

THESIS

TEMPERATURE SENSITIVITY IN ABOVEGROUND NET PRIMARY PRODUCTIVITY IN
SEMI-ARID GRASSLANDS

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ABSTRACT

TEMPERATURE SENSITIVITY IN ABOVEGROUND NET PRIMARY PRODUCTIVITY IN SEMI-ARID GRASSLANDS

Although climate models forecast warmer temperatures with a high degree of certainty, precipitation is the primary driver of aboveground net primary productivity (ANPP) in most grasslands. In contrast, variations in temperature seldom are related to patterns of ANPP. Thus forecasting responses to warming is a challenge, and raises the question: how sensitive will grassland ANPP be to warming? I evaluated climate and multi-year ANPP data (67 years) from eight western US grasslands arrayed along substantial mean annual temperature (MAT, ~7-14 °C) and mean annual precipitation (MAP, ~300 – 500 mm) gradients. I used regression and analysis of covariance (ANCOVA) to assess relationships between ANPP and temperature, as well as precipitation (annual and growing season) to evaluate temperature sensitivity of ANPP. I also related ANPP to the Standardized Precipitation Evaporation Index (SPEI), which combines precipitation and evapotranspiration estimates. Regression models indicated that variation in growing season temperature was negatively related to total and graminoid ANPP, but precipitation was a better predictor than temperature. Growing season temperature was also a significant parameter in more complex models, but again precipitation was consistently a stronger predictor of ANPP. Surprisingly, neither annual nor growing season SPEI was as strongly related to ANPP as was precipitation alone. I conclude that warming will affect ANPP in these grasslands, but that predicting temperature effects from natural climatic gradients is

difficult. This is because unlike precipitation, warming effects are likely to be complex and site specific as well as moderated by regional shifts in the C₃/C₄ ratios of plant communities.

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CHAPTER ONE: INTRODUCTION

Global temperatures have been on the rise and are expected to increase between 1.1-6.4 °C by 2100 (IPCC 2007) and rate of warming in the United States over the past decade was approximately 50% higher than the global average (Hansen et al. 2010). Although it is vital that we understand how ecosystem functioning of all biomes will be affected by warming temperatures, grasslands are particularly important to study because they comprise approximately a third of the earth's terrestrial surface. One of the most important ecosystem functions is the conversion of inorganic carbon to organic forms often measured as aboveground net primary productivity (ANPP).

In grassland ecosystems, precipitation has been shown to be the best predictor of the variation in ANPP (Lauenroth 1979, Sala et al. 1988, Harpole et al 2007, Knapp et al. 2008, Merbold et al. 2009, Jung et al 2011, Zhang et al. 2014). Other abiotic variables have been shown to be important as well, such as soil-texture (Noy-Meir 1973, Sala 1982, Lane et al. 1988, Epstein et al. 1997) and temperature. However, temperature sensitivity has only been detected in warming experiments (Niu et al. 2008, 2011, Cantarel 2013), but not in observational studies that use natural gradients (Sala et al. 1988). One exception is a gradient study conducted by Epstein et al. (1997) in which temperature was shown to be negatively correlated to, and a significant predictor of ANPP.

Unlike precipitation, temperature can have both positive and negative effects (Wu et al. 2011), as well as direct and indirect effects on productivity. Increased temperatures can have a negative and indirect effects on plants under low levels of soil moisture by decreasing stomatal conductance to avoid water loss (through evapotranspiration), resulting in a reduction in carbon

fixation (Ryan et al. 1991, Niu et al. 2008). Alternatively, temperature can have positive effects when soil moisture is high in grasslands by escalating microbial activities that make nutrients available (an indirect effect) or increasing basic plant growth processes and the length of the growing season (direct effects; (Ryan et al. 1991, Kardol 2010). Therefore, mean annual precipitation (MAP) and resulting mean soil moisture content can affect the direction (Xia et al. 2009, Wu et al. 2011) and magnitude (Epstein et al. 1997) of the effects of temperature in grasslands. Soil moisture varies throughout the year, meaning the effects of temperature could sometimes be negative (Cantarel et al. 2013) or positive (Bloor et al. 2010), potentially making the net effect minimal and difficult to detect. Even if a temperature signal could be found, warming experiments indicate that the negative effects of warming often take years to offset the positive effects (Cantarel et al. 2013), highlighting the importance of long-term studies.

There are two primary ways to examine climate-ANPP relationships: site-based experimental studies and natural gradient, observational studies. Although site-based experimental studies are important for identifying the key drivers and their interactions at a given site, such studies are often relatively short (1-5 years) and it is difficult to extrapolate these findings to a larger scale due to many other confounding variables that are altered in unexpected ways (Dunne et al. 2004). Gradient studies, however, can best serve as ‘natural’ laboratories for climate-ANPP studies because they incorporate a range of abiotic and biotic variables (De Frenne et al 2013). Also, these studies can be used to substitute “space-for-time” (Rustad 2008), meaning researchers could potentially examine the future effects of warming for one region by examining similar regions that currently exhibit higher temperatures.

Epstein et al. (1997) was able to utilize a gradient approach and detected temperature sensitivity in ANPP by minimizing the variation in precipitation and maximizing the temperature

gradient across grassland types. He did this by analyzing the temperature-ANPP relationship within 5-mm bins of MAP. However, even in this tightly constrained analysis, temperature sensitivity was only found in more xeric grasslands (MAP <80 cm), but not in mesic grasslands (MAP >80 cm). This indicates at lower levels of precipitation, the negative effects of elevated temperature outweigh the positive effects (Epstein et al. 1997).

Epstein et al. (1997) conducted simple regressions and a stepwise-regression within each bin of MAP, using ANPP as the dependent variable and soil texture (clay and sand content) and mean annual temperature (MAT) as the independent variables. However, the stepwise-regression was conducted to determine whether MAT or soil texture were better predictors of ANPP within each bin of MAP and did not search for a model that could best explain the variation in productivity. It also did not include MAP in the stepwise-regression as an independent variable, therefore the relative importance of MAT and soil texture in comparison to MAP is unknown.

Due to the variety of ecosystem services grasslands provide, it is important to identify statistical models that best explain the variation in ANPP in grasslands, as well as the relative importance of each parameter in the selected model. Akaike's Information Criterion (AIC; Johnson and Omland 2004) is a common model selection process that examines all potential parameters and selects the simplest model with the best fit. If a particular term is included in the model, it can be concluded that the parameter is important. The relative importance of each model can be found by calculating the Akaike weights (Johnson and Omland 2004) for each model by summing the models that included the term of interest and assigning each term a weight on a scale of 0-1, with 1 being the most important.

Although Epstein et al. (1997) was able to identify a negative relationship between temperature and productivity in relatively dry grasslands, there has been no independent

verification of this relationship. I used the Standardized Precipitation Evaporation Index (SPEI, Vicente-Serrano 2010) as a tool to confirm that the primary effects of temperature on ANPP are through increased evapotranspiration (a negative indirect effect on soil-moisture content). The SPEI destimates the severity of drought, by taking into account the level and timing of precipitation events and the corresponding negative effects of temperature on evapotranspiration. By regressing SPEI against ANPP and comparing it to precipitation vs. ANPP regressions, one could determine if including the evapotranspiration component (built into SPEI) improves the model. If SPEI is a significantly better predictor of ANPP than precipitation alone, that would indicate the primary effects of temperature on ANPP are the negative effects on the soil moisture status.

The overarching goal of this thesis was to evaluate temperature sensitivity of ANPP in semi-arid grasslands. In chapter 2, I present the results of my analysis of 67 years of data from eight western US grasslands arrayed along substantial mean annual temperature (MAT, ~7-14 °C) and mean annual precipitation (MAP, ~300 – 500 mm) gradients. This was done to address the prediction that if there were direct effects of variation in temperatures ANPP then either a positive or negative effect of higher temperatures on ANPP would be detected. Positive effects could result from lengthening the growing season, which would be particularly important along the northern end of the gradient. Negative effects could result from exceeding the thermal optima of the dominant plants, which would likely be more important at the southern end of the gradient. Similarly, if the effects of increasing temperatures were indirect then a negative effect of temperature on ANPP would also be detected, but this would be the result of the effects of soil drying.

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CHAPTER TWO: TEMPERATURE SENSITIVITY IN ABOVEGROUND NET PRIMARY PRODUCTIVITY IN SEMI-ARID GRASSLANDS

INTRODUCTION

Of the predicted climatic changes forecast to occur due to anthropogenic disruption of the global climate system, the most certain of these is for increased atmospheric temperatures (Stocker et al. 2013). Moreover, there is abundant evidence that warming is already occurring across much of the globe (Rummukainen 2012). While virtually every biome may be impacted by warming, the degree of impact is likely to vary, and it is therefore essential to understand how sensitive different ecosystems are to temperature change. For grassland ecosystems, precipitation has long been considered the dominant climatic driver of ecosystem function over much of the globe (Harpole et al. 2007, Merbold et al. 2009, Jung et al. 2011, Zhang et al. 2014). This has been repeatedly demonstrated for aboveground net primary production (ANPP) in site-based observational studies (Briggs and Knapp 1995, Jobbágy et al. 2002, Derner et al. 2008) studies across broad geographic gradients (Webb et al. 1978, Knapp and Smith 2001, Reed et al. 2009, Guo et al. 2012), and in a number of experiments in grassland ecosystems (Yahdjian and Sala 2006, Sherry et al. 2008, Cherwin and Knapp 2012). Indeed, at large spatial scales, mean annual precipitation (MAP) may account for 90% of the variation in ANPP (Sala et al. 1988).

Temperature on the other hand is seldom statistically related to spatial or temporal variation in ANPP in grasslands (Sala et al. 1988, Del Grosso et al. 2008, Guo et al. 2014) except perhaps at global scales (e.g., Whittaker 1975, Frank and Inouye 1994, Gang et al. 2013). In experiments with warming treatments, results have been mixed with some studies showing positive responses (Lin et al. 2010), others negative responses (Niu et al. 2008, 2011, Cantarel et al. 2013), while

others found little response (Fay et al. 2011, Xu et al. 2013) to increased temperatures. In one of the few studies demonstrating temperature effects on grassland ANPP across natural climatic gradients, Epstein et al. (1997) reported negative effects of temperature on ANPP in the central US. Although regression coefficients were not strong (average $r^2 \sim 0.2-0.3$) temperature effects were greater in drier (< 600 mm MAP) than more mesic grasslands. Similarly, Wu et al. (2011) in a meta-analysis of warming experiments reported that warming often had a negative effect on productivity unless additional precipitation was added. These and other studies suggest that the primary effect of higher temperatures in many grassland ecosystems may be direct through negative effects on water balance (Peñuelas et al. 2007, Xu et al. 2012, Dulamsuren et al. 2013).

Grasslands cover approximately a third of the earth's land surface and provide vital ecosystem services that include the sequestration of carbon in the soil, forage production and habitat critical for many species (Lal 2004, Chou et al. 2008). Because many of these grassland ecosystem services depend on productivity (often measured as ANPP), it is important to better understand the drivers of spatial and temporal patterns of productivity. ANPP is an important integrative variable of ecosystem function as well as a key component of the global carbon cycle. Given the high degree of certainty in forecasted increases in air temperatures, insight into how grassland ANPP may be affected is critical. If effects of increasing temperatures are primarily manifest through negative impacts on water balance, semi-arid and arid grasslands should be among the most sensitive ecosystems to this consequence of warming. For example, Huxman et al. (2004) inferred that ecosystems with low precipitation inputs should be the most responsive to changes in water availability, and Knapp and Smith (2001) reported that grasslands were more responsive to precipitation variability than most other ecosystem types in North America.

Studies on other continents have found similar patterns (Li et al 2011, Sala et al. 2012). Recently, De Frenne et al. (2013) advocated the use of natural gradients of climatic variation to assess ecological responses to climate change, and I adopted this approach to assess the temperature sensitivity of ANPP in semi-arid grasslands. As in past ANPP precipitation studies (Sala et al. 1988, Epstein et al 1997, Huxman et al. 2004, Veron et al. 2005), I assessed sensitivity from a spatial perspective by relating variation in ANPP to temperature variables across a range of sites. The analysis was based on data from eight semi-arid native grasslands with collectively 67 years of ANPP data. These sites occurred along a western US climatic gradient in which both mean annual temperature (MAT) and MAP varied two-fold. I predicted that if there were direct effects of variation in temperatures ANPP then either a positive or negative effect of higher temperatures on ANPP would be detected. Positive effects could result from lengthening the growing season, which would be particularly important along the northern end of the gradient. Negative effects could result from exceeding the thermal optima of the dominant plants, which would likely be more important at the southern end of the gradient. Similarly, if the effects of increasing temperatures were indirect then a negative effect of temperature on ANPP would also be detected, but this would be the result of the effects of soil drying. To further examine this indirect effect, I also incorporated the Standardized Precipitation Evaporation Index (SPEI, Vicente-Serrano et al. 2010) into my analysis as an independent variable. The SPEI adjusts precipitation inputs by estimates of evapotranspiration (largely driven by temperature) and thus explicitly includes the potential negative effects of temperature on water balance (Vicente-Serrano et al. 2010).

METHODS AND MATERIALS

Annual net primary production (ANPP; g/m^2) precipitation and temperature data (annual and growing season, April 1st-September30th) were compiled from eight semi-arid grasslands

sites located in the Great Plains region of the United States (Fig. 1, Table 1). I defined the growing season for all grasslands as April 1st-September 30th even though growing season length is variable across this latitudinal gradient. However, analyses with shorter growing seasons in the north and longer seasons in the south only marginally altered the results reported below. Thus, I opted to maintain a consistent growing season period for all grasslands. Across these sites, 30-yr MAT varied ~ 2-fold, from 7.8 °C to 14.2 °C, as did MAP (280 to 500 mm). Distances between sites usually exceeded 100 km except for the two sites at the southern end of the gradient. These were located at the Sevilleta LTER site and both were included because the dominant grass species differed between sites (*Bouteloua gracilis* vs. *B. eripoda*). Data availability for ANPP varied from 3 to 16 years at individual sites (Table 4 – Appendix A), and my primary focus was on relating patterns of ANPP and temperature across this 1,600 km latitudinal gradient, although temporal variation was included, consistent with past studies that have assessed the sensitivity of ANPP to precipitation in grasslands (Sala et al. 1988, Huxman et al. 2004, Wu et al. 2011, Jobbágy et al. 2002, Peñuelas et al. 2007). Soils varied from sandy loams to clay (Table 1), and as expected for the central US, grassland communities were dominated by C₃ plants in the northern sites grading to C₄ dominance in the southern sites (Terri and Stowe 1976, Epstein et al. 1997, Table 1). Sites were not burned or grazed by livestock during the years that ANPP data were collected.

ANPP ESTIMATES

Methods used for estimating ANPP differed among sites. In the six northern sites, ANPP was estimated by harvesting peak or end of season biomass, sorting by species, then drying and weighing. Plot sizes varied from 0.1-0.25 m² and the number of harvested plots was > 10/yr at each site except at Cheyenne, where n=5. ANPP estimates from the two southern sites were based on non-destructive allometric methods in which volume estimates were made for

individual plants and ANPP was estimated using species-specific equations (Muldavin et al. 2008). For each site, total ANPP and ANPP of specific functional types including graminoids (grasses and sedges), forbs, and C₃ and C₄ photosynthetic pathways were estimated. Woody plants were included when estimating total ANPP, but they were a minor component of ANPP at all sites, therefore they were not analyzed as a functional group.

Climate data (including annual temperature and precipitation, as well as growing season temperature and precipitation) were compiled from site weather records or nearby weather stations (< 15 km from study site). Further details on each site can be found in Supplementary Information.

DATA ANALYSIS

I related patterns of ANPP to variation in temperature and precipitation in three ways. First, I combined the 67 years of data available from all sites with corresponding climatic data to evaluate simple and multiple linear regression models relating temperature and precipitation to ANPP. I focused on simple linear and multiple regressions, (procREG, SAS version 9.3, Cary, NC, USA) initially in order to more directly compare my results with other regional scale analyses. Because the number of years of data varied among sites and those sites with the greatest number of years (the most northern and the two southern sites; Table 4 – Appendix A) could dominate and bias relationships, I calculated site means for ANPP and climate data. This eliminated temporal variability and limited my statistical power to the number of sites (8), but allowed us to determine if using all 67 years of data led to qualitatively different relationships from those based on site means. Second, the combined data set was analyzed with analysis of covariance (ANCOVA, proc MIXED) models that included site as a fixed effect, along with temperature and precipitation variables and all interaction terms. Finally, I downloaded SPEI values (Vicente-Serrano et al. 2010, from www.sac.csic.es) based on annual and growing season

periods for each site and related these to patterns of ANPP. SPEI includes an estimate of evapotranspiration (ET) driven primarily by temperature, thus by comparing SPEI-ANPP relationships to precipitation-ANPP relationships, I could explicitly assess the negative and indirect effects of temperature on water balance and consequently ANPP. My expectation was that combining precipitation inputs with the negative effects of temperature on water balance would yield a model that explained a greater variation in ANPP than precipitation or temperature alone.

All models were evaluated for total ANPP, graminoid, forb, and the proportion of ANPP comprised of C₃ species, as dependent variables. The latter dependent variable (which ranged in magnitude from ~ 90 to <5 %) was included because relative abundance of photosynthetic types was less variable from year to year than absolute ANPP values. This allowed us to focus more on broad scale climatic drivers of ANPP by photosynthetic pathway.

Akaike's Information Criterion (AIC; Johnson and Omland 2004) was used to select those models that best fit the patterns of variation in ANPP (see Table 6 - Appendix A, Supplementary Information for all candidate models). The AIC model selection procedure (SAS proc GLMselect) compared each candidate model and assigned them an AIC value based on the each model's goodness of fit, taking into account the number of parameters by penalizing each model for additional terms. The model with the lowest AIC value was selected as the best model. To estimate the relative importance of particular model parameters, Akaike weights (w) were summed from those models that included the term of interest (Johnson and Omland 2004). On a scale of 0-1, the parameters were assigned a weight based on model comparisons. Parameters in which w was near 1 were deemed the most important. I calculated Akaike weights with 'MuMIn' in R version 3.0.2 (www.r-project.org).

Finally, following Epstein et al. (1997), data were parsed into narrow ranges of precipitation (100 mm and 200 mm bins) to minimize variation in precipitation and increase the potential for temperature sensitivity to be manifest. Simple linear regression analyses were then conducted for those subsets of the data ($n = 7$ to 56 years depending on the particular range of precipitation binned).

RESULTS

Both annual and growing season precipitation were positively correlated with total ANPP in simple regression models (Table 2, Figure 2) and accounted for 39% and 31% of the variance in ANPP respectively. In contrast, annual and growing season temperatures were negatively correlated with ANPP (Table 2, Figure 2) and explained 8% and 14% of the variance, respectively. When site means were used, precipitation-ANPP relationships remained statistically significant ($p < 0.0001$; Fig. 2 left inset), whereas temperature-ANPP relationships were not significant (although trends were similar; Fig. 2 right set). The addition of temperature variables in multiple regression models did not improve the explanatory power of precipitation alone. However, despite temperature's relatively minimal predictive power in simple and multiple regressions, ANCOVA models selected by AIC included growing season temperature along with site, annual precipitation and a growing season temperature x annual precipitation interaction term (Table 3, Figure 5). Although site and annual precipitation were the most influential parameters in the model ($w = 1.0$), growing season temperature contributed substantially ($w = 0.81$), while the interaction term was the least important variable ($w = 0.55$; Table 3).

Graminoids comprised a large proportion of total ANPP at all sites and thus both annual and growing season precipitation were also strongly correlated with graminoid ANPP; annual precipitation again was the best predictor (Figure 3, Table 2). In simple regression models,

annual and growing season temperatures were highly correlated with graminoid ANPP, but similar to total ANPP, annual and growing season temperatures explained much less of the variability ($r^2 = 0.15$ and 0.20 respectively, Figure 3, Table 2). Similar to the results for total ANPP, when data were combined at the site level, relationships were statistically significant for precipitation but not temperature (Figure 3 inset).

The best ANCOVA model for graminoid ANPP included the same parameters important for total ANPP (site, growing season temperature, annual precipitation, and a temperature x annual precipitation interaction term). For graminoids, site and annual precipitation were the most important model parameters, both with a weight of 1.0, whereas growing season temperature was less important ($w = 0.58$; Table 3). In contrast to graminoids, forbs comprised a much smaller and more variable proportion of total ANPP among sites and as a result, no simple or multiple regression models with temperature or precipitation parameters were significant. The best ANCOVA model for forb ANPP included site, annual precipitation, and an interaction between these two terms (Table 3).

In contrast to absolute ANPP values, the proportion of ANPP from C_3 plants was strongly correlated with both growing season and annual temperature, but not with precipitation. In simple regressions, annual temperature was a better predictor of relative C_3 ANPP than growing season temperature ($r^2 = 0.43$ and 0.27 respectively; Table 2), and was inversely related to C_3 productivity (Figure 4). The best model selected using Akaike weights included site, growing season temperature, annual precipitation and the interaction terms annual precipitation x site and growing season temperature x annual precipitation (Table 3).

Despite the combination of precipitation and temperature effects in SPEI values, simple regressions of growing season ($r^2 = 0.30$) and annual SPEI ($r^2 = 0.28$), although highly

significant, explained less of the variation in ANPP than precipitation alone. Furthermore, parsing the data into 100 mm and 200 mm ranges of precipitation after Epstein et al. (1997) did not improve relationships between ANPP and temperature variables along this gradient.

Discussion

The goal of this study was to assess the temperature sensitivity of ANPP in semi-arid grasslands along a natural climatic gradient where temperature (C °) and precipitation (mm) both varied by 2-fold from north to south and west to east in the central US. Although growing season temperature was found to be negatively related to both total and graminoid ANPP with simple linear regression models. Annual precipitation was a much stronger predictor of patterns of ANPP than temperature. Thus, my study was consistent with previous studies (Lauenroth and Sala 1992, Li et al. 2011, Knapp and Smith 2002, Vermeire et al. 2009, Sala et al. 1988), but the amount of variance explained by precipitation was substantially less along this latitudinal gradient than in many of these other studies. Because temperature and precipitation were negatively correlated across these sites, inferences regarding temperature sensitivity are limited. With models that accounted for site variation and interactions between temperature and precipitation, growing season temperature was again identified as a significant model parameter explaining variation in ANPP, yet secondary to precipitation.

Past studies (experimental and observational) have demonstrated negative effects of temperature on ANPP, and these have been argued to be indirect due to increased evapotranspiration (ET) and reduced water availability to plants with warming (Epstein et al. 1997, Niu et al. 2007, Engel et al. 2009, Dulamsuren et al. 2013, Xu et al. 2013). I was unable to demonstrate such a negative statistical relationship between temperature and ANPP when I analyzed subsets of the data in which precipitation variation was restricted to narrow ranges

(Epstein et al. 1997). Furthermore, simple linear regression models based on the SPEI explained even less variance along this natural climatic gradient than precipitation alone. This suggests that across these eight semi-arid grasslands, the indirect effect of temperature on site water balance was not the primary effect of temperature on ANPP. This result and the inclusion of significant precipitation*temperature interaction terms in the best-fit models suggests that the relationship between temperature and ANPP may be more complex than the precipitation-ANPP relationship.

Why is ANPP sensitivity to temperature difficult to detect along natural climate gradients?

The strong interdependency of temperature and precipitation in determining ecosystem function is well known (Rosenzweig 1968, Kardol et al. 2010; Frank and Inouye 1994, Rustad et al. 2001), yet at local to global scales, ecosystem function and structure are usually much better correlated with precipitation patterns than temperature (e.g., Sala et al. 1988, Del Grosso and Parton 2008). The exception to this generalization is in ecosystems with abundant water (Huxman et al. 2004, Kirwan et al. 2009). Below I explore several potential reasons why temperature sensitivity is difficult to detect and why as a result, predicting responses of ANPP to forecast warming is likely to be better informed by experiments than by using natural climatic gradients.

A fundamental difference between plant and ecosystem responses to varying temperatures vs. precipitation is that for all but the most hydric ecosystems (Knapp et al. 2008), significant reductions in precipitation will always have a negative (or at best neutral) effect on ecosystem processes. This includes both leaf level photosynthesis and ANPP (Fig. 4, Sala et al. 1981, Heitschmidt et al. 2005). In contrast, most C gain processes at both the leaf and ecosystem

levels have distinct thermal optima. Thus, alterations in temperature can have negative or positive impacts contingent upon temperatures shifting towards or away from thermal optima (Fig. 4). Such contingent positive or negative effects can occur on diurnal as well as seasonal time scales. Temperature impacts on C gain can also vary with soil moisture such that warm temperatures might positively affect ecosystem processes for several days after a substantial rain event, but have negative effects during dry periods when soil water is low (Niu et al. 2008, Zhou et al. 2008). Such contingent effects are likely reflected in the temperature*precipitation interaction term in the models that explained variation in ANPP the best (Table 3).

In addition, precipitation tends to vary much more than temperature at interannual time scales. Based on long-term (30-yr) climatic records for these eight sites, coefficients of variation (CV) for annual temperature ranged from 5-20% whereas CV's for precipitation varied from 18-32%. This pattern was also evident in the 67 year data set. Thus, even if ANPP were equally sensitive to alterations in temperature and precipitation, greater interannual variability in precipitation would increase the chance of detecting significant precipitation sensitivity relative to temperature.

Less interannual variation in temperature vs. precipitation may also lead to the strong correlation of MAT with the distribution of species with C₃ and C₄ photosynthetic pathways at regional to continental scales in grasslands (Terri and Stowe 1976, Tieszen et al. 1979; Wittmer et al. 2010). Indeed in this study, precipitation better explained the variance of ANPP but variation in temperature explained more variance in the contribution of C₃ species to ANPP. Greater stability in temperatures may allow species with different photosynthetic traits to align more strongly along temperature than precipitation gradients. This strong sorting of C₃/C₄ photosynthetic pathways was clearly evident along the natural climatic gradient in this study

(Table 1, Fig. 4). Differences in temperature optima of the dominant C₃ and C₄ grasses and their shift in abundance from north to south along a temperature gradient, combined with variable effects of alterations in temperature (Fig 4) all likely contribute to low apparent temperature sensitivity of ANPP in this region and perhaps in many others.

Despite low apparent sensitivity of ANPP to variations in temperature along this natural climatic gradient, I am hesitant to conclude that these grasslands will be insensitive to forecasted warming. Indeed, because of low interannual variability in temperature, directional shifts in MAT by only a few degrees may lead to temperatures that routinely exceed historic levels (Mora et al. 2013), particularly for temperature extremes (Smith 2011). Further, because shifts in community composition and species distributions (including alterations in C₃/C₄ composition) to directional changes in climate require more time than physiological responses of extant species (Smith et al. 2009; Vermeire et al. 2009), sensitivity of ANPP to future warming may lag the more immediate responses to changes precipitation. Thus, although using natural climatic gradients for ecological climate change research may have many advantages (De Frenne et al. 2013) and such gradients have been particularly useful for providing insights into precipitation as a driver of ANPP, assessing responses to warming may require long-term experimentation to better forecast ecosystem responses (Knapp et al. 2012).

TABLES

Table 1: Description of the eight grassland sites along a latitudinal gradient of semi-arid grasslands in the western US. Climate data are from NOAA (www.ncdc.noaa.gov/cdoweb/datasets). Mean annual precipitation (MAP), growing season precipitation (GS. Precip), mean annual temperature (MAT), and growing season temperature (GS. Temp) are based on 30yr of data. The C₃:C₄ ratio was determined using ANPP data collected from this study, and calculated as the proportion of C₃ and C₄ biomass (g/m²) relative to the total. More detailed information for each site can be found in the references provided after the soil type description.

SITE CHARACTERISTICS

Site	MAP (mm)	GS. Precip (mm)	MAT (°C)	GS. Temp (°C)	C₃:C₄	Soil Type
Fort Keogh	316.0	246.1	7.83	16.86	87:13%	Silty clay loam ¹
Wind Cave	499.1	378.7	8.4	15.8	75:25%	Sandy Loam ²
Cheyenne	404.9	306.8	8.1	14.9	59:41%	Fine-loamy ³
SGS	389.7	290.6	8.4	15.2	42:58%	Sandy loam ⁴
Sand Creek	393.9	312.7	10.9	19.0	14:86%	Clay ⁵
Fort Union	427.0	317.3	9.9	16.2	25:75%	Sandy clay loam ⁵
Sevilleta Blue	281.4	178.8	14.2	21.6	22:78%	Sandy loam and sandy clay loam ⁶
Sevilleta Black	281.4	178.8	14.2	21.6	20:80%	Sandy loam and sandy clay loam ⁶

Heitschmidt et al. 2005¹, Smith, A.², Dijkstra et al. 2001³, Lauenroth and Burke 2008⁴, Cherwin and Knapp 2011⁵, Muldavin et al. 2008⁶

Table 2: Results for simple linear regression models relating climatic variables to ANPP (total, graminoid and the proportion of ANPP from C₃ plants). Only significant relationships are shown. When temperature and precipitation variables were combined in multiple regression models, none were significant, nor were any regression models significant for forb ANPP. Standardized Precipitation Evaporation Index (SPEI) measures the severity of droughts by combining precipitation inputs with estimates of evapotranspirational losses.

Dependent Variable	Parameter	Regression Coefficient	p-value	r²
Total ANPP				
	Annual Temperature	-5.32	0.019	0.08
	Annual Precipitation	0.33	<.0001	0.39
	Annual SPEI	31.86	<.0001	0.28
	Growing Season Temperature	-7.67	0.002	0.14
	Growing Season Precipitation	0.31	<.0001	0.31
	Growing Season SPEI	31.65	<.0001	0.30
Graminoid ANPP				
	Annual Temperature	-6.38	0.0002	0.15
	Annual Precipitation	0.31	<.0001	0.43
	Growing Season Temperature	-8.30	0.001	0.20
	Growing Season Precipitation	0.30	<.0001	0.40
Relative C₃ ANPP				
	Annual Temperature	-0.07	<.0001	0.43
	Growing Season Temperature	-0.06	<.0001	0.27

Table 3: Results from ANCOVA analyses relating climatic variables and site as a fixed effect to total ANPP and functional types. Akaike’s Information Criterion (AIC) was used to select models with the best fit and the least complexity. Simple and multiple regression models were included as candidate models, but none were selected. The weights of the individual parameters are denoted as w . Models were selected for each of the functional types: total ANPP, graminoid, forb, and relative C₃ ANPP. Akaike weights were used to assess how individual parameters improved the model selected. GS = growing season, An = annual, Temp = temperature, Precip = precipitation.

Selected Models Using AIC					
Dependent Variable	Model	Parameters	AIC	w	R₂
Overall ANPP	Site GS.Temp An.Precip GS.Temp * An.Precip		572.35		0.61
		Site		1.00	
		GS.Temp		0.81	
		An.Precip		1.00	
		GS.Temp * An.Precip		0.55	
Graminoid	Site GS.Temp An.Precip GS.Temp*An.Precip		544.24		0.63
		Site		1.00	
		GS.Temp		0.58	
		An.Precip		1.00	
		GS.Temp*An.Precip		0.20	
Forb	Site An.Precip An.Precip*Site		398.44		0.52
		Site		1.00	
		An.Precip		1.00	
		An.Precip*Site		0.99	
Relative C ₃	Site GS.Temp An.Precip An.Precip*Site GS.Temp*An.Precip		-189.96		0.89
		Site		1.00	
		GS.Temp		0.98	
		An.Precip		1.00	
		An.Precip*Site		0.98	
		GS.Temp*An.Precip		0.96	

FIGURES

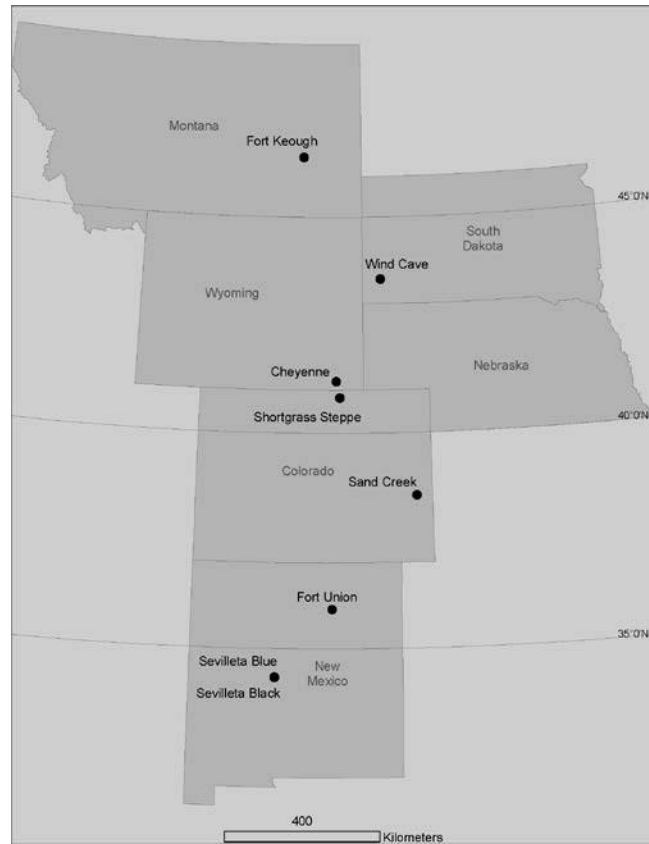


Figure 1: Locations of eight grasslands included in this study. Additional information for each site can be found in Tables 1 and 4.

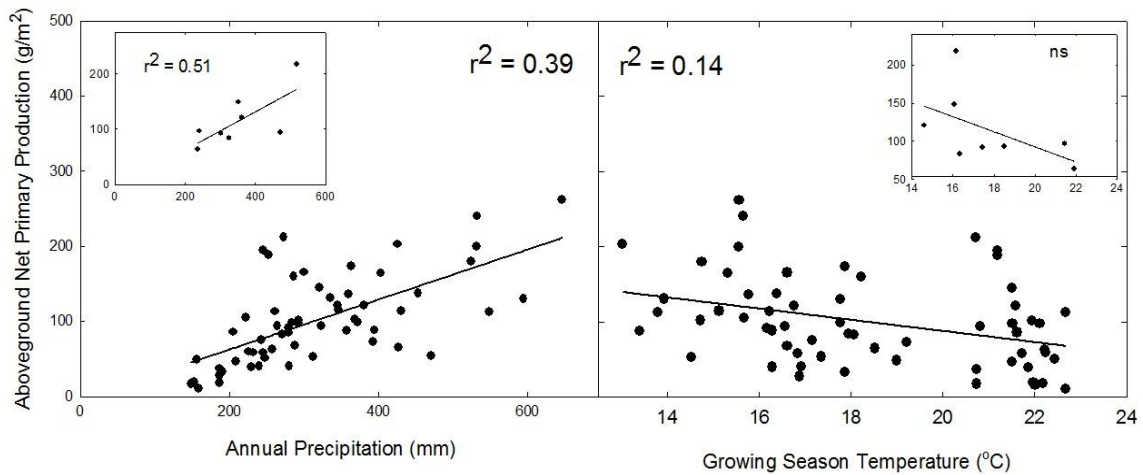


Figure 2: Simple linear regression models that best fit patterns of ANPP. Left: Relationship between annual precipitation and aboveground net primary productivity (ANPP) across eight grasslands ($ANPP = -2.90 + 0.33 * An.Precip$; Left inset: $ANPP = -7.32 + 0.35 * An.Precip$). Inset: Relationship based on site means of ANPP and precipitation. Right: Relationship between ANPP and growing season temperature across eight grasslands. Inset: Relationship based on site means of ANPP and temperature ($ANPP = 240.87 - 7.67 * GS.Temp$).

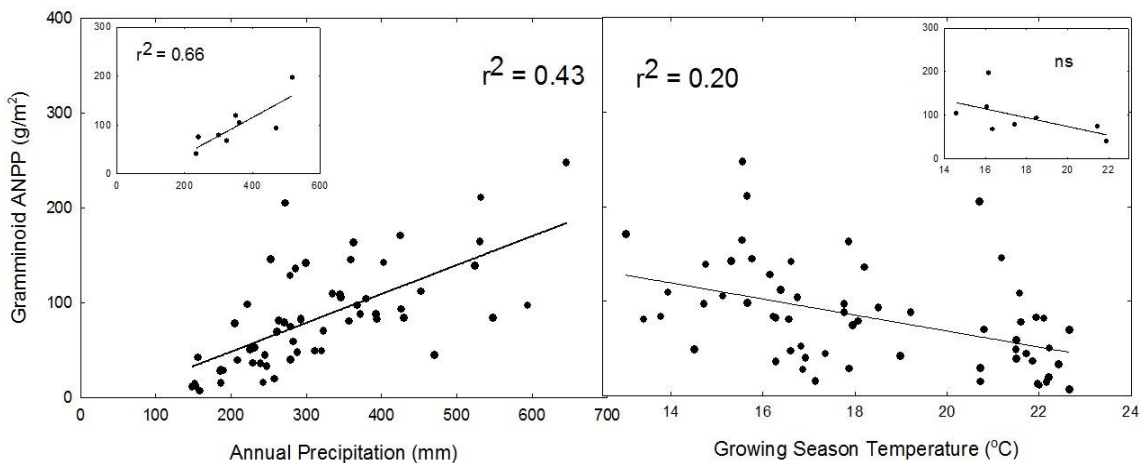


Figure 3: Simple linear regression models that best fit patterns of graminoid ANPP. Left: Relationship between annual precipitation and graminoid ANPP ($Graminoid\ ANPP = -14.58 + 0.31 * An.Precip$; Left inset: $Graminoid\ ANPP = -36.78 + 0.38 * An.Precip$). Right: Relationship between growing season temperature and graminoid ANPP. Insets: Relationships based on site means for each of the eight grasslands ($Graminoid\ ANPP = 233.20 - 8.30 * GS.Temp$).

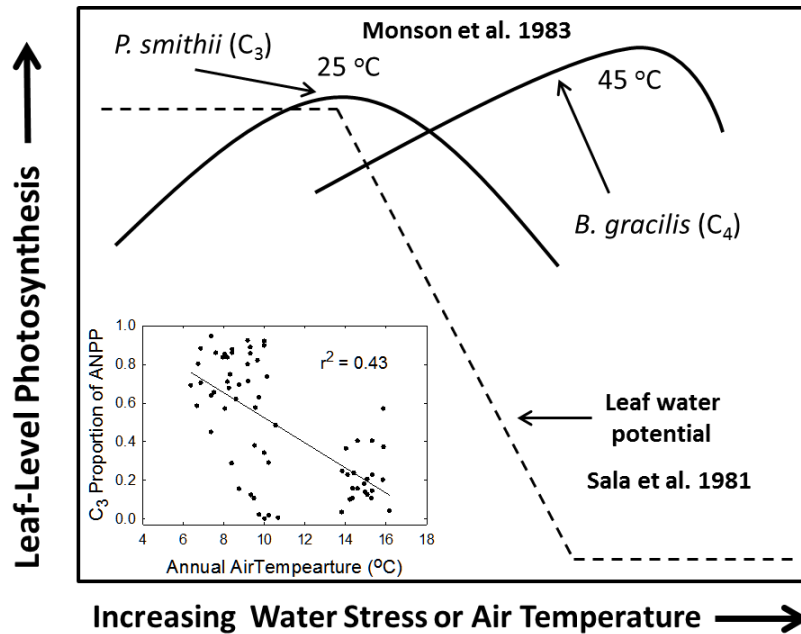


Figure 4: Contrasting responses of leaf-level photosynthesis in two dominant semi-arid grassland grasses to alterations in temperature and increasing water stress. Along the north to south climatic gradient in this study (Fig. 1), there is a shift in the proportion of ANPP resulting from plants with the C₃ vs. C₄ photosynthetic pathways (inset, relationship from this study, Table 1). The two dominant grasses along this gradient, *Pascopyrum smithii* and *Bouteloua gracilis*, both have broad photosynthetic response surfaces to varying temperatures and their respective temperature optima differ by 20 °C (Monson et al. 1983). Shifts in the abundance of C₃ and C₄ species along this gradient may moderate apparent temperature sensitivity of ANPP, whereas effects of temporal changes in temperature for both C₃ and C₄ grasses will depend upon whether temperatures are shifting towards or away from thermal optima. In contrast to temperature, responses of photosynthesis to water stress (dashed line) show a strong threshold response for all plant species (example shown is for *B. gracilis*, Sala et al 1981) and thus ANPP responses to changes in precipitation inputs are more likely to be consistently strong along the entire climatic gradient (spatially and temporally). Combined, spatial shifts in species-level traits and differences in the nature of physiological responses to change in water vs. temperature are key mechanisms explaining why precipitation but not temperature is a strong predictor of latitudinal variation in ANPP in western US semi-arid grasslands.

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CHAPTER THREE: CONCLUSIONS AND FUTURE WORK

I examined the relationships between ANPP and temperature, as well as precipitation (annual and growing season) across a north-south temperature and precipitation gradient, in the semi-arid region of the Great Plains. Consistent with previous observational gradient studies, precipitation accounted for the most variation in productivity (Webb et al. 1978, Sala et al. 1988, Knapp and Smith 2001, Reed et al. 2009, Guo et al. 2012) while I could only detect a minor sensitivity to increases in temperature. In addition, the effects of temperature were found to be dependent on the level of precipitation. This is consistent with previous studies which have shown the effects of temperature on productivity can be positive, negative, or have no effect, depending on soil moisture status (Epstein et al 1997, Wu et al. 2011). In contrast, precipitation is consistently positively correlated with productivity (Jobbágy et al. 2002, Yahdjian and Sala 2006, Cherwin and Knapp 2012), with the exception of the most xeric environments (Knapp et al. 2008). This indicates the relationship between temperature and ANPP is more complex than that of ANPP and precipitation, and requires further investigation.

Despite my inability to find a strong temperature-ANPP relationship, it is possible that increasing global temperatures will have a significant, indirect effect on productivity in semi-arid grasslands by changing the species composition (Cantarel 2011). In my study, temperature was the most significant predictor of the distribution of C₃ and C₄ species. It is possible the effects of increased temperatures will alter community compositions to reflect more xeric communities (more C₄ species) with lower maximum growth potential, resulting in decreased productivity. Because changes in community composition takes place over the course of many years, there will be a significant need for long-term, site base studies that monitor not only total ANPP, but

the productivity of individual species. By doing this, it can also be determined if there is a shift in dominance towards species that are better adapted to new climatic conditions, which could alter total ecosystem response to changes in the environment over time.

Precipitation is typically more variable than temperature at interannual time scales, making it easier to detect a significant precipitation sensitivity than a temperature sensitivity. Despite my efforts to minimize the variation in precipitation by examining these relationships along a north-south gradient, the coefficient of variation was still much higher (5-20%) than temperature (18-32%). However, many experimental studies have been successful in minimizing the variation in precipitation and detecting a significantly negative temperature effect on productivity (Niu et al. 2008, 2011, Cantarel 2013). This highlights the need for more site-based, experimental studies that can control precipitation and soil moisture to highlight the effects of temperature.

As seen in the models selected using AIC model selection, the effects of temperature on ANPP depend on the levels of precipitation, however this relationship is still not fully understood. It will be beneficial to have more site-level studies that manipulate temperature and soil moisture content to better understand the mechanisms behind the temperature-precipitation interaction effect. To further investigate this interaction, it would be informative to monitor the physiological responses (such as leaf water potential, leaf temperature, stomatal conductance, and photosynthetic yield) to increased temperature, under each soil moisture treatment. By varying soil moisture levels and monitoring corresponding plant stress, I could better identify when the positive effects of increased temperature are outweighed by the negative effects of increasing temperatures. This would be particularly helpful in understanding the underlying mechanisms responsible for plant-level response to warming.

Physiological plant-based studies should focus on the dominant species because dominant species drive ecosystem-level responses to environmental change (Whittaker 1965, Smith et al. 2009, Engel 2009, Niu et al. 2011). By better understanding how the dominant species respond to climatic changes, we can more accurately predict how the overall ecosystem will be affected. However, due to numerous abiotic interactions and these interactions changing over time, it will be difficult to ever predict future effects of climate change with full certainty by studying individual plant responses alone (Engel 2009).

It is also very likely that abiotic factors other than soil moisture will change the severity and direction of the effects of temperature on productivity. For instance, CO₂ experiments have shown that elevated [CO₂] decreases stomatal conductance, resulting in a decrease in water loss and higher soil moisture content (Morgan et al. 2004). Therefore, it is possible that if an increase in temperature coincides with an increase in [CO₂], as climate models predict (IPCC 2007), an increase in temperature may increase productivity. An increase in biomass will lead to a higher rate of N intake, a highly limiting nutrient in semi-arid regions, potentially limiting the positive effects of increased [CO₂] (Morgan et al. 2004, Bachman et al. 2009, Dijkstra et al. 2010). It is clear that there is a need for more factorial experiments to study how different possible combinations of abiotic factors alter the effects of temperature on ecosystem functioning. Other abiotic factors to consider examining in a factorial design include: soil texture, the timing and intensity of rainfall, the timing of temperature extremes, and other limiting nutrients (K and P). Climate-productivity studies primarily examine aboveground primary productivity, leaving the belowground (BNNP) responses largely understudied (Frank 2007, Li et al. 2011). However, studies have shown that the ratio of photosynthates allocated to belowground and aboveground shifts, depending on environmental conditions (Tilman 1988, Li et al. 2011). Therefore, it cannot

be assumed that BNPP increases or decreases linearly with ANPP. In fact, it is possible that while we may see an increase in ANPP in response to a change in climate (such as increased warming), there is a total net decrease in net primary productivity due to a loss in belowground production. Including belowground productivity in addition to ANPP, will provide a better estimate of the true ecosystem response to changes in climate (Wu et al. 2011).

Grasslands cover approximately 33% of the terrestrial earth and serve an integral role in the carbon cycle by storing approximately between 28–37% of the terrestrial soil organic carbon (SOC) (Chou et al. 2008). Understanding the drivers of productivity in grasslands will help us better understand how anthropogenic changes, such as global warming, will alter grassland ecosystem functioning.

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APPENDIX A: SUPPLEMENTARY INFORMATION

Detailed Site Descriptions

Table 4: Additional site data for the eight grasslands. Longitude, latitude and elevation estimates were gathered using earth.google.com. Years of data are the number of years of data used in the analyses.

Site	Years of Available Data	Longitude	Latitude	Elevation (m)
Fort Keogh	16	-105°57' 20 "W	46°22'55 "N	820
Wind Cave	4	-103° 25' 16"W	43° 36' 16"	1045
Cheyenne	7	-104°53' 12" W	41°11' 5.2" N	1920
SGS	9	-104°46' 38"W	40°48'46"N	1655
Sand Creek	3	-102° 30' 22" W	38° 32' 51 " N	1210
Fort Union	3	-105° 0' 36"W	35° 54' 35 "N	2060
Sevilleta Blue	12	-106° 58' 0"W	34° 20' 0"N	1670
Sevilleta Black	11	-106° 58' 0"W	34° 20' 0 "N	1615

MIXED GRASS PRAIRIE

Fort Keogh, MT (46° 22' 55"N -105° 57'20" W) is an upland site in south eastern Montana that is dominated by two C₃ grasses, *Hesperostipa comata* and *Pascopyrum smithii*. Both climate and productivity data collected for the Fort Keogh site were provided by the Fort Keogh United States Department of Agriculture (USDA) Agricultural Research Service (ARS) station

Wind Cave, SD (41°11' 5.2" N -103° 25' 16"W) is a lowland site that is dominated by *Pascopyrum smithii* (C₃) and *Bouteloua gracilis* (C₄). Climate data were collected from the High Plains Regional Climate Center (HPRCC). Biomass data were provided by Anine Smith from

Colorado State University and the U.S. Geological Survey (USGS) Northern Prairie Wildlife Research Center.

Cheyenne, WY (41° 6' N -104°53' 12" W) is an upland site. The plant community is approximately 55% C₃ grasses and 25% C₄ grasses (Bachman et al 2010). *Pascopyrum smithii* is the dominant C₃ grass, while *Bouteloua gracilis* is the dominant C₄ grass. The Cheyenne United States Department of Agriculture (USDA) Agricultural Research Service (ARS) station provided multiples years of both productivity data and climate data collected from the Prairie Heating and CO₂ Enrichment (PHACE) experiment. Additional biomass data were collected by participants of The Extreme Drought in Grasslands Experiment (EDGE) project.

SHORT GRASS STEPPE

Short Grass Steppe, CO (40°48'46"N -104° 27' W), is an upland site in which the C₄ grass *Bouteloua gracilis* accounts for approximately 70% of canopy cover and 90% of total biomass (Dalglish et al. 2006, Cherwin et al. 2011). Short Grass Steppe is located in the north east portion of Colorado. It is less than 50 km south east of the Cheyenne site, but it is approximately 265 meters lower in elevation. Short Grass Steppe Long Term Ecological Research (SGS LTER) provided both climate and productivity data for the Short Grass Steppe site. Additional biomass data was collected by participants of The Extreme Drought in Grasslands Experiment (EDGE) project.

Sand Creek Massacre Historical Site, CO (38° 32' 51 " N -102° 30' 22" W) and *Fort Union, CO* (35° 54' 35 "N -105° 0' 36"W) are also dominated by *Bouteloua gracilis* (C₄). Karie Cherwin, from Colorado State University, provided productivity data and the National Oceanic and Atmospheric Administration (NOAA) (www.ncdc.noaa.gov/cdo-web/datasets) provided the climate data for both Sand Creek and Fort Union.

DESERT GRASSLAND

Sevilleta Blue and *Sevilleta Black* (-106° 58' 0"W 34° 20' 29 "N), are both located in central New Mexico. Their names are derived from their distinctively different plant community compositions. *Sevilleta Blue*, is dominated by blue grama (*Bouteloua gracilis*) while *Sevilleta Black*, is dominated by black grama (*Bouteloua eriopoda*). Both ANPP data and climate data were provided by *Sevilleta* Long Term Ecological Research Site (LTER). Additional biomass data were also collected by participants of The Extreme Drought in Grasslands Experiment (EDGE) project.

Table 5: Coefficient of variation (%) for each of the independent variables in a simple regression with ANPP as the dependent variable. Each regression was conducted within site using 30-year means.

Site Characteristic				
Site	MAP (mm)	GS. Precip (mm)	MAT (°C)	GS. Temp (°C)
Fort Keogh	26.83	32.51	14.04	5.49
Wind Cave	26.15	30.94	12.13	6.31
Cheyenne	19.64	24.94	9.15	5.87
SGS	18.11	23.43	15.09	5.24
Sand Creek	35.22	36.35	19.64	8.04
Fort Union	24.47	29.57	5.19	3.71
Sevilleta Blue	31.97	45.88	18.74	10.91
Sevilleta Black	31.97	45.88	18.74	10.91

Table 6: Dependent variables and candidate models used to assess patterns of ANPP in the eight grasslands.

Dependent Variables	Parameters	
Total ANPP Graminoid ANPP Forb ANPP Relative C3 ANPP	Simple Regression	Multiple Regression
	Annual Temperature	Annual Temperature
	Annual Precipitation	Annual Precipitation
	Growing Season Temperature	Growing Season Temperature
	Growing Season Precipitation	Growing Season Precipitation
	Annual SPEI	Temperature and Precipitation
	Growing Season SPEI	
	ANCOVA	
	Site	
	Annual Temperature	
	Annual Precipitation	
	Growing Season Temperature	
	Growing Season Precipitation	
	All combinations and interactions	

SUPPLEMENTAL LITERATURE CITED

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