

THESIS

RESPONSE AND RECOVERY OF GRASSLAND PLANT COMMUNITIES EXPOSED TO
MULTIYEAR DROUGHT DIFFERS ACROSS A PRECIPITATION GRADIENT

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ABSTRACT

RESPONSE AND RECOVERY OF GRASSLAND PLANT COMMUNITIES EXPOSED TO MULTIYEAR DROUGHT DIFFERS ACROSS A PRECIPITATION GRADIENT

Drought events are expected to increase in grassland ecosystems in many regions of globe due to climate change. Much is known about the effects of drought on grassland plant communities, yet it is difficult to compare responses across different grassland ecosystems because studies impose drought with varying characteristics. Further, few studies have documented plant community recovery, even though the impacts of drought can persist for multiple years. We experimentally imposed four years of extreme, growing season drought at four sites representing the major Central US grassland types (shortgrass steppe, mixed grass prairie, tall grass prairie) spanning a precipitation gradient. Growing season drought was imposed in two ways: 1) by reducing each rainfall event by 66% (chronic) or 2) by completely excluding rainfall until a similar reduction in precipitation as the chronic treatment was achieved (intense). Plant community responses to the two drought treatments were monitored for each year of the four-year drought treatments and four years following the drought to assess recovery. Overall, plant communities at the drier sites responded sooner to drought and took longer to recovery than the wetter sites. Plant composition was altered at all sites, which was largely driven by shifts in the dominant C₃-C₄ grasses and subsequent species reordering and to a lesser extent by changes in richness in evenness. There was a significant decrease in C₄ graminoid abundance in response to drought at all sites with a corresponding increase of C₃ annual grasses during the drought at the mixed grass sites but not until the recovery period at the shortgrass

steppe. Cheatgrass (*Bromus tectorum*) invaded the shortgrass steppe during the drought and proliferated during the recovery period, which likely pushed the communities into an alternate state, and inhibited recovery after four years of ambient conditions. The northern mixed grass prairie also did not fully recovery after four years, which indicates that full plant community recovery can extend longer than the drought itself at these drier sites. While there is some indication that intense drought had a greater impact on communities than chronic drought, there is limited evidence to suggest that drought type significantly influenced plant community responses or recovery. These findings indicate that while the shortgrass steppe is water limited with drought adapted species, these xeric grassland plant communities are less resistant and resilient to multiyear drought than those in mesic grasslands.

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Introduction

Atmospheric warming is expected to intensify droughts in the 21st century (Dai 2011, IPCC 2013) by increasing the severity, duration, and frequency of these events. While these changes are forecast for many regions, the Central Plains of the US, in particular, is projected to undergo unprecedented drying and drought periods (Cook et al. 2015, Rahmani and Harrington 2019). This is concerning given that this region houses the most economically important and extensive, intact grasslands in the US. Drought can be detrimental to grassland productivity (Knapp et al. 2015) and have a devastating economic cost. For instance, an estimated \$30 billion in damages resulted from the 2012 US drought, which was largely attributed to agricultural losses (Rippey 2015). Grasslands may also lag in their recovery from drought as evidenced by having longer recovery times than other ecosystems (Zhen Yu et al. 2017), which suggests longer lasting effects of intensified drought events. If recovery is delayed, this may affect future vulnerability of grasslands as droughts continue to intensify and occur more frequently (Schwalm et al. 2017). The degree to which plant communities are affected by drought and the duration that these effects last can have major implications on ecosystem function the services ecosystems provide. Thus, it is critical to understand both how grasslands will respond to and recover from intensified drought events.

The effects of drought on grassland ecosystem functioning have been studied extensively (Sala et al. 2012, Hoover et al. 2014, Knapp et al. 2015, Arredondo et al. 2016, Knapp et al. 2020). It is well established that aboveground net primary production (ANPP) is more responsive in grasslands than other ecosystem types to variation in annual precipitation (MAP, Smith and Knapp 2001, Huxman et al. 2004). While it might be expected that xeric grasslands would be most resistant to drought because they have species adapted to chronic water limitation

(Tielborger et al. 2014), more xeric grasslands often experience greater losses in ANPP than more mesic sites (Knapp et al. 2015), in line with this differential sensitivity to interannual variation in precipitation (Huxman et al. 2004). The sensitivity of different grasslands to drought may also depend on characteristics of the drought. For example, mesic grasslands might be more vulnerable to periods without any precipitation (intense drought) whereas xeric sites might see greater effects when exposed to frequent events of reduced precipitation (chronic drought, Knapp et al. 2008, Heisler-White 2009)

Recent meta analyses show that sensitivity of plant communities to drought also depends on local climate conditions, with greater negative effects of drought on species richness and diversity at drier sites (Korrell et al. 2021, Lui et al. 2021). Different aspects of communities may also exhibit variable sensitivity to drought. For example, another meta-analysis summarized the effects of global change drivers on plant communities and found a higher proportion of sites experienced shifts in composition than changes in species richness in response to long-term (>10 year) drought (Komatsu et al. 2019). Changes in composition can result from shifts in species abundances (species reordering), which occurs when individual plants die after extended periods of drought, and the space made available by reduced abundances or loss of drought-intolerant species may in turn create opportunities for establishment of more drought tolerant species (Smith 2011). For instance, during the Dust Bowl drought of the 1930's, there were decreases in total grass cover driven by reduced abundance of dominate C₄ grass species, while at the same time C₃ grasses and ruderal species increased in abundance in some grasslands (Weaver 1968). Many other studies have shown that drought results in a decrease of total grass cover and declines in dominant species (Morecroft et al. 2004, Stampfli and Zeiter 2004, Evans et al. 2011, Rondeau et al. 2013, Batbaatar et al. 2021), and an increase of ruderal species after multiple

years (Evans et al. 2011). However, few studies explicitly link these responses with compositional change (except Batbaatar et al. 2021), or do not look at the effects of composition at all and only focus on richness (Korrell et al. 2021) even though composition is more responsive to drought than richness (Komatsu et al. 2019). In addition, different studies impose drought of varying magnitude and duration, making it difficult to synthesize these findings to predict plant community responses to drought.

Few studies have documented grassland plant community recovery after drought ends, but the effects of drought may persist for several years and take longer to recover than ecosystem functioning (e.g., ANPP). After the Dust Bowl, ANPP recovered three years after drought, but it took 20 years for C₃-C₄ grass abundances to return to predrought conditions (Weaver 1968, Knapp et al. 2020). In another study, an extreme, 2-year drought resulted in a significant shift in plant composition and large loss of ANPP, and while ANPP recovered 1-year post-drought, plant compositional changes persisted for at least two years after the drought (Hoover et al. 2014). In the shortgrass steppe, the dominant C₄ had not returned to predrought levels seven years after drought (Rondeau et al. 2013). These findings highlight the need for multiyear studies to better quantify length of recovery after drought, or at least to know the state plant communities are in several years post-drought. This is especially imperative given the projected increase in drought frequency, and the compounded effects drought can have on plant communities if they do not have time to recover between events (Schwalm et al. 2017).

The goal of this study was to compare how plant communities in different grassland types (shortgrass steppe, mixed grass prairie, and tall grass prairie), that encompass a ~500 mm precipitation gradient in the Central US, respond to four years of chronic and intense drought. In

addition, the communities were monitored under ambient conditions for four years following the drought treatments to assess recovery. I specifically aimed to answer the following questions:

- 1) What is the timing of plant community response to drought and what are the characteristics of this drought response (i.e., species loss, shifts in species abundance, etc.)?
- 2) How long does it take for plant communities to recover, and if they do not fully recover, what is impeding recovery?
- 3) Are there differences in response and recovery based on characteristics of the drought event (i.e., chronic vs. intense) or grassland type?

I hypothesized that plant community responses would mirror ecosystem responses observed at the study sites (Carroll et al. 2021), with drier sites affected by drought earlier than more mesic sites and having a greater magnitude of response that takes longer to recover than mesic sites. I anticipated shifts in C₃-C₄ graminoid abundance with composition as the greatest driver of change during drought based on previous findings (Weaver 1968, Evans et al. 2011, Knapp et al. 2020), rather than changes in numbers of species (richness, Komatsu et al. 2019). Moreover, in cases where communities did not recover, this lack of recovery would largely be due to C₃-C₄ abundances not being restored to pre-drought levels. Finally, I hypothesized chronic drought would have a greater impact on xeric grasslands and mesic grasslands would be more affected by intense drought. This is because xeric grasslands communities are adapted to dry periods, so they are likely less sensitive to longer dry periods and more responsive to changes in the size and frequency of precipitation events (Knapp et al. 2008, Heisler-White et al. 2009). Conversely, mesic grasslands communities experience frequent precipitation events, so extending the time between events would likely have a greater impact than changing the size and frequency of events (Knapp et al. 2008, Heisler-White et al. 2009).

Methods

Site descriptions

The Extreme Drought in Grasslands Experiment (EDGE) was established in 2013 at four grassland sites in the Central Plains region of the US (Fig. S1). The sites include shortgrass prairie at the Central Plains Research in northern Colorado (SGS); northern mixed grass prairie at the High Plains Grassland near Cheyenne, WY (HPG); southern mixed grass prairie the Hays Agricultural Research Station near Hays, KS (HYS); and tallgrass prairie at the Konza Prairie Biological Station near Manhattan, KS (KNZ). SGS, HYS, and KNZ are dominated by C₄ grasses, while HPG is dominated by a C₃ grass (Table 1). The sites vary by ~500 mm in mean annual precipitation (MAP, most of which falls during the growing season of April 1st-September 15th; Table 1). All sites have a history of cattle grazing, but none of the sites were grazed during the experiment. The grassland at KNZ is burned annually as per regional management practices, but the other three sites are unburned. For more information about site descriptions see Table 1 and Griffin-Nolan et al. (2019).

Drought treatments

At each site, thirty 6 x 6 m plots were established in 2013, which included 10 plots for each treatment (control, chronic drought, intense drought). We used a randomized complete block design to assign treatments to plots within a block. Plots were spaced 2 m or more apart and blocks were at least 5 m apart. Cold frame shelters (Stuppy Greenhouse Inc, North Kansas City, MO) were established over the chronic and intense plots to allow for the manipulation of precipitation. The perimeter of each plot (including control plots) was trenched to a depth of 50-100 cm (depending on soil conditions) and lined with plastic to hydrologically isolate each plot from the surrounding soil. In addition, aluminum flashing was installed to a depth of 15 cm, with

5 cm aboveground, to prevent overland flow into the plots. The two drought treatments began in 2014. The chronic drought treatment was simulated with roofs made of strips of corrugated polycarbonate roof panels that covered the roof so that each precipitation event was reduced by 66% throughout the growing season (approximately April 1- Sept. 15, Fig. 1). For the intense drought treatment, roofs were completely covered with corrugated polycarbonate roof panels so that all precipitation events were excluded. The intense treatments were in place until an equivalent amount of precipitation was excluded as the chronic treatment (early-late May until mid-late August, Fig. 1), and then at that time the roofs were removed. The chronic shelter roofs were removed at the end of the growing season. The drought shelters had little effect on sunlight penetration and microclimates (Yahdjian et al. 2002, English et al. 2005). For both drought treatments, gutters were installed to redirect water away from the shelters. Starting in 2018 when the recovery period began, both drought treatments received ambient precipitation year-round, and the control plots received ambient precipitation the duration of both the drought and recovery periods (Fig. 1). For more information about the drought treatments and attributes see Carroll et al. 2021.

Plant composition sampling

Each 6 x 6 m plot was divided into four 2 x 2 m subplots which were located 1 m from the sides of the shelters. One of the 2 x 2 m plots was randomly designated as the permanent plant species composition sampling plot, while the remaining were designated to destructive sampling. The 2 x 2 m² plant species composition sampling plot was divided into four 1x1 m² subplots, and absolute percent cover was estimated separately for each species in each subplot for each year of the study. Sampling occurred twice in early to mid-June and mid-to-late August to capture maximum cover of early and late season species. Percent cover of each species was

averaged across the four 1 x 1 m subplots, so there was one cover value for each species per 2 x 2 m plot.

Statistical analysis

To evaluate plant community responses to drought and subsequent recovery, I compared the drought treatments (chronic, intense) to the control plots. This allowed me to account for underlying change in plant communities that occurs naturally over time (Avolio et al. 2015). Grasslands also respond to variation in annual precipitation, especially at drier sites, making it more accurate to assess recovery by comparing previously droughted plots to control plots in the same year (Smith and Knapp 2001). In addition, the region experienced extreme drought in 2012, so pretreatment data from 2013 may not reliably determine recovery. However, I used pretreatment data (2013) to assess whether plots designated as future drought or control treatments had differences in community structure and composition. To test my central hypothesis, I compared plant community structure and composition between drought and control plots for each year of drought (2014-2017) and during the recovery period (2018-2021). All statistical analyses were conducted using R software version 4.2.1 (R Core Team 2021).

I calculated the total number of species (species richness) and distribution of species abundance (evenness) using the `community_structure` function in the `codyn` package (Hallett et al. 2020). Species richness values were not averaged at the 1 x 1 m subplot level and represent the total number of unique species in each 2 x 2 m plot. I also calculated the total cover of C₃ and C₄ graminoids (grasses and sedges) by treatment for each year. I assessed drought effects for each site separately using linear mixed effects models with the `lmer` function in the `lme4` package with treatment, year, and treatment*year as fixed effects with block and plot included as random effects (Bates et al. 2015). Separate models were created for each response variable (i.e.,

richness, evenness, C₃ cover, C₄ cover). We used the emmeans function for pairwise comparisons when there was a significant effect of treatment or the interaction ($p = <0.05$).

We assessed changes in community composition (the identity and abundances of species in a community) using permutational multivariate analysis of variance (PERMANOVA) models in the vegan package (Oksanen et al. 2020). Models were made for each year and site combination with treatment as a fixed effect and block as a random effect. This allowed us to use the pairwise.adonis2 function to get pairwise comparisons for each treatment comparison within a single year (Arbizu 2020). We used the multivariate_difference function in codyn to calculate the mean multivariate difference based on Bray-Curtis dissimilarity matrices between the control vs. chronic treatments, control vs. intense treatments, and chronic vs. intense treatments. Composition difference ranges from 0 (identical communities) to 1 (completely different communities). This measure was used to quantify the magnitude of compositional difference between the treatments within each year. I identified species that contributed most to compositional difference between treatments using the Similarity Percentage (SIMPER) analysis in vegan, and then calculated average percent cover of the species by treatment over time. Species with cover of one percent or less were excluded from community composition analyses.

I determined the timing of drought responses and recovery based on when the drought treatment versus control comparisons were significant in the mixed models and PERMANOVA models. When the treatment and/or the treatment*year interaction terms in a mixed model had a p-value of <0.05 , I examined pairwise contrasts of the treatments within each year to determine when each treatment comparison was significant. The first year that treatment was significant was when a drought response occurred, and recovery was deemed to have occurred the year in which treatment was no longer significant. This method enabled me to pinpoint the timing of the

response and recovery of each community metric (richness, evenness, C₃ cover, C₄ cover) for all treatment comparisons. Since the PERMANOVA models were separated by year, I looked at treatment comparisons when treatment was significant in the model to determine timing of response and recovery community composition.

Results

Precipitation during drought and recovery

The drought treatments reduced ambient growing season precipitation by an average of 67.99% at SGS, 66.60% at HPG, 57.26% at HYS, and 58.40% at KNZ across the four years of the treatment (Fig. 1a-d, Carroll et al. 2021). Ambient growing season precipitation was above the 30-year average during the second year of drought (2015) at SGS and HPG, but below average the other three years of the drought (Fig. 1a,b). At HYS, ambient precipitation was either around the average amount and exceeded the average in 2016 (Fig. 1c). The first and last years of drought at KNZ had below average precipitation, and above average during the two middle years of drought (2015-2016, Fig. 1d).

Ambient precipitation during the growing season continued to be less than average during the first three years of recovery at SGS and was slightly above average in the last year (2021, Fig. 1a). At HPG, ambient precipitation was above average in the first two years of recovery and below average the last two years (Fig. 1b). Ambient precipitation was above average all four years of recovery at HYS (Fig. 1c). During the third year of recovery at KNZ ambient precipitation was above average, but below average the other three years of recovery (Fig. 1d).

Timing of plant community response to drought and characteristics of the response

Richness and Evenness

Drought had a limited impact on species richness across the sites. Richness decreased by 3.6 species on average during the second year of chronic drought at SGS but returned to control levels the following two years of drought (Fig. 2a). Richness at HYS increased in chronic plots by 5.4 species on average in the third year of the chronic drought treatment, and remained higher

in the following year, although not significantly (Fig. 2c). At HPG and KNZ, richness was not affected by either the chronic or intense drought treatments (Fig. 2b, d).

All sites except KNZ experienced an increase in evenness during the drought period. At SGS, evenness increased in the last two years of chronic drought, and during the last year of the intense drought treatment (Fig. 3a). The first site to respond was HPG during the second year of intense drought. Differences in evenness diminished in the third year although both chronic and intense drought had slightly higher evenness than the control treatment. Evenness remained slightly elevated in the chronic treatment and became significantly higher again in the last year of intense drought (Fig. 3b). Evenness increased significantly in the third year of intense drought at HYS and remained higher the next year (Fig. 3c).

C₃-C₄ abundance

There was no significant difference in C₃ grass abundance between either drought treatment and the control at SGS or KNZ during the drought period (Fig 4a,d), but C₃ graminoid abundance increased in response to chronic and intense drought at the two mixed grass sites. In the chronic treatment at HPG, C₃ abundance started to increase after one year and became significantly higher than the control treatment in the second and third year of drought. C₃ abundance also increased in the intense treatment, but only significantly in 2016, and C₃ abundance returned to control levels in both treatments by the last year of drought (Fig. 4b). During the third year of both drought treatments at HYS, C₃ abundance significantly increased and remained elevated, albeit not significantly, in 2017 (Fig. 4c). At both sites, average C₃ cover increased more in the chronic plots than the intense plots, peaking at an average increase of ~40% at HPG in 2015 and ~50% at HYS in 2016 (Fig. 4b-c).

The abundance of C₄ graminoids decreased at all sites in response to extreme drought (Fig. 5a-d). In the second year of drought (2015), C₄ cover started to decrease in both drought treatments at SGS and reached a maximum average loss of ~32% in the third year of the drought and remained significantly lower in fourth year (Fig. 5a). During the first year of drought, average C₄ cover declined by 8% in the chronic treatment and 9% in the intense treatment at HPG and continued to decline until final year of drought when losses were 16% for both treatments (Fig. 5b). Declines in C₄ abundance peaked in third of both drought treatments at HYS, with an average loss in cover of just over 50% for both treatments, but C₄ grasses started to respond significantly one year sooner in the intense plots (fig. 5c). The abundance of C₄ grasses also declined in the first year of intense drought at KNZ and remained significantly lower throughout the drought. Average C₄ losses peaked at 66% less than the control treatment in the third year of the drought treatments. Average cover of C₄ graminoids also decreased in the chronic treatment at KNZ, but to a lesser extent, and only significantly in the third and fourth years of the drought treatments (Fig. 5d).

Community composition

Community composition responded to drought at all sites, but the timing and the magnitude of the response varied. Starting in the second year of intense and chronic drought at SGS and HPG, community composition began to significantly diverge from the control treatment (Fig. 6a-b). The differences in composition between the control and drought treatments at both sites were in part due to the decline of the dominant C₄ grass *Bouteloua gracilis* and a drastic increase of an annual C₃ grass *Vulpia octoflora* at HPG (Table 2; S2a-b, S3a-b). Composition of communities exposed to intense drought also started to diverge in the second year at HYS, but composition did not begin to respond to chronic drought until the third year (Fig. 6c). These

differences were partially driven by the decrease of *Bouteloua curtipendula*, one of the dominant C₄ grasses, and an increase of *Bromus japonicus*; an exotic, annual, C₃ grass (table 2, S4a-b). It took three years of chronic drought for composition to respond at KNZ, and composition was unaffected by the intense drought treatment (Fig. 6d).

The magnitude of the difference in composition between the drought treatments and control was greatest at SGS and HYS. The difference in composition, which ranges from 0-1, for the intense versus control comparison peaked at 0.47 at SGS and 0.44 at HYS, which was slightly higher than the difference between the chronic versus control at both sites (Fig. 6a, c). Compositional difference also peaked in 2016 at HPG for both treatments, but was highest in the chronic plots at 0.31, and became more like the control treatment in the last year of drought (Fig. 6b). Intense drought composition difference was also marginally higher than the chronic drought at KNZ but reached a maximum of 0.27 in year three of the drought, and then the difference for both treatments diminished in the final year of the drought treatments (Fig. 6d).

Timing of plant community recovery following drought and factors affecting recovery

Richness and Evenness

Both SGS and HYS saw the significant differences in richness with drought rebound during the recovery period, leading to incomplete recovery by the fourth year of the recovery period. At SGS, richness in both drought treatments was not different from the control until the last year of recovery, when the intense treatment had 1.8 fewer species on average than the control treatment (Fig. 2a). During the first year of recovery at HYS, richness in the chronic treatment dropped to the control level, but then increased again and was significantly higher than the control in the third and fourth years of recovery (Fig. 2c); the number of species in the

intense drought treatment was higher than the control throughout recovery but was never significantly different (Fig. 2c).

Evenness in both drought treatments at SGS decreased in the first year of recovery and was lower than the control in the last two years of recovery, although not significantly for the chronic drought in 2021 (Fig. 3a). Evenness also decreased starting in the third year of recovery in both drought treatments at HPG, and only recovered in the intense treatment in the last year of recovery (Fig. 3b). The chronic and intense treatments at HYS had higher evenness than the control treatment throughout the recovery period, but evenness was only significantly different from the control treatment in the first year of the recovery period for the chronic drought treatment and in the third year of recovery for the intense drought treatment (Fig. 3c).

C₃- C₄ abundance

While C₃ abundance was unaffected by drought at SGS and KNZ, cover of C₃ graminoids increased at SGS and decreased at KNZ during the recovery period. Average C₃ cover started to significantly increase in the first year of post-drought recovery and was ~25% higher in both drought treatments during the last year of recovery at SGS (Fig. 4a). During the second year of recovery at KNZ, C₃ abundance started to decrease in the intense treatment, and was 8% lower than the control treatment that last year of recovery (Fig. 4d). Cover of C₃ graminoids recovered at both mixed grass sites. At HYS, recovery in both drought treatments occurred during the first year of ambient conditions (Fig. 4c). C₃ cover returned to control levels in in the last year of drought at HPG but increased again in the second year of recovery and was 21% higher in the intense plots by the third year. After four years of ambient conditions, C₃ abundance remained higher in the drought treatments but was not significantly different from the control treatment (Fig. 4b).

Average C₄ abundance returned to control levels at all sites but at different times (Fig. 5a-d). The abundance of C₄ graminoids continued to decline in both drought treatments in the first two years of recovery at SGS but recovered the third year (Fig. 5a). While abundance returned to control levels in the last year of drought at HPG, differences remerged in the first year of recovery and recovered again the following year (Fig. 5b). At HYS, both drought treatments recovered after in the first year of ambient conditions (Fig. 5c). It took one year of ambient conditions for C₄ abundance to recover from intense drought at KNZ and two years for chronic drought, although cover remained slightly lower in the droughted plots throughout the recovery period (Fig. 5d).

Community composition

Composition in both drought treatments did not recover by the fourth year of the recovery period at SGS (Fig. 6a). Incomplete recovery at SGS was largely driven by a significant increase in *Bromus tectorum*, an annual invasive grass, that established in the plots in the third year of drought and increased in abundance throughout the recovery period and had higher average cover in both drought treatments versus the control treatment (Table 2, S2c). At HPG, composition in the chronic treatment recovered in the fourth-year post-drought but did not recover in the intense treatment. Overall C₃ cover recovered at HPG, but differences persisted in the cover of multiple C₃ grasses, which drove compositional differences and contributed to incomplete recovery in the fourth year post-drought. For instance, *Koeleria macranthra* had a higher average cover in the control versus the drought treatments, and *Hesperostipa comata* cover was higher in the drought treatments versus the control treatment (Table 2, Fig. S3c-d). Composition fully recovered at HYS and KNZ in the second year of the recovery period for both drought treatments. The magnitude of compositional difference was greatest for the intense plots

in the first year post-drought for all sites ranging from 0.27 at KNZ to 0.49 at SGS, and gradually declined over the recovery period. The chronic treatment had lower compositional differences overall than the intense treatment and remained relatively stable throughout recovery (Fig. 6a-d).

Comparing plant community responses/recovery between grassland and drought types

Richness and Evenness

There was no difference between the drought treatments in their effect on richness at any of the sites during the drought or recovery periods (Fig. 2a-d). Evenness values were also comparable between the intense and chronic drought treatments at all sites, except when evenness was higher in the chronic treatment during the second year of recovery (2019) at SGS and in the intense treatment during the second year of drought (2016) at HPG (Fig 3.a-b).

C₃-C₄ abundance

Overall, the drought treatments had a similar impact on C₃ and C₄ abundance. At SGS, C₃ abundance was similar between the chronic and intense treatments until the third year of drought when it was ~25% higher in the intense treatment, but C₃ abundance increased in the chronic plots the following year (2020) and was no longer different from the intense plots (Fig. 4a). The abundance of C₃ graminoids was slightly higher in the chronic treatment than the intense treatment during the first year of drought at HPG and that difference increased the next year and was 25% higher in the chronic treatment versus the control (Fig. 4b). Chronic drought also had ~25% higher cover of C₃ graminoids compared to the intense treatment during the third year of drought, and there was no difference in C₃ cover between the drought treatments during any other year. At KNZ, C₃ cover was ~10% higher in the chronic plots compared to the intense plots during the second year of recovery and remained slightly higher albeit not significantly the rest of the recovery period (Fig. 4d).

There was no difference between the drought treatments in their effect on C₄ abundance at SGS (Fig. 5a). Intense drought had a greater impact on C₄ abundance at HPG during the second year of drought when it was ~10% lower than in the chronic treatment, but there was no difference in C₄ cover between the treatments in any other year of the drought or recovery periods (Fig. 5b). A similar trend occurred at HYS in the third year of drought when C₄ cover was lower in the intense treatment but the same during the rest of drought and recovery (Fig. 5c). At KNZ, C₄ cover was lower in the intense treatment than in the chronic treatment throughout the drought and recovery, with the greatest difference in the third year of drought when C₄ cover was ~32% lower in the intense treatment.

Community composition

The drought treatments generally had a similar effect on composition at the sites (Fig 6a-d). At SGS, there was a significant difference in composition between the chronic and intense plots in the last year of drought (2017) and in the second year of recovery (2019). The species that contributed most to differences were *Carex eleocharis* in 2017, which had a higher cover in the chronic treatment compared to the intense treatment (Table 2, Fig. S2a). In 2019, *Bromus tectorum* contributed most to the difference in composition between the treatments, and was higher in the intense treatment (Table 2, Fig S2c). The magnitude of difference in composition was greatest in 2019 but was less than the difference between either drought treatment compared to the control (Fig. 6a). Composition never diverged between the drought treatments at HPG (Fig. 6b). At HYS, composition was significantly different between the drought treatments in the third year of drought (2016), which can likely be attributed to lower cover of *Bouteloua curtipendula* in the intense plots (Table 2, S4a). In 2018, *Bouteloua gracilis* contributed most to the difference in composition between the drought treatments and was higher in the intense plots

(Table 2, Fig. S4b). The magnitude of difference was greatest in 2018, which was similar to the level of difference for the drought versus control comparisons (Fig. 6c). There was a significant difference in composition between the drought treatments beginning in the third year of drought and persisted throughout the recovery period at KNZ. *Andropogon gerardii* contributed most to the differences in composition and was lower in cover in the intense treatment than the chronic treatment (Table 2, S5a). The level of composition difference was similar to the drought versus control comparisons and peaked during the first year of recovery (Fig. 6d).

Discussion

Grasslands will likely experience more long-term, extreme drought events in the future, and our results show that plant communities in the Central Plains of the US that span a broad precipitation gradient are all negatively impacted by these conditions but to differing extents. The four grassland sites in our experiment all underwent compositional change and shifts in C₃-C₄ abundances, and some experienced change in richness and evenness. We also found that plant community recovery can extend over several years. After four years of ambient conditions, some of which were natural drought years at SGS, HPG, and KNZ, at least one aspect of the communities had not recovered at all sites.

Timing of plant community response to drought and characteristics of the response

Drought caused significant shifts in C₃-C₄ graminoid abundance. Specifically, some C₄ species decreased in cover while some C₃ species increased in cover (species reordering), which drove compositional changes in all grassland types (Smith 2011). This is somewhat surprising given the general perspective that C₄ species are more water use efficient, but this has been observed previously (Weaver 1968, Knapp et al. 2015, Knapp et al. 2020). The drought imposed in this study likely disproportionately favored C₃ graminoids because of its timing during the growing season. Since C₃ species are active earlier than C₄ species, they can take advantage of late winter/early spring precipitation, allowing them to grow and reproduce before drought makes conditions unfavorable (Huxman et al. 2004, Knapp et al. 2020). Indeed, *Vulpia octoflora*, an annual C₃ grass, increased in the shortgrass steppe and the northern mixed grass prairie sites, as it was able to exploit space opened by reduced abundance of *Bouteloua gracilis*, the dominate C₄ grass (Weaver 1968, Grime 2001, Evans et al. 2011). These conditions also likely promoted the establishment of cheatgrass (*Bromus tectorum*) in the shortgrass steppe in the third year of

drought (2016), which is an invasive annual C₃ grass known to establish in disturbed areas and benefits from summer drought (Bradley 2009, Prevey and Seastedt 2014). *Bromus japonicus*, another exotic annual grass, also drove increased abundance of C₃ cover at HYS likely in response to decreased abundance of dominant C₄ grasses including *Bouteloua curtipendula*.

Changes in richness and evenness had less of an impact on plant composition than shifts in species abundances. Only the shortgrass steppe and southern mixed grass prairie experienced changes in richness that were transient, and evenness increased relatively small amounts in the shortgrass steppe (SGS) and both mixed grass prairies (HPG, HYS). While several studies have shown that drought leads to decreased richness due to the decline in abundance and subsequent loss of locally rare species (Tilman and Haddi 1992, Evans et al. 2011, Fry et al. 2014), it is possible that drought did not perturb the communities enough to cause a loss of species; or species were lost, but those losses were offset by species gains. Multiyear drought can eventually lead to increased richness when ruderal species establish after dominant species decline in abundance (Grime 2001, Evans et al. 2011), which was observed after three years of drought in the southern mixed grass prairie. Reduced abundance of dominant species in both mixed grass prairies and the shortgrass steppe may have also caused the subdominant species to increase, making species abundances in communities more similar overall, thus increasing evenness. While drought caused some changes in richness and evenness, the effects were less drastic and more ephemeral than the effects of drought on C₃-C₄ abundance. Together these findings suggest that changes in plant composition are more likely to result from shifts in cover of dominant graminoids and subsequent species reordering than from alterations in richness or evenness (Batbaatar et al. 2021).

Timing of plant community recovery following drought and factors affecting recovery

There was at least one aspect of the plant communities that did not recover after four years in all grassland types, suggesting complete recovery can take longer than the duration of the drought event itself. In addition, the full effects of drought may not be seen until several years after the drought ends (i.e., a lagged response), as differences did not emerge in C₃ abundance, richness, or evenness until the recovery period at some of the sites.

Composition did not fully recover at the two drier sites (SGS, HPG) after four years of ambient conditions, which can largely be attributed to incomplete recovery of C₃-C₄ graminoid abundances, and from changes in the identity of the most abundant species in a community. While the abundance of C₄ graminoids recovered in both drought treatments at SGS and HPG, it was not restored to predrought levels, due to the widespread loss of *Bouteloua gracilis*. After the drought ended, cover of *Bouteloua gracilis* also decreased in the control plots at both sites, leading to “recovery” of C₄ cover in the droughted communities because cover was low across all plots. This decline could be attributed to the cessation of grazing (Laurenroth and Burke 2008) that likely destabilized plant communities and hindered community recovery, especially in the shortgrass steppe, where *Bouteloua gracilis* regulates ecosystem processes (Hyder 1975, Evans et al. 2011). Dry conditions during the recovery period possibly impeded the establishment of *Bouteloua gracilis* seedlings, further inhibiting community recovery (Laurenroth et al. 1994, Fig. 1). In addition, lower than average growing season precipitation continued to benefit C₃ graminoids after the drought ended, likely making it more difficult for C₃-C₄ abundances to be restored and for communities to recover (Knapp et al. 2020, Fig. 1). Favorable conditions for C₃ plants in combination with altered composition in the droughted communities likely led to *Hesperostipa comata* becoming the most dominant species in the fourth year (2021) in the

droughted plots at HPG, and likely explains lingering compositional and evenness differences between the control and intense treatment.

Another factor inhibiting C₃-C₄ recovery in the shortgrass steppe was the invasion of cheatgrass and the increase in abundance of the native annual *Vulpia octoflora*. Cheatgrass increased throughout the recovery period, exposing communities to both biotic (invasion) and abiotic (drought) stressors (Fahey et al. 2018), and the interactive effects of these stressors may have made recovery less likely than if these communities had just been exposed to drought. The invasion of cheatgrass also inhibited recovery of richness and evenness in the intense treatment at SGS, because the high cover of cheatgrass presumably caused richness and evenness to decline (Prevey and Seastedt 2014). Together these findings suggest that declines of the dominant species from drought in the shortgrass steppe can promote establishment of annual grasses (primarily cheatgrass) and long-lasting alterations of composition.

The abundance of C₃-C₄ graminoids was fully restored at the southern mixed grass site (HYS) and consequently composition recovered. Since richness did not recover at HYS, this implies that the changes in richness had less of an impact on composition than shifts of C₃-C₄ graminoids. Composition also recovered in the tallgrass prairie (KNZ), but differences in C₃ graminoid abundance persisted in the fourth year of recovery. Since C₃ graminoids make up a much smaller proportion than C₄ graminoids of total graminoid cover at KNZ, it is logical that composition could recover without C₃ abundance recovering.

Composition at the wetter sites recovered sooner than drier sites, and overall, the plant community response to drought was less pronounced at the wetter sites. This suggests that recovery time is correlated with the magnitude of the response during drought. For instance, the

shortgrass steppe experienced the greatest magnitude of compositional change and did not recover after four years, while KNZ had the lowest magnitude compositional response and recovered after two years. Further, the mixed grass sites, which fall in middle of the precipitation gradient, experienced intermediate impacts of drought and recovery times.

Comparing plant community responses/recovery between grassland and drought types

Our findings indicate that drier grassland communities respond sooner to drought but took longer to recover than mesic sites. These results are in line with observations of greater sensitivity of ANPP to drought in more arid than mesic sites (Knapp et al. 2015, Griffin-Nolan et al. 2019, Carroll et al. 2021). This also challenges previous conclusions that semi-arid grassland communities are resistant to long-term water limitation because of drought tolerant species (Evans et al. 2011, Tielborger et al. 2014). However, the declines in C₄ cover that occurred at SGS and HPG, driven by reduced cover of *B. gracilis*, may have been expedited since plants were likely already drought stressed when treatments began because of natural drought conditions in 2012 and below average precipitation in 2013 (Fig. 1a). Moreover, these sites were historically grazed but not grazed during the study period, which could also have contributed to the overall decline in *B. gracilis* abundance at both sites.

There was limited support for our hypothesis that drought type would have differential impacts on communities based on site aridity, which was also true for ecosystem responses in ANPP (Carroll et al. 2021). While some community characteristics of the drier sites appeared to be more affected by chronic drought but by intense drought for the mesic site, neither drought type was consistently more impactful. There was some evidence to suggest that intense drought had a greater impact on plant communities overall since the magnitude of compositional

difference was greatest for intense drought at all sites, which was again true for ANPP responses at the sites (Carroll et al. 2021). However, composition of intensely droughted communities did not necessarily respond sooner or take longer to recover across sites. In addition, there were limited differences in the impact that the drought treatments had on richness, evenness, C₃-C₄ abundance, and composition. While composition was significantly different between the drought treatments at KNZ beginning the third year of drought through the last year of recovery, this was likely in part because cover of *Andropogon gerardii* was higher in the chronic plots before treatment began in 2013 (Fig. S5a). Overall, these findings imply the magnitude of drought is more important than other drought characteristics like the number and time between precipitation events for understanding the impact of drought on plant communities.

Conclusions

Extreme drought altered plant communities across four major grassland types in the US Central Plains and many aspects of plant communities did not recover after four years. The magnitude and timing of response and recovery differed based on MAP and grassland type, with the semi-arid shortgrass steppe being most vulnerable to extreme drought and the mesic tallgrass prairie being the most resistant to drought. Drought type (chronic, intense), however, did not have a consistent effect on plant communities based on site MAP. Across sites, the abundance of C₃-C₄ graminoids drove compositional responses and recovery. This was most evident at the shortgrass steppe, where communities were transformed from being C₄ dominated by *B. gracilis* to dominated by annual grasses in the recovery period, including cheatgrass, an invasive C₃ species. This shift will likely have lasting impacts on plant composition and ecosystem services because cheatgrass and other invasive bromes reduce carbon storage (Germino et al. 2016), increase fire risk (Brooks et al. 2004), cause severe erosion in disturbed areas (Knapp 1996; Wilcox et al. 2012), and are often not palatable for wildlife and livestock (Menalled et al. 2017). These findings can help prioritize drought mitigation and recovery efforts in the shortgrass steppe. For instance, various stakeholders including land managers and ranchers could work together to prevent invasive grasses such as cheatgrass from establishing after drought by seeding native species or altering grazing practices. This study also underscores the importance of studying how multiple aspects of communities respond to drought, since community composition was affected by drought at all sites, but richness and evenness were not (Avolio et al. 2019, Komatsu et al. 2019). In addition, this work shows that the effects of drought need to be monitored for several years after drought ends to understand the full effects of drought in

grasslands and the associated environmental, economic, and social implications in the context of climate change.

Future Directions

The results of this study showed that plant composition is affected by extreme drought largely due to shifts in C_3 - C_4 abundance, and in cases where composition did not recover, it was because C_3 - C_4 abundances were not restored to predrought conditions. However, there are many other aspects of communities that are responsive to drought that were not explored that could help explain compositional changes. For instance, previous work has shown that drought favors woody species (Rondeau et al. 2013), causes declines in grass cover (Stampfli and Zeiter 2004, Morecroft 2004, Babaataar et al. 2021), and over time can lead to an increase in ruderal species (Weaver 1968, Evans et al. 2011). Using existing species composition data, it would be easy to categorize the species into these functional groups based on their growth form (forb, grass, woody) and life form (annual vs. perennial) to see if drought caused differences in richness or cover of these groups, and if so, how long it takes for the differences to recover.

It would also be worthwhile to dig deeper into species-specific responses and recovery. For instance, richness decreased at SGS and increased at HYS during the drought, but it is not clear which species were lost and gained and if the same species were consistently lost or gained at the sites. This could be determined by tracking which species were present in each plot over time and could potentially uncover species that can exploit drought conditions (species gained) or are drought intolerant (species lost). This approach could also be used at KNZ and HPG to see if species losses offset by species gains explain why these sites did not see a response in overall richness to drought.

It would also be interesting to track species abundances over time to determine the timing of species reordering. This could be accomplished using rank abundance curves (RACs), which trace the identity and abundance of species over time (Avolio et al. 2019). For example, at SGS,

this would pinpoint when *B. gracilis* was no longer the most dominant species in the droughted plots, and which species took its place. It would also show which species were the most dominant each year and would uncover if communities transitioned from being dominated by one species to being codominated (Hoover et al. 2014). In addition, by looking at species absolute cover (instead of relative cover) for the RACs, comparisons could be made of total plant cover between the drought and control treatments to see if drought caused changes in total plant cover over time.

Information about species identity, abundances and rank could also be incorporated into studies of ecosystem (ANPP) responses and recovery by identifying which species drove changes in aboveground biomass. At SGS, for instance, biomass and composition data show the grassland shifted from being C₄ to C₃ dominated in response to drought, and knowing which species contributed to these shifts is important for quantifying the implications for ecosystem function and services. For example, by the end of the recovery period, the communities were mostly dominated by cheatgrass, which stores less carbon and is of poorer forage quality than other grasses. Overall, linking species, community, ecosystem scale observations will provide a more complete picture of the drought responses and recovery in these grasslands (Felton and Smith 2017).

While this study showed that the shortgrass steppe was the least resistant and resilient to drought, further research is needed to understand why this was the case. A future study could explore the combined effects of grazing, drought, and invasion on plant community responses and recovery at the shortgrass steppe by doing a factorial experiment with treatments for each combination of the levels of the factors (i.e., grazing yes, grazing no, drought yes, drought no, invasion yes, invasion no) and controls. While this would be a huge undertaking and potentially

difficult to manage, it would uncover if the lack of grazing led to loss of *B.gracilis* and the role this species plays in stabilizing communities. Further, it would untangle the individual and combined effects of drought and invasion on plant composition responses and incomplete recovery.

Given that drastic changes in composition have persisted after four years of ambient conditions at the shortgrass steppe, it is likely that these communities are in an alternative state and that drought relief alone will not facilitate restoration of C₃-C₄ abundances (Scheffer et al. 2001). A future study could explore if this is indeed the case by removing cheatgrass and seeding treated plots with native grasses to see if plant composition shifts back to the trajectory of the control communities or to predrought conditions. This could also help inform restoration practices of the shortgrass steppe that has been invaded by cheatgrass.

Finally, this study had some limitations that could be addressed in future work. For example, during the drought period, all sites experienced the same magnitude of drought, but conditions in the recovery period varied by site since the sites received ambient precipitation. For instance, three of the four years at SGS had below average precipitation while all recovery years at HYS received above average precipitation. Across site recovery comparisons would be more accurate if the level of ambient precipitation was standardized, either by irrigating plots or by continuing to restrict precipitation to some degree.

Tables and Figures

Table 1 Characteristics of the four grassland sites included in the study. Species: BOGR=*Bouteloua gracilis*, PASM=*Pascopyrum smithii*, BOCU=*Bouteloua curtipendula*, SCSC=*Schizachyrium scoparium*, SPAS = *Sporobolus asper*, ANGE=*Andropogon gerardii*, SONU=*Sorghastrum nutans*. Modified from Carroll et al. 2021.

Site	Grassland Type	MAP (mm)	MAT (°C)	Dominant species
SGS	Shortgrass steppe	289	9.5	BOGR
HPG	Northern mixed grass prairie	309	8.8	PASM, BOGR
HYS	Southern mixed grass prairie	570	13.1	BOCU, SCSC, SPAS
KNZ	Tall grass prairie	825	13.5	ANGE, SONU

Table 2 Species that contributed the highest percentage to differences in composition between each drought treatment vs. control comparison each year. Values are percentages rounded to the nearest tenth. Species: BOGR=*Bouteloua gracilis*, VUOC=*Vulpia octoflora*, PLPA=*Plantago patagonica*, BRTE=*Bromus tectorum*, HECO=*Hesperostipa comata*, HEVI=*Heterotheca villosa*, KOMA=*Koeleria macrantha*, CAEL=*Carex eleocharis*, BRJA=*Bromus japonicus*, BOCU=*Bouteloua curtipendula*, SCSC=*Schizachyrium scoparium*, ANGE=*Andropogon gerardii*, SONU=*Sorghastrum nutans*

Site	Treatment	Species	2013	2014	2015	2016	2017	2018	2019	2020	2021
SGS	control-chronic	BOGR	9.2		10.8	10.3	19.6				
		VUOC		8.7				14.3			
		PLPA							8.2		
	control-intense	BRTE								18.0	18.0
		BOGR	9.3	8.0	13.3	10.0	21.3				
		VUOC						14.9			
	chronic-intense	BRTE							20.4	27.5	24.7
		BOGR	6.0								
		VUOC		8.9	9.9	10.0		9.5			
		CAEL					5.8				
		BRTE							18.8	19.2	17.6
HPG	control-chronic	BOGR	5.9								
		HECO		5.5							11.4
		VUOC			13.7	15.2					
	control-intense	HEVI					6.7				
		KOMA						7.5	9.7	11.8	
		BOGR	6.1								
	chronic-intense	CAEL		5.2							
		VUOC			7.2	11.6		8.9			
		HEVI					6.2				
		KOMA							9.5	11.5	
		HECO									10.8
		CAEL	5.3	6.4							
HYS	control-chronic	VUOC			12.8	11.2		7.9			
		HECO					6.2		6.1		10.4
		BRTE								11.9	
	control-intense	BRJA	7.3			7.2					
		BOCU		9.3	10.1						
		SCSC					8.2	10.2	10.2	12.8	13.6
	chronic-intense	BRJA	6.7				8.1				
		BOCU		10.3	11.7	8.4					
		SCSC						10.3	9.1	13.2	13.9
	control-chronic	BRJA	6.7			7.9	6.1				
		BOCU		9.1	10.6						
		BOGR						7.8		9.7	10.0
		SCSC							6.4		
KNZ	control-chronic	ANGE	9.4	9.3	9.3	8.4	9.1	9.9	8.4	6.9	7.6
	control-intense	ANGE	11.4	10.6	10.4		9.5	12.5	11.9	8.3	9.3
		SONU				10.5					
	chronic-intense	ANGE	11.7	11.1	11.0	11.8	11.4	14.2	11.7	8.2	8.6

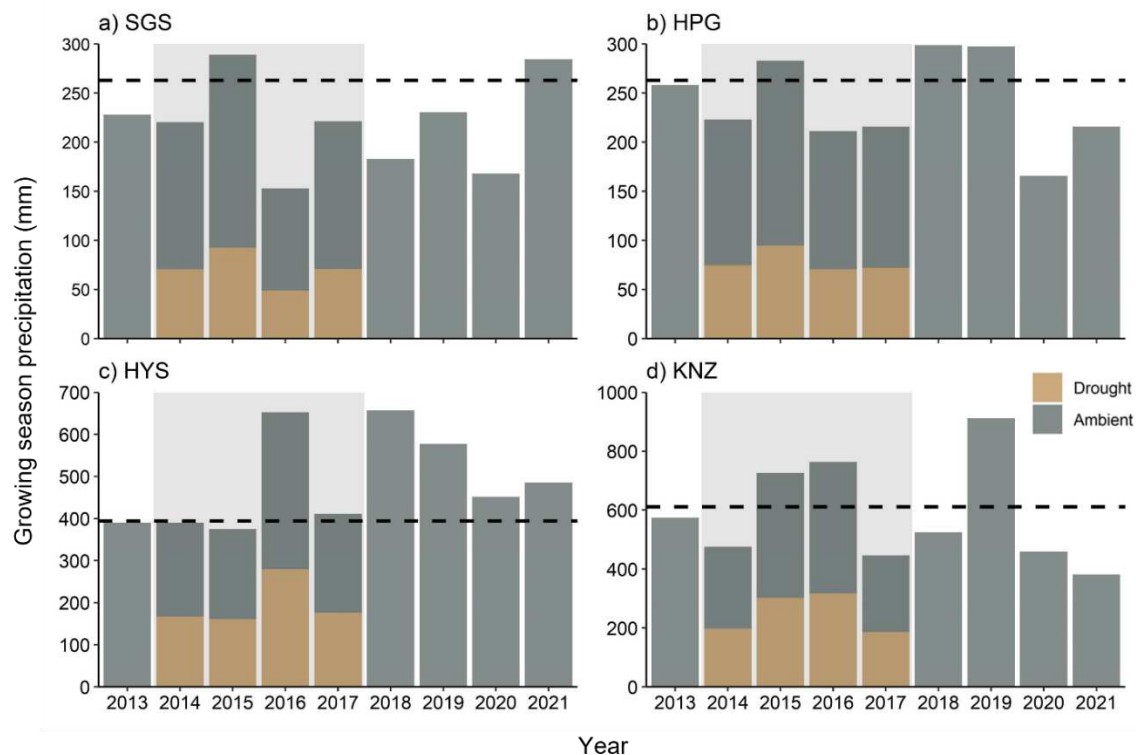


Figure 1 = Total ambient growing season precipitation (GSP) in millimeters (April 1st - September 15th) by year represented by the grey bars. The brown shading in the drought years shows the average amount of growing season precipitation received in both drought treatments, based on the average percent reductions in growing season precipitation across the four years of the drought treatments. Percent reductions at each site: SGS=67.99%, HPG=66.60%, HYS=57.26%, KNZ=58.40%. The black dashed line represents the 30-year average growing season precipitation for each site.

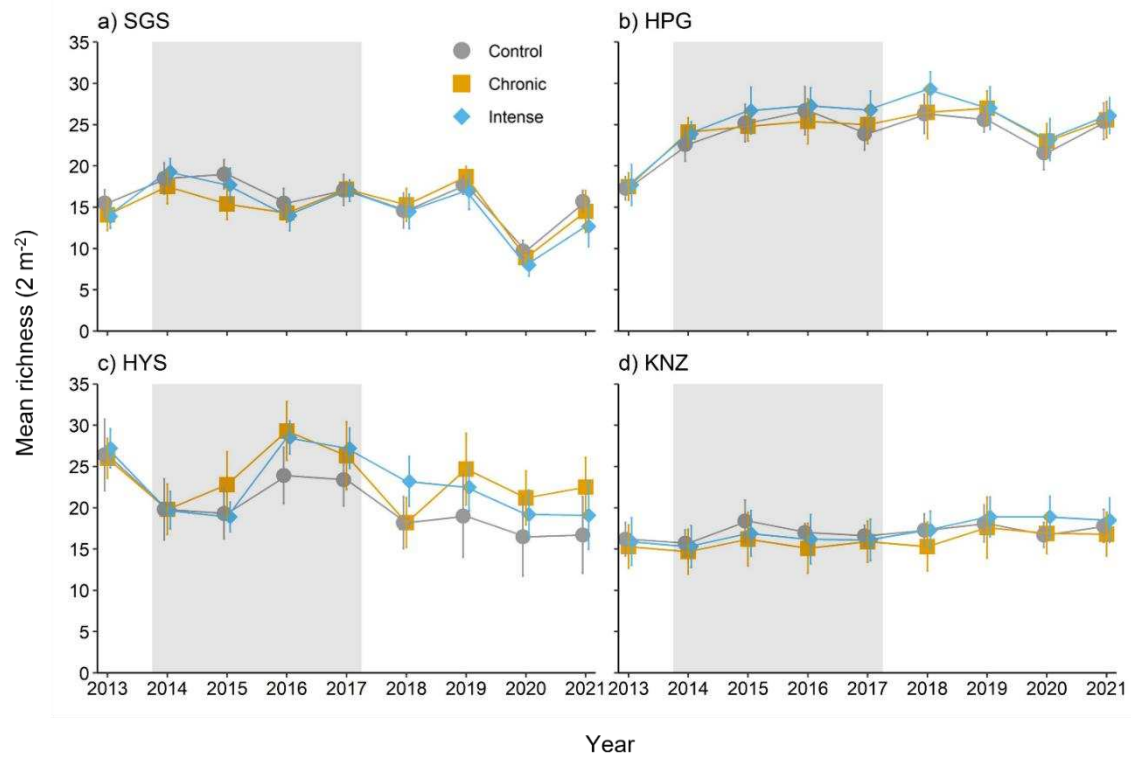


Figure 2 Mean species richness by treatment for each year at the 2 x 2 m plot level. Error bars represent 95% confidence intervals.

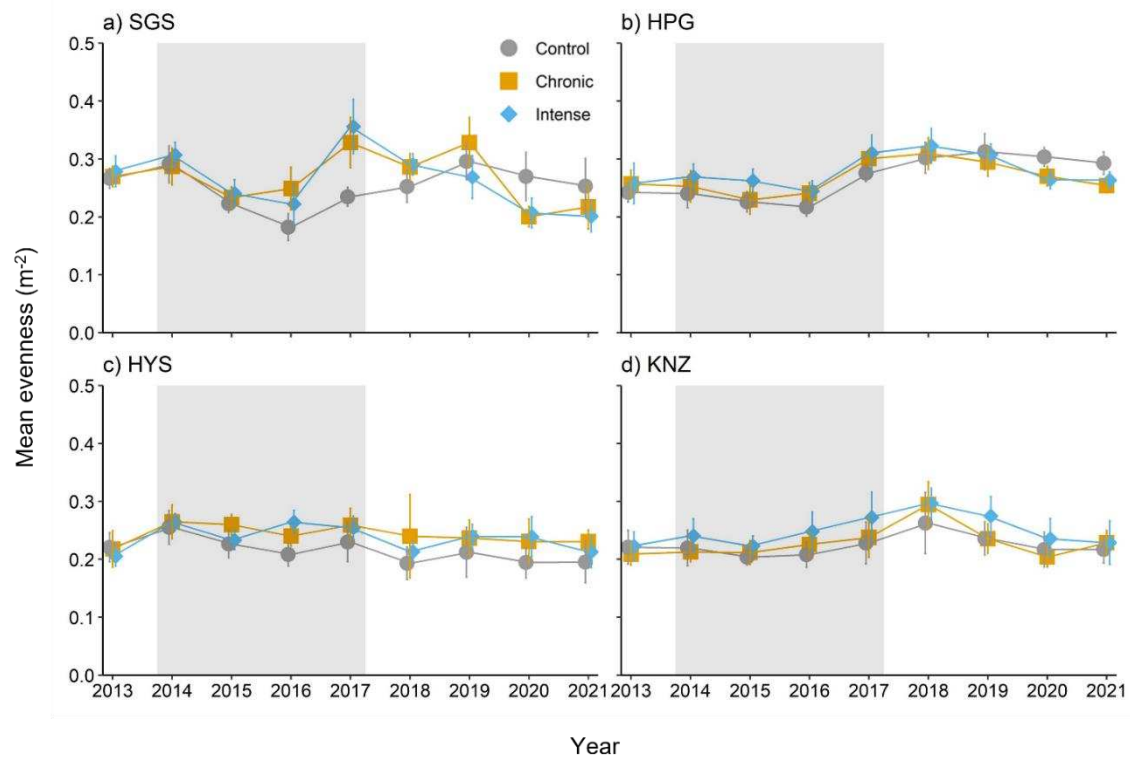


Figure 3 Mean evenness by treatment and year based on EVAR measure. Values range from 0 (relative abundance of species completely different) to 1 (relative abundances of species the same). Error bars represent 95% confidence intervals.

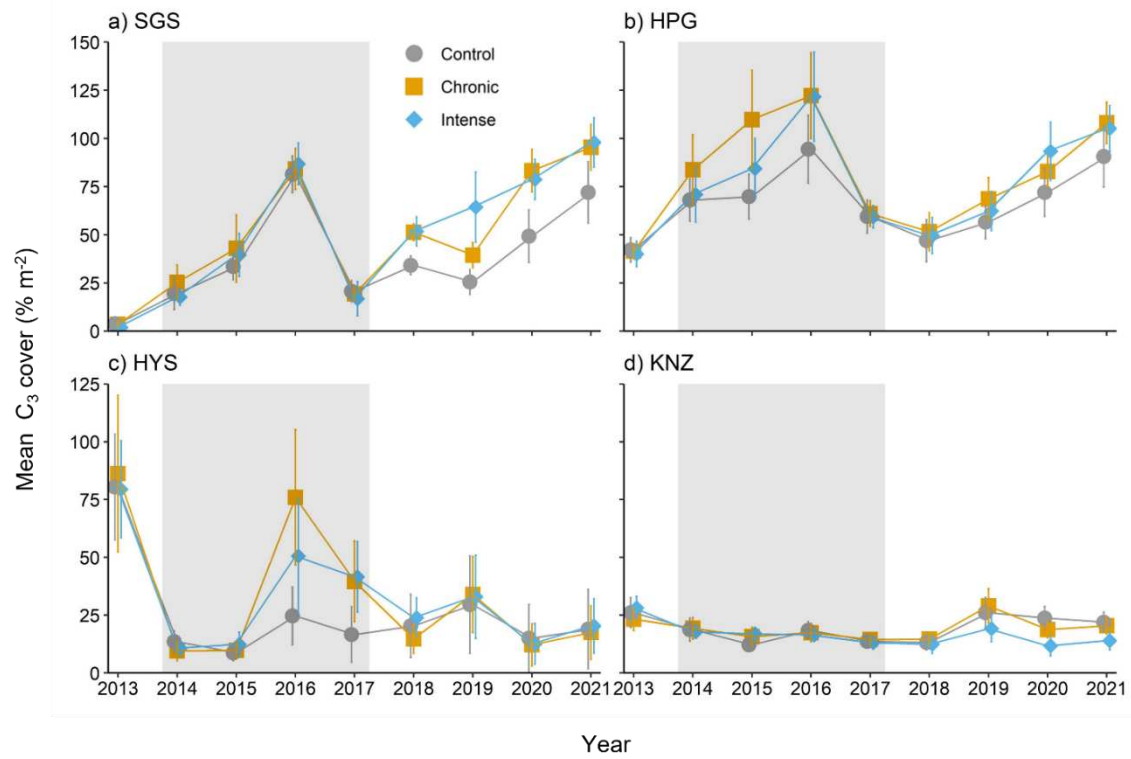


Figure 4 Mean cover of C_3 graminoids by treatment and year. Error bars show 95% Confidence intervals.

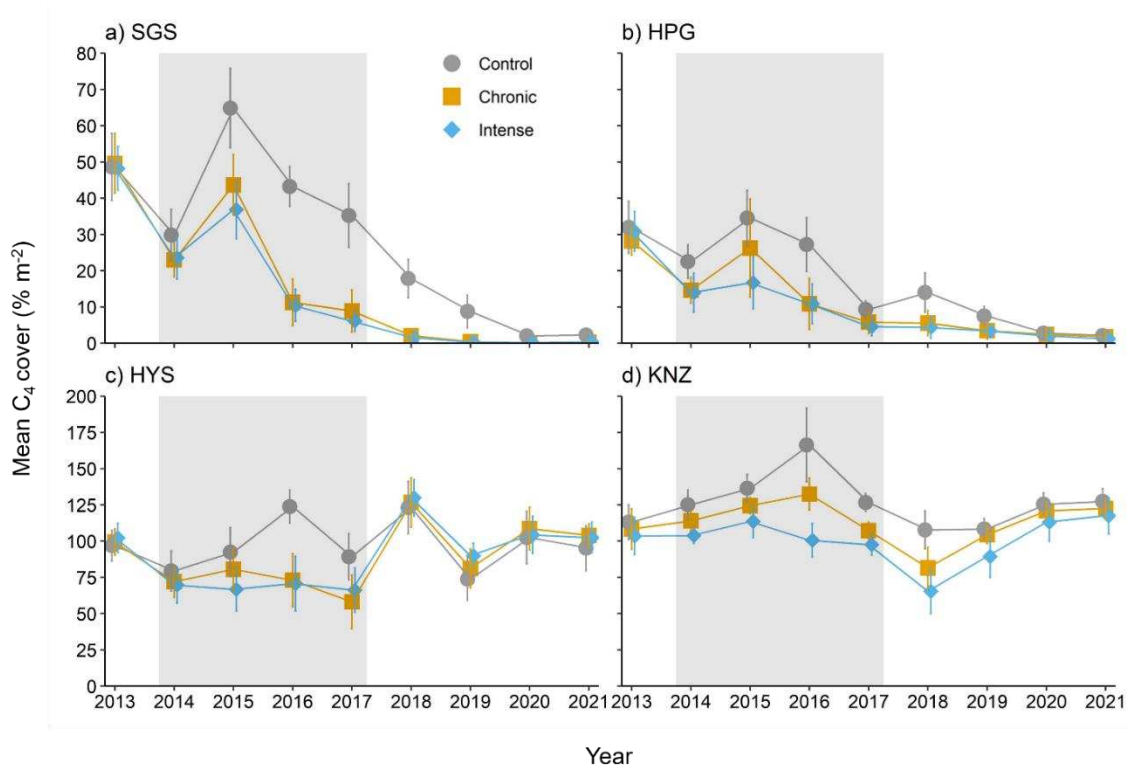


Figure 5 Mean cover of C_4 graminoids by treatment and year. Error bars show 95% confidence intervals.

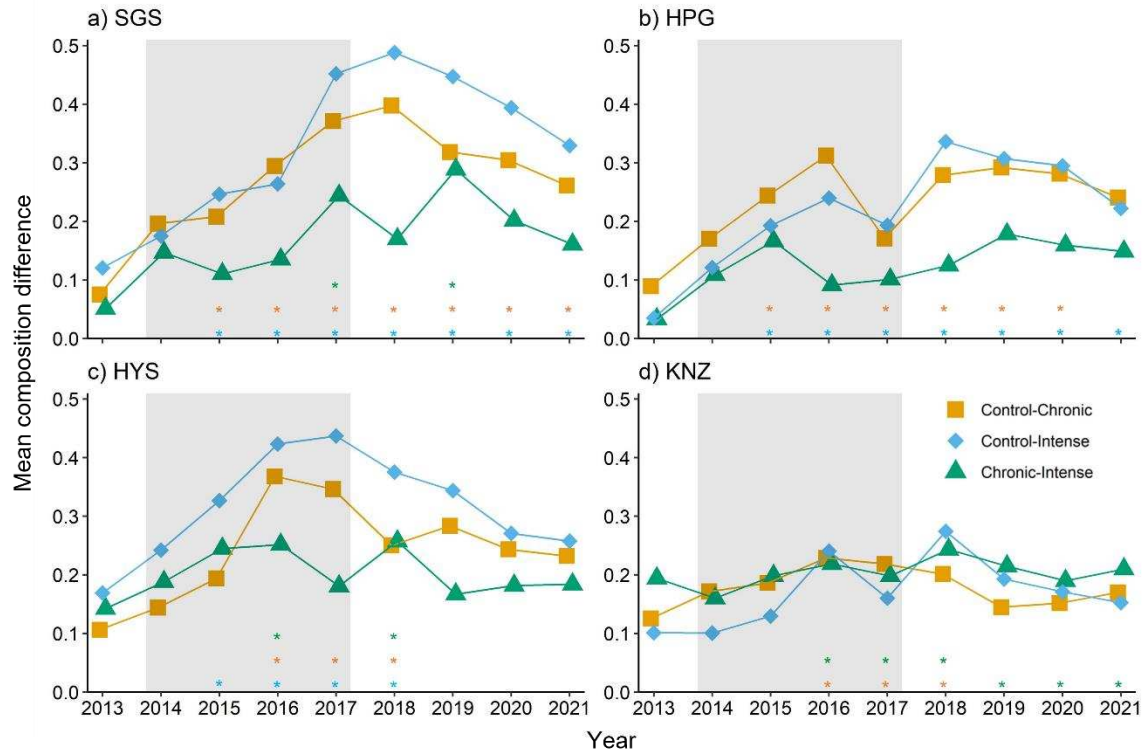


Figure 6 Mean composition difference between treatment comparisons based on Bray-Curtis dissimilarity matrix. Asterisk above year tick indicates significant difference between drought treatment and control based on PERMANOVA results. Orange asterisk = significant difference in composition between the control vs. chronic treatment. Blue asterisk = significant difference between the control vs. intense treatment. Green asterisk = significant difference between the chronic vs. intense treatment.

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Appendix: Supplemental figures and tables

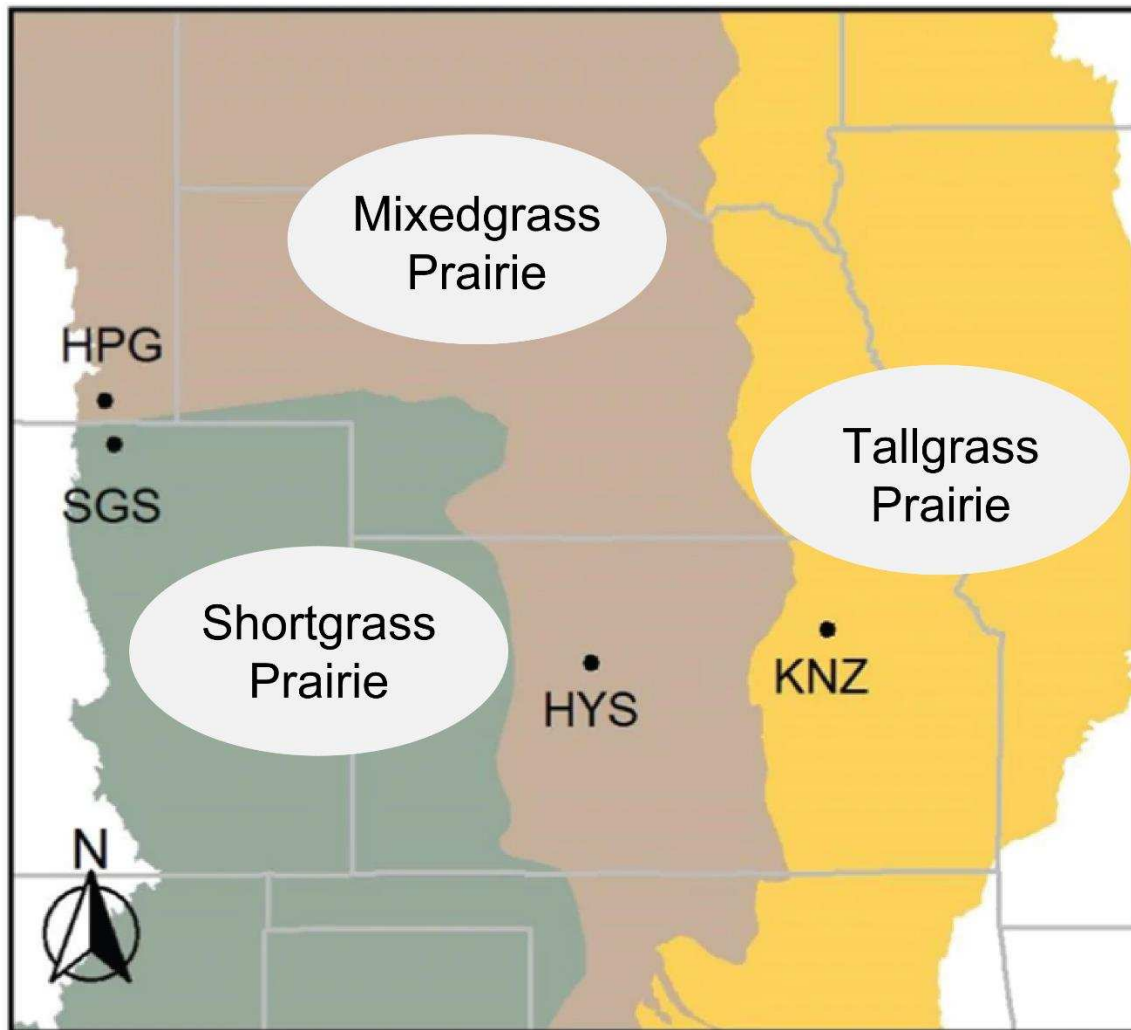


Figure S1 Map of the four grassland sites showing the location and grassland type. Modified from Carroll et al. 2021.

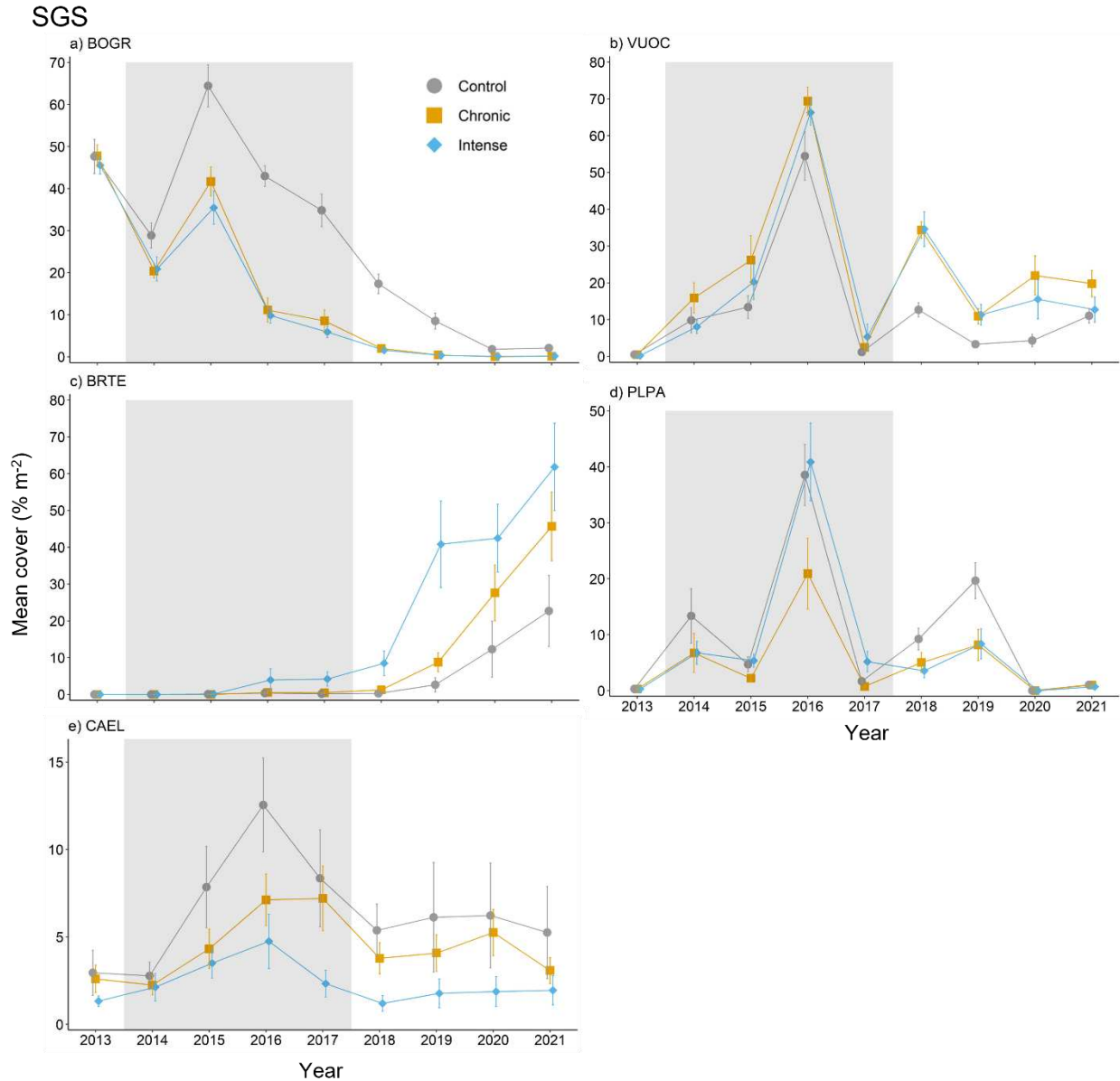


Figure S2 Mean absolute cover of species that contributed most to differences in composition between the drought treatments and control at SGS. See Table 2 to see the year(s) in which each species was the highest contributor to compositional differences. Error bars show standard error. Species: BOGR=*Bouteloua gracilis*, VUOC=*Vulpia octoflora*, BRTE=*Bromus tectorum*, PLPA=*Plantago patagonica*, CAEL=*Carex eleocharis*

HPG

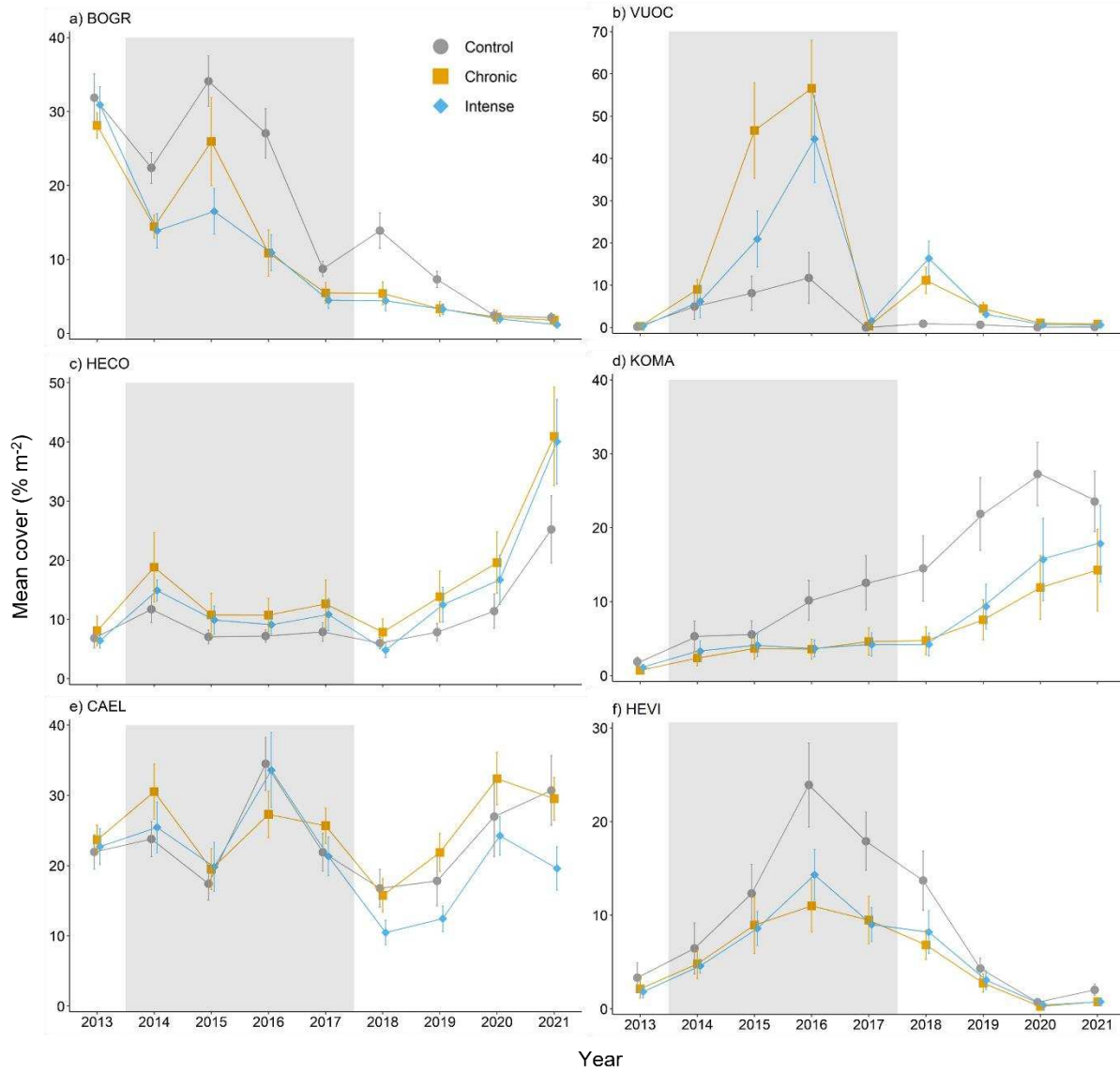


Figure S3 Mean absolute cover of species that contributed most to differences in composition between the drought treatments and control at HPG. See Table 2 to see the year(s) in which each species was the highest contributor to compositional differences. Error bars show standard error. Species: BOGR=*Bouteloua gracilis*, VUOC=*Vulpia octoflora*, HECO=*Hesperostipa comata*, KOMA=*Koeleria macrantha*, CAEL=*Carex eleocharis*, HEVI=*Heterotheca villosa*

HYS

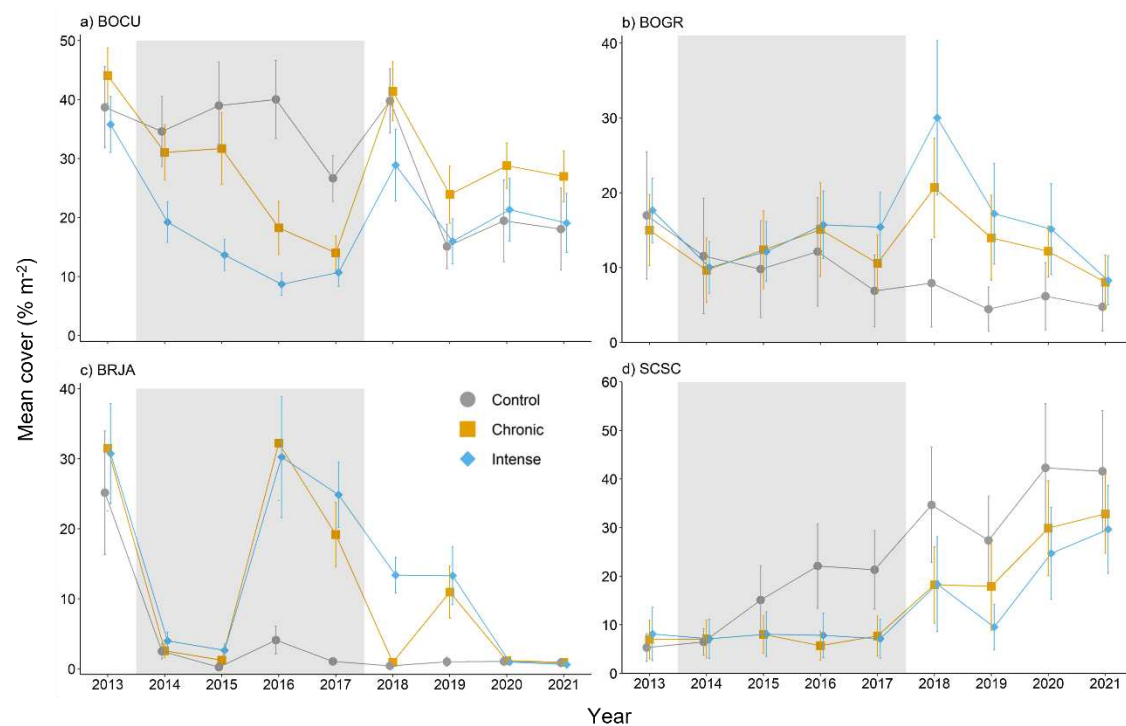


Figure S4 Mean absolute cover of species that contributed most to differences in composition between the drought treatments and control at HYS. See Table 2 to see the year(s) in which each species was the highest contributor to compositional differences. Error bars show standard error. Species: BOCU=*Bouteloua curtipendula*, BOGR=*Bouteloua gracilis*, BRJA=*Bromus japonicus*, SCSC=*Schizachyrium scoparium*

KNZ

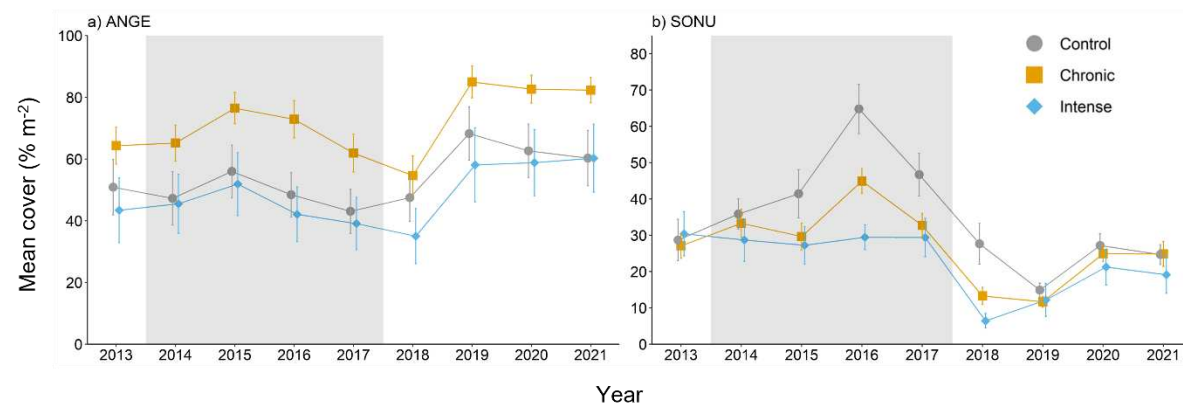


Figure S5 Mean absolute cover of species that contributed most to differences in composition between the drought treatments and control at KNZ. See Table 2 to see the year(s) in which each species was the highest contributor to compositional differences. Error bars show standard error. Species: ANGE=*Andropogon gerardii*, SONU=*Sorghastrum nutans*

Table S1 PERMANOVA pairwise contrast results. P-values <0.05 are bolded. A dash indicates a treatment p-value >0.05 in PERMANOVA model, so treatment comparisons were not made.

Site	Treatment	2013	2014	2015	2016	2017	2018	2019	2020	2021
SGS	control-chronic	-	-	.004	.002	.006	.002	.002	.025	.030
	control-intense	-	-	.015	.002	.002	.002	.002	.004	.015
	chronic-intense	-	-	-	-	.018	-	.048	-	-
HPG	control-chronic	-	-	.006	.004	.047	.004	.018	.017	-
	control-intense	-	-	.004	.004	.006	.002	.002	.024	.026
	chronic-intense	-	-	-	-	-	-	-	-	-
HYS	control-chronic	-	-	-	.002	.002	.014	-	-	-
	control-intense	-	-	.002	.002	.002	.002	-	-	-
	chronic-intense	-	-	-	.016	-	.016	-	-	-
KNZ	control-chronic	-	-	-	.005	.013	.020	-	-	-
	control-intense	-	-	-	-	-	-	-	-	-
	chronic-intense	-	-	-	.012	.036	.020	.041	.049	.018

Table S2 Mixed model results testing the main and interactive effects of drought treatment on community structure. F=F-values, df=degrees of freedom, P=p-value. Bold values represent significance (p<0.05)

Site	Predictor	Richness			Evenness			C ₃ cover			C ₄ cover		
		F	df	P	F	df	P	F	df	P	F	df	P
SGS	Treatment	12.56	2	.105	2.1	2	.157	19.6	2	<.0001	32.5	2	<.0001
	Year	50.42	8	<.0001	22.1	8	<.0001	160.2	8	<.0001	232.3	8	<.0001
	Treatment x Year	1.70	16	.048	3.0	16	<.0001	4.7	16	<.0001	11.3	16	<.0001
CHY	Treatment	2.26	2	.133	2.46	2	.11	8.8	2	.002	16.8	2	<.0001
	Year	33.66	8	<.0001	29.52	8	<.0001	69.6	8	<.0001	94.4	8	<.0001
	Treatment x Year	.61	16	.876	2.99	16	.0002	2.53	16	.001	3.8	16	<.0001
HYS	Treatment	3.03	2	.073	6.27	2	.009	1.3	2	.296	1.5	2	.241
	Year	21.51	8	<.0001	5.77	8	<.0001	63.4	8	<.0001	34.0	8	<.0001
	Treatment x Year	1.96	16	.017	1.07	16	.38	3.6	16	<.0001	5.7	16	<.0001
KNZ	Treatment	.74	2	.49	2.66	2	.097	1.4	2	.268	22.6	2	<.0001
	Year	10.36	8	<.0001	16.95	8	<.0001	26.7	8	<.0001	37.3	8	<.0001
	Treatment x Year	1.33	16	.180	1.44	16	.315	4.3	16	<.0001	5.19	16	<.0001

Table S3 Pairwise treatment contrasts by year for repeated measures mixed models. P-values only given when $p = < 0.05$.

Response	Site	Contrast	2013	2014	2015	2016	2017	2018	2019	2020	2021
Richness	SGS	control-chronic	-	-	.002	-	-	-	-	-	
		control-intense	-	-	-	-	-	-	-	-	.014
		chronic-intense	-	-	-	-	-	-	-	-	-
	HPG	control-chronic	-	-	-	-	-	-	-	-	-
		control-intense	-	-	-	-	-	-	-	-	-
		chronic-intense	-	-	-	-	-	-	-	-	-
	HYS	control-chronic	-	-	-	.033	-	-	.023	-	.020
		control-intense	-	-	-	-	-	-	-	-	-
		chronic-intense	-	-	-	-	-	-	-	-	-
	KNZ	control-chronic	-	-	-	-	-	-	-	-	-
		control-intense	-	-	-	-	-	-	-	-	-
		chronic-intense	-	-	-	-	-	-	-	-	-
Evenness	SGS	control-chronic	-	-	-	.002	<.0001	-	-	.001	-
		control-intense	-	-	-	-	<.0001	-	-	.004	.020
		chronic-intense	-	-	-	-	-	-	.006	-	-
	HPG	control-chronic	-	-	-	-	-	-	-	.032	.010
		control-intense	-	-	.018	-	.025	-	-	.009	-
		chronic-intense	-	-	.037	-	-	-	-	-	-
	HYS	control-chronic	-	-	-	-	-	.028	-	-	-
		control-intense	-	-	-	.006	-	-	-	.039	-
		chronic-intense	-	-	-	-	-	-	-	-	-
	KNZ	control-chronic	-	-	-	-	-	-	-	-	-
		control-intense	-	-	-	-	-	-	-	-	-
		chronic-intense	-	-	-	-	-	-	-	-	-
C3 cover	SGS	control-chronic	-	-	-	-	-	.011	.0497	<.0001	.0003

		control-intense	-	-	-	-	-	.008	<.0001	<.0001	<.0001
		chronic-intense	-	-	-	-	-	-	.0001	-	-
	HPG	control-chronic	-	-	<.0001	.008	-	-	-	-	-
		control-intense	-	-	-	.001	-	-	-	.013	-
		chronic-intense	-	-	.002	-	-	-	-	-	-
	HYS	control-chronic	-	-	-	<.0001	.023	-	-	-	-
		control-intense	-	-	-	.008	.012	-	-	-	-
		chronic-intense	-	-	-	.010	-	-	-	-	-
	KNZ	control-chronic	-	-	-	-	-	-	-	-	-
		control-intense	-	-	-	-	-	-	.029	<.0001	.011
		chronic-intense	-	-	-	-	-	-	.001	-	-
	C4 cover	SGS	control-chronic	-	-	<.0001	<.0001	<.0001	<.0001	.044	-
control-intense			-	-	<.0001	<.0001	<.0001	<.0001	.042	-	-
chronic-intense			-	-	-	-	-	-	-	-	-
HPG		control-chronic	-	.015	.009	<.0001	-	.008	-	-	-
		control-intense	-	.007	<.0001	<.0001	-	.002	-	-	-
		chronic-intense	-	-	.002	-	-	-	-	-	-
HYS		control-chronic	-	-	-	<.0001	.002	-	-	-	-
		control-intense	-	-	.0103	<.0001	.028	-	-	-	-
		chronic-intense	-	-	.010	-	-	-	-	-	-
KNZ		control-chronic	-	-	-	<.0001	.012	.0004	-	-	-
		control-intense	-	.005	.002	<.0001	.0001	<.0001	.014	-	-
		chronic-intense	-	-	-	<.0001	-	.044	-	-	-