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RESEARCH ARTICLE

Extreme drought has limited effects on soil seed bank composition in desert grasslands

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Abstract

Question: Does climate change affect vegetation and seed bank composition in desert grasslands?

Location: Sevilleta National Wildlife Refuge, New Mexico, USA.

Methods: Vegetation and seed bank species composition were recorded in black grama (*Bouteloua eriopoda*) and blue grama (*Bouteloua gracilis*) grasslands. At each site, two rainfall manipulations and ambient controls were established in 2013 ($n = 10$). Treatments included extreme drought (−66% rainfall reduction during the growing season) and delayed monsoon (precipitation captured during July–August and re-applied in September–October). Above-ground species composition was assessed, and composite soil samples were collected in 2017, five years after the experiment started. Seed bank was evaluated using the seedling emergence method.

Results: Rainfall treatments increased the above-ground vegetation and seed bank richness in the blue grama community, but not in the black grama community. Vegetation cover was reduced by both rainfall manipulations, but seed bank density increased or remained the same compared with controls. In above-ground vegetation, cover of annual and perennial forbs increased, and dominant perennial grasses decreased under drought. In the soil seed bank, species composition was similar among all treatments and was dominated by annual and perennial forbs.

Conclusions: The seed bank was more resistant to drought than above-ground vegetation. Because seed banks can enhance long-term community stability, their drought resistance plays an important role in maintaining ecosystem processes during and following drought in these grassland communities.

KEYWORDS
Black grama (*Bouteloua eriopoda*), Blue grama (*Bouteloua gracilis*), delayed monsoon, desert grassland, extreme drought

1 | INTRODUCTION

At a global scale, all ecosystems are, and will continue to be, impacted by global change, including alterations in temperature and precipitation, and more frequent and severe periods of climatic extremes (Min et al., 2011; Smith, 2011). The magnitude of climate change, and alterations in precipitation and temperature at a regional scale, are reasonably well constrained (Solomon et al., 2007; Schoof et al., 2010). However, local ecosystems vary dramatically in their response and sensitivity to changes in climate (Smith et al., 2009; Luo et al., 2011; Maurer et al., 2020) and there is a lack of knowledge about how ecosystems will respond to many aspects of climate change, including prolonged severe drought and changes in precipitation seasonality.

In southwestern North America, climate models predict a global increase in temperature (Gutzler & Robbins, 2011), whereas the effects of climate change on precipitation vary regionally and remain harder to forecast. Rainfall in this region is dominated by the North American Monsoon during which 60% of annual rainfall occurs from July through September following a two-month hyper-arid period with high temperatures and low average rainfall (Notaro et al., 2010). In general, models predict an increase in the frequency of extreme events, which is already evident in the climate record (Zhang et al., 2021). Of greater concern, climate models indicate a >90% probability of decadal scale, severe drought by the end of the century (Cook et al., 2015). Although models forecast little change in average summer precipitation, a change in the seasonality of the summer monsoon is predicted to occur, with decreased precipitation in June and July and more precipitation in September and October effectively extending the hyper-arid period (Solomon et al., 2007; Cook & Seager, 2013; Cook et al., 2015).

Changes in rainfall event size and lengthening the time between rain events may have several impacts on community composition and diversity (Knapp et al., 2002; Miranda et al., 2009; Talmon et al., 2011). In grassland ecosystems, droughts can rapidly alter plant community composition (Fynn & O'Connor, 2000) and ecosystem functioning (Wilcox et al., 2020). Drought can decrease the abundance of dominant perennial grasses (Báez et al., 2013), and increase the abundance of annual and perennial forbs during the drought and after it ends (Milton & Dean, 2000; Hodgkinson & Müller, 2005; Porensky et al., 2013; O'Connor, 2015; Munson et al., 2016; Swemmer et al., 2018). However, during drought, composition of the soil seed bank can give a more complete idea of how vegetation and seed production responds to extreme events (DeMalach et al., 2021). Seeds of many species have a bet-hedging strategy in unpredictable environments (Metz et al., 2010; Gremer & Venable, 2014; Tomiolo et al., 2020), maintaining a fraction of dormant seeds for future germination opportunities as an insurance against reproduction failure (Venable, 2007; Saatkamp et al., 2013). Therefore, seed banks may serve as a source of ecosystem resilience (Gremer & Venable, 2014; Ma et al., 2021), yet the response of this component of the plant community to climate change is rarely estimated in perennial-dominated dry grasslands.

Many seeds can withstand a much wider range of environmental conditions than adult plants, especially extremes of drought and temperature (Fenner & Thompson, 2005; Olano et al., 2012; Ooi et al., 2012). The ability of seeds to persist in a state of diapause during long periods gives them the ability to survive persistent periods of unfavorable climate conditions (Venable, 2007). Changes in above-ground plant species composition can be accelerated or decelerated by dry years (Kimball et al., 2010; Loydi et al., 2012; Funk et al., 2018). At the same time the soil seed bank may determine resilience of the community once drought ends. Nonetheless, the similarity between established vegetation and the soil seed bank is usually low (Hopfensperger, 2007). Moreover, seed rain can change due to drought since seed production may be reduced for some species but not for others (Zeiter et al., 2016) altering the composition of the seed bank. Large differences between below- and above-ground vegetation may cause a shift in species composition over the long term (Saatkamp et al., 2013). Thus, changes in the soil seed bank in response to drought can yield information on how total community composition may change following drought and, as a consequence, how other ecosystem attributes may change as well.

Many grasslands experience a complex disturbance regime that includes grazing, fire and periodic drought (Collins et al., 1998; Smith et al., 2016; Ratajczak et al., 2019). This complex disturbance regime partly determines the persistence of soil seed banks (Fenner & Thompson, 2005), and grassland species exhibit a wide spectrum of seed longevity. How seed bank composition and persistence are affected by drought remains relatively unknown since many factors may influence seed bank persistence and development. Yet, understanding how seed banks are affected by drought is important for restoration and community resilience following extreme climatic events. Current knowledge indicates the seed banks enhance the persistence of plant species particularly in ecosystems with recurrent disturbances (Olano et al., 2012). In arid systems, pulses of rain promote germination (Holmgren et al., 2006; Ooi et al., 2009), but if follow-up rains are not sufficient, or if high soil temperatures reduce humidity, seedling recruitment could fail, depleting the seed bank (Ooi, 2012).

Although numerous rainfall manipulation experiments have been conducted recently (Beier et al., 2012; Gherardi & Sala, 2013; Knapp et al., 2017), very few have studied how drought affects the soil seed bank. The seed bank is an important feature of plant communities, but seed persistence depends on several factors. Persistence is often species-specific, and viability will depend on environmental conditions (Ma et al., 2020). For example, some seeds germinate rapidly following a small moisture pulse (Nenzhelele et al., 2018; Siebert et al., 2020), but subsequent dry conditions may reduce their survival (Ooi et al., 2009). In contrast, those species with permanent seed banks and with bet-hedging strategies (i.e., with a high proportion of dormant seeds) have increased chances of survival during drought (Venable, 2007). Consequently, seed bank composition after drought can change, which can affect plant community composition after the dry period ends. Therefore, understanding how seed banks will respond to drought or changes in precipitation seasonality is particularly important for community composition and ecosystem functioning in dryland ecosystems. In the context of current climate change, knowing the response of the seed bank in dry environments is crucial to predict how these vulnerable ecosystems may respond in the future.

In this study, we used a multi-year field experiment in two semi-arid grassland ecosystems to determine the effects of drought and changes in precipitation seasonality on above-ground vegetation and soil seed bank communities. We hypothesized that vegetation and seed bank richness and diversity would decline with drought and species composition would change as the abundance of short-lived annual species increased with drought.

2 | METHODS

2.1 | Study area

This study was conducted at the Sevilleta National Wildlife Refuge (SNWR), a 100,000 ha area located along the Rio Grande Valley in central New Mexico, USA. The area was grazed by domestic cattle until 1973. Mean annual temperature at the study site is 13.2°C and average annual precipitation is 226.8 mm (1989–2018), approximately 60% (136 mm) of which occurs during the monsoon season from June through September (Notaro et al., 2010). Average annual precipitation during the experimental drought (2013–2017) was 230.9 mm and average monsoon precipitation was 150.6 mm. Soils are highly erodible Typic Haplargids derived from piedmont alluvium. Soil texture in the upper 20 cm, where root biomass is concentrated (Kurc & Small, 2007), is 68% sand, 22% silt, and 10% clay, with 2% calcium carbonate (Kieft et al., 1998). Water-holding capacity and nutrient reserves are very low (Zak et al., 1994).

The SNWR is located at the ecotone between Chihuahuan Desert and Great Plains grasslands at an elevation of ~1,600 m. The Great Plains grassland is dominated by blue grama (*Bouteloua gracilis*), whereas the Chihuahuan Desert grassland is dominated by black grama (*Bouteloua eriopoda*) (Kröel-Dulay et al., 2004). At both sites, vegetation covers about 60% of the soil surface (Pockman & Small, 2010) with plant interspaces supporting cyanobacterial crusts (Fernandes et al., 2018; Baldarelli et al., 2021). The sites differ in plant species richness (76 and 60 species in the above-ground vegetation at the blue and black grama sites, respectively), response to climate variability (Rudgers et al., 2018), and sensitivity to drought (Knapp et al., 2015). Vegetation dynamics across this ecotone depend strongly on short- and long-term fluctuations in precipitation (Muldavin et al., 2008; Collins & Xia, 2015; Mulhouse et al., 2017), and long-term data show that the Chihuahuan Desert species, black grama, is expanding at the expense of blue grama as aridity increases (Collins et al., 2020). Thus, it is important to determine how predicted climate change (chronic drought or changes in seasonality) will affect vegetation dynamics across this ecotone in the future.

2.2 | Experimental design

The experiment consisted of two rainfall manipulations and a control (ambient rainfall) in both Great Plains and Chihuahuan Desert grasslands (from now on referred to as blue and black grama sites respectively; Figure 1). The two sites are approximately 5 km apart with similar climate and soils (Ladwig et al., 2021). The two rainfall manipulations at each site were drought and a delayed monsoon treatment. The drought consisted of a 66% reduction in growing season (April through mid-September) precipitation over five growing seasons (2013–2017) using rainfall manipulation shelters (Yahdjian & Sala, 2002). For the drought treatment, 15.25-cm wide transparent polyethylene slats were arrayed at a spacing that reduced each rainfall event by 66%, thereby maintaining the natural precipitation pattern of each site (Knapp et al., 2017). This was the equivalent of a ca. 50% reduction in annual precipitation because 60%–75% of annual precipitation falls during the growing season. These passive shelters mimic rainfall patterns found during actual droughts (Knapp et al., 2015) and reflect the impacts of multi-year severe drought as predicted for this region by climate models (Cook et al., 2015).

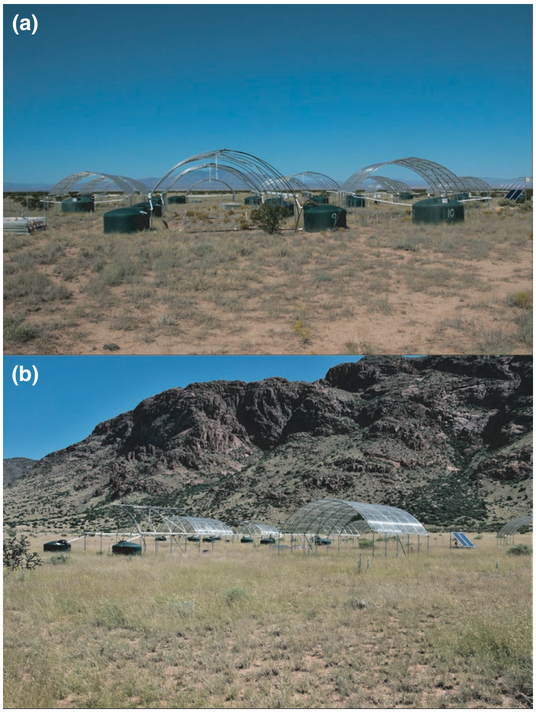

FIGURE 1 General view of (a) the black grama site and (b) the blue grama site

For the delayed monsoon, complete rainout shelters made of transparent polyethylene panels that covered the entire plot were deployed and all rain during July and August was captured in gutters and stored in opaque 4,165-l water tanks. The roof structures were removed 1 September each year and all water captured during summer was added onto each plot in several medium and large rain events (depending on total July–August rainfall) during September and early October using a pump and overhead sprinkler system with raindrop quality sprinkler heads. In 2017 a total of six watering events ranging in size from 10 to 30 mm were applied in September and October at each site. Thus, these plots received the same amount of precipitation as ambient rainfall, but under different seasonality simulating a situation in which the summer monsoon occurs later in the year, as predicted by models of climate change for this region (Cook & Seager, 2013).

Each site consisted of thirty 5 m × 5 m experimental areas ($n = 10$ plots per treatment) plus a 1-m buffer to allow access to the plots and minimize edge effects associated with the infrastructure. Each experimental site was established in relatively level, homogeneous

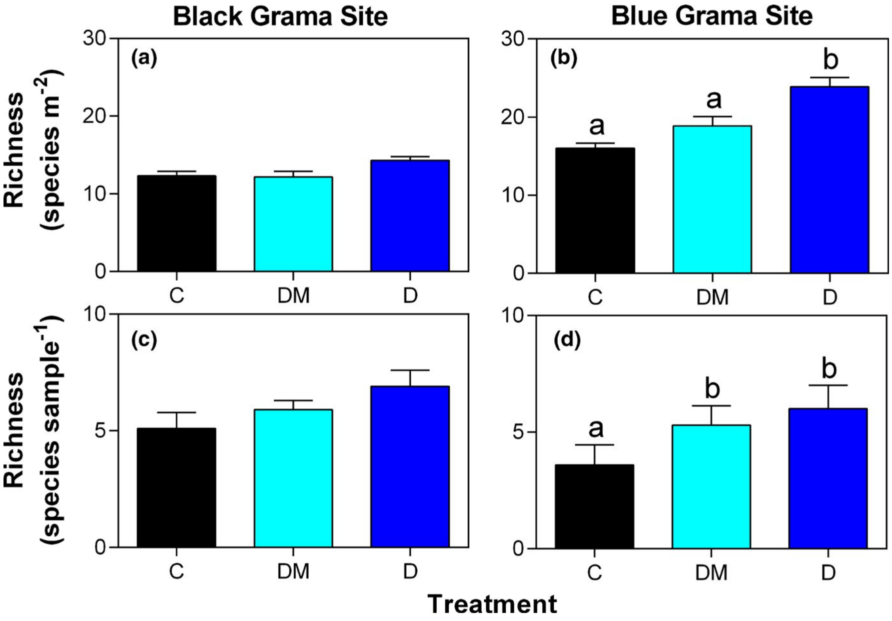

FIGURE 2 Total mean species richness (±standard error) in vegetation surveys (a and b) and soil seed bank samples (c and d) in the different treatments (C: Control, DM: delayed monsoon, D: drought) in blue and black grama-dominated grasslands. Different letters indicate significant differences among treatment means ($n = 10$)

areas of blue grama and black grama-dominated grassland starting in 2013 with 2012 as a pretreatment year. Plots were arrayed in a block design ($n = 10$ blocks per site) with 5–15 m between blocks at the blue grama and 5 m between blocks at the black grama sites. For each site, all plots within a block (including the control) were located at least 5 m apart, and trenched to 20 cm and surrounded by an aluminum flashing barrier to hydrologically isolate them from the adjacent soil. The most significant environmental artifacts of these shelters are a 0.4°C increase in temperature (Whitney et al., 2019), and 5%–10% reduction in light due to the polycarbonate roofing material used, which is still above saturating light levels in this system. The shelters have up to a ~20-cm edge effect (Yahdjian & Sala, 2002) which is well within the range of our 1-m buffer zone.

In each replicate plot cover of all species was visually assessed during spring and fall in four permanently marked 1-m^2 quadrats, two quadrats in the northwest and two in the southeast sections of each plot. Highest cover for each species registered during 2017 (spring or summer) was used. In mid-September 2017, after five seasons of experimental treatments, we took soil samples in each experimental plot ($n = 30$ per site). Each soil sample consisted of a composite sample of five soil cores, 6.45 cm^2 and 2.54 cm depth. Cores were randomly located at least 1 m apart in each plot excluding the 1-m^2 vegetation quadrats. Thus, each soil sample was 81.94 cm^3. After soil collection, soil seed bank densities and composition were evaluated using the seedling emergence method (Roberts, 1981). Soil samples were transferred to plastic trays (10 cm × 10 cm × 3 cm) and maintained in a climate-controlled greenhouse at the University of New Mexico with automatic irrigation for a period of 10 weeks (20/15°C day/night, 12 h day length and irrigation three times a day to keep trays constantly moist). Emerged seedlings were identified and removed every week. Unidentifiable seedlings were transferred into pots and grown until identification was possible. One species could not be identified at the end of the study. Raw data are available through the Environmental Data Initiative (https://doi.org/10.6073/pasta/0c1cfdf74faae96dd4d489f8b6c49c24).

2.3 | Statistical analysis

For all plots we calculated seed density (seeds per square meter) and vegetation cover (%) by species and life form (grass, forbs, shrubs and annual or perennial). We also calculated Shannon diversity index (H') and Berger–Parker Dominance index (D; Avolio et al., 2019) for vegetation at the plot scale based on average cover values from the four 1-m^2 quadrats and based on seedling emergence data from the soil seed bank. Differences in all estimated parameters among treatments within each site were analyzed using blocked ANOVA and Tukey's post-hoc test.

Vegetation and soil seed bank composition among treatments were analyzed separately using multi-variate analyses. A non-metric multi-dimensional scaling (NMS) ordination and a permutation multi-variate ANOVA (perMANOVA) were performed in each site for vegetation and soil seed bank data sets. The NMS was conducted using the Sørensen distance measure, a random starting configuration and 250 runs with real data (McCune & Grace, 2002). The perMANOVA was done using Euclidean distance. Pair-wise comparisons with Bonferroni correction were performed to detect significant differences between treatments. Next, we used Indicator Species Analysis for vegetation and soil seed bank samples to determine which species characterized each treatment using only the defined groups that differed significantly based on perMANOVA (Dufrêne & Legendre, 1997). All multi-variate analyses were made using PC-ORD (version 6.0, Wild Blueberry Media LLC, Corvallis, USA).

3 | RESULTS

In 2017, we found a total of 40 plant species at the black grama site (above-ground richness = 29 and seed bank richness = 23) and

64 species at the blue grama site (above-ground richness = 55 and seed bank richness = 27) across all treatments. Twelve and 18 species were common to above-ground vegetation and the soil seed bank in black and blue grama sites, respectively. In the black grama site, across all samples and treatments, most of the species were annuals (40.0%) or shrub or subshrub species (30.0%). Perennial grasses and forbs represented 15.0% and 12.5% each, while only one annual grass species (2.5%) occurred in the samples. Similarly, in the blue grama site, annual forbs were the most frequent (42.2%) followed by shrubs and subshrubs (32.8%). Perennial grasses and forbs represented 10.9% and 9.4% respectively, while 4.7% were annual grasses.

In the black grama site, neither chronic drought nor delayed monsoon affected species richness in above-ground vegetation or the soil seed bank. In contrast, in the blue grama site species richness of vegetation was significantly higher in the drought treatment compared to the control. In addition, species richness of the soil seed bank was also significantly higher in the drought treatment as well as the delayed monsoon compared to controls (Figure 2). In terms of plant cover, the drought treatment reduced species cover at both sites, but there were no differences in cover between the control and the delayed monsoon treatment. For the soil seed bank, both drought and delayed monsoon had higher seed density in the blue grama site relative to controls. In contrast, no significant differences in seed density were found among treatments at the black grama site (Figure 3).

For above-ground vegetation, Shannon species diversity (H') significantly changed only at the black grama site, where the drought treatment resulted in lower diversity than the control or delayed monsoon treatments. In addition, Berger–Parker dominance was lower in the drought treatments than in controls and delayed monsoon treatments at both sites. In contrast, neither dominance nor diversity of the soil seed bank differed among treatments at either site (Table 1).

Perennial grasses dominated vegetation cover at both sites. However, the drought treatment reduced significantly the cover of perennial grasses at both sites, while increasing the cover of annual species only at the blue grama site. On the other hand, the soil seed bank was dominated by annual species at both sites, and the drought and delayed monsoon treatments tended to increase dominance of annuals in the soil seed bank, although differences were not significant due to high variability among replicates (Table 2). As a result, drought increased forb species cover at both sites (represented mostly by annual species), while decreasing the cover of perennial grasses. The delayed monsoon treatment resulted in higher cover of shrub species compared to the other treatments only at the black grama site (Table 3). Contrary to changes in above-ground vegetation, seed density in the soil did not differ among treatments.

At the black grama site, community composition of the above-ground vegetation differed significantly among treatments (perMANOVA, $F_{2,16} = 46.60$, $p < 0.001$; Figure 4a), but not for the soil seed bank (perMANOVA, $F_{2,16} = 1.11$, $p > 0.30$; Figure 4b). In the former case, pair-wise comparisons among means showed that species composition differed between the drought and the delayed monsoon and control treatments ($p < 0.05$), whereas the delayed monsoon and control treatments did not differ significantly. Indicator species analysis showed that several species were responsible for these differences (i.e., control + delayed monsoon vs drought; Table 4). Control and delayed monsoon plots at the black grama site were characterized by two perennial grasses, *Bouteloua eriopoda* and *Muhlenbergia arenicola*, while drought plots were dominated by three forb species: the perennial *Astragalus feensis*, and the annuals *Cryptantha crassisepala* and *Salsola tragus*.

Similar differences in community composition also occurred with vegetation plots at the blue grama site. Pair-wise comparisons among means showed that the composition of above-ground vegetation differed between the drought and the delayed monsoon and control

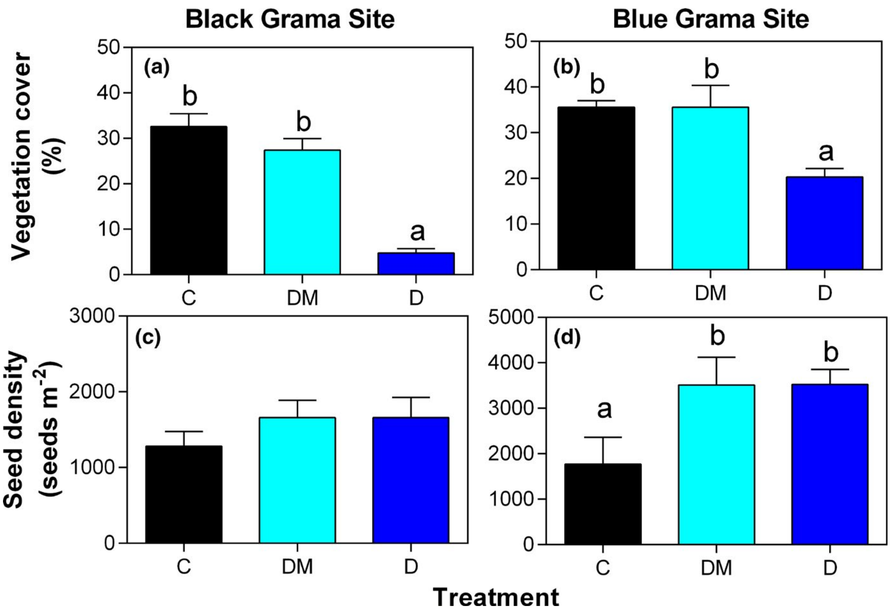

FIGURE 3 Total mean (±standard error) vegetation cover (a and b) and soil seed bank densities (c and d) in the different treatments (C: Control, DM: delayed monsoon, D: drought) in blue and black grama-dominated grasslands. Different letters indicate significant differences among treatment means ($n = 10$)

TABLE 1 Mean value ($n = 10$) of Shannon diversity index (H') and Berger–Parker Dominance index (D) in blue and black grama-dominated grasslands for vegetation surveys and soil seed bank samples

		Black grama site			**Blue grama site**		
		C	**DM**	**D**	**C**	**DM**	**D**
H'	Vegetation	**0.781^{b}**	**0.823^{b}**	**0.322^{a}**	1.100	1.106	1.113
	Soil seed bank	1.990	2.246	2.408	1.117	1.497	1.384
D	Vegetation	**0.284^{c}**	**0.198^{b}**	**0.023^{a}**	**0.211^{b}**	**0.227^{b}**	**0.058^{a}**
	Soil seed bank	0.073	0.025	0.068	0.684	0.653	0.719

Significant differences among means are marked in bold text and with different letters.
Abbreviations: C, Control; D, drought; DM, delayed monsoon.

TABLE 2 Abundance of annual and perennial species in blue and black grama-dominated grasslands for vegetation surveys and soil seed bank samples ($n = 10$)

	Black grama site			**Blue grama site**		
	C	**DM**	**D**	**C**	**DM**	**D**
Vegetation (cover, %)						
Annual	0.9 (±0.2)	0.7 (±0.2)	1.9 (±0.8)	**0.6 (±0.2)^{a}**	**1.2 (±0.3)^{a}**	**8.1 (±1.1)^{b}**
Perennial	**31.7 (±2.8)^{b}**	**26.7 (±2.5)^{b}**	**2.9 (±0.7)^{a}**	**34.9 (±1.3)^{b}**	**34.5 (±4.5)^{b}**	**12.2 (±1.2)^{a}**
Soil seed bank (seed density, seeds m^{-2})						
Annual	1025.2 (±180.1)	1357.7 (±157.5)	1342.5 (±252.2)	1598.8 (±587.2)	3148.8 (±635.1)	3283.1 (±315.4)
Perennial	256.3 (±70.3)	305.1 (±74.9)	352.6 (±87.4)	170.9 (±64.2)	366.1 (±83.6)	244.1 (±54.2)

Significant differences among means are marked in bold text and with different letters. Abbreviations: C, Control; D: drought; DM, delayed monsoon.

TABLE 3 Mean abundance ($n = 10$) of grass, forb and shrub species in blue- and black grama-dominated grasslands for vegetation surveys and soil seed bank samples

	Black grama site			**Blue grama site**		
	C	**DM**	**D**	**C**	**DM**	**D**
Vegetation (cover, %)						
Grass	**30.3 (±2.7)^{c}**	**20.6 (±2.0)^{b}**	**0.5 (±0.2)^{a}**	**32.0 (±1.4)^{b}**	**31.2 (±4.5)^{b}**	**8.1 (±1.4)^{a}**
Forb	**1.4 (±0.3)^{a}**	**1.2 (±0.3)^{a}**	**3.6 (±0.8)^{b}**	**2.2 (±0.7)^{a}**	**1.8 (±0.4)^{a}**	**9.6 (±0.7)^{b}**
Shrub	**0.9 (±0.2)^{a}**	**5.5 (±1.8)^{b}**	**0.7 (±0.2)^{a}**	1.3 (±0.3)	2.7 (±0.7)	2.5 (±0.5)
Soil seed bank (seed density, seeds m^{-2})						
Grass	207.5 (±71.9)	170.9 (±54.9)	231.9 (±44.8)	122.0 (±71.8)	341.7 (±78.6)	158.7 (±47.2)
Forb	1037.4 (±182.2)	1379.1 (±160.5)	1379.1 (±242.6)	1598.8 (±587.2)	3112.2 (±627.7)	3283.1 (±310.7)
Shrub	36.6 (±19.7)	109.8 (±44.8)	48.8 (±21.0)	48.8 (±21.0)	61.0 (±28.8)	85.4 (±43.1)

Significant differences among means are marked in bold text and with different letters. Abbreviations: C, Control; D, drought; DM, delayed monsoon.

treatments ($p < 0.05$), whereas the delayed monsoon and control treatments did not differ significantly (perMANOVA, $F_{2,16} = 14.30$, $p < 0.001$; Figure 4c). Indicator species analysis (Table 4) showed that control and delayed monsoon plots were dominated by *Bouteloua gracilis* and *Bouteloua eriopoda*. Vegetation cover in the drought plots was dominated by several species belonging to different vegetation groups. Most of the species were annual forbs (i.e., *Salsola tragus*, *Chamaesyce serpyllifolia*, *Lepidium densiflorum*, *Euphorbia exstipulata*, *Chamaesyce serrula*, *Descurainia pinnata* and *Allionia incarnata*), but there were other species from different groups: *Hymenopappus filifolius* (subshrub), *Astragalus feensis* (perennial forb), *Aristida adscensionis* (annual grass) and *Dasychloa pulchella* (perennial grass). No differences among treatments were found in the composition of the soil seed bank at the blue grama site (perMANOVA, $F_{2,16} = 2.42$, $p > 0.05$; Figure 4d).

4 | DISCUSSION

In this study, we used a multi-year rainfall manipulation experiment in two semi-arid grasslands to determine the effect of chronic, extreme drought and changes in precipitation seasonality on aboveground vegetation and soil seed bank attributes. We hypothesized that vegetation and seed bank richness and diversity would decline with alterations in precipitation and species composition would

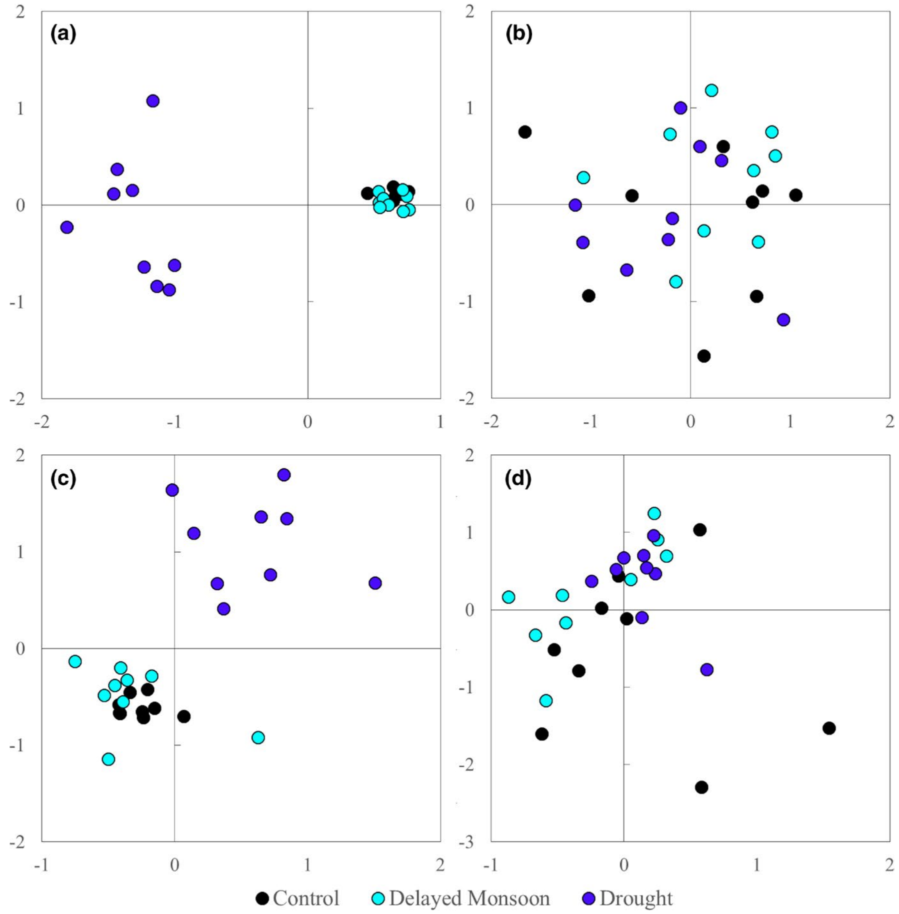

FIGURE 4 Non-metric multidimensional scaling ordination diagrams for vegetation surveys (a and c) and soil seed bank samples (b and d) for black (above) and blue (below) grama-dominated grasslands

change, increasing annual species' abundance. Contrary to our expectations, species richness did not decrease. However, drought, but not delayed monsoon, significantly affected above-ground vegetation composition. Furthermore, these changes in rainfall regimes had no effect on the composition of the seed bank.

Changes in above-ground vegetation in southwestern USA arid and semi-arid grasslands in response to rainfall manipulations have been reported in other studies (Báez et al., 2013; Gherardi & Sala, 2015; Knapp et al., 2015), where species richness increases and species composition changes toward annual-dominated grasslands. This may be partially explained by a reduction in competition intensity from dominant grasses (Suttle et al., 2007; Peters & Yao, 2012; LaForgia et al., 2018). Dry conditions may affect dominant species, like perennial grasses (Kardol et al., 2010; Mariotte et al., 2013; O'Connor, 2015; Swemmer et al., 2018), that are usually intolerant to drought (Breshears et al., 2005; Munson et al., 2016; Funk et al., 2019; Griffin-Nolan et al., 2019). This negative impact on dominance may benefit subordinate species that are usually less competitive than dominant grasses, as well as drought-adapted species (Kardol et al., 2010; Liu et al., 2018; Siebert et al., 2020), such as annual or short-lived forbs (Buitenwerf et al., 2011; Munson et al., 2016; Swemmer et al., 2018). These changes in above-ground vegetation composition occurred in both blue and black grama-dominated grasslands, and have also been reported in other studies (Suttle et al., 2007; Lloret et al., 2009; Báez et al., 2013).

In contrast, chronic drought increased species richness and seed density in the seed bank at the blue grama site. Neither treatment affected the composition and structure of the soil seed bank at the black grama site. In blue grama-dominated grasslands, annual forbs with high seed production are more frequent than in the black grama grassland, where subordinate species are characterized more by perennial forbs and shrubs (Kröel-Dulay et al., 2004). The higher species richness in the blue grama site increases the chances of having drought-tolerant or drought-avoidance species within the plots (Tilman et al., 2006), increasing species richness and seed density. Nonetheless, species composition did not change in either of the studied sites, indicating more limited effects of precipitation alterations in the soil seed bank compared to above-ground vegetation. The delayed monsoon treatment affected seed density and species richness only at the blue grama site. Changes in timing of precipitation instead of rainfall amount have been shown to influence community composition (Kimball et al., 2010). This was not observed in our case. Information about the impact of altered rainfall timing on seed bank composition is limited. Nevertheless, our data suggest that seed banks are resistant to these changes, but more studies are needed.

In general, similarity between vegetation and seed bank is usually low in terms of species identity (Hopfensperger, 2007; Ma et al., 2021), since in many perennial-dominated grasslands seed banks have a high abundance of annual and perennial forbs (Kinloch &

TABLE 4 Indicator species of vegetation surveys in blue and black grama-dominated grasslands

			Cover (%)		
Species	**IV**	***p***	**C**	**DM**	**D**
Black grama site					
Astragalus feensis	76.6	0.014	0.17	0.04	**0.35**
Bouteloua eriopoda	98.6	0.001	**28.67**	**19.52**	0.38
Cryptantha crassisepala	72.3	0.012	0.13	0.06	**0.89**
Muhlenbergia arenicola	51.7	0.044	**0.57**	**0.37**	0.01
Salsola tragus	79.3	0.001	0.01	0.01	**0.11**
Blue grama site					
Allionia incarnata	44.4	0.010	0.01	0.01	**0.84**
Aristida adscensionis	88.9	0.001	0.01	0.02	**0.48**
Astragalus feensis	67	0.008	0.01	0.01	**0.13**
Bouteloua eriopoda	79.1	0.001	**8.75**	**6.52**	2.21
Bouteloua gracilis	83.6	0.001	**22.11**	**21.65**	3.67
Chamaesyce serrula	83.5	0.001	0.09	0.11	**0.52**
Chamaesyce serpyllifolia	79.3	0.006	0.13	0.60	**1.10**
Dasyochloa pulchella	52.2	0.010	0.01	0.01	**0.09**
Descurainia pinnata	64.1	0.030	0.01	0.01	**0.10**
Euphorbia exstipulata	90.1	0.001	0.02	0.06	**0.26**
Hymenopappus filifolius	78.5	0.004	0.01	0.07	**0.52**
Lepidium densiflorum	75.4	0.006	0.03	0.17	**0.32**
Salsola tragus	94.7	0.006	0.05	0.33	**4.04**

Shaded numbers indicate the highest cover value and the treatment characterized by each indicator species. Abbreviations: C, Control; D, drought; DM, delayed monsoon; IV, indicator value; *p*, significance level.

Friedel, 2005; Loydi, 2019). As a consequence, perennial grasses comprise a small portion of the seed bank (Hild et al., 2001). This is partially explained because annual species tend to produce a large number of small seeds (Grime, 2001), increasing their relative abundance in the seed bank. These annual species may also benefit from dry conditions. While perennial grasses are reduced during drought, lowering their seed production (Marone & Pol, 2021), annual species are able to grow during periods of soil moisture availability (Levine et al., 2008; Mayfield et al., 2014) derived from pulses of rain, like those that occur during the summer monsoon (Muldavin et al., 2008; Mulhouse et al., 2017). Under these conditions annual species can complete their life cycle during relatively short time periods when soil moisture is available (Ruthven III, 2007; Nenzhelele et al., 2018; Siebert et al., 2020), contributing seeds to the soil seed bank, even during relatively dry years.

Our methodological approach (i.e., seedling emergence method) does not allow us to evaluate dormant seeds, and this method tends to underestimate seed bank density (Gross, 1990; Price et al., 2010). It could be possible that the observed results (i.e., higher species richness and seed density in drought and monsoon-delayed treatments) are related with a higher seed input of some species into the seed bank (Zeiter et al., 2016) rather than an the effect of the drought treatments, *per se*, since drought typically increases the fraction of dormant seeds (Saatkamp et al., 2013). Nonetheless, our methods do not allow us to evaluate density of dormant seeds. Future work could include a combination of seedling emergence and seed extraction methods to assess the density of the dormant seed pool (Gonzalez & Ghermandi, 2012).

We found that the composition of the soil seed bank proved to be more resistant to changes in response to altered rainfall regimes than above-ground vegetation in both blue grama and black grama grassland. For above-ground vegetation, we observed a strong decline in the relative abundance of dominant species due to drought. However, the effect of drought on seed bank composition was limited. Seed banks are important for long-term community stability in grassland ecosystems (Koopmann et al., 2017), buffering year-to-year variability (DeMalach et al., 2021). Therefore, it is expected that seed banks experience minor long-term changes in composition compared to above-ground vegetation (DeMalach et al., 2021). Nonetheless, the size of the seed bank and the abundance of dominant species may vary among years (Hild et al., 2001), but functional composition of the seed bank typically remains the same (i.e., dominated by annual species). This way, even under altered rainfall regimes some ecosystem characteristics (e.g., species richness; productivity) may be maintained (Báez et al., 2013; Ott et al., 2019; Muraina et al., 2021).

Overall, the soil seed bank plays an important role in vegetation recovery after disturbances, such as prolonged drought (Hild et al., 2001; Marone & Pol, 2021). In the future, drought-induced species loss might be compensated by a gain in drought-tolerant species that are already present in the seed bank. This might generate a shift in species composition for perennial-dominated desert grasslands, following observed changes in above-ground vegetation. Alternatively, this effect may not be in terms of vegetation composition in systems where the dominant species rely less on a persistent seed bank (Gibson, 2009). But, the high abundance of annual species in the seed bank might play an important role in ecosystem functioning after the dry period is over (e.g., Wilcox et al., 2020). These species develop rapidly and can cover and protect the soil, and create favorable niches facilitating the recruitment of perennial species. Dominant species may take longer to recover (from surviving individuals or from seeds) and during this transition, the establishment of new individuals from the seed bank will provide safe sites for the establishment of longer-lived species as grasslands recover from extreme climate events (Smith, 2011). In this way, the drought-resistant soil seed bank might contribute to vegetation recovery after drought.

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AUTHOR CONTRIBUTIONS

AL and SLC conceived and designed the study. SLC acquired permissions for sample collection. AL and SLC performed field work. AL collected and analyzed the data. AL and SLC wrote the manuscript.

DATA AVAILABILITY STATEMENT

Data supporting the findings of this study are available through the Environmental Data Initiative (https://doi.org/10.6073/pasta/0c1cfdf74faae96dd4d489f8b6c49c24).

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