

Semi-arid savanna herbaceous production and diversity responses to interactive effects of drought, nitrogen deposition, and fire

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Abstract

Question: Savannas are globally widespread and furnish a variety of ecological services through their structural heterogeneity. Unfortunately, those essential ecosystem services are threatened by climate changes including expected increases in duration of drought and nitrogen deposition. The objective of this study was to determine how overall herbaceous production, functional group production and diversity respond in the short-term to interactions between forecasted environmental conditions and prescribed fires.

Location: Western Edwards Plateau, Texas (latitude 31°N, longitude 100°W).

Methods: We randomly assigned full-factorial treatment combinations of rainout shelters, simulated nitrogen deposition and prescribed fires to field plots in an herbaceous-dominated area of a semi-arid savanna. Aboveground net primary productivity (assessed via destructive harvest) and diversity (using Shannon's index) were assessed as indicators of ecosystem functioning.

Results: Total aboveground net primary production was reduced by fire in the short-term (4 months), and reduced by drought at 8 months, but drought reductions were later overridden by lagged responses to large precipitation events (12 months). Forb production increased in response to nitrogen addition (8 months) and drought (12 months), but decreased as a result of fire (12 months). Live grass production was consistently reduced by drought. Plant species diversity was positively responsive to nitrogen addition, particularly in the absence of drought.

Conclusions: Our findings suggest that the concentrated precipitation events that are forecasted to follow extended droughts may aid rapid recovery of drought-induced production decreases. In addition, the small-scale diversity of this semi-arid savanna may be driven more by resource availability than light-competition in the short-term. Managers and ecologists can use these results to help disentangle the ecosystem functioning that may be observed in the presence of future droughts,

nitrogen deposition and prescribed fire. Understanding these processes will be key to protecting the integrity of savannas.

KEYWORDS

anthropogenic change, biodiversity, biomass, climate change, dryland ecosystem, erratic weather, extreme events, nutrient flux, rangeland

1 | INTRODUCTION

Precipitation, nutrient availability, and fires have been identified as key determinants of savanna composition, which is rich in biodiversity (Kraaij & Ward, 2006; Polley, Bailey, Nowak, & Stafford-Smith, 2017; Scholes & Walker, 1993). The characteristic codominance between grasses and trees in savannas provides valuable ecosystem services such as aquifer recharge, forage grazing, and nutrient cycling (Olenick, Kreuter, & Conner, 2005; Young & Solbrig, 1992). Therefore, human-induced perturbations to resources and disturbance patterns in savannas have the potential to reduce the high biodiversity and trigger a state-shift towards woodland or grassland (Breshears et al., 2016; Stringham, Krueger, & Shaver, 2003). This would have both ecological and economic implications of global significance in terms of ecological services such as grazing and carbon storage (Archibald & Scholes, 2007; Scholes, 2003; Zhao & Running, 2010). Conserving the herbaceous component of savannas is crucial as it limits woody encroachment both directly (through resource partitioning of rooting layers) and indirectly by serving as the fuel load for fires (Scholes & Archer, 1997; Walter, 1939; Weaver, 1935). Herbaceous diversity is key to buffering production fluctuations in response to both wet and dry climate events, thus increasing the inertia of the systems (Isbell et al., 2015; Westman, 1978).

Climate change models for the southwestern USA (IPCC, 2013) forecast concentrated precipitation events followed by prolonged droughts (Dai, 2013; Knapp et al., 2008; Trenberth, Dai, Rasmussen, & Parsons, 2003). Semi-arid grasslands have been identified as the most sensitive grassland to drought in terms of aboveground net primary productivity (ANPP) (Knapp et al., 2015), and ANPP growth and recovery is positively correlated to yearly precipitation (Knapp & Smith, 2001). A regime of less frequent, more intense precipitation events is, however, likely to reduce the amount of precipitation lost to soil water evaporation and slightly reduce periods of soil water deficit in those regions (Knapp et al., 2008; Schwinning & Sala, 2004); therefore, events of concentrated precipitation may be the most important driver of variation in inter-annual ANPP (Heisler-White, Knapp, & Kelly, 2008).

Water stress also constrains photosynthesis and causes ANPP and ground cover to decline, opening the potential for desertification and erosion (Herbel, Ares, & Wright, 1972; Wonkka, Twidwell, Franz, Taylor, & Rogers, 2016). For these reasons, water is considered the most limiting resource in arid and semi-arid ecosystems followed by nitrogen (N) availability (Chapin, Bloom, Field, & Waring, 1987; Yahdjian & Sala, 2010).

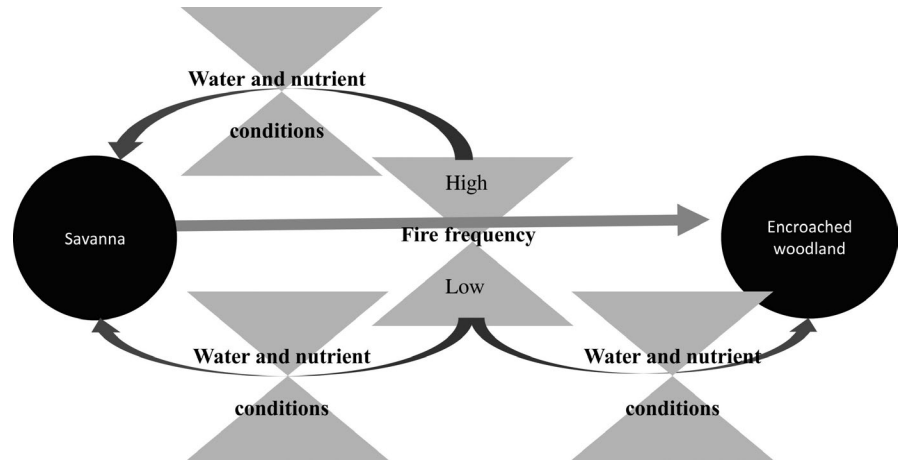
The addition of N to these systems via atmospheric deposition is expected to have an impact on native systems by inducing changes in both plant production and diversity (Collins et al., 2008; Polley et al., 2017; Yahdjian, Gherardi, & Sala, 2011). Bennett and Adams (2001) found that although the timing of herbaceous production is regulated by precipitation, the amount of ANPP is regulated by N availability at a semi-arid site. Thus, the addition of N commonly causes ANPP to increase (Borer, Seabloom, Mitchell, & Cronin, 2014; Mbatha & Ward, 2010; Snyman, 2002; Yahdjian et al., 2011).

Although increased N availability commonly enhances ANPP, plant species richness and diversity generally decline (Borer et al., 2014; Mbatha & Ward, 2010; Yahdjian et al., 2011; Zeng et al., 2010). Even low levels of novel N availability can trigger a dramatic loss of species diversity (Clark & Tilman, 2008). Declines in diversity can then degrade the system's ecological services as higher levels of heterogeneity have been tied to increased ecosystem functioning in savannas (Guo, Weise, Fiedler, Lohmann, & Tietjen, 2018). Because C3 plants are less nutrient use efficient (NUE), they uptake N more rapidly and may outcompete NUE C4 grasses (Christie, 1981; Reich et al., 2001; Sage, Pearcy, & Seemann, 1987; Wedin & Tilman, 1997). A significant interaction between extended droughts and N deposition is also expected as N uptake is dependent on soil water availability for transport to roots (Polley et al., 2017; Scholes, 2003).

Using historical aerial photographs (Archer, Scifres, Bassham, & Maggio, 1988), isotope analysis (Boutton, Archer, Midwood, Zitzer, & Bol, 1998), and general observations (Fuhlendorf, Smeins, & Grant, 1996), a trend of increasing woody plant density has been documented in savannas and grasslands worldwide, including those in Australia (Fensham, Fairfax, & Archer, 2005) and South Africa (Kraaij & Ward, 2006). Fire suppression has been identified as a leading cause for this phenomenon (Twidwell, Fuhlendorf, Taylor, & Rogers, 2013; Van Auken, 2009). In addition to fire intensity, season and frequency, the water and nutrient conditions present following fires determine community responses (Figure 1) (Buis et al., 2009; Mbatha & Ward, 2010; Solbrig, Medina, & Silva, 1996).

Within semi-arid regions where the climate is unpredictable, prescribed fire effects have been variable (Blair, 1997; Smith et al., 2016; Wink & Wright, 1973). Increased bare ground and subsequent soil erosion are both risks when conducting prescribed fires in semi-arid and arid regions (Ludwig, Wilcox, Breshears, Tongway, & Imeson, 2005; Snyman, 2003). Savanna fires, however, are crucial to maintaining heterogeneous structure, diversity and herbaceous production (Fuhlendorf, Fynn, McGranahan, & Twidwell, 2017; Savadogo, Tiveau, Sawadogo, & Tigabu, 2008; Twidwell et al., 2013).

FIGURE 1 The interactions between resource availability, fires, and savanna encroachment where resource availability regulates the progression of an ecosystem towards an encroached woodland and/or community composition as a savanna



Fires are able to increase diversity by suppressing a few dominant species (Brockway & Lewis, 1997).

As key determinants of savanna communities are anthropogenically altered, key local and global services of those systems will also be disrupted. The interactions between precipitation, soil nutrients and prescribed fires are the cornerstones of semi-arid savanna conservation under changing environmental conditions.

The objective of this study was to investigate (a) how ANPP and diversity within the herbaceous layer of a semi-arid savanna will respond in the short-term to drought, N deposition and prescribed fire and (b) how these factors will interact to alter those responses. To answer these questions, we implemented rainout shelters, N additions, and prescribed fire treatments on herbaceous-dominated plots in a semi-arid savanna system in Texas, USA. Predictions were that (H1) ANPP would be stimulated by the N treatment but would be reduced by the drought treatment; (H2) drought and N treatments would cause diversity to decline because of increasing dominance in either C4 grasses or C3 plants, respectively, while fire would enhance diversity through competitive release; (H3) interactions, including drought, were predicted to demonstrate constrained responses to the other factors.

2 | METHODS

2.1 | Study site

This study took place at the Texas A&M AgriLife Sonora Research Station (SRS) on the western edge of the Edwards Plateau (56 km south of Sonora, Texas (30°16'N, 100°33'W)). The ecoregion is a semi-arid savanna system with heterogeneous, shallow-depth soils and a historic fire return interval of 4–8 years (Guyette, Stambaugh, Dey, & Muzika, 2012). The mean January temperature is 8°C and the mean July temperature is 26°C with a mean growing season length of 240 days (SRS records and Fuhlendorf, Briske, & Smeins, 2001). The annual precipitation pattern is bimodal (spring/autumn). While inter-annual precipitation is variable, the annual mean is 567.88 mm.

The study site lies primarily on 1%–3% slopes Valera clay soils with a petrocalcic layer 51–102 cm below the surface (Garbiel & Loomis, 2017). Soils were moderately alkaline clay loam soil. Characteristic vegetation includes *Quercus virginiana* (live oak), *Juniperus* spp. (juniper species), *Nassella leucotricha* (Texas wintergrass), *Hilaria belangeri* (common curly mesquite), *Aristida wrightii* (Wright's threeawn), *Bothriochloa ischaemum* (King Ranch bluestem), *Bouteloua curtipendula* (sideoats grama) and *Glandularia bipinnatifida* (prairie verbena).

Based on records from the National Atmospheric Deposition Program (National Trends monitoring site TX16), the SRS is currently receiving 0.2 g/m² of total N deposition annually. The Oak Ridge National Laboratory (ORNL) Distributed Active Archive Center (<https://daac.ornl.gov/>) forecasts that this amount could increase to 1.7 g/m² annually as soon as the year 2050 in this region.

2.2 | Study design

We established sixty-four 5 × 5 m plots in a primarily herbaceous area with minimum 2 m alleyways separating the plots. Livestock and wildlife were excluded from the study area. Treatments were drought (rainout shelter or ambient), N deposition (N addition or control) and fire (prescribed ring fires or control). A 2 × 2 × 2 full-factorial experimental design was used to assign the eight treatment groups to the 64 plots resulting in eight replicates for each combination of treatments.

A 3 × 3 m area was covered by rainout shelters which were constructed on March 2, 2018, and simulated the 1st percentile extreme drought for the site (175.65 mm/year) following the Drought-Net protocol (www.drought-net.colstate.edu). In order to calculate this value, we used site-specific precipitation records from 1919–2013. Exclusion of rainfall was by clear polycarbonate roofing strips affixed to PVC frames at c. 1.4 m tall. Experimental plots with shelters were also trenched to 25–38 cm depending on depth of petrocalcic layer and 6 mm sheet plastic was installed to protrude 7–12 cm above the ground. The shelter size covered a 2 × 2 m core sampling area in addition to a 50 cm buffer to minimize edge effects, safely surpassing

the 20 cm edge effect noted by Yahdjian and Sala (2002). Ammonium nitrate fertilizer (NH_4NO_3 ; 34% N) was applied in a granular form on April 18, 2018, using a hand-held spreader. Our application rate was 5 g N/m², reflecting the rate that interacted with drought to trigger alterations to semi-arid plant diversity in Vourlitis (2017). A rate exceeding the current ambient deposition was selected as the Distributed Active Archive Center (<https://daac.ornl.gov/>) predictions indicate that N deposition has the potential to drastically increase in the future as intensive manufacturing activities continue. We conducted prescribed ring fires on March 1 and 2, 2018, using a propane vapour torch to allow for the low fuel loads. Burn plots were contained using wet lines. These fires simulate prescribed fires that are used to manage woody encroachment on these landscapes. In the herbaceous layer of semi-arid savannas where fuels are low, low-intensity fires are common (Kraaij & Ward, 2006; Skarpe, 1992).

2.3 | Sampling

2.3.1 | Aboveground net primary productivity

A 0.25 m² square quadrat was used for destructive total ANPP (biomass) sampling in each of the plots before treatment and 4, 8, and 12 months after treatment. All vegetation rooted within the quadrat was clipped to the ground level. Location of harvest was modified at each sampling to avoid any compensatory growth effects. Biomass was then sorted to dead and live vegetation then further sorted to grass, forb, and woody groups. Functional group classes per plot were dried in an oven at 60°C for 48 h. After drying, each category was weighed separately and recorded on a per-plot basis to the nearest 0.01 g.

2.3.2 | Diversity

A static, 1 m² quadrat was designated in each of the plots to assess density of individuals before treatment, and 8 and 12 months after treatment. The location of community diversity sampling was not used for destructive ANPP sampling. The density of species representing >1% was recorded. Shannon's H' was calculated based on species density using the *diversity(index = 'shannon')* function in the VEGAN package (Okasanen et al., 2018) of RSTUDIO (RStudio Team, 2018). Plant traits and species names (based on USDA Plant Database) are available in Appendix S1.

2.4 | Statistical analysis

Differences in Shannon's diversity (H') and ANPP between treatments were assessed parametrically. Log_{10} transformations were applied as needed to achieve assumptions of normality and homogeneity of variance. While normality was evaluated visually, as suggested by Zuur, Ieno, and Elphick (2010), the homogeneity of variance was tested using the Levene's test with $p > 0.05$ considered homogenous

(Van Der Waal et al., 2009). Three-way, factorial ANOVAs were performed to test the interactive effects of drought, N and fire on ANPP (biomass) and Shannon's diversity changes. Drought (shelter or ambient), N (addition or control), and fire (burned or unburned) were used as fixed effects with function *Fit Model*, Standard Least Squares in JMP Pro 13.0 (SAS Institute Inc., 2016). Live grass ANPP failed to meet the assumptions of full-factorial ANOVA in the spring of 2019, so a Generalized Linear Model (GLM) based on Maximum Likelihood was performed on $\text{log}_{10}(\text{live grass})$ with the link function, 'Identity' in the *Fit Model* function of JMP Pro 13.0 (SAS Institute Inc., 2016). This model was selected based on the Pearson Goodness of Fit Test ($p > 0.05$). Aboveground net primary productivity sampling dates were analysed individually as we sought to understand treatment effects at unique phenological stages rather than changes over this short period of time; location of sampling was also altered between dates. Diversity assessments accounted for pre-treatment diversity by analysing the change in diversity from pre-treatment values while still enabling the identification of treatment effects during multiple seasons. Effect significance ($p < 0.05$) indicated that a treatment significantly altered the ANPP or diversity variable. Significant interactions between the effects indicated that one treatment altered how the variable responded to other treatment(s).

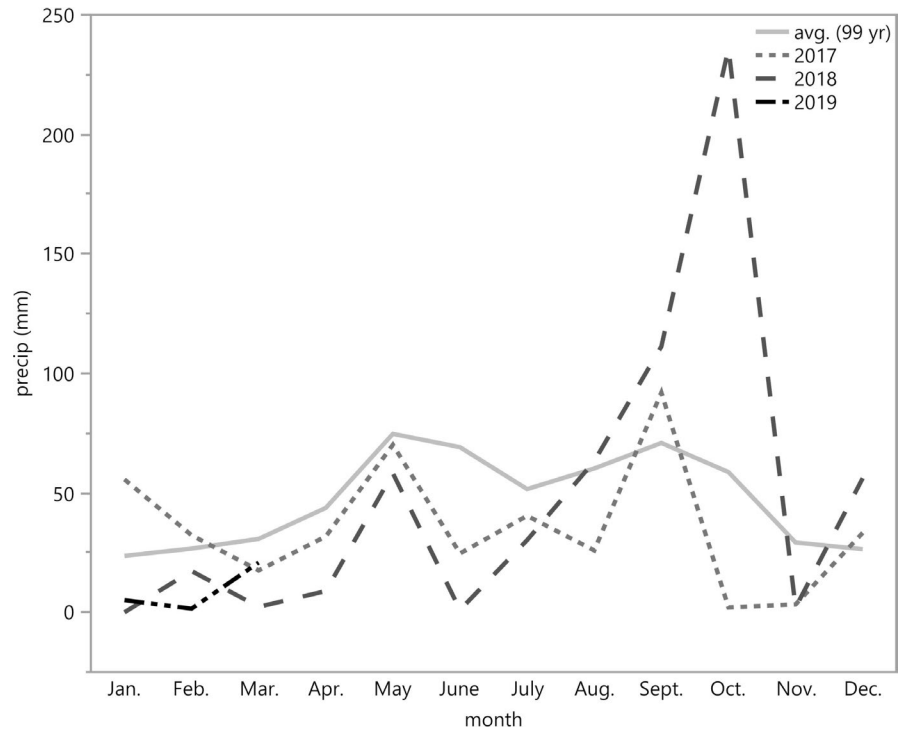
3 | RESULTS

Precipitation during the primary study year was atypical, with low precipitation in the first 7 months and high precipitation in the autumn (Figure 2). This novel pattern resulted in slightly above-average annual precipitation in 2018 (586.49 mm) and likely affected our observed results. However, these results are presented as an aspect of a larger interaction that merits further investigation (Smith, Wilcox, Power, Tissue, & Knapp, 2017). In the spring of 2019, the mean cover by annual plants was 61% compared with 11% in the winter of 2018.

3.1 | Aboveground net primary productivity

In the full-factorial ANOVA of pre-treatment (spring 2018) transformed total ANPP, no significant differences were detected ($p > 0.05$, Appendix S2). A summer ANPP sampling revealed that log_{10} -transformed, total ANPP was significantly reduced by fire 4 months after treatment ($p < 0.05$, Appendix S2). This indicates that ANPP was unable to recover from the prescribed fires within 4 months during a time of ambient drought. After 8 months, the drought treatment caused a significant reduction ($p < 0.01$) in total ANPP and no significant difference was attributed to the N or fire treatment ($p > 0.05$) (Appendix S2). Increased precipitation during the late summer and autumn of 2018 allowed the drought treatment to produce an observable decrease in ANPP, but also facilitated the full recovery from the fire treatment (Figure 3). In the spring of 2019 (12 months after treatment initiation), no differences in overall ANPP were detected as a result of the treatments either independently or interactively.

FIGURE 2 Monthly precipitation totals (in mm) during and preceding the study. Treatments implemented in March–April 2018. The 99-year monthly average is also plotted for comparison



In the spring of 2018 (pre-treatment), the back-transformed mean ANPP was 47.62 g/m². In the summer of 2018, 4 months post-treatment, the back-transformed mean ANPP was 21.01 g/m² (44.12% of spring 2018 amount). The winter of 2018 (8 months post-treatment) back-transformed mean was 47.78 g/m² (100.36% of spring 2018 amount). The ANPP in the spring of 2019 was significantly higher than other sampling dates (Kruskal–Wallis Rank Sums Test, $p < 0.05$, Data Appendix S2) with a back-transformed mean ANPP of 97.14 g/m² (203.99% of spring 2018 amount).

In the winter of 2018, forbs and grasses comprised an average of 46.37% (28.86 g/m²) and 53.63% (33.38 g/m²), respectively, of total ANPP. In the spring of 2019, forbs and grasses comprised an average of 70.65% (78.73 g/m²) and 29.35% (32.71 g/m²), respectively, of total ANPP. ANOVAs on growth-form ANPP were conducted to understand more specific responses within live grass and forb functional groups. The winter 2018 sampling ANOVA indicates that live forb ANPP was increased by the N treatment ($p < 0.01$, Appendix S3 and Figure 4). The spring 2019 transformed live forb group (Appendix S3) was significantly increased by drought ($p < 0.05$, Figure 4) and significantly reduced by fire ($p < 0.01$, Figure 4). Live grass ANPP was significantly reduced by the drought treatment after 8 months ($p < 0.05$, Appendix S4). The generalized linear model analysis revealed that drought also significantly reduced live grass production ($p < 0.01$, Appendix S4) 12 months after imposition in the spring of 2019.

3.2 | Vegetation diversity

The effect of each treatment on the magnitude of change in diversity from the winter of 2017 to the winter of 2018 and winter 2018

to spring 2019 was analysed using a full-factorial ANOVA on the change in Shannon's diversity (H') (Appendix S5). This method was used in order to attain data normality as well as to assess how the treatments induced change in diversity of the vegetative community. The addition of N significantly increased diversity and thus magnitude of change in diversity ($p < 0.05$) after 8 months of treatment (Appendix S5) from the winter of 2017 to the winter of 2018.

The Drought * N interaction was also significant ($p < 0.05$) after 8 months, with the addition of N increasing mean plant diversity only when the plots were not experiencing drought (Appendix S5). The control and fire treatment groups experienced less mean change in diversity 8 months after treatment application compared with other groups (Figure 5).

Diversity was greater overall in the winter of 2018 compared with the winter of 2017 and greatest in spring 2019, highlighting the seasonality of plant communities, (Appendix S5, $p < 0.001$).

4 | DISCUSSION

4.1 | Aboveground net primary productivity responses

The drought-induced reduction in ANPP during the fall of 2018 demonstrated the water limitation of ANPP as expected in H1 (Hoover, Knapp, & Smith, 2014; Koerner & Collins, 2014). The lack of reduction in ANPP from drought in the spring of 2019 likely resulted from a lagged response to the large precipitation events that occurred during the autumn of 2018. Cherwin and Knapp (2012) identified a similar lack of drought-induced ANPP

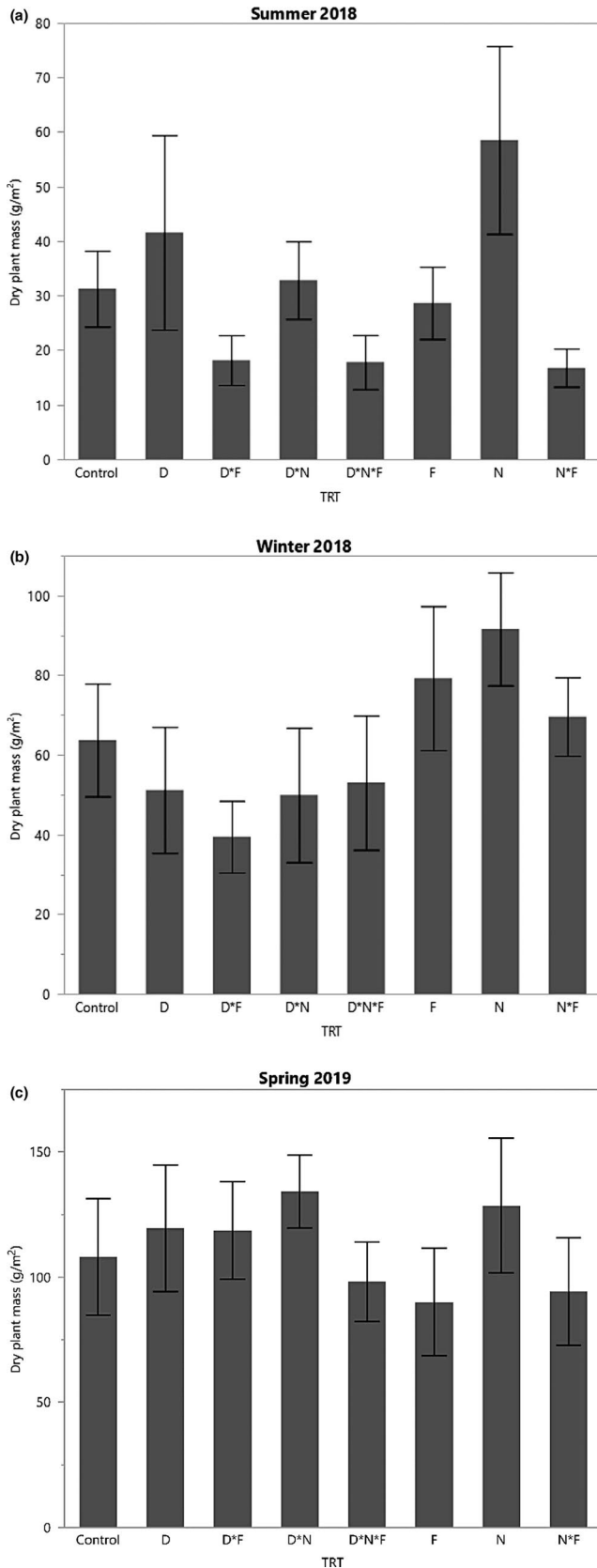


FIGURE 3 Mean total dry plant mass (ANPP) graphed by treatment group for the summer 2018, winter 2018, and spring 2019 samplings. Drought significantly ($p < 0.05$) reduced total ANPP at the winter 2018 sampling. All other treatment effects and interactions were non-significant. D signifies drought, N is ammonium nitrate addition, and F indicates that prescribed fires were conducted. Error bars are graphed for one standard error from the mean of each category

precipitation events lead to higher amounts of ANPP and may be the most important variable to explain inter-annual ANPP fluctuations (Heisler-White et al., 2008).

Counter to our predictions in H1, no significant increase in overall ANPP was observed in response to the N treatment at any of the samplings. Adaptations to the semi-arid environment such as slow growth and low resource requirements may have limited the native species' response to N supplementation (Chapin, 1991; Chapin et al., 1987). This concept is corroborated by the findings of Ladwig et al. (2012) who also found no response in ANPP to N in four out of six years of a study in the arid Chihuahuan desert. Furthermore, there was an extended period of below-average precipitation during our study (January–July of 2018 based on 99 years of SRS precipitation records). White, Moore, and Craig (2004) found that N is not co-limiting with precipitation in ANPP immediately following drought such as was the case during this study. Consequently, this system could have still been experiencing recovery from water limitation at the time of N supplementation and for the duration of its availability (Snyman, 2002). The lack of ANPP response to N can also be attributed to the trade-off between increased N uptake and decreased plant NUE (Lü, Dijkstra, Kong, Wang, & Han, 2015). These findings reinforce that the total ANPP of this system is water-limited in the short-term, rather than N-limited, with event size being more important than amount of precipitation received.

Aboveground net primary productivity showed a reduction from the fire treatment for a short period of time (4 months after fires) but then had recovered by 8 months following the fire. Thus, fire had only short-term negative impacts on productivity/ANPP even when burned during a period of drought (Taylor et al., 2012). Further investigation is merited as this principle could alleviate managers' reluctance to utilize prescribed fire during droughts.

An analysis of ANPP by functional groups provided insights into the functioning and stability of this savanna system. The live forb group responding positively to N in the winter of 2018 partly supported our prediction that dominance of C3 plants may increase in response to N addition (H2) (Reich et al., 2001). These findings demonstrate the low-NUE growth strategy of C3 plants, which exhibit more rapid N uptake and growth compared with slower-growing C4 grasses (Chapin et al., 1987; Wedin & Tilman, 1997; Zeng et al., 2010).

The reduction of live grass ANPP in the autumn of 2019 and spring of 2019 supports H1 that drought would limit production and alludes to the water limitation of grass ANPP. The increase in forb ANPP in plots receiving drought treatment in the spring 2019 fails to support our prediction that ANPP would decline in

sensitivity in a semi-arid grassland and suggest that reductions in the amount of precipitation may be over-riden by the size of precipitation events occurring naturally. These more concentrated

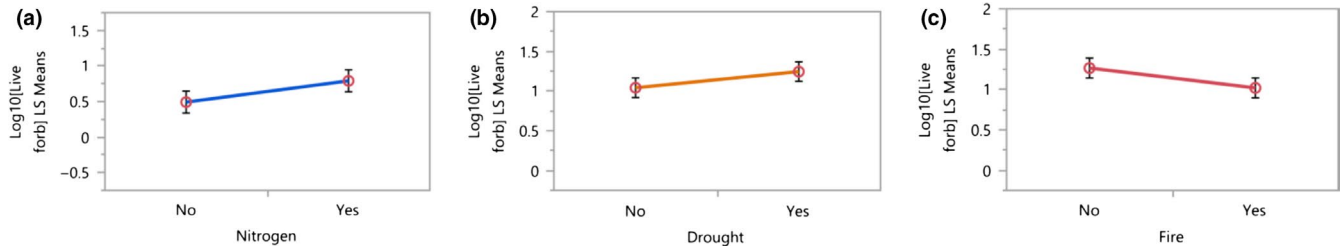
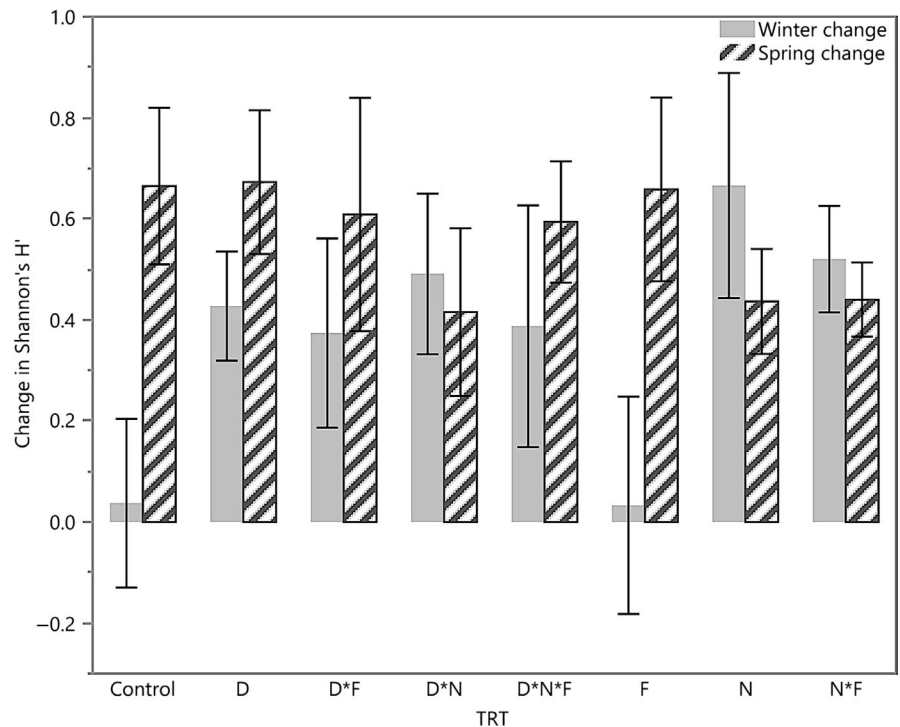


FIGURE 4 Least square (LS) means graphed comparing live forb ANPP with treatment addition (yes) or control (no) in the winter of 2018 (a) and spring of 2019 (b and c). Change indicated in LS means is the result of the treatment indicated for each graph. Only significant differences in treatments are shown. Nitrogen significantly enhanced forb production ($p < 0.01$) at the winter 2018 date. In the spring of 2019, drought significantly increased forb production ($p < 0.05$) while fire significantly reduced it ($p < 0.01$). Vertical lines represent the 95% confidence intervals of the LS means of each response variable [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 5 Change observed in Shannon's H' between sampling dates (Winter 2018-Winter 2017 and Spring 2019-Winter 2018) of the eight treatment groups where D signifies drought, N is ammonium nitrate addition and F indicates that prescribed fires were conducted. Nitrogen significantly increased diversity in the winter sampling ($p < 0.05$). Drought significantly interacted with nitrogen to alter that outcome at the same sampling ($p < 0.05$). No treatments or interactions were significant in the spring change. Error bars are constructed for one standard error from the mean of each group



response to drought and likely results from differences in growth form and seasonal precipitation. While forbs are stimulated by winter precipitation in semi-arid environments, long-lived native grasses are more responsive to summer precipitation which was lacking during this experimental period (Clarke, Latz, & Albrecht, 2005). Rather than being directly increased by the presence of the drought shelters, the increased forb production may have been an incidental consequence of perennial grass mortality under the combined ambient and experimental drought. Briggs and Knapp (1995) observed this phenomenon in a mesic grassland as grass production was limited by water stress and forb density was able to increase because of competitive release. On a larger scale of management, this increase in forb production would further alter the forage availability for cattle, nutrient cycling, and potential for effective fires following droughts.

The timing of prescribed fires determines the responses of growth forms. If vegetative tissue is removed during a period of reproduction or active growth, forb mortality can occur (Brockway,

Gatewood, & Paris, 2002). The reduced forb production in the spring of 2019 owing to fire in 2018 demonstrated prescribed fire-induced winter forb mortality the previous year. Because burns occurred during the spring, many of these cool-season forbs were actively growing or producing seeds. Growing season fires can cause forb mortality (Brockway et al., 2002) and their removal by fire limited the regrowth of that functional group the following year.

4.2 | Vegetation diversity

The implementation of the drought treatment had a significant effect on the system's diversity response to the N treatment at 8 months of treatment, as seen through the significant Drought * N interaction. The N treatment only increased (the magnitude of change in) diversity when the drought treatment was not applied. This finding supports our prediction that treatment combinations including drought would exhibit water limitation through

constrained responses to the other factors (H3); the magnitude of change in diversity was lower when both N and drought were applied compared with when N was applied and drought was not. As predicted, water availability and drought alter the vegetation response to N availability (Huang et al., 2018; Scholes, 2003). Because nutrient uptake requires water for solubility and use, changes to diversity via deposition impacts may be lessened by the concurrent effects of drought (Alam, 1999; Scholes & Archer, 1997; Van Der Waal et al., 2009). However, care should be taken with this interpretation as overall diversity was found to be lower at times of lower precipitation and these results are considered preliminary (Prieto, Peñuelas, Lloret, Llorens, & Estiarte, 2009).

In H2, we hypothesized that N addition would cause diversity to decline; we instead found that N addition caused diversity to increase between winter samplings, thus failing to support our hypothesis. These results resemble those of Ladwig et al. (2012) who also found an increase in Shannon's H' as a result of fertilization during 1 year of study in an arid grassland, but contrast the findings of decreased diversity by others (Clark & Tilman, 2008; Yahdjian et al., 2011). The combination of heavy rains and supplemental N likely interacted to maximize diversity in the winter 2018 sampling as diversity is positively associated with growing season precipitation (Prieto et al., 2009). Thus, plot diversity was likely constrained more by ambient environmental conditions than by competitive interactions which would have limited diversity in plots experiencing increased growth from N addition (Grime, 1973; Valone, 2003). Competition in these ecosystems is dependent upon environmental conditions and species assemblages (Van Auken, 2000). Because the rate of change caused by fertilization is highly dependent on the level of application and environmental conditions (Snyman, 2002; Wedin & Tilman, 1997; Xu et al., 2014; Zhou, Bowker, Tao, Wu, & Zhang, 2018), expected results may have been obscured by the short length of study or supplemented N losses to volatilization prior to uptake.

Although we expected diversity to increase as a result of competitive release (Boughton, Bohlen, & Steele, 2013), fires failed to increase diversity as predicted in H2. This can be attributed to the low-intensity nature of the burns and the short duration of the study.

A lack of detectable response in diversity or magnitude of change in diversity in the spring of 2019 may be attributed to the high proportion of annual species canopy cover (61%) that did not express diversity responses to treatments. These results contrast the decline in annual richness and diversity in response to N both in the short- and long-term (Borer et al., 2014). We expect that the diversity responses throughout this study were largely attributable to the uncharacteristic precipitation (below- and then above-average) regimes overriding other disturbance responses (McPherson, 1994) in addition to the small-scale nature of this study.

4.3 | Notes on interpretation

Our results should be interpreted with consideration of the scale of the study, as these small-scale findings may not directly translate to

the landscape scale (Fuhlendorf et al., 2017); rather, we seek to reveal processes that may become amplified under altered climate regimes. In addition, the precipitation pattern during the primary year of our study (2018) was highly atypical for the site. Precipitation was below-average early in the year, but was then high in the late summer and early autumn. Interruption of the typical bimodal regime may have induced exaggerated responses to treatments in the autumn of 2018. This pattern of low precipitation followed by concentrated events may simulate forecasted conditions, however.

5 | CONCLUSIONS

Savannas hold a significant portion of global primary productivity (Field, Behrenfeld, Randerson, & Falkowski, 1998) and a tremendous amount of biodiversity. Both of those valuable qualities are at risk of alteration because of lengthened drought and increased N deposition interacting with prescribed fires. Such alterations could have both global (e.g. carbon storage (Archibald & Scholes, 2007; Zhao & Running, 2010)) and local impacts (e.g. grazing potential (Young & Solbrig, 1992)). The lagged response to large precipitation events overshadowing the ANPP response to passively reduced precipitation demonstrates that the system ANPP may benefit from a pattern of intense precipitation periods forecasted to follow lengthened droughts. We also expect that total ANPP changes would become clearer with a spectrum of precipitation alteration over a lengthened period of time (Wilcox et al., 2017). Forbs exhibited their superior capacity for nutrient uptake and opportunistic strategy by responding positively to both N addition and drought. Prescribed fires may have the potential to mediate this increased forb production as growing season fires (although low-intensity) reduced forb production the following year. The diversity of the system appears to be more resource-limited and seasonally driven than it is competition-limited as it was higher overall in response to increased precipitation and as a result of N supplementation. In addition, the potential impacts of N deposition on diversity appear to be dependent on whether a drought is also occurring. Further studies should be conducted in order to understand these mechanisms at a larger scale and longer time-frame in order to identify trends within the community.

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AUTHOR CONTRIBUTIONS

H.H. implemented the design, collected data, performed statistical analysis, and wrote the manuscript. W.R. conceived the study, obtained funding, and oversaw project. A.L. assisted with project establishment, and data collection. H.S. served as burn boss. D.T. served as site-contact, and maintenance of project infrastructure. All authors commented on manuscript.

DATA AVAILABILITY STATEMENT

Original datasets and code are permanently archived via a Texas A&M Google Docs cloud storage data repository and may be made available upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Supporting information for species included in diversity analysis.

Appendix S2. Tables related to statistical analysis of total ANPP.

Appendix S3. Table showing statistical analysis of forb ANPP.

Appendix S4. Table showing statistical analysis of grass ANPP.

Appendix S5. Tables related to supporting statistical analysis of diversity.

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