THESIS

ASSESSING DROUGHT SENSITIVITY ACROSS THE SHORTGRASS STEPPE BIOME

Submitted by

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ABSTRACT

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Net primary productivity (NPP) of grassland ecosystems is dependent on many biotic and abiotic factors. However, water availability is generally considered the primary determinant of NPP, as well as being key for defining grassland community structure, and thus it is imperative to understand how grasslands respond to drought in a climate where droughts are expected to become more frequent and severe. There is a well-documented negative relationship, described by the Huxman-Smith model, between drought sensitivity and mean annual precipitation (MAP) at spatial scales that span multiple biomes. In other words, drier ecosystems are usually more sensitive to drought than more mesic ecosystems. While this cross-biome pattern has been independently confirmed with a variety of research approaches, there is limited research that has explored how patterns of drought sensitivity vary with MAP *within* a single biome where the dominant species do not vary. My goal was to determine if this negative relationship is evident within a regionally extensive grassland biome generally dominated by a single grass species (*Bouteloua gracilis* or blue gramma).

I characterized the spatial pattern and relationship between drought sensitivity and MAP across the shortgrass steppe biome of the North American Great Plains using satellite-derived Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) data (from 2000-2022) as proxies for vegetation productivity. Gridded annual precipitation data were obtained at a comparable spatial scale. I found a negative relationship between drought sensitivity and MAP within the shortgrass steppe biome, indicating that the Huxman-Smith model is also supported within a single biome. Thus, my results suggest that while changes in the dominant vegetation may contribute to the patterns observed between MAP and drought sensitivity at large spatial scales that include multiple biomes, gradients in MAP within a biome can also drive this negative relationship. As a result, directional changes in annual precipitation amounts have the potential to alter drought sensitivity directly, even if the dominant plant species do not change.

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CHAPTER 1: INTRODUCTION

1.1 Overview

Grasslands are important and highly biodiverse ecosystems, comprising about 30-40% of the global terrestrial surface (Hoover et al., 2021; Liu et al., 2023). These biomes support a large variety of plant and animal communities, providing habitat and food for pollinators, grassland fauna, and grazing livestock (Blair et al., 2014; Hoover et al., 2021; Richter et al., 2021). Grassland and steppe ecosystems are also important for carbon sequestration as carbon sinks, storing approximately one-third of global terrestrial carbon (Guo et al., 2023; Hoover & Rogers, 2016).

Grassland ecosystems face several anthropogenic threats. Most of the world’s agriculture occurs within grassland regions, and consequently, these ecosystems have been heavily degraded as a result of land use changes (Blair et al., 2014). Further, climate change poses a large risk to these vulnerable ecosystems with associated changes in precipitation regimes. With climate change, precipitation events have shifted to fewer and larger rainfall events (Peng et al., 2013; Tank and Können, 2023; Trenberth et al., 2014), resulting in increased interannual precipitation variability (Gherardi & Sala, 2019). In conjunction with shifts in precipitation amount and frequency, rising temperatures can increase evaporative demand and, therefore, impact overall surface and subsurface water balances (Pachanaparn et al. 2022), leading to a predicted increase in drought frequency and severity worldwide (Knapp et al., 2017; Lau et al., 2013; Pachanaparn et al., 2022; Polade et al., 2014; Slette et al., 2019; Vicente-Serrano 2010).

Drought is characterized as an anomalous period of low water availability of sufficient duration to potentially alter ecosystem structure and function on annual or longer time scales (Knapp et al., 2024; Shantz 1927; Zhao et al., 2022). Commonly, drought is caused by a reduction in precipitation inputs, however, drought can also be caused by an increase in evaporative demand from high vapor pressure deficits (Knapp et al., 2024; Zhao et al., 2022). Drought is an unpredictable phenomenon, implying that a drought event differs from predictable dry seasons, and can therefore be defined as a deviation from normal precipitation regimes (Knapp et al., 2024; Slette et al., 2019).

As droughts are anticipated to increase in severity and frequency globally, grasslands face particular peril because these ecosystems strongly rely on precipitation to maintain soil moisture (Blair et al., 2014; Noy-Meir, 1973; Post et al., 2021; Schwinning & Sala, 2004). Further, precipitation is the primary limiting factor of vegetation growth in semiarid grassland biomes (Burke et al., 1997; Stuart-Haëntjens et al., 2018), therefore, these ecosystems are highly responsive to changes in precipitation (Almeida-Ñauñay et al. 2022; Knapp & Smith., 2001; Knapp et al., 2015). Mean annual precipitation (MAP) is an important factor driving grassland aboveground net primary productivity (ANPP; Dong et al., 2023), with MAP explaining 90% of the variation in ANPP in the North American Great Plains (Sala et al., 1988). Shifts in precipitation have been found to have notable impacts on vegetation productivity (Augustine 2010; Knapp & Smith, 2001), highlighting the importance of precipitation in grassland ecosystems.

Drought impacts many ecosystem processes that are linked to grassland productivity. Hoover et al. (2014) and Wang et al. (2022a) found a decrease of 20-30% of total ANPP in grassland ecosystems during a drought event, alongside smaller yet significant declines in belowground net primary productivity (BNPP) and larger ANPP reductions in two consecutive drought years. Decreases in primary productivity has significant negative effects on carbon storage and cycling, which threatens the capacity of these ecosystems to remain carbon sinks (Ciais et al., 2005; Dong et al., 2023; Hoover & Rogers, 2016; Zscheischler et al., 2014), and could ultimately result in positive feedback mechanisms further exacerbating climate change (Ivits et al., 2014; Ma et al., 2012). Because of the documented impacts of drought on ecosystem structure and the threats that these ecosystems face from climate change, it is imperative to understand the patterns of drought sensitivity and the impacts that this has on ecosystem functioning (Crausbay et al., 2017).

There is well-documented evidence for a negative relationship between MAP and ecosystem sensitivity to precipitation at spatial scales spanning multiple biomes (the Huxman-Smith model; Huxman et al., 2004). Generally, arid and semiarid sites with lower MAP have been found to be more sensitive, and thus, less resistant to drought than more mesic ecosystems (Huxman et al., 2004; Knapp et al., 2024). The Huxman-Smith model (Huxman et al., 2004) describes this pattern as an exponentially decreasing relationship between MAP and ANPP across a precipitation gradient spanning multiple biomes. This conclusion is further supported by meta-analyses of field studies that showed ecosystem resistance increasing and sensitivity decreasing with MAP (Stuart-Haëntjens et al., 2018; Wang et al., 2022a). Maurer et al. (2020) and Wang et al. (2022b) also found similar negative relationships between MAP and remotely sensed proxies of ANPP in the continental U.S. and China, respectively. These studies imply that more arid and chronically drier sites are more likely to experience ANPP declines in extreme drought years. Huxman et al. (2004) explained this pattern with a ‘Resource Limitation Hypothesis’, claiming that sites with a higher MAP likely have other limiting resources aside from precipitation, and thus would not respond as strongly to shifts in precipitation, such as drought. To support this, Huxman et al. (2004) found that in sites with a higher MAP, ANPP was more often influenced by temperature and the ANPP in the previous year, rather than precipitation alone.

However, there is a contrasting hypothesis to the ‘Resource Limitation Hypothesis’ that depicts the opposite relationship between MAP and drought sensitivity- the ‘Stress Adaptation Hypothesis’ (Knapp et al., 2024). This hypothesis suggests that plants in more arid sites can adapt to drier conditions through stress tolerance strategies and thus have higher water-use efficiency (Knapp et al., 2015; Knapp et al., 2024). This implies that vegetation in drier environments would be more resistant to drought, meaning that these sites could remain productive under disturbance (Isbell et al., 2015) and would therefore exhibit smaller decreases in ANPP with drought (Al-Yaari et al., 2020). Grime et al. (2008) found little change in grassland productivity as a result of changes in climate, indicating that the vegetation may be adapted to stress and able to withstand variation in climatic factors, supporting the ‘Stress Adaptation Hypothesis’. Metz and Teilbörger (2023) further supported this hypothesis with a reciprocal transplant experiment along an aridity gradient, finding that individuals originating in more arid sites had a higher fitness than individuals originating from less arid sites when exposed to drought, suggesting evidence of local adaptation.

Overall, there is more support from drought experiments for the ‘Resource Limitation Hypothesis’ compared to the ‘Stress Adaptation Hypothesis’ (Du et al., 2018; Knapp et al., 2024; Maurer et al., 2020). The Huxman-Smith Model is supported primarily by studies spanning multiple biomes at landscape, continental or even global scales (Huxman et al., 2004; Maurer et al., 2020; Smith et al., 2024; Stuart-Haëntjens et al., 2018; Wang et al., 2022a; Wang et al., 2022b). Many of these studies span biomes ranging from deserts to forests, comprised of drastically different dominant vegetation. Thus, vegetation turnover could be partially responsible for the pattern described by the Huxman-Smith model. Knapp et al. (2015) performed a similar study using data from only grassland sites in the North American Great Plains, and also found a negative relationship between drought sensitivity and MAP. However, even among the Great Plains grassland biomes, species composition varies along the precipitation gradient from shortgrass dominated to tallgrass dominated prairies. It is currently unknown how drought sensitivity relates to MAP in an extensive region where the dominant vegetation is more homogenous. The exponentially decreasing relationship described by the Huxman-Smith model could be present across biomes regardless of whether there is a negative or no relationship between sensitivity and precipitation in each individual biome (Figure 2.1). This study aims to assess if the negative relationship described by the Huxman-Smith model is present within a single biome to better characterize the patterns of drought sensitivity in a region with relatively homogenous vegetation.

1.2 Study System

Grasslands are important ecosystems to assess differential drought sensitivity due to their vulnerability and responsiveness to shifts in precipitation (Knapp et al., 2024). Compared to shrubland and forested biomes, there is evidence that grasslands exhibit the highest vulnerability to drought (Dong et al., 2023; Sun et al., 2024; Zeng et al., 2022), making them an appropriate model ecosystem to assess the relationship between drought sensitivity and precipitation.

Within the North American Great Plains, the shortgrass steppe biome stretches from northern Colorado south to central Texas (Figure S1). The shortgrass steppe biome is the driest, most water-limited, and least productive biome within the North American Great Plains, due to the rain shadow east of the Rocky Mountains (Hoover et al., 2021; Pielke & Doesken, 2008). Within the shortgrass steppe, water is the primary factor determining community composition and function and is the strongest predictor of vegetative productivity (Noy-Meir 1973; Pielke & Doesken, 2008). The topography of the shortgrass steppe is characterized by rolling hills and flat terraces (Yonker et al., 1988), which has experienced an extensive history of grazing (Milchunas et al., 1988).

The vegetation across the shortgrass steppe is relatively homogenous, dominated by *Bouteloua gracilis* (blue grama), a warm season perennial C_4 grass species, that is dominant across all soil types in the biome (Hoover et al., 2021; Irisarri et al., 2016; Lauenroth, 2008). Additional important vegetation in the region includes: C_4 grass *B. dactyloides* (buffalo grass); cool season perennial C_3 graminoids *Pascopyrum smithii* (western wheatgrass) and *Carex duriuscula* (needle leaf sedge); and annual grass *Vulpia octoflora* (Irisarri et al., 2016; Lauenroth, 2008).

Throughout the region, MAP ranges from 250mm to 625mm, following a longitudinal pattern with drier regions in the west and wetter in the east, with a biome-wide average of 440mm (Figure 2.2a; Lauenroth et al., 2008). This precipitation range is consistent with the strongest relationship between sensitivity and MAP observed by Huxman et al. (2004). In addition to the general west-east MAP gradient, monsoonal periods between July and September are responsible for over half of the annual precipitation in the southern portions of the shortgrass steppe (Felton & Goldsmith, 2023). The year-to-year variability in precipitation also differs across the biome, with more consistent precipitation in the north and more variable precipitation in the south. Mean annual temperature in the shortgrass steppe ranges from 6°C to 20°C, largely following a north-to-south latitudinal gradient, with a majority of the area (50%) between 10°C and 15°C (Figure 2.2b). As a result of the variation in both temperature and precipitation across the biome, aridity also varies across the region, with the most arid regions in the southwest and most humid regions in the northeast. Between 2000 and 2022, the study period for this analysis, vegetation was neither browning nor greening within the shortgrass steppe biome (Figure S2), in contrast to a global greening trend over that time period (Li et al., 2024).

1.3 Objectives

This thesis assesses the relationship between drought sensitivity and MAP within the shortgrass steppe biome, dominated by *B. gracilis*, across a precipitation gradient. This study aims to determine 1) how drought sensitivity varies across the shortgrass steppe biome; and 2) if the negative relationship between MAP and drought sensitivity, as described by the Huxman-Smith model, is evident within a single grassland biome. Analyses were performed across the entire biome using gridded precipitation data and satellite-derived Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) data as proxies for vegetation productivity. The shifts and uncertainties that climate change brings to precipitation frequency and duration may leave grasslands under threat of further ANPP loss and habitat degradation (Byrne et al., 2017). Thus, a better understanding of drought sensitivity can inform future research and management to protect these sociologically and ecologically important ecosystems.

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CHAPTER 2: DOES WITHIN-BIOME DROUGHT SENSITIVTY REFLECT PATTERNS ACROSS BIOMES? [1]

2.1 Summary

With climate change increasing the likelihood of precipitation extremes globally, particularly drought, it is important to identify those ecosystems that are most sensitive to negative precipitation anomalies. Currently, there is considerable evidence for the existence of a general negative relationship between mean annual precipitation (MAP) and ecosystem sensitivity to drought, often measured as reductions in aboveground net primary production (ANPP). In other words, more arid ecosystems are more likely than mesic systems to experience dramatic reductions in functioning during drought events. However, most evidence for this pattern is based on studies conducted at regional to continental spatial scales, which span multiple biomes and a wide range in MAP. But it is uncertain if similar relationships exist within a single biome where the gradients in MAP are much reduced and the dominant vegetation does not vary substantially. If such a relationship does not exist within biomes, this suggests that shifts in the dominant vegetation are likely the primary determinant of the observed negative relationship. We used 23 years of satellite derived vegetation indices (157,929 pixels at 1 km^2 resolution) and corresponding gridded precipitation data to determine if a relationship between drought sensitivity and MAP was evident across the semiarid shortgrass steppe biome of the western U.S. We focused our analyses of vegetation responses to individual drought years, as well as average responses to multiple, usually non-consecutive, dry years. Consistent with

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[1] Hedberg, S.L., P.D. Dao, and A.K. Knapp. (2024). Does within-biome drought sensitivity reflect patterns across biomes? Manuscript in prep.

previous large scale and multi-biome studies, we found a strong negative relationship between MAP (varying from 250-625 mm) and drought sensitivity within this single biome. This relationship was observed for both Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) proxies for ANPP, and regardless of how many drought years were included in the analyses. From these results, we conclude that while differences in vegetation types and growth forms (grasses, shrubs, forests) may contribute to the well-documented patterns of drought sensitivity at large spatial scales, the long-term precipitation history of an ecosystem (e.g. MAP) can be directly linked to patterns of differential drought sensitivity within a biome. Such information should improve predictions of drought vulnerability both within as well as across biomes.

2.2 Introduction

Precipitation regimes including amounts and variability have shifted with climate change (Peng et al., 2013; Tank & Können, 2023; Trenberth et al., 2014), and coupled with rising temperatures, drought events are predicted to increase in frequency, severity and duration worldwide (Knapp et al., 2017; Lau et al., 2013; Pachanaparn et al., 2022; Polade et al., 2014; Slette et al., 2019; Vicente-Serrano, 2010). Drought, defined as an anomalous period of low water availability of sufficient duration to potentially alter ecosystem structure and function (Knapp et al., 2024; Slette et al., 2019), can occur from a reduction in precipitation inputs and/or an increase in evaporative demand. Drought is well-documented to have widespread impacts on ecosystem functioning, including reductions in ANPP (Hoover et al., 2014; Wang et al., 2022a), belowground net primary productivity (BNPP; Wang et al., 2022a), carbon cycling, and carbon storage (Ciais et al., 2005; Dong et al., 2023; Hoover & Rogers, 2016; Zscheischler et al., 2014). It is also well known that ecosystems differ in their drought sensitivity, with a number of biotic and abiotic factors proposed to explain why some ecosystems are more resistant to drought than others (Crausbay et al., 2017, Huxman et al., 2004; Knapp et al. 2024, Smith et al. 2024).

Long-term precipitation history, or mean annual precipitation (MAP), is one proposed abiotic determinant of differential drought sensitivity, as first proposed by the Huxman-Smith model (Huxman et al., 2004). This negative relationship (Fig. 2.1), typically observed across large spatial scales that cross multiple biomes, occurs because arid and semiarid regions with low MAP often exhibit heightened sensitivity and lower resistance to drought compared to more mesic ecosystems. A negative relationship has been supported through global meta-analyses of drought field experiments (Stuart-Haëntjens et al., 2018; Wang et al., 2022a), multi-site field observational studies (Huxman et al., 2004; Knapp et al., 2015, 2024), and multi-site field experimental manipulations that impose drought using consistent methodologies, such as the International Drought Experiment (Bondaruk et al., 2022; Luo et al., 2021; Smith et al., 2024). The Huxman-Smith model has also been supported using satellite-derived products as proxies for net primary productivity and precipitation (Maurer et al., 2020; Wang et al., 2022b). Huxman et al. (2004) proposed a resource limitation hypothesis to explain this pattern, arguing that productivity in regions with higher MAP is often limited by factors other than precipitation, such as light and nutrient availability, and thus ANPP in these ecosystems would be less responsive to drought or other alterations in precipitation.

It's important to note that alternate models of the relationship between MAP and drought sensitivity have been proposed and supported, such as the stress adaptation hypothesis (Knapp et al. 2024). This model predicts a contrasting pattern – that because species in chronically drier sites are better adapted to water limitation, more arid ecosystems should be more resistant (less sensitive) to drought periods than more mesic ecosystems (Funk et al., 2013; Grime et al., 2008; Gutschick & BassiriRad, 2003; Reynolds et al., 1999; Metz & Teilbörger, 2023).

The Huxman-Smith Model is primarily supported by studies spanning several biomes at large spatial scales and or studies encompassing large MAP gradients (Huxman et al., 2004; Maurer et al., 2020; Stuart-Haëntjens et al., 2016; Wang et al., 2022a; Wang et al., 2022b). Since these studies are conducted at landscape, continental, or even global scales, vegetation turnover across biomes is always present and may influence, or largely drive, this relationship. This is because different growth forms may respond to drought differentially (Gharun et al., 2020; Sankaran, 2019). While drought sensitivity studies limited to grassland or rangeland ecosystems also support the Huxman-Smith model (Bondaruk et al., 2022; Knapp et al., 2015; Luo et al., 2021) significant turnover of the dominant grassland species co-occurred with the MAP gradients assessed, and thus, the question remains whether or not drought sensitivity varies with MAP directly or whether shifts in the dominant vegetation alter patterns of drought sensitivity.

The shortgrass steppe in the North American Great Plains is a grassland type that spans a significant range in MAP, from 250-625 mm, and yet is largely dominated by a single grass species, *Bouteloua gracilis* (blue grama, Lauenroth et al., 2008b). Importantly, this range in precipitation corresponds to the strongest relationship between drought sensitivity and MAP as described by the Huxman-Smith model (Huxman et al., 2004). Thus, the shortgrass steppe is uniquely valuable for understanding the relationship between drought sensitivity and MAP within a single biome. Here we present the results of a biome-wide analysis of drought sensitivity and its relationship with MAP using gridded precipitation data and satellite-derived proxies for productivity. Our goal was to test whether the negative relationship between drought sensitivity and MAP is evident within a single biome with little vegetation turnover across the region.

Specifically, we asked the following:

1) How does drought sensitivity vary across the shortgrass steppe biome?
2) Is there a negative relationship between MAP and drought sensitivity within a single biome, as described by the Huxman-Smith model?

We predicted that we would not find a relationship between MAP and drought sensitivity within this single biome, suggesting that the turnover in dominant vegetation (desert, grassland, forest) is the primary driver of patterns of drought sensitivity at regional to continental scales. These contrasting within vs. between biome patterns of drought sensitivity are not necessarily inconsistent with each other (Fig. 2.1), but differentiating between them would enhance our ability to forecast drought responses in the future.

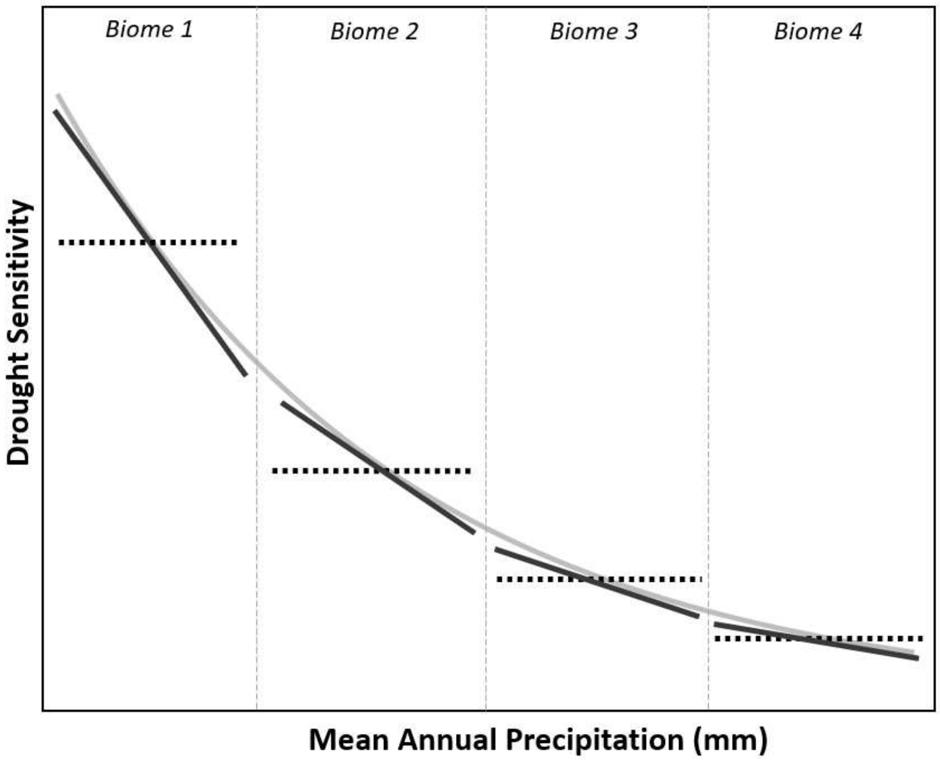

Figure 2.1 Conceptual depiction of potential relationships between cross-biome patterns of drought sensitivity and within biome sensitivity across a gradient in mean annual precipitation (MAP). The continuous light gray depicts how drought sensitivity varies at large spatial scales (across multiple biomes) with MAP. This pattern of high sensitivity in arid biomes and decreasing sensitivity as MAP increases was first proposed by Huxman et al. (2004, the Huxman-Smith model) and has since been supported by Knapp et al., (2015), Maurer et al. (2020), and Wang et al., (2022a). This pattern has been assumed to be driven, in large part, by responses of the different vegetation types that also vary along MAP gradients. But within biomes, drought sensitivity may track the Huxman-Smith model (solid black line) or may not be related to the smaller gradients in MAP within a biome (dashed black line). The former relationship would indicate that MAP is a primary driver of the Huxman-Smith model whereas the latter would indicate that the turnover of dominant vegetation types are mostly responsible for the cross-biome pattern. Note that it is also possible that a positive relationship might exist between MAP and drought sensitivity within biomes (not shown), as predicted by the stress adaptation hypothesis (see text).

2.3 Methods

2.3.1 Study Area

The shortgrass steppe is the driest and least productive grassland type within the North American Great Plains, due to the rain shadow created by the Rocky Mountains to the west (Pielke & Doesken, 2008). Precipitation amounts and aridity levels vary longitudinally across the shortgrass steppe, with wetter and more humid regions to the east. Overall, precipitation in the biome ranges from 250 mm in the west to 625 mm in the southeast (Figure 2.2a; Lauenroth et al., 2008b). Mean annual temperature follows a latitudinal gradient with warmer temperatures in the south (Figure 2.2b). For our analysis, the spatial boundary of the shortgrass steppe biome was first obtained from the USDA Forest Service and World Wildlife Foundation's ecoregion classification map and then subsequently constrained to the shortgrass steppe precipitation amounts (MAP between 250 and 625mm as defined by Lauenroth et al. 2008b).

The study area was further constrained to only include grassland land cover pixels, excluding cropland, urban and miscellaneous land types from the analysis. Land cover data from the year 2020, with a spatial resolution of 55 meters, was downloaded from the Moderate Resolution Imaging Spectroradiometer (MODIS) data product MCD12Q1 Version 6 (Friedl & Sulla-Menashe, 2019). Land cover information was derived via supervised classification with enhanced post-processing. Land cover types were defined by the Annual International Geosphere-Biosphere Programme (IGBP) land type classification, and the study area was constrained to grassland pixels (IGBP class 10), defined as herbaceous vegetation less than 2 meters in height.

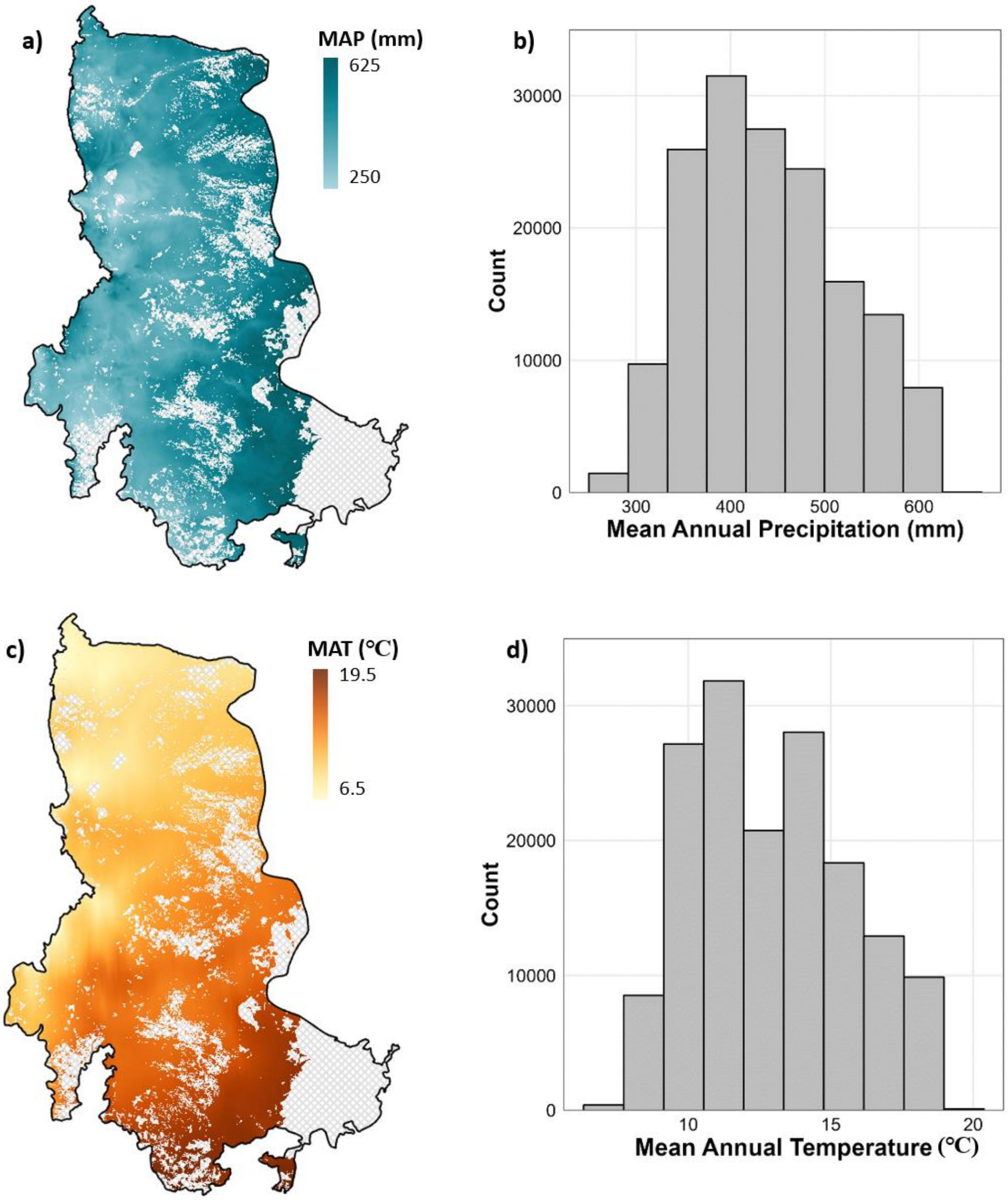

Figure 2.2 Spatial distributions (a, c) and histogram distributions (b, d) of mean annual precipitation (MAP) and mean annual temperature (MAT) across the shortgrass steppe biome. For this analysis, the spatial boundary of the shortgrass steppe biome was first obtained from the USDA Forest Service and World Wildlife Foundation’s ecoregion classification map, masked to exclude non-grassland pixels, and subsequently constrained to the shortgrass steppe precipitation amounts (MAP 250-625mm) defined by Lauenroth et al. (2008b). Thus, the stippled regions represent regions that do not have grassland land cover or fall outside of the precipitation amounts consistent with shortgrass steppe vegetation.

2.3.2 Datasets

Raster surfaces of annual precipitation data were downloaded from DAYMET Version 4 Data (Thornton et al., 2022). These data are derived from precipitation ground-based measurements with a spatial resolution of 1 kilometer. Data were downloaded from all years inclusive of 2000 to 2022 and smoothed using a 3x3 low pass convolution filter in ArcGIS Pro to minimize spatial noise in the dataset. Three time periods of precipitation data acquisition were compared for each year of the time series: annual (January-December) precipitation, growing season (April-September) precipitation, and January-September precipitation to assess the impact of seasonal precipitation regimes. Differences in the relative proportions of precipitation among these time periods differed only modestly among years, so we used annual precipitation for the remainder of the study.

Gridded annual average maximum and minimum temperature surfaces were downloaded from DAYMET Version 4 Data for all years 2000-2022 (Thornton et al., 2022). Average annual temperature was then calculated as the mean of the maximum and minimum temperature surfaces for each pixel. Gridded aridity index (AI) and potential evapotranspiration (PET) surfaces were downloaded, providing the average AI and PET values for each pixel from a 30-year period from 1970-2000 (Zomer et al., 2022).

NDVI data has been widely used as a proxy for vegetation productivity (Hermance et al., 2015; Maurer et al., 2020), and is generally consistent with gross primary productivity (GPP) values in grassland ecosystems, even in drought years (Zhou et al., 2014). NDVI determines the amount of visible red light absorbed by chlorophyll within a plant compared to the amount of reflected near-infrared light. Measurements range from -1 to 1, with -1 indicating water, snow, cloud, bare soil, dry or dead vegetation and 1 indicating healthy vegetation, with grassland NDVI values typically between 0.2 and 0.5. To corroborate our results derived from NDVI data, Enhanced Vegetation Index (EVI) data was also downloaded. EVI data is derived from the near infrared, red and blue bands, and is often more representative of vegetation in areas with dense vegetation, often forests and shrublands, though outperforms other vegetation indices in dense grasslands. NDVI and EVI data (250-meter spatial resolution) was derived from MODIS product, MOD13Q1 Version 6.1 (Didan, 2021). This data product averages the best pixel value across acquisitions from a 16-day period, based on low cloud cover, low view angle and high vegetation values. Time-series NDVI and data was downloaded spanning the growing season (3/22-10/15, or 3/21-10/14 in leap years) for each year between 2000 and 2022.

Pixels that had one or more negative NDVI or EVI value throughout the growing season (<1% of the total pixels) were removed, as negative values are not representative of vegetation. Furthermore, any pixel that had never greened up to reach NDVI or EVI values greater than 0.2 across the entire growing season, even in wet years, was excluded since it is likely that these pixels were misclassified as grassland vegetation. To encapsulate the NDVI and EVI dynamics throughout each year, growing-season integrated NDVI ($NDVI_{int}$) and growing-season integrated EVI (EVI_{int}) via trapezoidal approximation were used as vegetation proxies in this study. The vegetation indices were spatially resampled using bilinear interpolation to match the 1-km spatial resolution of the precipitation dataset.

To confirm that $NDVI_{int}$ data is related to ANPP, we compared this satellite metric to empirical field data from the Central Plains Experimental Range (CPER) field site in the northwestern shortgrass steppe (Hoover et al., 2020). From the years 2000 to 2018, plot-level ANPP data from a variety of topographic positions and management activities was averaged by year (Hoover et al., 2020) and $NDVI_{int}$ values were averaged by year for all pixels that lie within the CPER site boundary (n =42). $NDVI_{int}$ data were then regressed against the field ANPP data, and a positive relationship was found ($R^2 = 0.49$; P-value < 0.001; Figure 2.3a). Similarly, to ensure that satellite derived vegetation productivity data responded predictably to precipitation, mean $NDVI_{int}$ values were regressed against MAP values for the 2000-2022 time series and were found to be significantly related ($R^2 = 0.39$, P-value < 0.0001; Figure 2.3b).

Temporal regressions were run on all time-series datasets to ensure that there wasn't a substantial significant trend in MAP, MAT, or NDVI over the yearly time series. Between 2000 and 2022, only 0.04%, 4.2%, and 2.96% of total pixels had significant temporal regressions ($\alpha = 0.05$) for annual precipitation, temperature and NDVI datasets, respectively (Table S2).

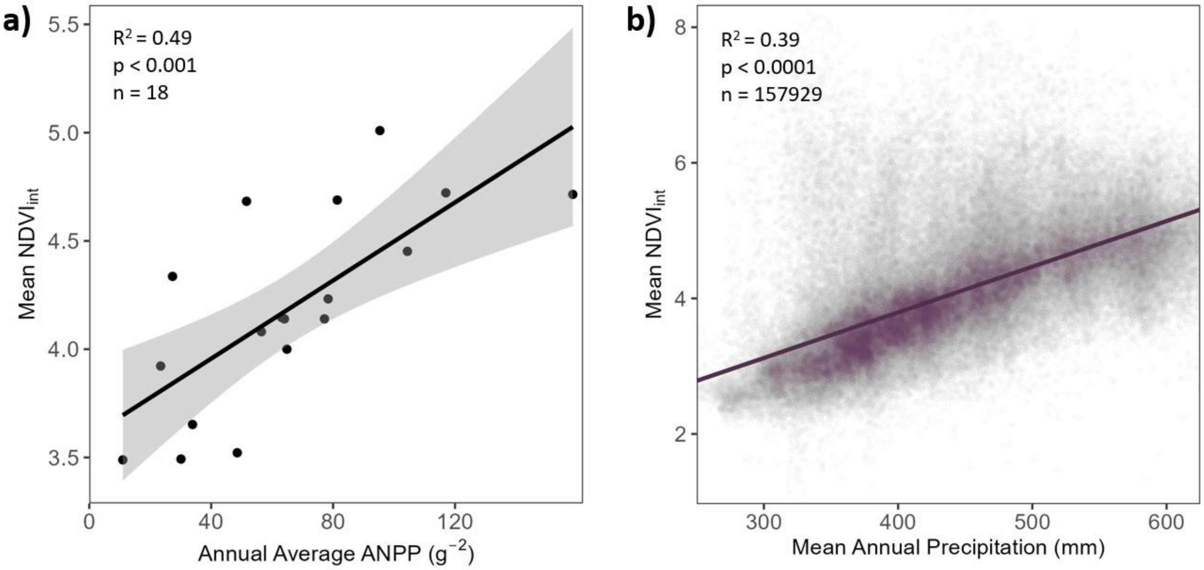

Figure 2.3 Validation of $\mathrm{NDVI}_{\mathrm{int}}$ values with empirical aboveground net primary productivity (ANPP) field data from the Central Plains Experimental Range (CPER) (a); and the relationship between $\mathrm{NDVI}_{\mathrm{int}}$ values and Mean Annual Precipitation (MAP) (b). This confirms the use of $\mathrm{NDVI}_{\mathrm{int}}$ as a proxy for ANPP (R2 = 0.49; P-value < 0.001) and that satellite derived productivity data responded predictably to precipitation (R2 = 0.39, P-value < 0.0001). The second scatterplot is symbolized by density, with darker purple areas representing many overlapping points.

2.3.3. Analysis

Drought sensitivity was calculated as the relative reduction in $NDVI_{int}$ or EVI_{int} per unit reduction in precipitation in drought vs. normal years using the following equations:

$$\frac{[(NDVIint_n - NDVIint_d)/NDVIint_n] \text{ x } 100}{\text{Precipitation}_n - \text{Precipitation}_d} \quad (1)$$

$$\frac{[(EVIint_n - EVIint_d)/EVIint_n] \text{ x } 100}{\text{Precipitation}_n - \text{Precipitation}_d} \quad (2)$$

where normal precipitation (Precipitation_n) values were calculated for each pixel as the mean precipitation from all years within ±10% of the 2000-2022 mean. Normal $NDVI_{int}$ ($NDVIint_n$) and EVI_{int} ($EVIint_n$) values for each pixel were subsequently calculated as the mean $NDVI_{int}$ and EVI_{int} values from all normal precipitation years. Pixels were excluded from the analysis (~3%) if there were less than 4 normal precipitation years during the 23-yr period. Drought years and the precipitation levels during those years (Precipitation_d) were determined three different ways: 1) as the single year with the lowest precipitation between 2000-2022; 2) the mean precipitation from the three driest years between 2000-2022; and 3) the mean precipitation from all years with precipitation values less than 30% of the 2000-2022 mean. Similarly, the $NDVI_{int}$ and EVI_{int} values in drought years ($NDVIint_d$ and $EVIint_d$) and were calculated for each pixel from the years identified as drought years from each drought scenario, and drought sensitivity was calculated for each scenario (Equations 1 and 2). To assess the relationship between MAP and drought sensitivity, linear regressions were used to relate the two variables for each drought scenario.

2.4 Results

There were five spatially expansive drought years between 2000 and 2022 in the shortgrass steppe biome: 2002, 2011, 2012, 2020, and 2022. These five years made up the driest year for 93% of the biome and on average precipitation was decreased by 181.5mm (45.1%) with a corresponding 21% decrease in $NDVI_{int}$ (Table S1). 2011 was the most extreme and spatially expansive drought year, concentrated in the southeastern portion of the shortgrass steppe, with the 2002 and 2012 droughts having large impacts across the northern and southwestern regions of the biome (Figure 2.4b).

Drought sensitivity varied substantially across the biome, largely following a longitudinal pattern, with the western half of the biome exhibiting a higher sensitivity to drought than the eastern half (Figure 2.4a). High drought sensitivity values were clustered in the northwestern quarter of the biome, with a smaller area of high sensitivity in the south-central region. A small southwestern section of the biome, located in central New Mexico, deviated from this pattern as it exhibited the lowest drought sensitivity (Figure 2.4a).

Within the shortgrass steppe biome, the drought sensitivity of primary production decreased with increasing MAP regardless of whether the driest year, the three driest years, or all years with annual precipitation below 30% of the mean were used to define drought periods (Figure 2.5). The negative relationship between MAP and sensitivity was the strongest in the latter two drought scenarios, however (Figure 2.5). The weakest relationship between drought sensitivity and MAP was observed when only the driest year was used when defining drought years. The EVI_{int} data, used as an additional satellite-proxy for primary production, further confirmed this negative relationship (Figure S3).

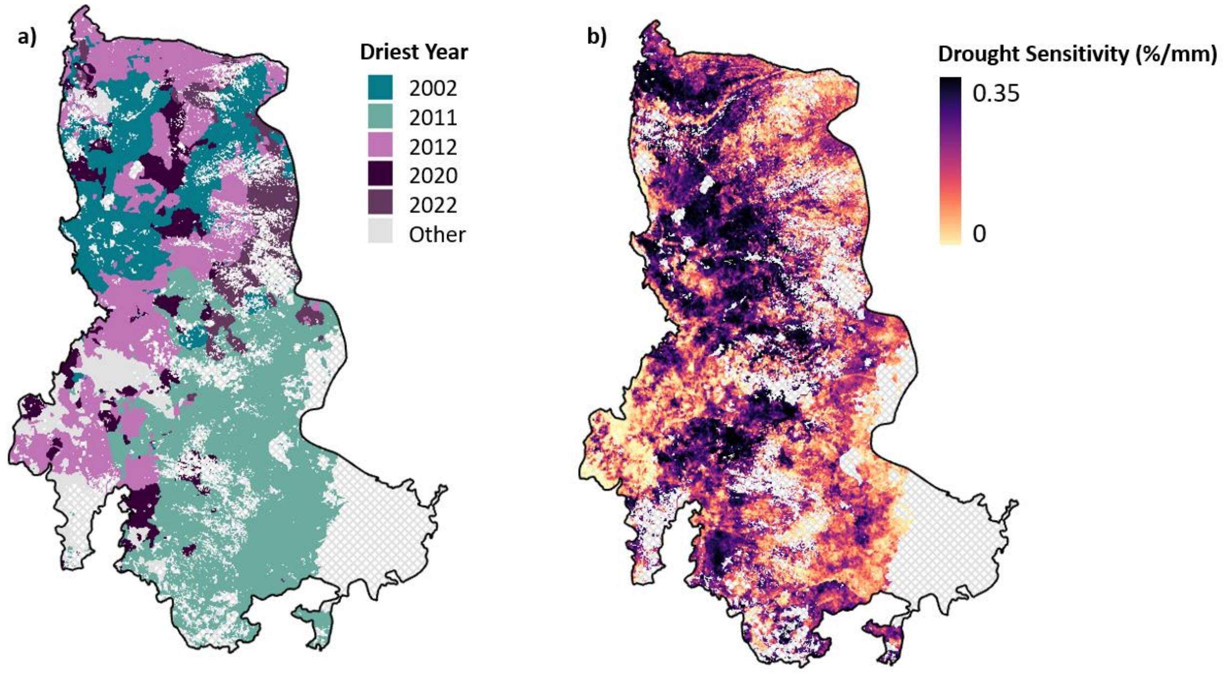

Figure 2.4 Spatial distributions of the driest year between 2000 and 2022 (a) and drought sensitivity across the shortgrass steppe (b). For this analysis, the spatial boundary of the shortgrass steppe biome was first obtained from the USDA Forest Service and World Wildlife Foundation's (WWF) ecoregion classification map, masked to exclude non-grassland pixels, and subsequently constrained to the shortgrass steppe precipitation amounts (MAP 250-625mm) defined by Lauenroth et al. (2008b). Thus, the stippled regions represent regions that do not have grassland land cover or fall outside of the precipitation amounts consistent with shortgrass steppe vegetation. Drought sensitivity was calculated as $(\text{NDVI}_{\text{normal}}-\text{NDVI}_{\text{drought}})/\text{NDVI}_{\text{normal}})*100/(\text{Precipitation}_{\text{normal}}-\text{Precipitation}_{\text{drought}})$, where all normal years fell within ± 10% of the 2000-2022 precipitation mean, and all drought years fell below 30% of the 2000-2022 precipitation mean.

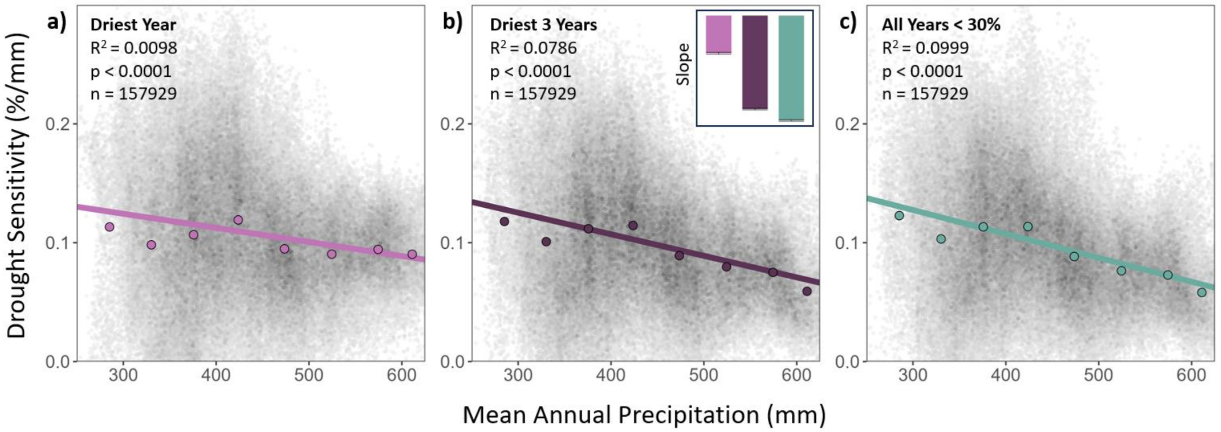

Figure 2.5 Relationship between mean annual precipitation (MAP) and drought sensitivity. Drought sensitivity was calculated as $(\mathrm{NDVI}_{\mathrm{normal}}-\mathrm{NDVI}_{\mathrm{drought}})/\mathrm{NDVI}_{\mathrm{normal}})*100/(\mathrm{Precipitation}_{\mathrm{normal}}-\mathrm{Precipitation}_{\mathrm{drought}})$, where all normal years fell within ± 10% of the 2000-2022 precipitation mean, and drought years were calculated from the driest year (a), the mean of the driest three years (b), and the mean of all years below 30% of the 2000-2022 precipitation mean (c). The background scatterplots (n=157,929) are shaded by density, with darker areas representing many overlapping data points. Binned data points represent the mean drought sensitivity values for each 50mm MAP increment to better visualize the trend, though trend lines were derived from the entire dataset (n=157,929). The inset compares the slopes (± SE) of the linear regressions for each scenario: driest year (pink), the driest 3 years (purple), and all years <30% of the mean (teal).

2.5 Discussion

We had predicted that within a biome, a reduced range in MAP and a lack of turnover in the dominant vegetation would make it challenging to find relationships between MAP and drought sensitivity. But contrary to our expectations, we found a strong and consistent negative relationship between drought sensitivity and MAP within the shortgrass steppe biome. Importantly, this indicates that the patterns of sensitivity reported by Huxman et al. (2004) across biomes are also evident within biomes. We calculated drought sensitivity in three ways based on different criteria for drought years: the driest year, the mean of the three driest years, and the mean precipitation in years at least 30% below the mean, and found a negative relationship in all three scenarios, albeit a weaker relationship when only the driest year was used to define drought years (Figure 2.5). The differences between the first and latter two drought scenarios may have resulted because the latter two scenarios included multiple years, increasing the likelihood of including a strong drought response that is representative of a typical drought response. Further, this negative pattern was also supported by drought sensitivity values derived from both $NDVI_{int}$ and EVI_{int} data in all 3 drought scenarios (Figure S3), increasing our confidence in this negative relationship.

The negative pattern of differential drought sensitivity that we observed within the shortgrass steppe suggests that MAP can be a direct driver of drought sensitivity both within and across biomes. Our results do not preclude vegetation turnover also influencing drought sensitivity patterns across biomes as described by the Huxman-Smith model, but they do indicate that long-term precipitation history plays a role as well. Several previous studies support our conclusions. For example, Knapp et al. (2015) analyzed differential drought sensitivities among six grassland field sites in the Great Plains, two of which were *B. gracilis* (blue grama) dominated. Of the two sites with the same dominant species and different climatic conditions, they found that the more arid site was more sensitive to drought than the more mesic site (Knapp et al., 2015). Similarly, Luo et al. (2021) imposed an experimental drought at two sites along an aridity gradient with the same dominant species and found a greater drought sensitivity at the drier site.

We used MAP to be able compare our results to the patterns observed in previous studies (Huxman et al., 2004; Knapp et al., 2015; Maurer et al., 2020; Stuart-Haëntjens et al., 2022; Wang et al., 2022a), and because of the strong importance of precipitation in grassland productivity, structure and function (Noy-Meir, 1973; Pielke & Doesken, 2008; Sala et al., 1988). However, reductions in precipitation alone may not be the most representative metric of drought, especially in a region where evaporative demand varies spatially. To address this, we also correlated drought sensitivity with the mean aridity index (P/PET), which is more representative of the overall water balance (Zomer et al., 2022). Significant negative relationships between drought sensitivity and aridity index were also observed for all three drought scenarios, though this relationship was slightly weaker than the one derived with MAP (Table S3). Similarly, multiple regressions were run using both MAP and potential evapotranspiration (PET) to assess the relative importance of each variable, and MAP was found to be the primary driver of sensitivity in all three drought scenarios (Table S3). This suggests that precipitation inputs play a dominant role in determining in drought sensitivity, consistent with past studies (Maurer et al., 2020).

Finally, it’s worth noting that drought sensitivity was lowest in a small region of the shortgrass steppe in central New Mexico, located in the Chihuahuan Desert, despite low MAP in this region (Figure 2.4b). Here, monsoonal precipitation, usually beginning in July and ending in September, accounts for about half of the annual precipitation and is the main driver of ANPP, especially in drier areas (Felton & Goldsmith, 2023; Higgins et al., 1997; Muldavin et al., 2014; Petrie et al., 2014). This contrasts the spring and early summer precipitation patterns in the rest of the biome (Lauenroth et al., 2008a). Monsoons are often characterized by heavy rainfall events (Higgins et al., 1997) which can wet deeper soil depths and provide more effective precipitation, lowering drought sensitivity compared to areas that receive many smaller rainfall events (Cherwin & Knapp, 2012). The differential drought sensitivity patterns that are observed between the New Mexico region and the remainder of the biome highlight the importance of seasonality, precipitation event sizes, and MAP in mediating drought sensitivity (Hajek & Knapp, 2022). Thus, the contrasting patterns of drought sensitivity in this monsoonal region relative to the rest of the biome may be due to the approaches used to assess drought responses (observational vs. experimental).

In conclusion, our findings generally support the hypothesis that sensitivity to drought decreases as MAP increases, supporting earlier studies (Bondaruk et al., 2022; Huxman et al., 2004; Knapp et al., 2015; Luo et al., 2021; Maurer et al., 2020; Smith et al., 2024; Stuart-Haëntjens et al., 2022; Wang et al., 2022a). But we have also shown that this relationship exists within a single biome where the dominant vegetation is relatively constant. By extending the analysis of drought sensitivity patterns from across biomes to within biomes, we demonstrate that long-term precipitation history can be directly related to ecosystem drought sensitivity. Such knowledge extends our ability to forecast responses to drought from regional to more local scales.

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CHAPTER 3: SUMMARY AND DIRECTIONS FOR FUTURE RESEARCH

3.1 Summary

In this thesis, I quantified the relationship between drought sensitivity and mean annual precipitation (MAP) within an extensive grassland biome where the dominant species were relatively constant despite a 3-fold range in MAP. Huxman et al. (2004) first proposed the Huxman-Smith model to describe the patterns of higher drought sensitivity in arid biomes, which has since been supported by several large-scale studies (Maurer et al., 2020; Smith et al., 2024; Stuart-Haëntjens et al., 2018; Wang et al., 2022a; Wang et al., 2022b). By constraining our analysis to a single biome dominated by *Bouteloua gracilis*, I have disentangled the effects of MAP and vegetation turnover as drivers of drought sensitivity and assessed the applicability of the Huxman-Smith model within a single biome. I predicted that the cross-biome Huxman-Smith model was largely driven by turnover in dominant vegetation (desert, grassland, forest) at large spatial scales, thus the negative relationship between drought sensitivity and MAP within a single biome was unexpected. This negative pattern is present in a majority of the biome, aside from a small area in eastern New Mexico, where the precipitation patterns are largely monsoonal.

My results support previous studies that compare drought sensitivity among a few grassland sites across an aridity gradient (Bondaruk et al., 2022; Knapp et al., 2015; Luo et al., 2021), and suggests that the Huxman-Smith model of drought sensitivity isn't driven solely by vegetation turnover across biomes. By extending the analysis of drought sensitivity patterns from across biomes to within biomes, our study further establishes the importance of MAP in driving grassland drought sensitivity and across-biome drought sensitivity.

3.2 Directions for Future Research

This study primarily focused on the relationship between drought sensitivity and MAP, although mean potential evapotranspiration (PET) and aridity index (P/PET) were also assessed. There are, of course, other variables that can influence drought sensitivity. Water and nutrient availability vary with landscape position with both often most abundant at lower topographic positions, and thus landscape position may impact grassland sensitivity to precipitation (Hoover et al., 2021). Edaphic attributes influence soil water retention and holding capacity, and these can also affect resistance and susceptibility to drought (Qi et al., 2018; Salley et al., 2016). In general, soils with low clay concentrations, and low organic matter correspond to a lower water holding capacity, and consequently, a higher susceptibility to drought (Qi et al., 2018; Salley et al., 2016). Further, temperature and its associated impacts on evapotranspiration and aridity can impact drought severity and thus how ecosystems respond to drought (Vicente-Serrano et al., 2010; Zomer et al., 2022). Given the documented impacts of these other variables on drought sensitivity, a multiple regression approach (including slope, aspect elevation, soil type and soil edaphic properties, and climatic variables such as MAP, temperature, humidity) could be used to assess the relative importance of each variable in driving drought sensitivity.

In my analysis, normal and drought years were derived from a time series of annual precipitation data. An alternative approach would be to repeat this analysis with a time series of high-resolution gridded soil moisture data or standardized precipitation evapotranspiration index

(SPEI) data. Both datasets can detect and characterize drought events, as soil moisture data reflects the hydrologic conditions of the soil and thus can detect hydrological drought, while SPEI data accounts for several variables due to its inclusion of PET, thus can capture the spatial variation in evaporative demand.

This analysis was also performed using annual precipitation, and thus didn’t take into account the patterns in precipitation timing, event size, or seasonality. Regions that receive fewer and larger rainfall events have been found to be less sensitive to drought when compared to regions that receive many small rainfall events (Cherwin & Knapp, 2012). Due to the differences in sensitivity that we observed between the monsoonal regions of the biome compared to those that are not monsoonal, this suggests that both the timing and amount of precipitation can lead to differential drought sensitivities, which can be further explored in future analyses.

Finally, previous studies suggest that MAP drives drought sensitivity across biomes and our local-scale study within a relatively homogenous grassland ecosystem suggests that conclusion also holds true within biomes. However, this study only assessed this relationship within the shortgrass steppe and not other biomes. Consequently, results cannot yet be generalizable across additional biomes, but future analysis could assess if the negative relationship between MAP and drought sensitivity described by the Huxman-Smith model is present in other biomes that have little vegetation turnover.

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Appendix

Figure S1. Map of shortgrass steppe biome (black outline) in the context of the North American Great Plains (light blue), made up of the tallgrass prairie, the northern and central mixed prairies, and the shortgrass steppe. The spatial boundary of the shortgrass steppe biome was first obtained from the USDA Forest Service and World Wildlife Foundation's (WWF) ecoregion classification map, masked to exclude non-grassland pixels, and subsequently constrained to the shortgrass steppe precipitation amounts (MAP 250-625mm) defined by Lauenroth et al. (2008b). Thus, the shaded gray region within the shortgrass steppe boundary represents the study area for this analysis.

Table S1: Summary of drought years

Drought Year	Area of SGS (%) of Driest Year	Mean Precipitation Decrease (mm)	Mean % Decrease in Precipitation	Mean % Decrease in $NDVI_{int}$
2002	18.04%	170.55	45.90%	25.18%
2011	36.22%	240.37	54.00%	28.98%
2012	24.52%	158.95	42.81%	16.41%
2020	7.96%	148.70	39.83%	15.04%
2022	6.42%	189.16	42.54%	19.35%

Table S2: Temporal Regression Summaries

Variable	Time Series	Mean Slope	Sig. positive pixels	Sig. negative pixels
Precipitation	1980-2022	-0.61	0.4%	2.89%
Precipitation	2000-2022	0.153	0.041%	0%
$NDVI_{int}$	2000-2022	0.00264	1.47%	1.6%
Temperature	2000-2022	0.0095	4.2%	0%

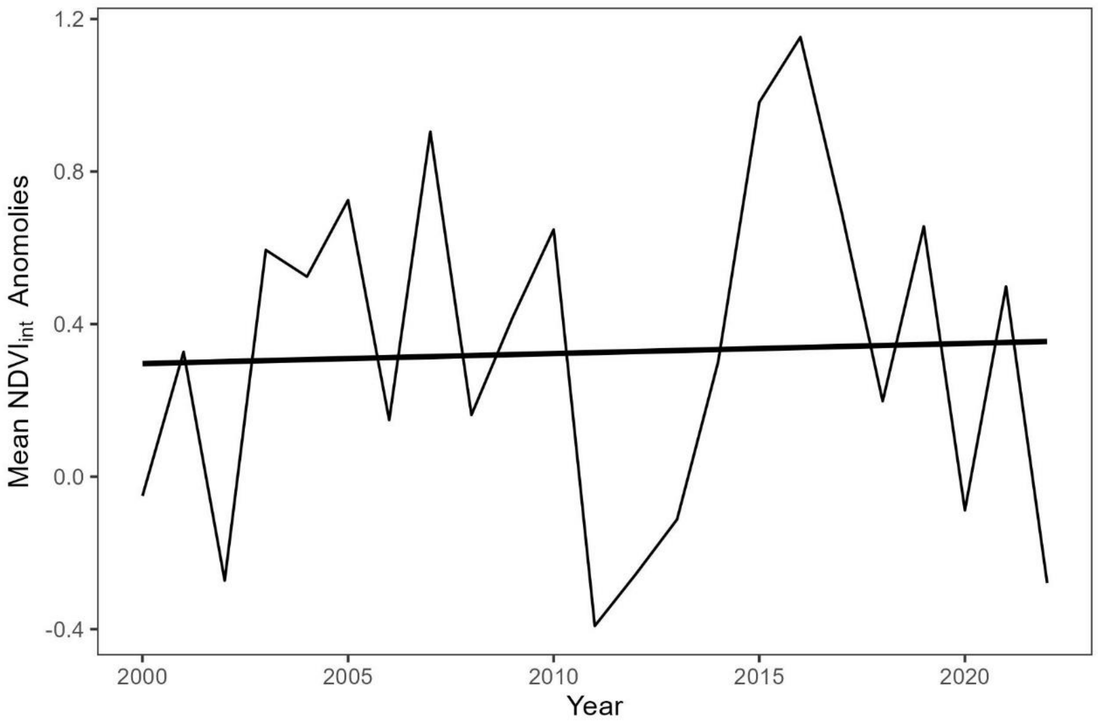

Figure S2. Mean annual NDVI$_{int}$ anomalies relative to the 2000-2022 NDVI$_{int}$ mean within the shortgrass steppe biome.

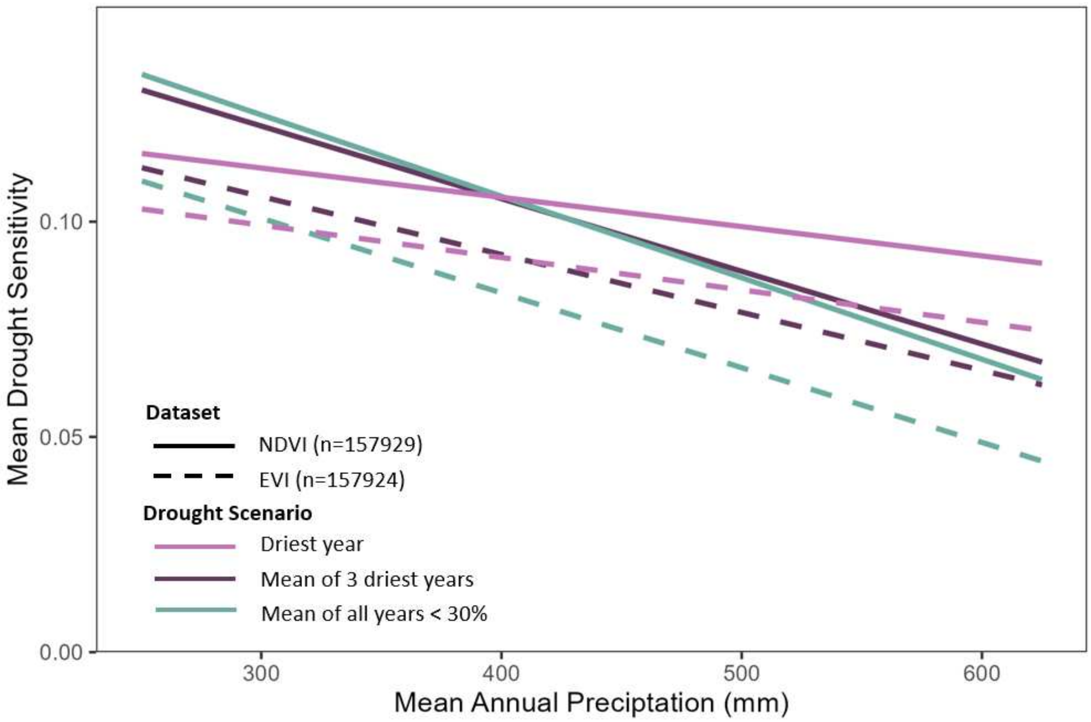

Figure S3. Comparison of the drought sensitivity relationship with mean annual precipitation (MAP) derived from Normalized Difference Vegetation Index ($NDVI_{int}$) data and Enhanced Vegetation Index (EVI_{int}) data from the MOD13Q1 Version 6.1 data product.

Table S3: Results from Regressions

	Driest Year			**Mean of Driest 3 Years**			**Mean of all years <30% Mean**		
	Slope	Adj. R^2	P-value	Slope	Adj. R^2	P-value	Slope	Adjusted R^2	P-value
MAP	-6.8×10^{-5}	0.0098	**<0.0001**	-1.7×10^{-4}	0.0786	**<0.0001**	-1.9×10^{-4}	0.0999	**<0.0001**
Aridity Index	-1.4×10^{-5}	0.0115	**<0.0001**	-2.1×10^{-5}	0.0325	**<0.0001**	-3.3×10^{-5}	0.0793	**<0.0001**
MAP	-1.1×10^{-3}	0.0346	**<0.0001**	-8.9×10^{-4}	0.1268	**<0.0001**	-8.5×10^{-4}	0.1135	**<0.0001**
PET	-2.3×10^{-4}		**<0.0001**	-1.9×10^{-4}		**<0.0001**	-1.5×10^{-4}		**<0.0001**
MAP + PET	4.9×10^{-7}		**<0.0001**	3.5×10^{-7}		**<0.0001**	3.2×10^{-7}		**<0.0001**