs were apparently equal between species, *E. lehmanniana*'s DS was lower than that of *B. eriopoda*.

Plant cover

Results of studies on the relationship between *B. eriopoda* and water availability in the Chihuahuan Desert are varied. For example, Muldavin et al. (2008) attributed summer and fall primary productivity patterns of *B. eriopoda* and other C4 grasses to soil moisture in the top 30 cm of soil. In this study by Muldavin et al., the annual net

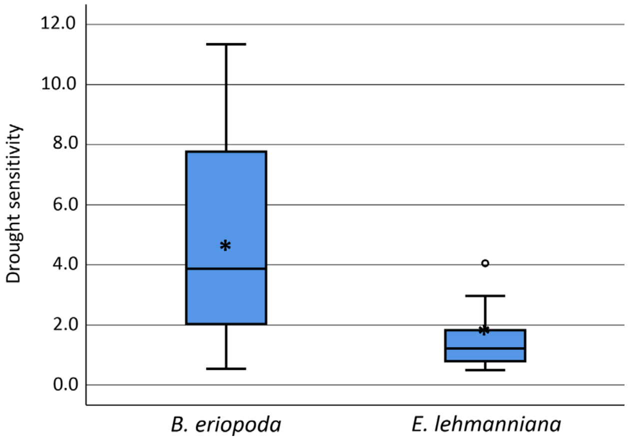

FIGURE 5 Sensitivity of *Bouteloua eriopoda* and *Eragrostis lehmanniana* to drought treatment. Drought sensitivity (DS) is defined as square millimeters reduction in cover per millimeter reduction in precipitation. The boxes represent 25%–75% interquartiles. The bold black lines inside the box represent the medians. Top and bottom whiskers indicate the maximum and minimum values, respectively. Open circles indicate outliers. Asterisks represent mean DS. Drought sensitivity differed between species ($p < 0.005$, $F_{1,22} = 9.586$). $n = 6$ per treatment. Precipitation data include 2016–2017, 2017–2018, and 2018–2019

primary productivity patterns of these grasses were reflective of annual precipitation with no lag in response. Munson et al. (2013) determined that *B. eriopoda* net primary production was more closely linked to summer than to annual precipitation. More recently, Reichmann and Sala (2014) showed a legacy effect of the prior years' precipitation. The studies by Muldavin et al. (2008), Munson et al. (2013), and Reichmann and Sala (2014) were carried out in different sites on different landforms and geographic scales.

We have shown the effect of extended year-round extreme drought on live cover of *B. eriopoda* and *E. lehmanniana*. It is important to note that the effect of cool-season drought combined with low temperatures may have differential effects on these two species at our site. Hamerlynck et al. (2012) determined that cool-season drought had a greater effect on *E. lehmanniana* than on native grasses, and when combined with sub-freezing temperatures, cool-season drought induces greater mortality in *E. lehmanniana* than in native grass species. *Eragrostis lehmanniana* has the ability to respond to cool-season precipitation by producing green growth (Cable, 1971) unless air temperatures are low (Cox et al., 1990). Because *B. eriopoda* does not have the same response, it is likely that cool-season drought has a greater influence on *E. lehmanniana* survival than on *B. eriopoda* survival. Cool-season rainout shelter research is needed to ascertain the relative influence of drought seasonality on drought response in these two species in this community.

We found a response to drought that was similar to that observed by others. For example, an 82.2% reduction in precipitation resulted in mortality of *B. eriopoda* similar to that of *E. lehmanniana* during a natural drought in winter 1988 and spring 1989 in Pima County, AZ (Robinett, 1992). The lack of difference between treatments in *B. eriopoda* and *E. lehmanniana* percent cover may be attributed to the annual precipitation amounts received at the site in 2017 and 2018. In 2016 and 2017, annual precipitation was well above, and in 2018, well below the long-term average of the site. Because the rainout shelters are designed to remove 80% of precipitation, our results may indicate that there is a threshold of precipitation above which no drought effects manifest.

Plant responses to drought are influenced by soil type and physical characteristics (Hamerlynck & McAuliffe, 2008; McAuliffe & Hamerlynck, 2010). The geologic and soil properties of our site may have been responsible for the differences between our results and other similar studies (e.g., Muldavin et al., 2008; Munson et al., 2013; Reichmann & Sala, 2014). This upland grassland is located on an alluvial fan collar (Monger, 2006) of Mt. Summerford. The collar is the topmost area of the alluvial fans, which was created from the deposition of alluvial particles eroded from the granitic pediment of Mt. Summerford (Wondzell et al., 1996). It is characterized by high run-on, high infiltration, and low runoff (Wondzell et al., 1996). The alluvial sedimentary soil is coarse with a high percentage of sand and coarse (>2 mm) particles, leading to a high rate of infiltration and percolation to the deeper layers (Duniway et al., 2018).

Our results were very similar to those of Griffin-Nolan et al. (2019) in which 4-year 66% drought treatment resulted in the mortality of >95% of *B. eriopoda*. Under a long-term 80% reduction in precipitation, it is unlikely that mature plants of either *B. eriopoda* or *E. lehmanniana* will survive. The appearance of some live green cover under the drought treatment in 2019 may indicate that a mature *B. eriopoda* is more resilient than *E. lehmanniana* to extreme drought conditions. While conditions supporting *B. eriopoda* reproduction are rare (Peters, 2000), large numbers of highly viable *E. lehmanniana* seeds exist in the seedbank (Sumrall et al., 1991). Robinett (1992) reported that *E. lehmanniana* population flourished via germination and establishment after a severe drought. Therefore, if the ability of *B. eriopoda* to survive drought through dormancy confers any population-level advantage, it is likely offset by the greater reproductive ability of *E. lehmanniana*.

Precipitation pivot point

The relationship between drought response and plant cover is complicated by plant morphology and growth form, and plant responses to climatic variation may be influenced by plant maturity and size. Drewa et al. (2006) defined *B. eriopoda* clones as distinctive clumps separated from others by more than 3 cm and identified clones that were 30–350 cm in basal diameter on the Jornada Experimental Range. In contrast, *E. lehmanniana* has smaller plant basal areas (Moran et al., 2009) than clones of *B. eriopoda*. In a glasshouse experiment, Fernández et al. (2002) reported that in drought-exposed, similarly sized, *B. eriopoda* and *E. lehmanniana* individuals, final biomass was reduced by 60% and that the species exhibited similar drought responses. Therefore, to account for the potential interaction between drought response and biomass, we standardized by using percent change of cover of the prior year for our PPP analysis. This allowed us to account for differences between species in initial cover. Future research should address the response of mature *B. eriopoda* and *E. lehmanniana* plants to imposed drought to elucidate the influence of individual plant size on drought response.

Our results differed from those of Munson et al. (2013), likely because of the differences in geomorphic variation. Munson et al. (2013) drew on data from eight sites in New Mexico, Texas, and Mexico. Within the Chihuahuan Desert, Munson et al. (2013) used data from five sites ranging from Big Bend National Park in southern Texas to Sevilleta National Wildlife Refuge in central New Mexico and including the Jornada Experimental Range. These sites encompassed a range of geomorphic features, while our study was specific to an alluvial fan collar on the Jornada Experimental Range. The difference between our PPPs and those of Munson et al. (2013) was not attributed to the greater range in precipitation values derived from our drought treatments. When calculated from ambient-only precipitation values in our study, neither monsoon nor annual PPP was similar to that of Munson et al. (2013) (Appendix S1: Figure S1 and Table S2).

Grasslands may respond more quickly to long-term drought than shrublands, indicated by PPPs. For example, Scott et al. (2015) determined that the carbon balance PPP for Walnut Gulch Kendall grassland, in which *E. lehmanniana* and *B. eriopoda* were dominant grass species, showed a positive carbon balance pivot point offset, indicating that the ecosystem had already adjusted to the change in precipitation over the last 10 years. Because this response is not uniform across all desert grassland ecosystems (Scott et al., 2015), our research can be used as a starting point for exploring the effect of drought on changing PPPs in our ecosystem.

Drought sensitivity

High plant diversity contributes to ecosystem resistance and resilience to environmental extremes (Isbell et al., 2015). Knapp et al. (2015) showed that grassland DS is inversely related to mean annual precipitation; as precipitation increased, DS decreased. In response to 1 year of 40% decrease in precipitation, *B. eriopoda*-dominated grasslands in New Mexico had the highest DS of North American grasslands, attributed to the DS of *B. eriopoda* (Knapp et al., 2015). Knapp et al. (2015) estimated the DS of *B. eriopoda*-dominated grasslands in New Mexico at $>0.7\ \mathrm{g \cdot m^{-2} \cdot mm^{-1}}$, which converts to 2.65 $\mathrm{mm^2/mm}$ (Reichmann & Sala, 2014). This was intermediate between our species-specific DS values for *B. eriopoda* (4.71 $\mathrm{mm^2/mm}$) and *E. lehmanniana* (1.56 $\mathrm{mm^2/mm}$). We have shown that DS responses can be evaluated per individual species.

The overlap in ranges of *B. eriopoda* and *E. lehmanniana* DS indicates that both species may be considered important biotic influences on the DS of this ecosystem. Additional research is needed to address both the biotic and abiotic mechanisms that influence the DS of this ecosystem (Knapp et al., 2015). In our study, perennial plant diversity was very low, and annual forbs and grasses were extremely short-lived due to drought during the experiment. Therefore, it is unlikely the community drought response differs from that of *B. eriopoda* and *E. lehmanniana* and we believe the drought responses of *B. eriopoda* and *E. lehmanniana* are representative of the community response to drought. However, future research may address the relative contribution of these two species to drought resistance by including additional perennial and annual plant species in a similar experimental design in this plant community.

While drought may temporarily halt *E. lehmanniana* invasion or reduce *E. lehmanniana* biomass production, these reductions in *E. lehmanniana* performance disappear with a return to normal precipitation (Scott et al., 2015). The characteristics that make *E. lehmanniana* a successful invader may allow populations to overcome extended drought in response to returning precipitation. These characteristics, including copious seed production and distribution (Anable et al., 1992), high seed desiccationtolerance (Emmerich & Hardegree, 1996), long seedbank persistence (Voight et al., 1996), increased seed production in response to drought (Fernández and Reynolds, 2000), and ability to germinate in response to moisture (Tapia & Schmutz, 1971), need to be investigated under conditions of returning precipitation after extended drought conditions.

CONCLUSIONS

If *E. lehmanniana* was better adapted to drought than *B. eriopoda*, we expected *E. lehmanniana* to show a less dramatic reduction in percent cover than *B. eriopoda*. Conversely, if *B. eriopoda* was better adapted to drought than *E. lehmanniana*, *E. lehmanniana* would have shown a greater reduction in percent cover than *B. eriopoda*. A combination of PPP and DS (Cherwin & Knapp, 2012) analyses provides insight into native–invader plant community responses to prolonged drought. This research contributes toward understanding (1) whether extended drought might benefit *E. lehmanniana* populations, (2) whether *E. lehmanniana* has drought tolerance superior to *B. eriopoda*, and (3) how these two species will respond as the climate becomes drier.

While it is unlikely that future droughts will reduce precipitation to the levels applied in this study, we have estimated the response *B. eriopoda* and *E. lehmanniana* will likely have as precipitation decreases due to climate change. We have concluded that it is unlikely that extended drought will benefit *E. lehmanniana* populations, *E. lehmanniana* and *B. eriopoda* have similar responses to drought, and both species will decline as the climate becomes drier. This study used an extreme level of experimental drought (i.e., 80% reduction in precipitation) to quantify the effects of drought on *B. eriopoda* and *E. lehmanniana*. The use of an extreme drought treatment provides future opportunities to evaluate the post-drought recovery of each species in our plots when drought is decreased incrementally.

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CONFLICT OF INTEREST

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

AUTHOR CONTRIBUTIONS

Conceptualization: Erik A. Lehnhoff. *Methodology*: Erik A. Lehnhoff and Sherri L. Buerdsell. *Investigation*: Sherri L. Buerdsell and Erik A. Lehnhoff. *Data analysis*: Sherri L. Buerdsell and Brook G. Milligan. *Writing—original draft*: Sherri L. Buerdsell. *Writing—review and editing*: Erik A. Lehnhoff and Brook G. Milligan. *Funding acquisition*: Erik A. Lehnhoff. All authors have read and agreed to the published version of the manuscript.

DATA AVAILABILITY STATEMENT

Data (Buerdsell et al., 2022) are available from Dryad: https://doi.org/10.5061/dryad.n02v6wwzd.

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