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Potential Effects of Altered Precipitation Regimes on Primary Production in Terrestrial Ecosystems

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POTENTIAL EFFECTS OF ALTERED PRECIPITATION REGIMES ON

PRIMARY PRODUCTION IN TERRESTRIAL ECOSYSTEMS

by

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ABSTRACT

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Utah State University, 2011

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In addition to causing an increase in mean temperatures, climate change is also altering precipitation regimes across the globe. General circulation models project both latitude-dependent changes in precipitation mean and increases in precipitation variability. These changes in water availability will impact terrestrial primary productivity, the fixation of carbon dioxide into organic matter by plants. In my thesis, I addressed the following three questions: 1.) What will be the relative effect of changes in the mean and standard deviation of annual precipitation on mean annual primary production? 2.) Which ecosystems will be the most sensitive to changes in precipitation? 3.) Will increases in production variability be disproportionately greater than increases in precipitation variability?

I gathered 58 time series of annual precipitation and aboveground net primary production (ANPP) from long-term ecological study sites across the globe. I quantified the sensitivity of ANPP at each site to changes in precipitation mean and variance. My results indicated that mean ANPP is about 40 times more sensitive to changes in precipitation mean than to changes in precipitation variance. I showed that semi-arid ecosystems such as shortgrass steppe in Colorado or typical steppe in Inner Mongolia may be the most sensitive to changes in precipitation mean.

At these sites and several others, a 1% change in mean precipitation may result in a change in ANPP that is greater than 1%.

To address how increases in interannual precipitation variability will impact the variability of ANPP, I perturbed the variability of observed precipitation time series and evaluated the impact of this perturbation on predicted ANPP variability. I found that different assumptions about the precipitation-ANPP relationship had different implications for how increases in precipitation variability will impact ANPP variability. Increases in ANPP variability were always directly proportional to increases in precipitation variability when ANPP was modeled as a simple linear or a lagged function of precipitation. However, when ANPP was modeled as a nonlinear, saturating function of precipitation, increases in ANPP variability were disproportionately low compared to increases in precipitation variability during wet years but disproportionately high during dry years.

My thesis addresses an existing research gap regarding the long-term impact of increases in interannual precipitation variability on key ecosystem functioning. I showed that increases in precipitation variability will have negligible impacts on ANPP mean and have disproportionately large impacts on ANPP variability only when ANPP is a concave down, nonlinear function of precipitation. My work also demonstrates the importance of the precipitation-ANPP relationship in determining the magnitude of impacts to ANPP caused by changes in precipitation. Finally, my thesis highlights the potential for considerable changes in ANPP variability due to increases in precipitation variability.

(80 pages)

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Joanna S. Hsu

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CHAPTER 1

INTRODUCTION

Primary production is an essential component of the global carbon cycle. The capacity for terrestrial vegetation to function as a carbon sink depends on how much carbon dioxide is fixed by plants. Annual net primary production (NPP) of the planet is about 105 Pg of carbon (Field et al. 1998, Geider et al. 2001). Terrestrial ecosystems cover about one-third of the earth's surface, but fix more than half of this carbon (Field et al.1998, Geider et al. 2001). At local scales, primary production is a key ecosystem function, influencing virtually all other ecosystem properties. In addition to being a direct resource for primary consumers, plant biomass determines the carrying capacity of an ecosystem by setting the energy available for all organisms.

Quantifying how climate change will impact aboveground terrestrial primary production has become an important goal for ecologists. A large body of research shows that increases in atmospheric carbon dioxide and temperature both stimulate primary production, at least initially (Riedo et al. 2001, Nemani et al. 2003, Ainsworth et al. 2005, Boisvenue et al. 2006, Heimann and Reichstein 2008, Wu et al. 2011). Though some studies indicate that warming can lead to drought and decreases in primary production, one meta-analysis showed that warming led to increases in aboveground biomass by an average of 27% (Wu et al. 2011).

This thesis focuses on a different another way climate change is impacting primary production: through changes in the precipitation regime. Water availability may be the biggest limitation to plant growth in over 40% of the planet's vegetated surface (Nemani et al. 2003). Precipitation variability is a major driver of aboveground net primary production (ANPP) dynamics, especially in arid and semi-arid ecosystems (Smoliak 1986, Sala et al. 1988, Lauenroth and Sala 1992, O'Connor et al. 2001, Khumalo and Holechek 2005, Knapp et al. 2006, Patton et al. 2007).

Global warming is altering precipitation patterns by increasing evaporation rates and the moisture holding capacity of the lower atmosphere (Boer 1993, Allen and Ingram 2002, Trenberth et al. 2003). General circulation models (GCMs) project two types of changes in precipitation that are already evident (Räisänen 2002, Salinger 2005, Sun et al. 2007, Zhang et al. 2007, Allan and Soden 2008, Stephens and Hu 2010). First, latitude-dependent changes in mean precipitation are causing some regions to become wetter and others to become drier. Second, increases in precipitation variability are resulting in fewer rainfall days, longer droughts, and more extreme events. In one study across 19 GCMs, a doubling of atmospheric CO_2 led to increases in the mean and standard deviation of annual precipitation of 2.5% and 4.2%, respectively (Räisänen 2002).

This thesis utilizes 58 long-term data sets of rainfall and ANPP from across the globe to examine how these two types of changes in precipitation regime might impact the mean and interannual variability of ANPP in terrestrial ecosystems. Using relationships between precipitation and primary production derived empirically from my data sets, I make predictions about the size of potential changes in ANPP relative to the size of potential changes in precipitation.

In Chapter 2, I examine how changes in precipitation mean and variance will impact mean annual ANPP. I characterize the precipitation-production relationship at each site using linear and nonlinear regression models and use partial derivatives to quantify the sensitivity of primary production to changes in precipitation mean and variance. The sensitivity of production to precipitation mean depends on the slope of the precipitation-production relationship, while the sensitivity to precipitation variance depends on the nonlinearity of this relationship. I also test whether production sensitivities correlate with abiotic variables such as mean annual temperature and precipitation.

In Chapter 3, I explore how increases in the interannual variability of precipitation will affect the interannual variability of ANPP in grasslands. Increases in the variability of precipitation should cause increases in the variability of ANPP since ANPP is a function of precipitation. These increases in ANPP variability will pose challenges for natural resource management. However, depending on how vegetation responds to precipitation variability, increases in ANPP variability may be relatively less than, equal to, or greater than increases in precipitation variability. In this chapter, I model three likely ways that ANPP responds to precipitation: linearly, nonlinearly, and with a time lag. I directly perturb the variability of observed precipitation time series and quantify how ANPP variability is affected in each of these three cases.

In Chapter 4, I summarize my findings, synthesizing across chapters. I discuss the contributions of my work to our understanding of how changes in precipitation will affect ANPP mean and variability.

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CHAPTER 2

SENSITIVITY OF MEAN ANNUAL PRIMARY PRODUCTION TO PRECIPITATION[1]

Abstract. In many terrestrial ecosystems, variation in aboveground net primary production (ANPP) is positively correlated with variation in interannual precipitation. Global climate change will alter both the mean and the variance of annual precipitation, but the relative impact of these changes in precipitation on mean ANPP remains uncertain. At any given site, the slope of the precipitation-ANPP relationship determine the sensitivity of mean ANPP to changes in mean precipitation, while the curvature of the precipitation-ANPP relationship determines the sensitivity of ANPP to changes in precipitation variability. We used 58 existing long-term data sets to characterize precipitation-ANPP relationships in terrestrial ecosystems and to quantify the sensitivity of mean ANPP to the mean and variance of annual precipitation. We found that most study sites have a nonlinear, saturating relationship between precipitation and ANPP, but these nonlinearities were not strong. As a result of these weak nonlinearities, ANPP was nearly 40 times more sensitive to precipitation mean than variance. A 1% increase in mean precipitation caused a -0.2% to 1.8% change in mean ANPP, with a 0.64% increase on average. Sensitivities to precipitation mean peaked at sites with a mean annual precipitation near 500 mm. Changes in species composition and increased intra-annual precipitation variability could lead to larger ANPP responses to altered precipitation regimes than predicted by our analysis.

Introduction

Primary production influences many soil and ecosystem properties. Primary production is also an important component of the global carbon cycle, and anticipating future changes in mean primary production is a goal of global change ecology.

Water availability is a key control of plant productivity, and aboveground net primary

1 Coauthored by Joanna Hsu, James Powell, and Peter Adler

production (ANPP) is positively correlated with mean annual precipitation (MAP) at regional scales (Lieth 1973, Sala et al. 1988, Huxman et al. 2004, Jobbagy et al. 2002, Bai et al. 2004). Interannual variability in ANPP is also correlated with interannual variability in precipitation at many sites, especially in water-limited ecosystems (Smoliak 1986, Lauenroth and Sala 1992, O'Connor et al. 2001, Khumalo and Holechek 2005, Knapp et al. 2006, Patton et al. 2007).

General circulation models (GCMs) project latitude-dependent changes in MAP due to climate forcing (Giorgi and Francisco 2000, Zhang et al. 2007, John et al. 2009). In addition to changes in mean precipitation, GCMs also project changes in the distribution of precipitation as the global hydrological cycle intensifies (Räisänen 2002, Salinger 2005, Sun et al. 2007, Allan and Soden 2008, Wetherald et al. 2009). However, while GCMs sometimes disagree on the magnitude and direction of changes in regional mean precipitation (Neelin et al. 2006, Zhang et al. 2007), they consistently predict increases in the intra- and interannual variability of precipitation. Observational studies and experimental manipulations both suggest that production is sensitive to the timing and size of precipitation inputs (Fay et al. 2003, Swemmer et al. 2007, Heisler-White et al. 2009), indicating that increases in precipitation variance will affect ANPP. Thus, mean ANPP may respond to changes in both the mean and the variance of the precipitation regime.

At a given site, the response of mean ANPP to changes in mean annual precipitation will depend on the slope and intercept of the relationship between precipitation and ANPP. Assuming that ANPP is a positive function of precipitation, the steeper this slope, the greater the effect of increases in mean precipitation on mean ANPP. How changes in precipitation variability can affect mean ANPP is less intuitive, but two mechanisms are possible. If precipitation across years is not symmetrically (normally) distributed around a mean, then an increase in precipitation variance may alter the precipitation mean, which in turn could alter mean ANPP. In addition, if the precipitation-ANPP relationship is nonlinear, changes in precipitation variance will alter mean

ANPP according to the curvature of the response function due to a mathematical property known as Jensen's inequality (Jensen 1906) (Fig. 2-1). Specifically, if the precipitation-ANPP relationship is concave down, then increases in precipitation variance will decrease mean ANPP even when MAP is held constant.

Nonlinear, concave-down relationships have been documented for regional precipitation-ANPP relationships (Huxman et al. 2004, Yang et al. 2008), but few studies have explored nonlinearities in temporal precipitation-ANPP relationships (but see Khumalo and Holechek 2005). In fact, we might expect nonlinear, concave-down relationships in any ecosystem where other resources, such as nitrogen, limit production in wet years more than in dry years. Where such nonlinear relationships exist, Jensen's inequality would apply. However, we do not know how common these nonlinearities are or how large a change in mean ANPP they would cause given changes in interannual precipitation variability.

We used existing long-term time series of precipitation and ANPP to pursue three objectives. First, we characterized temporal precipitation-ANPP relationships for all terrestrial ecosystems for which data was available. Second, we calculated the sensitivity of mean ANPP to the mean and variance of annual precipitation. Third, we tried to explain cross-system variation in ANPP sensitivities as a function of ecosystem type and abiotic covariates. To address these objectives, we built linear and nonlinear regression models to predict ANPP from precipitation and selected the best model for each data set using Akaike's Information Criterion (AICc). We then used partial derivatives to quantify the sensitivity of ANPP mean to precipitation mean and variance. Finally, we used regression to test for cross-system patterns in ANPP sensitivities to precipitation.

Methods

Data collection

We located long-term time series of annual precipitation and ANPP in three different ways. First, we used data sets previously analyzed for other rainfall and production patterns by Knapp and Smith (2001) and by Lehouerou (1988). The Knapp and Smith data sets are from Long-Term Ecological Research (LTER) sites across North America. We added updated data from these LTER sites when it was available. The Lehouerou data sets are from semi-arid and arid sites. In a few cases, updated data from these sites was also available. Secondly, we electronically searched ISI Web of Knowledge for articles published to date that might contain precipitation and ANPP data sets. We used “precipitation” and “primary production” as topic search algorithms in the subject area of ecology. We extracted raw data from papers by using the published tabular data or by digitizing figures. Finally, we used net primary productivity data sets from the Oak Ridge National Laboratory Distributed Active Archive Center, accessible at http://daac.ornl.gov/.

To ensure that studies had reasonable power to detect linear and nonlinear trends, we excluded data sets with fewer than 10 years of precipitation and ANPP data. We also excluded studies in which productivity was estimated using remote sensing approaches. In studies where productivity was experimentally manipulated via fertilization, only data from non-fertilized plots was used. Finally, we excluded studies from agricultural systems.

Model fitting

We fit a linear and nonlinear model to each data set using least squares regression. The nonlinear model we used (ANPP=a-b/precipitation) is a concave down, saturating function when a and b are positive. This nonlinear function is parsimonious, linear in its parameters (so that unique least squares parameter estimates are guaranteed to exist), and fit the data better than other saturating, quadratic, and sigmoidal models that we tested. We used AICc model weights to compare linear and nonlinear model fits and to select a best model for each data set.

In cases where growing season precipitation was available and accounted for more variation in ANPP than total annual precipitation, we used growing season precipitation as the predictor variable. We did not remove outliers and influential observations due to their important contribution to the precipitation-ANPP relationship. In many cases, ANPP during very wet years determines the nonlinearity of precipitation-ANPP relationship, and the frequency of these “outlier” years is increasing with climate change (Frich et al. 2002, Svoma and Balling et al. 2010).

We fit normal and lognormal distributions to each precipitation time series using maximum likelihood estimation. We determined which distribution best described each time series using AICc, and obtained the mean ($\bar{x}$) and variance (σ^2) of each precipitation time series from that distribution. When precipitation is lognormally distributed, an increase in precipitation variance will increase precipitation mean, which in turn may increase ANPP.

Sensitivity analysis

We used a quadratic approximation (Chesson et al. 2005) to quantify the expected value of ANPP (R) for each data set :

$$R \approx f(\bar{x}, a, b) + .5 f''(\bar{x}, a, b)\sigma^2. \tag{1}$$

In Equation 1, a and b are the fitted parameters of the linear or nonlinear precipitation-ANPP model, while ($\bar{x}$) and (σ^2) are the mean and variance of the precipitation time series. The second term in Equation 1 is the source of Jensen's inequality; it is negative when f is concave down, positive when f is concave up, and zero when f is linear. Equation 1 accounts for both ways that changes in precipitation variance can cause changes in ANPP: 1) directly, by changing the precipitation mean in lognormally distributed precipitation time series, and 2) indirectly, through

Jensen's inequality.

Next, we calculated ANPP sensitivities to the mean and variance of precipitation by taking the partial derivative of Equation 1 with respect to the mean and variance of precipitation. Details of the sensitivity analysis are given in Appendix A. We scaled the sensitivities to the mean response so that they are relative, not absolute, measures: a sensitivity of 1 implies that a 1% change in precipitation mean results in a 1% change in ANPP mean in the same direction. For each data set, we calculated separate sensitivities for linear and nonlinear models. Rather than choosing between the two sensitivities, we obtained the final sensitivities for each data set using a weighted average based on AICc weights from the model fitting. In cases where multiple data sets of the same vegetation type were available from the same study, we averaged across data sets to obtain mean sensitivities.

Cross-system patterns in sensitivities

Previous studies have assumed a linear relationship between precipitation and production, and used the slopes of temporal precipitation-ANPP relationships to quantify ANPP sensitivity to precipitation mean. These studies suggest that the highest ANPP sensitivities to precipitation may be at the driest, most water-limited sites (Huxman et al. 2004) or at sites that receive an intermediate amount of precipitation (Paruelo et al. 1999, Bai et al. 2008). To the best of our knowledge, cross-system studies of primary production sensitivity to changes in precipitation variance have been limited to comparing different measures of variability, such as coefficient of variation (Noy-Meir and Walker 1984, Lehouerou et al. 1988, Knapp et al. 2001). To determine which ecosystems might be affected most by altered precipitation patterns, we used regression to test whether ANPP sensitivities to mean and variance were correlated with patterns in precipitation, precipitation seasonality (summer or winter), temperature, or data set length.

Results

Data set description

We collected a total of 58 precipitation and ANPP data sets, representing 37 different study sites (Table 2-1, Table 2-2). The average length of our data sets was 19 years. Many of the study sites are in North America, including 8 LTER sites, but we also used data sets from Eurasia, South America, and Africa. We collected 46 data sets from grasslands, 6 from alpine meadows, 3 from shrub-dominated ecosystems, and 3 from forests. Peak live biomass was used to approximate ANPP at most sites, but peak standing crop was used at several sites. The Jornada, Sevilleta, and Bonanza LTER sites used non-destructive measurements combined with allometric equations to estimate ANPP.

Model fitting

A nonlinear relationship between precipitation and ANPP best described 31 out of the 58 data sets. Fig. 2-2 shows examples of linear and nonlinear data sets. Within the linear data sets, precipitation explained an average of 33% of the variation in ANPP. The nonlinear precipitation model explained an average of 30% of the variation in ANPP within the nonlinear data sets. A chi-square goodness of fit test indicated that the probability of having a nonlinear precipitation-ANPP relationship was not different across biomes (χ^2=1.68, df=3, p=0.69).

Of the 31 nonlinear data sets, 27 were concave down; an increase in precipitation variability at these sites will lead to a decrease in mean ANPP. Four data sets exhibited a concave up precipitation-ANPP relationship, three of which were from Niwot Ridge LTER. However, AICc model weights suggest that the nonlinear model is not overwhelmingly supported by the data, especially when the pattern is concave up. Across all data sets, the AICc weight for the nonlinear model averaged only 0.49. Within the 27 nonlinear, concave down data sets, the AICc weight of the nonlinear model ranged from 0.50 to 0.97, averaging 0.66. AICc support for concave up models was especially weak, averaging 0.54 across the 4 concave up data sets.

There were 45 unique precipitation time series within the 58 data sets. Based on AICc weights, precipitation was normally distributed for 18 data sets and lognormally distributed for 27 data sets. However, AICc only showed clear support (AICc weight > 0.8) for a normal distribution in 4 cases and for a lognormal distribution in 8 cases. If precipitation is lognormally distributed, then precipitation mean and variance are not independent of each other, and changes to precipitation variance will affect the mean of both precipitation and ANPP.

Sensitivity analysis

The sensitivity of mean ANPP to changes in mean precipitation ranged from -0.2 to 1.81 with a mean of 0.64, indicating that on average, a 1% change in mean precipitation will translate into a 0.64% change in ANPP. Eight sites showed sensitivities greater than one and two sites had negative sensitivities.

In almost all data sets, mean ANPP exhibited negative sensitivities to precipitation variance due to concave down precipitation-ANPP relationships (Table 2-1, Fig. 2-3). For every data set, the sensitivity of mean ANPP to changes in precipitation variance was smaller than the sensitivity to changes in precipitation mean (Fig. 2-3). In Appendix B, we demonstrate that this result would not change had we chosen a different saturating function to characterize the precipitation-ANPP relationship. The mean sensitivity to changes in variance was -0.016. Across data sets, ANPP was 39 times more sensitive to changes in precipitation mean than to changes in precipitation variance.

Cross-system patterns in sensitivities

A quadratic regression model (sensitivity = .20 + .002(MAP) - $2.26*10^{-6}(MAP)^2$) fit the relationship between MAP and ANPP sensitivity to precipitation mean better than a linear regression model, according to AICc (Fig. 2-4). In this model, which explains 17% of the variation in sensitivities to precipitation mean, sensitivity to mean peaks at sites with 505 mm MAP. Sensitivities to precipitation mean were not correlated with mean annual temperature alone (p=0.09), but a multiple regression with mean annual temperature and a quadratic MAP effect explained 28% of the variation in sensitivity to precipitation mean and had stronger AICc support (AICc weight=0.79) than the quadratic MAP model alone. In the multiple regression model, sensitivity to precipitation mean was positively correlated with mean annual temperature. ANPP sensitivities to precipitation mean were not correlated (p>0.1) with data set length or precipitation seasonality. Shrublands exhibited the highest sensitivities to precipitation mean (mean =0.87, followed by grasslands (mean=0.69), forests (mean=0.06), and then alpine meadows (mean=0.04), but these differences were only marginally significant (p=0.06).

There was a significant, negative correlation between sensitivity to precipitation variance and mean annual temperature (p=0.01 ,r^2=0.16). However, because the range of sensitivities to precipitation variance was so small, this trend is not ecologically important. There was no correlation (p>0.1) between sensitivity to precipitation variance and MAP, data set length, biome, or precipitation seasonality.

Discussion

Relative effect of changes in precipitation mean and variance

The precipitation-ANPP relationship at the majority of sites was best described by a nonlinear, concave down function. However, in most cases, the nonlinearity was not very strong and AICc model weights indicated that a linear model fit the precipitation-ANPP relationship almost as well as a nonlinear model. Similarly, skewness in precipitation distributions was common but weak. As a result, sensitivities to changes in precipitation variance caused by

Jensen's inequality or skewed precipitation distributions were very small compared to sensitivities to changes in precipitation mean. When comparing the magnitude of potential impacts on mean ANPP, the low sensitivities to precipitation variance override the fact that changes in variance are projected to be about 1.5 times greater than changes in mean (Räisänen 2002). Overall, our results suggest that changes in the interannual variability of precipitation will have negligible effects on mean ANPP.

This conclusion is accompanied by several caveats. First, the linear sensitivity analysis is valid only for relatively small (on the order of 10% or less) perturbations to means and variances, so large changes in precipitation are outside the scope of our inference. For a doubling of CO_2, almost all GCMs project changes in interannual precipitation that fall within this range (Räisänen 2002). Second, though ANPP sensitivities to interannual precipitation variability were small, primary production could be more sensitive to intra-annual precipitation variability (Lázaro et al. 2001, Fay et al. 2003, Snyder and Tartowski 2006, Swemmer et al. 2007, Heisler-White et al. 2009, Medvigy et al. 2010). Finally, our approach does not account for potential changes in species composition or long-term shifts in vegetation structure that could alter ANPP (Silvertown et al. 1994, O'Connor et al. 2001, Shaver et al. 2001, Lett and Knapp 2005).

Cross-system patterns in sensitivities

While the wettest sites are insensitive to changes in mean precipitation, small changes in mean precipitation could cause large changes in ANPP in some arid to semi-arid grasslands and shrublands. On average, a 1% change in mean precipitation will lead to a 0.72% change in ANPP at sites that receive less than 600 mm rainfall each year. At eight sites, sensitivities to precipitation mean are greater than 1. With more data from non-grassland sites, the trend showing shrublands and grasslands ecosystems to be more sensitive to MAP would likely become clearer.

The unimodal relationship between MAP and sensitivity to precipitation mean is consistent with several other studies that also found a peak in ANPP sensitivity at sites that receive 475 to 500 mm MAP (Paruelo et al. 1999, Bai et al. 2008, Hu et al. 2010). Our results strengthen the evidence for this pattern, especially given that this study uses a different measure of ANPP sensitivity. Semi-arid sites with MAP between 300 mm and 600 mm such as mixed prairie or shortgrass steppe in the U.S. or typical steppe in Inner Mongolia have the highest sensitivities to precipitation mean. (Noy-Meir 1973, Schlesinger 1997, Austin et al. 2004, Yahdjian et al. 2006). At the driest sites, ANPP sensitivities may be low due to low relative growth rates, density limitations, and high evaporation rates (Noy-Meir 1973, Paruelo et al. 1999, Bai et al. 2008). At sites with more than 500 mm MAP, ANPP responses to precipitation may be constrained by nutrient or light limitation (Paruelo et al. 1999, Knapp and Smith 2001).

Although our analyses show that semi-arid sites are most sensitive to precipitation mean, we have little data for sites receiving over 1000 mm annual rainfall. Long-term ANPP data comes chiefly from grassland sites, due to the interest in predicting forage availability in these ecosystems and the difficulties associated with quantifying ANPP in ecosystems dominated by woody species (Gower et al. 1999, Clark et al. 2001). Because we have so few data sets from wet or forested sites, we cannot rule out the possibility that changes in precipitation regime could have stronger effects on ANPP at wet sites than our analysis suggests.

Conclusion

Climate change will alter both the mean and variance of interannual precipitation. This analysis quantifies the sensitivity of mean ANPP to these changes; how ANPP variability might respond is addressed in Chapter 4. Our analysis indicates that the impact of increases in interannual precipitation variability on ANPP will be very small; ANPP is about 40 times more sensitive to precipitation mean than to interannual variance in precipitation. Semi-arid ecosystems are the most sensitive to changes in mean precipitation. Our sensitivity analysis quantifies the likely magnitude of these changes, at least over short time scales before species composition shifts take place. Many semi-arid regions such as the southwest United States are projected to become even drier (NAST 2000), and resulting decreases in mean ANPP will have implications for the function and management of the ecosystems in these regions.

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TABLE 2-1. Summary of the sensitivity of ANPP mean to precipitation mean and variance.

Data sets	Reference	Years	Location	Study site	Biome	Mean annual precip. (mm)	Mean annual temp. (ºC)	Mean annual ANPP (g/m^2)	Sensitivity to mean	Sensitivity to variance
1	Andales et al. 2006	18	Cheyenne, Wyoming, United States	High Plains Grasslands Research Station	grassland	384	7.6	144	0.73	-0.0149
1	ORNL	31	Badkyz, Mary, Turkmenistan	Badkhzy Nature Reserve Station	grassland	266	14.8	61	0.94	-0.0576
1	Bai et al. 2001	12	Ewenke Qi, Inner Mongolia, China	Ewenke Grassland Management Station	grassland	330	-1.9	243	0.29	-0.0081
1	Bai et al. 2001	11	Xiwu Qi, Inner Mongolia, China	Xiwu Grassland Management Station	grassland	330	1.1	190	0.1	-4e-04
1	Bai et al. 2001	12	Damao Qi, Inner Mongolia, China	Damao Grassland Management Station	grassland	256	4.7	28	0.55	-0.0057
1	Bentley and Talbot 1951	13	Oneals, California, United States	San Joaquin Experimental Range	grassland	527	15.8	184	0.46	-0.0214
1	Blaisdell 1958	13	Dubois, Idaho, United States	USDA Sheep Station	shrubland	324	6	92	0.94	-0.0237
2	Bonanza Creek LTER	14	Fairbanks, Alaska, United States	Bonanza Creek LTER	forest	276	-1.4	212	0.02	-5e-04
4	Cedar Creek LTER	11	Bethel, Minnesota, United States	Cedar Creek Ecosystem Science Reserve	grassland	803	6.7	124	0.5	-0.0138
1	ORNL	34	Dzhanybek, West Kazakhstan, Kazakhstan	Dzhanybek Research Station	grassland	274	6.6	140	0.49	-0.0043
1	Wang et al. 1998, Guo et al. 2006	14	Haibei, Qinghai, China	study site near Haibei	alpine meadow	350	0.6	340	0.27	-0.0066
1	Guo et al. 2006	14	Zhenglan Qi, Inner Mongolia, China	Inner Mongolia study site	grassland	365	1.7	140	0.4	-0.0068
1	Hubbard Brook LTER	10	Grafton County, New Hampshire, United States	Hubbard Brook LTER	forest	1196	5.3	704	0.1	-0.0012
1	Hulett and Tomanek 1969	24	Hays, Kansas, United States	near Fort Hays Experiment Station	grassland	580	12	291	0.81	-0.0074
1	Jobbagy and Sala 2000	10	Rio Mayo, Chubut, Argentina	near Rio Mayo	shrubland	152	8.1	56	0.5	-0.0523
3	Jornada LTER	19	Las Cruces, New Mexico, United States	Jornada LTER	grassland	138	14.7	249	0.37	-0.0214

1	Kellogg Biological Station LTER	18	Hickory Corners, Michigan, United States	Kellogg Biological Station LTER	grassland	888	9	398	-0.05	6e-04
3	Konza Prairie LTER	27	Manhattan, Kansas, United States	Konza Prairie Biological Station	grassland	810	12.5	415	0.37	-0.0074
1	ORNL	30	Kursk, Kursk Oblast, Russia	Kursk long-term ecological study site	grassland	560	5.6	367	0.23	-0.0038
1	Ma et al. 2010	20	Xilinhot, Inner Mongolia,China	Inner Mongolia Grassland Ecosystem Research Station	grassland	342	0.6	208	0.18	-0.0025
1	ORNL	11	Texcoco, Mexico, Mexico	Colegio de Postgraduodos site	grassland	580	14.8	298	0.76	-0.0116
1	Murphy 1970	16	Hopland, California, United States	Hopland grassland Station	grassland	930	13.9	228	0.34	-0.0106
5	Niwot LTER	16	Boulder, Colorado, United States	Niwot Ridge LTER	alpine meadow	901	7.3	181	-0.18	0.0074
1	O'Connor et al. 2001	19	Bloemfontein, Free State, South Africa	Sydenham farm, Univ. of Orange Free State	grassland	560	15.6	125	1.71	-0.1425
2	Patton et al. 2007	21	Streeter, North Dakota, United States	Central Grasslands Research Extension Center	grassland	454	5	299	0.19	-0.0116
1	Rogler and Haas 1947	20	Mandan, North Dakota, United States	Northern Great Plains grassland Station	grassland	406	5.6	42	1.81	0.0000
1	Sevilleta LTER	10	Albuquerque, New Mexico, United States	Sevilleta LTER	shrubland	254	14.5	66	1.19	-0.0117
1	Sevilleta LTER	10	Albuquerque, New Mexico, United States	Sevilleta LTER	grassland	247	13.4	95	0.51	-0.0129
7	Shortgrass Steppe LTER	28	Nunn, Colorado, United States	Shortgrass Steppe LTER	grassland	332	9.5	79	1.14	-0.0419
1	Smoliak 1986	50	Manyberries, Alberta, Canada	Agriculture Canada Research Substation	grassland	327	4.7	39	0.81	-6e-04
1	Towne and Owensby 1984	42	Manhattan, Kansas, United States	Kansas Flint Hills	grassland	828	12.9	327	0.68	-0.0276
1	ORNL	41	Bela-Bela, Limpopo, South Africa	Towoomba Research Station	grassland	645	18.7	132	1.14	-0.0302
3	Knapp et al. 2006	22	Pietermaritzburg, KwaZulu-Natal, South Africa	Ukulinga Research Farm	grassland	838	18.6	396	0.71	-0.0100

1	ORNL	10	Tumugi, Inner Mongolia, China	Inner Mongolia study site	grassland	411	4.3	152	1.28	-0.0023
1	ORNL	10	Tumugi, Inner Mongolia, China	Inner Mongolia study site	grassland	411	4.3	162	1.22	-0.0025
1	ORNL	10	Tumugi, Inner Mongolia, China	Inner Mongolia study site	grassland	411	4.3	152	1.25	-0.0026
1	Xiao1995b	10	Xilinhot,Inner Mongolia, China	Inner Mongolia study site	grassland	313	0	144	0.9	-0.0277

Table 2-2. Sensitivity of ANPP mean to precipitation mean and variance (detailed version).

Data set	Reference	Years	Location	Study site	Biome	Dominant species	Mean annual precip. (mm)	Mean annual temp. (ºC)	Precip. data	Mean of precip. time series	Std. dev. precip.	Precip. distribution	Mean ANPP (g/m^2)	Std. dev. ANPP	Linear model AICc wt.	Linear model slope	Linear model intercept	Linear model r^2	Nonlin. model parameter a	Nonlin. model parameter b	Nonlin. model r^2	Sensitivity to mean	Sensitivity to variance
Andales	Andales et al. 2006	18	Cheyenne, Wyoming, United States	High Plains Grasslands Research Station	grassland	unknown	384	7.6	April-Aug.	281	63.8	normal	144	53	0.54	0.38	38.5	0.2	241	25820	0.19	0.73	-0.01
Badkhzy	ORNL	31	Badkyz, Mary, Turkmenistan	Badkhzy Nature Reserve Station	grassland	Poa bulbosa	266	14.8	Jan.-May	236	68.78	normal	61	36	0.12	0.19	16.9	0.12	114	11286	0.23	0.94	-0.06
Bai1	Bai et al. 2001	12	Ewenke Qi, Inner Mongolia, China	Ewenke Grassland Management Station	grassland	Stipa baicalensis	330	-1.9	Jan.-Dec.	348	83.18	normal	243	53	0.42	0.2	174.8	0.09	307	20876	0.14	0.29	-0.01
Bai2	Bai et al. 2001	11	Xiwu Qi, Inner Mongolia, China	Xiwu Grassland Management Station	grassland	Stipa grandis	330	1.1	Jan.-Dec.	369	31.1	normal	190	33	0.5	0.03	177.9	0	214	8800	0	0.1	-4e-04
Bai4	Bai et al. 2001	12	Damao Qi, Inner Mongolia, China	Damao Grassland Management Station	grassland	Stipa klemenzii	256	4.7	Jan.-Dec.	255	40.4	normal	28	11	0.52	0.06	11.4	0.06	41	3262	0.05	0.55	-0.01
Bentley	Bentley and Talbot 1951	13	Oneals, California, United States	San Joaquin Experimental Range	grassland	Hordeum marinum	527	15.8	Sept.-Aug.	495	154.89	lognormal	184	39	0.4	0.14	113.3	0.32	265	36689	0.36	0.46	-0.02
Blaisdell	Blaisdell 1958	13	Dubois, Idaho, United States	USDA Sheep Station	shrubland	Artemisia tripartita, Pseudoroegneria spicata	324	6	July-June	283	52.46	lognormal	92	19	0.13	0.26	17.8	0.55	176	22920	0.66	0.94	-0.02
BNZ FP4	Bonanza Creek LTER	15	Fairbanks, Alaska, United States	Bonanza Creek LTER	forest	Picea glauca	276	-2.5	April-Aug.	204	48.26	lognormal	239	46	0.49	-0.02	243.3	0	251	2383	0	0.02	0
BNZ UP3	Bonanza Creek LTER	13	Fairbanks, Alaska, United States	Bonanza Creek LTER	forest	Picea glauca	276	-0.3	April-Aug.	210	47.01	lognormal	185	59	0.5	0.04	175.5	0	183	-419	0	0.02	2e-04
CC 1927	Cedar Creek LTER	11	Bethel, Minnesota, United States	Cedar Creek Ecosystem Science Reserve	grassland	Poa pratensis	803	6.7	Jan.-Dec.	842	198.55	lognormal	116	33	0.47	0.05	72.1	0.1	165	38969	0.12	0.42	-0.01
CC 1941	Cedar Creek LTER	11	Bethel, Minnesota, United States	Cedar Creek Ecosystem Science Reserve	grassland	Poa pratensis	803	6.7	Jan.-Dec.	842	198.55	lognormal	143	47	0.4	0.11	53.1	0.2	246	82139	0.25	0.72	-0.02
CC 1943	Cedar Creek LTER	11	Bethel, Minnesota, United States	Cedar Creek Ecosystem Science Reserve	grassland	Poa pratensis	803	6.7	Jan.-Dec.	842	198.55	lognormal	111	36	0.5	0.05	70.5	0.07	151	32292	0.07	0.38	-0.01
CC 1947	Cedar Creek LTER	11	Bethel, Minnesota, United States	Cedar Creek Ecosystem Science Reserve	grassland	Poa pratensis	803	6.7	Jan.-Dec.	842	198.55	lognormal	127	32	0.43	0.06	73.8	0.16	188	48755	0.2	0.48	-0.01
Dzhanybek	ORNL	34	Dzhanybek, West Kazakhstan, Kazakhstan	Dzhanybek Research Station	grassland	Agropyron desertorum	274	6.6	Jan.-May	104	36.42	normal	140	36	0.88	0.68	69.4	0.47	189	4372	0.4	0.49	0
Guo4	Guo et al. 2006	14	Zhenglan Qi, Inner Mongolia, China	Inner Mongolia study site	grassland	Stipa krylovii	365	1.7	Jan.-Dec.	375	77.69	lognormal	140	51	0.51	0.15	85	0.05	193	18988	0.04	0.4	-0.01
HB	Hubbard Brook LTER	10	Grafton County, New Hampshire, United States	Hubbard Brook LTER	forest	unknown	1196	5.3	Jan.-Dec.	1413	227.78	lognormal	704	24	0.46	0.05	640.4	0.18	777	99924	0.21	0.1	0
Hulett	Hulett and Tomanek 1969	24	Hays, Kansas, United States	near Fort Hays Experiment Station	grassland	Bouteloua gracilis, Buchloe dactyloides	580	12	Jan.-Dec.	606	171.31	normal	291	118	0.82	0.41	43.5	0.35	454	90291	0.26	0.81	-0.01
Jobbagy	Jobbagy and Sala 2000	10	Rio Mayo, Chubut, Argentina	near Rio Mayo	shrubland	Senecio filaginoides, Stipa speciosa, Poa ligularis, Adesmia campestris	152	8.1	Jan.-Dec.	154	61.65	normal	56	15	0.03	0.14	34.4	0.35	79	2974	0.68	0.5	-0.05
JOR BASN	Jornada LTER	19	Las Cruces, New Mexico, United States	Jornada LTER	grassland	Bouteloua eriopoda	138	14.7	Jan.-Dec.	138	64.98	lognormal	242	75	0.44	0.55	166	0.23	339	11311	0.25	0.44	-0.04

Data set	Reference	Years	Location	Study site	Biome	Dominant species	Mean annual precip. (mm)	Mean annual temp. (ºC)	Precip. data	Mean of precip. time series	Std. dev. precip.	Precip. distribution	Mean ANPP (g/m^2)	Std. dev. ANPP	Linear model AICc wt.	Linear model slope	Linear model intercept	Linear model r^2	Nonlin. model parameter a	Nonlin. model parameter b	Nonlin. model r^2	Sensitivity to mean	Sensitivity to variance
JOR IBPE	Jornada LTER	19	Las Cruces, New Mexico, United States	Jornada LTER	grassland	Bouteloua eriopoda	106	14.7	Jan.-Dec.	106	57.4	lognormal	242	92	0.82	0.83	153.5	0.27	293	3878	0.14	0.36	-0.01
JOR SUMM	Jornada LTER	19	Las Cruces, New Mexico, United States	Jornada LTER	grassland	Bouteloua eriopoda	146	14.7	Jan.-Dec.	146	113.72	lognormal	263	87	0.83	0.48	193.8	0.39	331	5882	0.28	0.3	-0.02
Kellogg	Kellogg Biological Station LTER	18	Hickory Corners, Michigan, United States	Kellogg Biological Station LTER	grassland	Setaria faberi	888	9	Jan.-Dec.	859	143.86	lognormal	398	78	0.5	-0.02	417.2	0	380	-15829	0	-0.05	6e-04
KNZ 001d	Konza Prairie LTER	34	Manhattan, Kansas, United States	Konza Prairie Biological Station	grassland	unknown	810	12.5	Jan.-Dec.	812	188.44	lognormal	457	92	0.68	0.29	218	0.36	681	172661	0.33	0.53	-0.01
KNZ 004b	Konza Prairie LTER	24	Manhattan, Kansas, United States	Konza Prairie Biological Station	grassland	unknown	810	12.5	Jan.-Dec.	795	186.55	lognormal	400	89	0.43	0.17	268.1	0.12	536	102149	0.14	0.36	-0.01
KNZ 020b	Konza Prairie LTER	24	Manhattan, Kansas, United States	Konza Prairie Biological Station	grassland	unknown	810	12.5	Jan.-Dec.	795	186.55	lognormal	389	70	0.59	0.11	301.8	0.08	455	50331	0.06	0.21	0
Kursk	ORNL	30	Kursk, Kursk Oblast, Russia	Kursk long-term ecological study site	grassland	Bromus riparius	560	5.6	April-Oct.	390	91.63	normal	367	124	0.56	0.26	267	0.04	428	22281	0.02	0.23	0
Ma 2010	Ma et al. 2010	20	Xilinhot, Inner Mongolia,China	Inner Mongolia Grassland Ecosystem Research Station	grassland	Leymus chinensis, Stipa grandis	342	0.6	Jan.-Dec.	344	67.47	lognormal	208	36	0.53	0.1	172.3	0.04	243	11634	0.03	0.18	0
Montecillo	ORNL	11	Texcoco, Mexico, Mexico	Colegio de Postgraduodos site	grassland	Distichlis spicata	580	14.8	April-July	312	59.3	lognormal	298	79	0.5	0.69	82.8	0.27	522	67604	0.27	0.76	-0.01
Murphy	Murphy 1970	16	Hopland, California, United States	Hopland grassland Station	grassland	Bromus, Festuca, Avena, Hordeum spp.	930	13.9	Nov.-May	901	256.6	lognormal	228	77	0.51	0.08	157.8	0.07	305	64754	0.06	0.34	-0.01
NiwotDM	Niwot LTER	16	Boulder, Colorado, United States	Niwot Ridge LTER	alpine meadow	unknown	901	7.3	Jan.-Dec.	825	237.17	lognormal	202	44	0.37	-0.1	285	0.29	101	-77151	0.34	-0.51	0.02
NiwotFF	Niwot LTER	15	Boulder, Colorado, United States	Niwot Ridge LTER	alpine meadow	unknown	901	7.3	Jan.-Dec.	800	221.59	lognormal	220	68	0.45	-0.13	325.4	0.19	92	-96264	0.21	-0.57	0.02
NiwotMM	Niwot LTER	16	Boulder, Colorado, United States	Niwot Ridge LTER	alpine meadow	unknown	901	7.3	Jan.-Dec.	825	237.17	lognormal	209	26	0.43	-0.06	255.3	0.26	155	-41747	0.28	-0.26	0.01
NiwotSB	Niwot LTER	15	Boulder, Colorado, United States	Niwot Ridge LTER	alpine meadow	unknown	901	7.3	Jan.-Dec.	800	221.59	lognormal	105	25	0.51	0.02	88.7	0.03	123	13256	0.03	0.17	-0.01
NiwotWM	Niwot LTER	16	Boulder, Colorado, United States	Niwot Ridge LTER	alpine meadow	unknown	901	7.3	Jan.-Dec.	825	237.17	lognormal	170	35	0.5	0.05	131.8	0.1	213	33206	0.1	0.26	-0.01
O'Connor	O'Connor et al. 2001	19	Bloemfontein, Free State, South Africa	Sydenham farm, Univ. of Orange Free State	grassland	Themeda triandra, Cymbopogon plurinodes	560	15.6	Jan.-Dec.	533	193.83	lognormal	125	74	0.08	0.28	-21.5	0.52	305	85694	0.63	1.71	-0.14
Patton overflow	Patton et al. 2007	21	Streeter, North Dakota, United States	Central Grasslands Research Extension Center	grassland	Poa pratensis, Bromus inermis, Symphoricarpos occidentalis	454	5	Nov.-Oct.	416	138.42	normal	314	45	0.4	0.05	291.1	0.03	339	9161	0.07	0.09	0
Patton silty	Patton et al. 2007	21	Streeter, North Dakota, United States	Central Grasslands Research Extension Center	grassland	Poa pratensis, Nassella viridula, Carex inops spp. heliophila	454	5	Nov.-Oct.	415	138.49	normal	283	57	0.25	0.21	195.4	0.26	356	26537	0.33	0.3	-0.02
Rogler Haas	Rogler and Haas 1947	20	Mandan, North Dakota, United States	Northern Great Plains grassland Station	grassland	Bouteloua gracilis, Hesperostipa comata	406	5.6	April-July	223	80.89	normal	42	36	1	0.33	-32.8	0.57	52	1580	0.15	1.81	0

Data set	Reference	Years	Location	Study site	Biome	Dominant species	Mean annual precip. (mm)	Mean annual temp. (ºC)	Precip. data	Mean of precip. time series	Std. dev. precip.	Precip. distribution	Mean ANPP (g/m^2)	Std. dev. ANPP	Linear model AICc wt.	Linear model slope	Linear model intercept	Linear model r^2	Nonlin. model parameter a	Nonlin. model parameter b	Nonlin. model r^2	Sensitivity to mean	Sensitivity to variance
SEV creosote	Sevilleta LTER	10	Albuquerque, New Mexico, United States	Sevilleta LTER	shrubland	Larrea tridentata	254	14.5	Jan.-Dec.	254	58.7	normal	66	21	0.76	0.32	-15.3	0.83	129	15201	0.79	1.19	-0.01
SEV grass	Sevilleta LTER	10	Albuquerque, New Mexico, United States	Sevilleta LTER	grassland	Bouteloua eriopoda	247	13.4	Jan.-Dec.	238	49.34	normal	95	67	0.45	0.15	59.3	0.01	150	12421	0.05	0.51	-0.01
SGS ESA1	Shortgrass Steppe LTER	38	Nunn, Colorado, United States	Shortgrass Steppe LTER	grassland	Bouteloua gracilis	332	9.5	Jan.-Dec.	338	82.56	lognormal	88	34	0.58	0.2	23	0.21	159	22259	0.19	0.79	-0.02
SGS forage	Shortgrass Steppe LTER	52	Nunn, Colorado, United States	Shortgrass Steppe LTER	grassland	Bouteloua gracilis	332	9.5	Jan.-Dec.	323	92.72	normal	68	26	0.98	0.17	13.1	0.39	100	9065	0.29	0.8	-6e-04
SGS midslope	Shortgrass Steppe LTER	25	Nunn, Colorado, United States	Shortgrass Steppe LTER	grassland	Bouteloua gracilis	332	9.5	Jan.-Dec.	345	84.43	lognormal	65	23	0.34	0.21	-8.6	0.6	136	23180	0.62	1.19	-0.04
SGS OC	Shortgrass Steppe LTER	17	Nunn, Colorado, United States	Shortgrass Steppe LTER	grassland	Bouteloua gracilis	332	9.5	Jan.-Dec.	347	97.08	lognormal	108	44	0.25	0.26	17.9	0.34	205	30971	0.42	0.97	-0.05
SGS ridge	Shortgrass Steppe LTER	25	Nunn, Colorado, United States	Shortgrass Steppe LTER	grassland	Bouteloua gracilis	332	9.5	Jan.-Dec.	345	84.43	lognormal	58	21	0.16	0.19	-7.3	0.55	123	21293	0.61	1.23	-0.05
SGS sec25	Shortgrass Steppe LTER	17	Nunn, Colorado, United States	Shortgrass Steppe LTER	grassland	Bouteloua gracilis	332	9.5	Jan.-Dec.	347	97.08	lognormal	62	29	0.27	0.25	-25.8	0.71	147	27505	0.74	1.54	-0.07
SGS swale	Shortgrass Steppe LTER	25	Nunn, Colorado, United States	Shortgrass Steppe LTER	grassland	Bouteloua gracilis	332	9.5	Jan.-Dec.	345	84.43	lognormal	103	47	0.22	0.4	-35.5	0.52	240	44803	0.57	1.46	-0.06
Smoliak 1986	Smoliak 1986	50	Manyberries, Alberta, Canada	Agriculture Canada Research Substation	grassland	Hesperostipa comata, Pascopyrum smithii	327	4.7	April-July	164	64.76	lognormal	39	17	0.99	0.19	7.3	0.55	72	4773	0.45	0.81	-6e-04
Towne	Towne and Owensby 1984	42	Manhattan, Kansas, United States	Kansas Flint Hills	grassland	Schizachyrium scoparium, Koeleria macrantha	828	12.9	Jan.-Dec.	831	191.55	lognormal	327	130	0.19	0.21	152.1	0.1	540	167818	0.16	0.68	-0.03
Towoomba	ORNL	41	Bela-Bela, Limpopo, South Africa	Towoomba Research Station	grassland	Cymbopogon pospischilii	645	18.7	Sept.-April	619	145.13	lognormal	132	73	0.47	0.24	-15.2	0.27	281	84484	0.27	1.14	-0.03
Ukulinga C3	Knapp et al. 2006	22	Pietermaritzburg, KwaZulu-Natal, South Africa	Ukulinga Research Farm	grassland	Themeda triandra, Heteropogon contortus	838	18.6	Sept.-March	546	102.47	lognormal	413	111	0.54	0.71	38.4	0.46	796	195357	0.05	0.92	-0.01
Ukulinga D1	Knapp et al. 2006	23	Pietermaritzburg, KwaZulu-Natal, South Africa	Ukulinga Research Farm	grassland	Themeda triandra, Heteropogon contortus	838	18.6	Sept.-March	532	117.4	normal	424	80	0.71	0.46	179	0.44	619	98024	0.34	0.55	-0.01
Ukulinga D3	Knapp et al. 2006	22	Pietermaritzburg, KwaZulu-Natal, South Africa	Ukulinga Research Farm	grassland	Themeda triandra, Heteropogon contortus	838	18.6	Sept.-March	546	102.47	lognormal	352	73	0.52	0.42	129.4	0.39	581	116782	-0.08	0.65	-0.01
Wang1998	Wang et al. 1998, Guo et al. 2006	14	Haibei, Qinghai, China	study site near Haibei	alpine meadow	Kobresia humilis	350	0.6	Jan.-Dec.	589	136.74	lognormal	340	54	0.46	0.13	263.2	0.11	435	53550	0.13	0.27	-0.01
Xiao FISI Tumugi	ORNL	10	Tumugi, Inner Mongolia, China	Inner Mongolia study site	grassland	Filifolium sibiricum	411	4.3	Jan.-Dec.	411	100.96	normal	152	55	0.94	0.49	-48.3	0.79	257	39388	0.64	1.28	0
Xiao LECH Tumugi	ORNL	10	Tumugi, Inner Mongolia, China	Inner Mongolia study site	grassland	Leymus chinensis	411	4.3	Jan.-Dec.	411	100.96	normal	162	56	0.93	0.49	-41.5	0.79	269	40332	0.64	1.22	0
Xiao STBA Tumugi	ORNL	10	Tumugi, Inner Mongolia, China	Inner Mongolia study site	grassland	Stipa baicalensis	411	4.3	Jan.-Dec.	411	100.96	normal	152	54	0.93	0.48	-43.9	0.79	256	38899	0.65	1.25	0
Xiao STGR Xilin	Xiao1995b	10	Xilinhot,Inner Mongolia, China	Inner Mongolia study site	grassland	Stipa grandis	313	0	Jan.-Dec.	314	73.79	normal	144	38	0.35	0.4	17.2	0.62	261	34982	0.67	0.9	-0.03

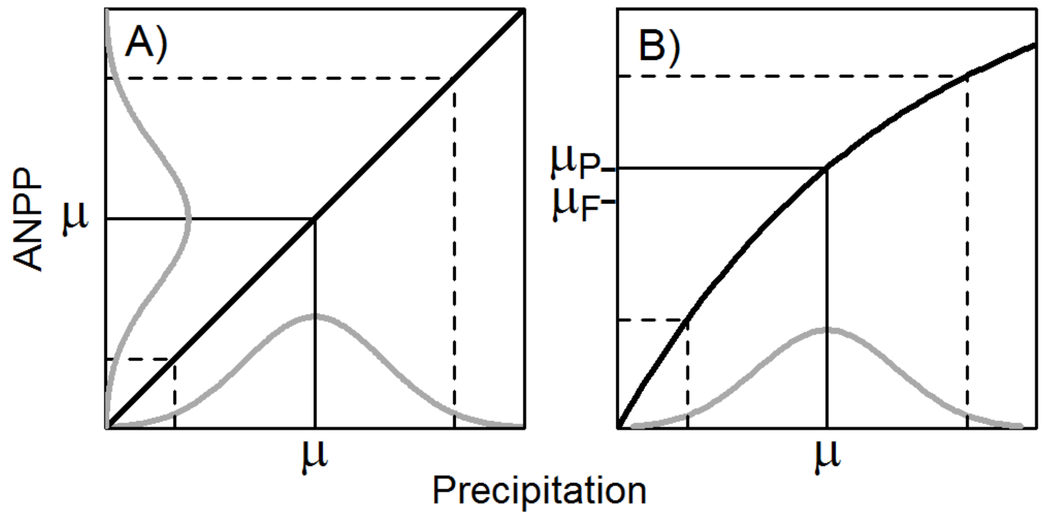

FIG. 2-1. An increase in precipitation variance will not affect mean ANPP if the relationship between precipitation and ANPP is linear (A). A concave down relationship (B) skews the distribution for decreasing values of ANPP, such that the future mean of ANPP (μ_F) will decrease relative to the present mean (μ_P).

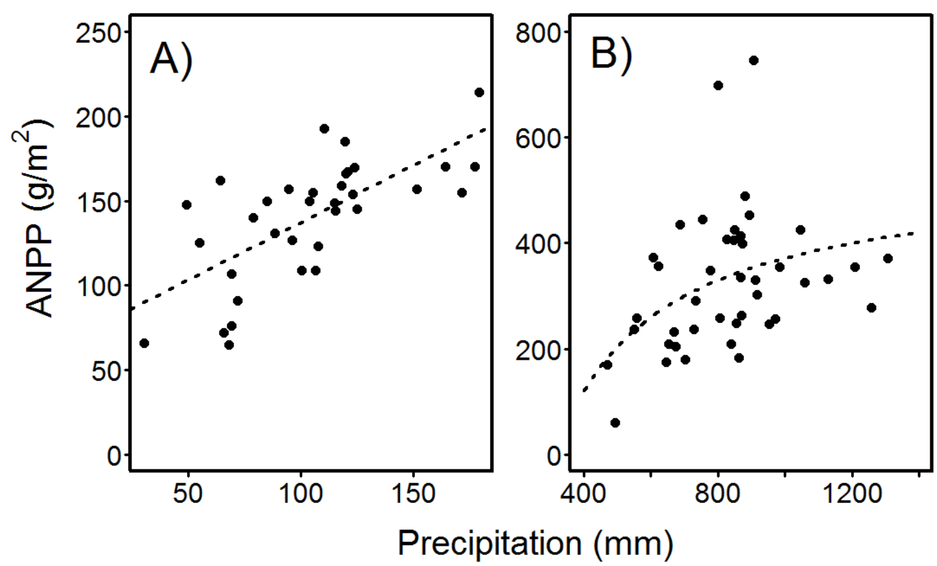

FIG. 2-2. Linear (A) and saturating (B) models fit to precipitation-ANPP relationships. Data shown is from semi-desert steppe in Dzhanybek, Kazakhstan (A) and tallgrass prairie in Manhattan, Kansas (B). The AICc weights for the linear model for the Dzhanybek and Manhattan data sets are 0.88 and 0.19, respectively.

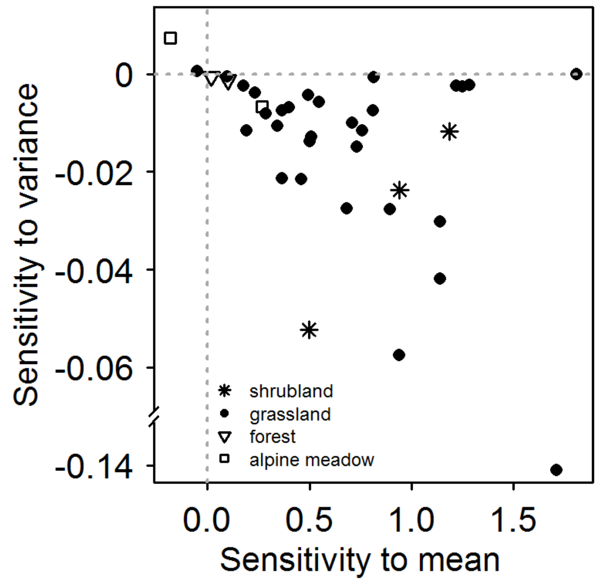

FIG. 2-3. Mean ANPP is more sensitive to precipitation mean than to precipitation variance. Most sites exhibit a positive sensitivity to precipitation mean and a negative sensitivity to precipitation variance. The long-term data shown here is from 37 different study sites.

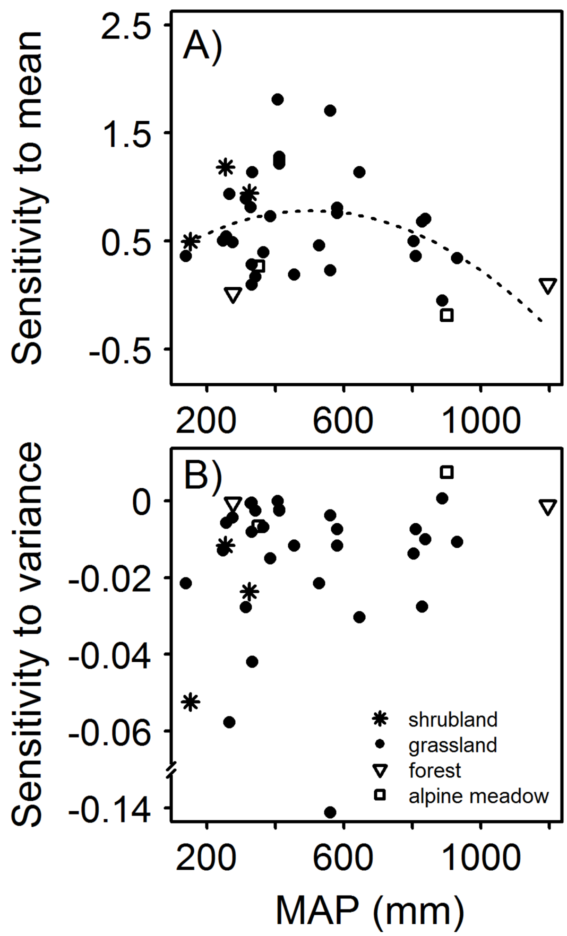

Fig. 2-4. ANPP sensitivity to precipitation mean is highest at sites that receive between 300 and 600 mm precipitation each year (A). The quadratic pattern shown in (A), $0.20 + 0.002(\mathrm{MAP}) - 2.26*10^{-6}(\mathrm{MAP})^2$, explains 16.5% of the variation in ANPP sensitivity to mean precipitation. Sensitivity to precipitation variance was not correlated with mean annual precipitation (B).

CHAPTER 3

ANTICIPATING CHANGES IN VARIABILITY OF GRASSLAND PRIMARY PRODUCTION DUE TO INCREASES IN INTERANNUAL PRECIPITATION VARIABILITY

Abstract. Increases in interannual precipitation variability will lead to increases in the variability of primary production, with potentially important consequences for natural resource management. However, previous work has suggested that vegetation might amplify or buffer precipitation variation, implying disproportionately large or small changes in production variability depending on how we model the production response to precipitation. I used 27 long-term data sets from grasslands across the globe to evaluate whether relative increases in the interannual variability of aboveground net primary production (ANPP) will be relatively less than, equal to, or greater than increases interannual precipitation variability. For each data set, I used three models to predict ANPP from precipitation: 1) a simple linear model, 2) a nonlinear model, and 3) a lag model, in which ANPP is a function of previous year production in addition to current year precipitation. I then perturbed the standard deviation of the observed precipitation time series and quantified the effect of this perturbation on the standard deviation of predicted ANPP. Using the simple linear model, relative increases in ANPP variability were always equal to the relative increases in precipitation variability. Under the lag effect model, an increase in precipitation variability also led to a proportional increase in ANPP variability, in spite of previous research suggesting that lag effects might buffer or amplify precipitation variability. When I modeled ANPP as a nonlinear, saturating function of precipitation, increases in ANPP variability were disproportionately high. In 6 out of 27 cases, increases in variability were twice as large as increases in precipitation variability. After using AICc model weights to account for which ANPP models best fit each site's precipitation and production data, a 5% increase in precipitation variability led to a 6.3% increase in ANPP variability on average.

INTRODUCTION

General circulation models (GCMs) consistently predict that climate change is bringing increasing levels of precipitation variability at a variety of time scales (Räisänen 2002, Salinger 2005, Sun et al. 2007, Allan and Soden 2008). One projected change in variability is an increase in the standard deviation and variance of annual precipitation (Räisänen 2002, Boer 2009, Wetherald 2009). GCMs vary in their predictions of how much interannual precipitation variability is changing (Räisänen 2002, Boer 2009). In one study across 19 GCMs, predictions on the high end are over 10%, but on average, the predicted increase in the standard deviation of annual precipitation for a doubling of CO_2 concentrations was 4.2% (Räisänen 2002).

This change in rainfall distribution could impact ecosystem processes, including primary productivity (Weltzin et al. 2003, Heisler and Weltzin 2006, Knapp et al. 2008). Since interannual variability in production depends on interannual variability in precipitation in water-limited ecosystems, an increase in precipitation variability will lead to an increase in primary production variability. However, depending on how vegetation responds to increased variability in precipitation, increases in production variability could be disproportionately high or low relative to increases in precipitation variability.

Given a simple, linear relationship between precipitation and aboveground net primary production (ANPP), the absolute increase in ANPP variability due to an increase in precipitation variability will depend on the slope of the precipitation-ANPP relationship. However, the relative increase in ANPP variability will always match the relative increase in precipitation variability: a 1% increase in precipitation variability will lead to a 1% increase in the portion of ANPP variability that is explained by precipitation variability. If the precipitation-ANPP relationship is more complex, then the increase in ANPP variability is harder to predict. In this chapter, I examine two ways in which increases in interannual precipitation variability could lead to disproportionately large or small changes in interannual ANPP variability.

First, I consider the influence of lag effects: current year production might reflect previous year production in addition to current year precipitation (e.g. Oesterheld et al. 2001, Wiegand et al. 2004, Yahdjian and Sala 2006, Arnone et al. 2008, Sherry et al. 2008). Such lagged responses to precipitation could occur when ecosystems store the effects of previous years in soils, seed banks, and structural organs. For example, ANPP may not be lower than expected given current-year rainfall if drought the previous year reduced plant densities (Yahdjian and Sala 2006).

Previous authors (Oesterheld et al. 2001, Wiegand et al. 2004) have suggested that lag effects can amplify or dampen precipitation variability depending on the sequence of precipitation years (Fig. 2 in Oesterheld et al. 2001). Positive lag effects can amplify ANPP variability if consecutive wet or dry years ratchet production up or down up. In contrast, lag effects would dampen precipitation variability if wet and dry years alternate (negative autocorrelation in precipitation), "evening out" the differences in production. These studies seem to imply that lag effects might amplify or buffer future increases in precipitation variability, depending on precipitation autocorrelation.

However, Oesterheld et al. (2001) and Wiegand et al. (2004) did not explicitly address the consequences of an increase in precipitation variability. While lag effects might generate more variability in ANPP for a given precipitation time series compared to a linear model, it is not clear whether the same logic applies to a perturbation in the variability of precipitation.

Second, I consider the possibility that the relationship between precipitation and ANPP is nonlinear, concave down. Nonlinear, concave-down relationships may characterize ecosystems (Nicholson and Farrar 1994) where resources other than water limit production in wet years more than in dry years. Chapter 1 showed that relationships between precipitation and ANPP often take this form. If the relationship between precipitation and ANPP is concave down at a site, then an increase in precipitation variability will lead to a disproportionately large increase in ANPP variability. Large decreases in ANPP in dry years drive ANPP variability higher, and this effect outweighs the buffering of variability (relative to a linear model) that occurs in wet years.

In this study, I use 27 long-term data sets of precipitation and primary production from grasslands to evaluate whether increases in precipitation variability are likely to cause disproportionately high or low changes in ANPP variability. I fit linear, nonlinear, and lag regression models to predict ANPP from precipitation. For each of these ANPP models, I quantify the effect of a perturbation of precipitation variability on ANPP variability.

METHODS

Data sets

I collected 37 long-term time series of annual precipitation and ANPP from grassland sites. For sites where growing season precipitation was available and accounted for more variation in ANPP than total annual precipitation, I used growing season precipitation in my analyses. All time series contained at least 11 consecutive years. Most of the data sets are from long-term ecological research sites in the United States, Eurasia, and South Africa. Remotely sensed data and data from fertilized plots were excluded. For more details about data collection, please see Chapter 1. All analyses were conducted in R version 2.8.1.

ANPP models

Using least squares regression, I fit three models to each data set to predict ANPP in year y: linear ($ANPP_y = k + m * precipitation_y$), lag effect ($ANPP_y = d + f * precipitation + g * ANPP_{y-1}$), and nonlinear ($ANPP_y = a - b / precipitation_y$). In the lag model, the lag parameter g controls how much ANPP is influenced by previous-year conditions. The nonlinear model is a concave down, saturating function when a and b are positive. This nonlinear function is parsimonious, linear in its parameters (so that unique least squares parameter estimates are guaranteed to exist), and fit the data better than other saturating models that I tested. Fig. 3-1 shows the linear, lag, and nonlinear models fit to a data set.

Next, I used F-tests to determine whether any of these precipitation-based models predicted interannual variation in ANPP better than a simple mean. For 10 data sets, a precipitation model did not fit the data significantly better ($p>0.05$) than a model with only a mean. These 10 data sets were excluded from subsequent analyses. For the remaining 27 data sets from 18 different study sites, I used Akaike's Information Criterion (AICc) weights to compare linear, nonlinear, and lag model fits. The average length of these data sets was 22 years.

Perturbation of precipitation variability

I used the fitted model parameters and the observed precipitation time series to generate predictions of ANPP for each data set based on the linear, lag, and nonlinear models. Variability in these "predicted" ANPP time series reflects variability in precipitation and not any other sources of variability. Thus, my analysis focuses only on the portion of ANPP variability deterministically related to precipitation. This approach assumes that the unexplained variation in ANPP (the model residuals) is not sensitive to precipitation variability, an assumption I return to in the Discussion.

To directly examine changes in ANPP variability due to increases in precipitation variability, I perturbed the interannual variation of the observed precipitation time series and quantified the effect of this perturbation on predicted ANPP variation. I increased the standard deviation of each precipitation time series by 5% without changing precipitation mean (Fig. 3-2A). This approach preserves the observed sequence and distribution of precipitation. I then used these perturbed precipitation time series to generate a second set of predicted ANPP values for each of the models (Fig. 3-2). Again, these predicted ANPP time series reflect only precipitation variability .

I compared absolute and relative variability between the two sets of predicted ANPP time series (e.g. linear ANPP predictions based on observed precipitation were compared with linear ANPP predictions based on perturbed precipitation). I calculated absolute changes in ANPP variability as the difference in ANPP standard deviation. I divided these differences in standard deviation by the standard deviation of the unperturbed time series to yield relative changes in ANPP variability. Finally, I compared relative changes in ANPP variability with the change in precipitation variability (5%) to determine whether changes in ANPP variability were proportional to changes in precipitation variability.

To obtain the final result for each data set, I calculated a weighted average of the relative changes in ANPP standard deviation using AICc weights from the model fitting. In cases where multiple data sets of the same vegetation type were available from the same study, I averaged across data sets to obtain mean changes in ANPP variability for that site.

Results

Linear and nonlinear precipitation models each explained an average of 35% of the interannual variability in ANPP. A lag model did slightly better, explaining 43% of the variability in ANPP, on average. Of the 27 data sets, 9 best fit a linear model, 3 best fit a lag model, and 15 best fit a nonlinear model. The average AICc weight for the linear, lag, and nonlinear models were 0.36, 0.21, and 0.42, respectively. Within the data sets that best fit each model, the average AICc weights for the best fit model were 0.60, 0.91, and 0.62 for the linear, lag, and nonlinear models, respectively. Across data sets, there were no patterns between mean annual precipitation or temperature and AICc weights for any of the models.

In the lag model, estimates for the lag parameter ranged from -0.5 to 0.54 across data sets, but were statistically significant (p<.05) at only the following 4 sites: Shortgrass Steppe LTER; Bloemfontein, South Africa; Kursk, Russia; and Alberta, Canada. All of these data sets except for Bloemfontein best fit a lag model over a linear or nonlinear model; estimates for the lag parameter within these data sets ranged from 0.42 to 0.46. On average, adding a lag parameter to a linear precipitation-ANPP model explained an additional 7.5% of the variability in ANPP across all data sets, but explained an additional 17.4% of the variability in ANPP in these four data sets.

A 5% increase in precipitation standard deviation led to an absolute increase of 1.49, 1.48, and 2.66 g/m^2 in the standard deviation of ANPP across the linear, lag, and nonlinear models, respectively. As expected, a 5% increase in precipitation standard deviation always led to a 5% increase in ANPP standard deviation when ANPP was modeled as a linear function of precipitation. The relative increase in ANPP standard deviation for the lag model was also always very close to 5% (ranging from 4.91% to 5.01%), meaning that the lag model did not cause a disproportionate increase in ANPP for any of the data sets (Fig. 3-2C).

The relative increase in ANPP standard deviation for the nonlinear model across data sets ranged from 4.9% to 20%, averaging 8.6%. Within the data sets that best fit a nonlinear model, the relative increases averaged 7.3%. A nonlinear, concave down precipitation-ANPP model produces an ANPP distribution that is left-skewed compared to the distribution of precipitation (Fig. 3-2D). As a result, ANPP variances predicted by this model, as well as changes in ANPP variance due to perturbations, are not symmetric about the mean of ANPP. On average, a 5% increase in precipitation standard deviation caused an 8.6% increase in ANPP standard deviation, which was comprised of a 2.7% increase in variability in years where precipitation was below mean and an 11.3% increase in years precipitation was above mean. In one data set, the relative increase in ANPP standard deviation (4.9%) was less than the increase in precipitation standard deviation (5%).

Note that these estimates for increases in variability under a nonlinear model are a little high because the nonlinear model generates negative ANPP predictions for one very dry year in each of three data sets, which leads to artificially high standard deviations, especially in the perturbed time series. Removing these three data sets from my analysis does not change the overall conclusions.

After accounting for AICc model weights and averaging across multiple data sets from the same study site, relative increases in ANPP standard deviation ranged from 5.0% to 10.7%, averaging 6.3% across 18 different study sites (Fig. 3-3). The extent to which nonlinearity amplifies precipitation variability depends on the size of the perturbation. Perturbations of 1%, 2%, 5%, and 10% led to median relative increases in ANPP variability of 1.2%., 2.4%, 6.0%, and 12.5%, respectively (Table 3-1). See Appendix C for a complete list of the fitted model parameters and the results from the 5% perturbation trial for each data set. Appendix D shows that direct comparisons of the relative variability in observed precipitation and ANPP time series should account for the fact that ANPP is a function of precipitation.

Discussion

My results indicate that different assumptions about the functional relationship between precipitation and production have different implications for the impact of climate change on the interannual variability of annual ANPP in grasslands. If ANPP has a linear or lagged response to precipitation, an increase in precipitation variability is simply matched by a proportional increase in ANPP variability. However, if ANPP is a nonlinear, saturating function of precipitation, an increase in precipitation variability will lead to a change in ANPP variability that is disproportionately high.

Lag effects did not cause disproportionate changes in predicted ANPP variability because a lag model maintains the linear relationship between precipitation and ANPP. The amplification of precipitation variability reported by Oesterheld et al. (2001) and Wiegand et al. (2004) occurs when comparing variance explained by two different regression models for a given precipitation sequence, not when evaluating the effect of increased precipitation variability. My perturbation of precipitation variability preserved the sequence of precipitation, so it did not lead to a disproportionate change in ANPP variability via lag effects. However, if climate change alters precipitation autocorrelation, then we could see disproportionate responses in ANPP variability due to lag effects.

In addition, the evidence for lag effects in grasslands was weak. ANPP at most sites did not exhibit a lagged response to precipitation. Only 4 sites had significant lag effects, and the average extra variability explained by a lag model over a linear model was only 7.5%. Very strong lag effects such as those observed at the shortgrass steppe (Oesterheld et al. 2001) are not common. However, lag effects may still operate on time scales that my data sets do not capture; many studies report intra-annual lag effects in production (e.g. Nicholson and Farrar 1994, Wiegand et al. 2004, Nippert et al. 2006, Sherry et al. 2008, Ma et al. 2010).

Where ANPP is a nonlinear, concave down function of precipitation, increases in precipitation variability will lead to disproportionately high increases in predicted ANPP variability (Figs. 3-2D, 3-3). In fact, most sites exhibit precipitation-ANPP relationships that are somewhat nonlinear. Even when nonlinearities in ANPP are not very strong (Chapter 2), they result in considerable amplification of precipitation variability. On average, relative increases in predicted ANPP variability were over 1.5 times larger than increases in precipitation variability when ANPP was modeled as a nonlinear function of precipitation.

The disproportionately high increase in ANPP variability is caused by the asymmetric change in ANPP variability in wet and dry years. Increases in precipitation variability lead to disproportionately large decreases in ANPP in dry years, where the slope of the precipitation-ANPP relationship is steep. However, in wet years, increases in precipitation variability lead to disproportionately small increases in ANPP due to shallow precipitation-ANPP slopes. The overall change in ANPP variability, then, depends on the distribution of precipitation. Since a nonlinear model produces a distribution of ANPP that is skewed towards dry years (Fig. 3D), the overall change in ANPP variability is usually disproportionately high. In only 1 of my 27 data sets was the observed precipitation distribution skewed strongly enough towards wet years such that the buffering effect of wet years slightly outweighed the amplifying effect of dry years. In most cases, an increase in interannual precipitation variability will lead to relative increases in primary production in wet years that are smaller than decreases in production in dry years.

The average predicted increase in the interannual variability of precipitation is 4.2% (Räisänen 2002) for a doubling of CO_2 concentrations. According to my analysis, a 5% increase in precipitation variability will lead to a 6.3% increase in grassland ANPP variability, on average. At some sites, increases will be much larger: 10.5% in mixed prairie in North Dakota and 7.5% in desert grasslands in New Mexico. These considerable increases in ANPP variability make ANPP more difficult to forecast and could create other challenges for natural resource management.

My analysis utilized only the portion of ANPP variability related to precipitation and assumed that remaining variation in ANPP is not sensitive to interannual precipitation variability. However, other drivers of ANPP may be indirectly influenced by precipitation and precipitation variability. For example, nitrogen availability, especially in arid and semi-arid regions, is strongly controlled by water availability (Noy-Meir 1973, Schlesinger 1997, Austin et al. 2004, Yahdjian et al. 2006). Increases in precipitation variability could lead to changes in the duration and timing of nitrogen mineralization and plant uptake, which would impact ANPP variability. Within the data sets used in this study, which represent grasslands where precipitation influences ANPP, an average of 35% of the variability in ANPP is directly explained by precipitation, but the percentage of ANPP that is indirectly affected by precipitation could actually be higher.

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TABLE 3-1. Relative increases in the standard deviation of annual ANPP with 1%, 2%, 5%, and 10% increases in the standard deviation of annual precipitation.

Data sets	Reference	Years	Location	Study site	Ecosystem	Mean annual precip. (mm)	Mean annual ANPP (g/m^2)	Std. dev. precip.	Std. dev. ANPP	1%	2%	5%	10%
1	Andales et al. 2006	18	Cheyenne, Wyoming, United States	High Plains Grasslands Research Station	mixed prairie	384	144	64	53	1.06	2.12	5.33	10.71
1	ORNL	31	Badkyz, Mary, Turkmenistan	Badkhzy Nature Reserve Station	desert steppe	266	61	69	36	1.37	2.75	6.99	14.41
1	Bai et al. 2001	12	Ewenke Qi, Inner Mongolia, China	Ewenke Grassland Management Station	meadow steppe	330	243	83	53	1.36	2.74	6.96	14.34
1	Bentley and Talbot 1951	13	Oneals, California, United States	San Joaquin Experimental Range	annual grassland	527	184	155	39	1.1	2.21	5.56	11.24
4	Cedar Creek LTER	11	Bethel, Minnesota, United States	Cedar Creek Ecosystem Science Reserve	old field	803	124	199	37	1.07	2.14	5.36	10.78
1	ORNL	34	Dzhanybek, West Kazakhstan, Kazakhstan	Dzhanybek Research Station	semi-arid steppe	274	140	36	36	1.16	2.34	5.93	12.26
1	Hulett and Tomanek 1969	24	Hays, Kansas, United States	near Fort Hays Experiment Station	mixed prairie	580	291	171	118	1.21	2.43	6.16	12.69
3	Jornada LTER	19	Las Cruces, New Mexico, United States	Jornada LTER	desert grassland	138	249	78	85	1.42	2.88	7.48	16.22
3	Konza Prairie LTER	27	Manhattan, Kansas, United States	Konza Prairie Biological Station	tallgrass prairie	810	415	187	84	1.11	2.23	5.6	11.31
1	ORNL	30	Kursk, Kursk Oblast, Russia	Kursk long-term ecological study site	meadow steppe	560	367	92	124	1.29	2.6	6.6	13.58
1	Ma et al. 2010	20	Xilinhot, Inner Mongolia,China	Inner Mongolia Grassland Ecosystem Research Station	typical steppe	342	208	67	36	0.99	1.98	4.95	9.92
1	O'Connor et al. 2001	19	Bloemfontein, Free State, South Africa	Sydenham farm, Univ. of Orange Free State	Semi-arid grassland	560	125	194	74	1.27	2.55	6.48	13.31
2	Patton et al. 2007	21	Streeter, North Dakota, United States	Central Grasslands Research Extension Center	old field	454	299	138	52	2.03	4.11	10.74	23.24
1	Rogler and Haas 1946	20	Mandan, North Dakota, United States	Northern Great Plains grassland Station	mixed prairie	406	42	81	36	1.15	2.3	5.81	11.78

Data sets	Reference	Years	Location	Study site	Ecosystem	Mean annual precip. (mm)	Mean annual ANPP (g/m^2)	Std. dev. precip.	Std. dev. ANPP	1%	2%	5%	10%
7	Shortgrass Steppe LTER	28	Nunn, Colorado, United States	Shortgrass Steppe LTER	shortgrass steppe	332	79	89	32	1.25	2.51	6.38	13.09
1	Smoliak 1986	50	Manyberries, Alberta, Canada	Agriculture Canada Research Substation	mixed prairie	327	39	65	17	1.11	2.22	5.59	11.36
1	Towne and Owensby 1984	42	Manhattan, Kansas, United States	Kansas Flint Hills	tallgrass prairie	828	327	192	130	1.22	2.46	6.2	12.64
1	ORNL	41	Bela-Bela, Limpopo, South Africa	Towoomba Research Station	mesic grassland	645	132	145	73	1.15	2.3	5.79	11.73

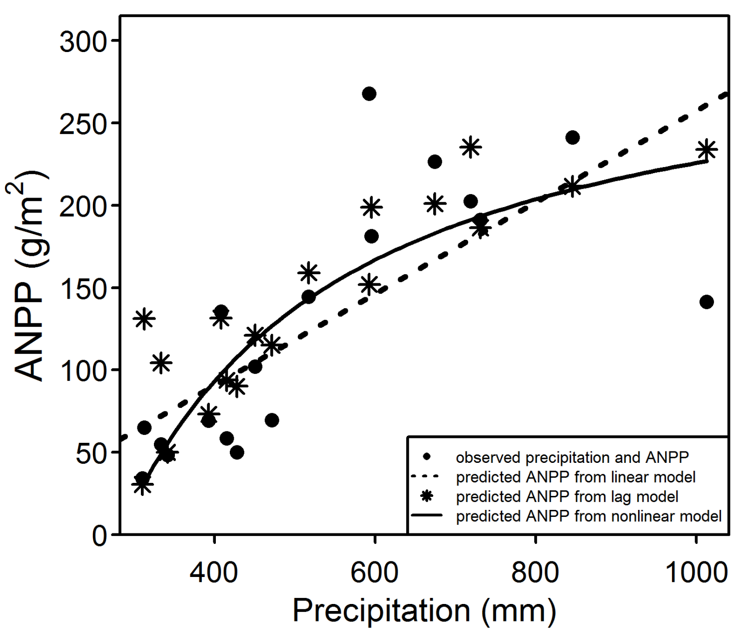

FIG. 3-1. Examples of the three types of precipitation-ANPP models used in this study. Data shown is from grasslands near Bloemfontein, South Africa (O'Connor et al. 2001). At this site, the linear, nonlinear, and lag models explain 53%, 66%, and 68% of the observed interannual variability in ANPP, respectively. A nonlinear model best fits the precipitation-ANPP relationship at this site (AICc weight=73%).

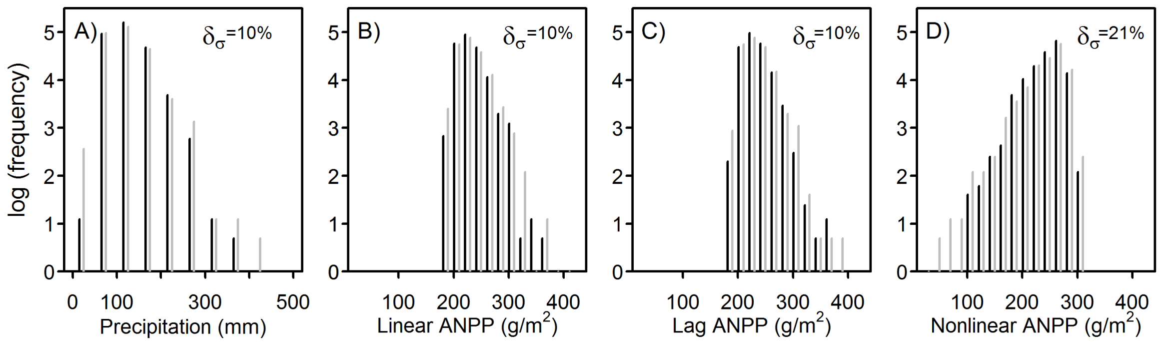

FIG. 3-2. Histograms of observed (black) and high-variability (gray) annual precipitation time series from Jornada Long-Term Ecological Research site between 1990 and 2008 (A). The high-variability precipitation time series was obtained by increasing the standard deviation of each observation by 10% without changing the precipitation mean. Panels B through D show histograms of ANPP predicted from the observed and high variability precipitation time series depicted in (A). When ANPP is a linear (B) or lagged (C) function of precipitation, a 10% increase in the variability of precipitation leads to a 10% increase in the variability of ANPP. However, when ANPP is a nonlinear, concave down function of precipitation (D), a 10% increase in the variability of precipitation leads to a 4% increase in ANPP variability during wet years and a 29% increase during dry years. Since a nonlinear model produces a distribution of ANPP that is skewed towards dry years, the overall increase in ANPP variability was 21%, much greater than the 10% increase in precipitation variability used in this simulation.

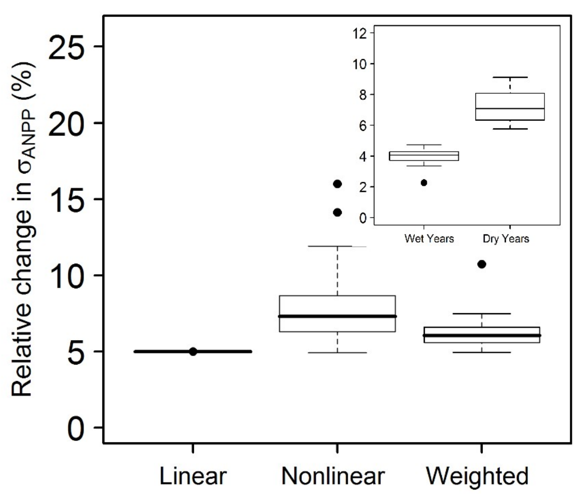

FIG. 3-3. Relative changes in ANPP standard deviation (%) given a 5% increase in the standard deviation of annual precipitation for 27 data sets from 18 different grassland sites. A 5% increase

in the variability of precipitation always results in a 5% increase in the variability of ANPP when the relationship between precipitation and ANPP is linear or lagged (not shown), and usually results in a disproportionately large increase in ANPP variability when the precipitation-ANPP relationship is nonlinear. The weighted ANPP model accounts for AICc weights for the linear and nonlinear models fitted to each data set. The inset of the weighted model shows that the change in ANPP variability is disproportionately high for dry years and disproportionately low for wet years due to the contribution of the nonlinear model.

CHAPTER 4

CONCLUSIONS

Precipitation is an important driver of primary production in water-limited ecosystems and changes in precipitation regime are already impacting primary production. A recent study showed that global net primary production (NPP) decreased between 2000 and 2009 due to large-scale regional droughts and a general drying trend in the southern hemisphere (Zhao and Running et al. 2011). Temperature-driven changes in the global hydrological cycle will continue to alter the mean and variability of primary production as greenhouse gases continue to accumulate in the atmosphere.

My work used the longest field-collected primary production time series available to evaluate potential aboveground net primary production (ANPP) responses to alterations in precipitation. My thesis makes two important contributions towards our understanding of how changes in precipitation will impact ANPP: it 1) establishes the importance of the precipitation-production relationship in determining the size of impacts and 2) quantifies the impacts of altered precipitation variability on ANPP.

First, my thesis shows clearly that the impacts of changes in precipitation on ANPP are highly dependent upon site-specific precipitation-production relationships (Table 4-1). In Chapter 2, I demonstrated that ANPP sensitivity to precipitation mean is controlled by the slope of the precipitation-ANPP relationship and that ANPP sensitivity to precipitation variance is controlled by the nonlinearity of this relationship. Because nonlinearities in the precipitation-ANPP relationship were weak at most sites, mean ANPP was nearly 40 times more sensitive to precipitation mean than to precipitation variance. In Chapter 3, I showed that increases in ANPP variability relative to increases in precipitation variability also depend on the form of the precipitation-production relationship. If we assume a nonlinear relationship between precipitation and ANPP, increases in ANPP variability were over 1.5 times greater than increases in precipitation variability on average.

Second and perhaps more importantly, my research meets the gap in knowledge about how an increase in precipitation variability will impact key ecosystem functions. Despite the abundant evidence from climate models indicating that an intensification of the global hydrological cycle is driving an increase in the frequency of extreme events, most climate change studies have focused on how ecosystems will be impacted by increases in mean temperatures (e.g. Petchey et al. 1999, Yvon-Durocher et al. 2010, Traill et al. 2010). In Chapter 2, I demonstrated that long-term mean primary production levels may be insensitive to interannual precipitation variability. Primary production may respond more strongly to increases in intra-annual variability in precipitation. Both rainfall manipulation experiments and analyses of long-term precipitation and primary production data indicate that mean ANPP is sensitive to the size of precipitation events, independent of precipitation amount (Lázaro et al. 2001, Fay et al. 2003, Snyder and Tartowski 2006, Nippert et al. 2006, Swemmer et al. 2007, Heisler-White et al. 2009, Medvigy et al. 2010). For example, in one experiment in the Chihuahua Desert, plots that received a single large rainfall event each month during the monsoon season had higher soil moisture content and aboveground production than plots receiving the same total rainfall in multiple smaller events (Thomey et al. 2011).

In Chapter 3, I showed that increases in ANPP variability were greater than increases precipitation variability only when production was assumed to be a nonlinear function of precipitation. Since most sites exhibit temporal precipitation-ANPP relationships that are at least slightly nonlinear (Chapter 2), the increase in ANPP variability given a 5% increase in precipitation variability averaged 6.3% across data sets. Furthermore, also due to the nonlinearity of the precipitation-ANPP relationships, increases in ANPP in wet years will be much less than decreases in ANPP during dry years. My thesis suggests that although increases in interannual precipitation variability will have negligible impacts on ANPP mean, they could have considerable impacts on ANPP variability. At most sites in fact, impacts to ANPP variability will be greater than impacts to ANPP mean. The average sensitivity of ANPP mean to changes in precipitation mean was only 0.65% (Chapter 1).

My thesis highlights the potential for changes in ANPP due to increases in precipitation variability. These increases in ANPP variability will have implications for natural resource management (Landres et al. 1999, le Roux and McGeoch 2008). On rangelands, land managers will have more difficulty forecasting forage availability for grazers. An increase in the interannual variability of ANPP will also increase the chances of stochastic extinction for rare species (Boyce 1992, Menges 2000) dependent upon the availability of primary production.

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TABLE 4-1. Summary of how precipitation changes impact ANPP.

Change in precipitation	Response of ANPP mean	Response of ANPP variability
Altered mean	Depends on slope of precipitation-ANPP relationship. Can be relatively higher or lower than change in precipitation mean.	Not considered in thesis.
Altered variability	Depends on the nonlinearity of precipitation-ANPP relationship. Decreases in mean are expected with nonlinear, concave-down relationships due to Jensen's inequality.	Depends on nonlinearity of precipitation-ANPP relationship. Impacts are always proportional if this relationship is linear. Always relatively higher if relationship is nonlinear, concave-down.

APPENDICES

Appendix A

Sensitivity analysis[1]

For each data set, we used a quadratic approximation (Chesson et al. 2005) to quantify the expected value of ANPP (R) given the distribution of precipitation:

$$R \approx f(\bar{x}, a, b) + .5 f''(\bar{x}, a, b)\sigma^2. \quad (1)$$

where f is the linear or nonlinear model describing the precipitation-ANPP relationship, a and b are the fitted parameters of f, and ($\bar{x}$) and (σ^2) are the mean and variance of precipitation. The second term in Equation 1 is the source of Jensen's inequality; it is negative when f is concave down, positive when f is concave up, and zero when f is linear. We fit normal and lognormal distributions to each precipitation time series using maximum likelihood estimation, obtaining $\bar{x}$ and σ^2 from the distribution with the lower AIC value. Thus, Equation 1 accounts for both ways that changes in precipitation variance can cause changes in ANPP: 1) directly, by changing the precipitation mean in lognormally distributed precipitation time series, and 2) indirectly, through Jensen's inequality.

To obtain the sensitivity of ANPP to changes in the variance of precipitation, we took the partial derivative of R with respect to σ^2:

$$\frac{\partial R}{\partial(\sigma^2)} = .5 f''(\bar{x}, a, b).$$

Approximating the derivative by using a difference equation ($\frac{\partial R}{\partial(\sigma^2)} \approx \frac{\Delta R}{\Delta(\sigma^2)}$) yields the expected change in ANPP (ΔR) given a change in precipitation variance ($\Delta(\sigma^2)$) :

$$\Delta R \approx .5 f''(\bar{x}, a, b)\Delta(\sigma^2).$$

1 Coauthored by Joanna Hsu, James Powell, and Peter Adler

Note that Jensen's inequality controls whether ΔR is positive or negative, though both Jensen's inequality and lognormal precipitation distributions can decrease ΔR . To obtain the proportional change in ANPP, we multiplied the right side of the equation by σ^2/σ^2 and divided both sides by *R:*

$$\frac{\Delta R}{R} \approx \frac{.5\sigma^2 f''(\bar{x},a,b)}{f(\bar{x},a,b)+.5 f''(\bar{x},a,b)\sigma^2} \quad \frac{\Delta\sigma^2}{\sigma^2}. \tag{2}$$

The first term on the right hand side of Equation 2 is the sensitivity of ANPP to changes in precipitation variance. Using similar steps, we obtained the sensitivity of ANPP to changes in mean precipitation:

$$\frac{\Delta R}{R} \approx \frac{[f'(\bar{x},a,b)+.5 f'''(\bar{x},a,b)\sigma^2]\bar{x}}{f(\bar{x},a,b)+.5 f''(\bar{x},a,b)\sigma^2} \quad \frac{\Delta\bar{x}}{\bar{x}}. \tag{3}$$

This analytic sensitivity analysis assumes that perturbations to mean precipitation mean and variance ($\Delta\sigma^2$ and $\Delta\bar{x}$) are small so that differentials can be reasonably approximated by finite changes to the mean and variance. Equations 2 and 3 indicate that ANPP sensitivity to changes in precipitation variance is dependent on the second derivative of *f*, while sensitivity to changes in mean precipitation is dependent on the first and third derivatives of *f.* For each data set, we calculated separate sensitivities for linear and nonlinear models. We obtained the final sensitivities for each data set using a weighted average of model sensitivities using AICc weights from the model fitting.

Note that quantifying *R* with a quadratic approximation (Equation 1) does not capture the changing concavity of the nonlinear models. To avoid this limitation, we also used a Monte Carlo simulation approach to quantify *R*, sampling precipitation distributions using maximum likelihood parameter estimates. *R* obtained from the simulations was very close to *R* obtained from the quadratic approximation (not shown).

Other studies have used slopes from linear precipitation-ANPP regressions or precipitation use efficiencies to approximate ANPP sensitivities to precipitation mean (Paruelo et al. 1999, Lauenroth et al. 2000, Huxman et al. 2004, Bai et al. 2008). Unlike those measures of sensitivities, our sensitivities account for nonlinearity in the precipitation-ANPP relationship and are relative (not absolute) measures: a sensitivity of 1 implies that a 1% change in precipitation mean results in a 1% change in ANPP mean in the same direction. Relative sensitivities change with precipitation; this sensitivity measure quantifies the sensitivity at mean precipitation. When the slope is positive, as it typically is in temporal precipitation-ANPP relationships, this measure underestimates sensitivity in wet years and overestimates it in dry years.

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Appendix B

Comparison of sensitivities[2]

In this appendix, we demonstrate that for any reasonable concave down, saturating curve we might use to model a precipitation-ANPP relationship, sensitivity to mean will always be greater than sensitivity to variance. "Reasonable" saturating curves include all those that approach their constant value a like a power law or decaying exponential function for large precipitation values. We use an asymptotic argument that holds for large values of mean precipitation ($\bar{x}$.), far to the right of any inflection point on the curve such that $f'(\bar{x},a,b)$, $f''(\bar{x},a,b)$, and $f'''(\bar{x},a,b)$ are monotonically decreasing and the odd derivatives have the same sign.

To indicate that a function *g(x)* behaves like *h(x)* at large *x*, we will use the notation *g(x)* ~ *h(x)*, which is defined to mean $g(x)/h(x)\rightarrow 1$ as $x\rightarrow\infty$ (Holmes 1995). For example, for the saturating curve $g(x)=\dfrac{ax^n}{b^n+x^n}$, $g'(x)=\dfrac{ab^n n x^{(n-1)}}{(b^n+x^n)^2}\sim\dfrac{n ab^n}{x^{(n+1)}}$ because

$$\frac{ab^n n x^{(n-1)}/(b^n+x^n)^2}{n ab^n/x^{(n+1)}}=\frac{x^{2n}}{(b^n+x^n)^2}\rightarrow 1 \text{ as } x\rightarrow\infty .$$

This particular *g(x)* is the Michaelis-Menten curve when $n = 1$ and is an example of a saturating curve whose first derivative is bounded by a power law. The curve that we chose, $f(x) = a - b/x$, is also bound by a power law.

Negative exponential functions could also be used to model precipitation-ANPP relationships. Both the logistic model, $g(x)=\dfrac{a}{(c+e^{-bx})}$, and the common type II model

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$g(x)=a(1-e^{-bx})$ have the property that $g'(x)\sim abe^{-bx}$. Thus, the first derivative of common saturating curves used in ecology behave asymptotically like (~) either a power law or like a decaying exponential. We will show that in both of these cases, sensitivity to mean always dominates the sensitivity to variance.

We begin by establishing the ratio of sensitivity to variance (Equation 2): sensitivity to mean (Equations 3): $\frac{\textit{sensitivity to}\,\sigma^2}{\textit{sensitivity to}\,\bar{x}}=\frac{.5\sigma^2 f''(\bar{x},a,b)}{[f'(\bar{x},a,b)+.5f'''(\bar{x},a,b)\sigma^2]\bar{x}}$. Note that this ratio reflects the quadratic approximation for Jensen's inequality (Equation 1) because our ANPP sensitivities to mean and variance (Equations 3 and 2) use this approximation. Since *f '(x)* and *f' '(x)* must have the same sign, $\frac{\textit{sensitivity to}\,\sigma^2}{\textit{sensitivity to}\,\bar{x}}\leqslant\frac{.5\sigma^2|f''(\bar{x},a,b)|}{[f'(\bar{x},a,b)]\bar{x}}$.

If the first derivative of a saturating curve behaves asymptotically like a power law with constant *k* and scaling exponent *z*, then $|f'(\bar{x})|\sim\frac{k}{\bar{x}^z}$, $|f''(\bar{x})|\sim\frac{zk}{\bar{x}^{z+1}}$, and

$\frac{\textit{sensitivity to}\,\sigma^2}{\textit{sensitivity to}\,\bar{x}}\leqslant\frac{.5\sigma^2\frac{zk}{\bar{x}^{z+1}}}{\frac{k}{\bar{x}^z}\bar{x}}$. Therefore,

$$\frac{\textit{sensitivity to}\,\sigma^2}{\textit{sensitivity to}\,\bar{x}}\leqslant\frac{.5\sigma^2 z}{\bar{x}^2}. \tag{4}$$

We can also model the precipitation-ANPP relationship with a saturating function whose first derivative behaves like a negative exponential with constant *C* and exponent *m.* In this case, $|f'(\bar{x})|\sim Ce^{-m\bar{x}}$, $|f''(\bar{x})|\sim Cbe^{-m\bar{x}}$, and $\frac{\textit{sensitivity to}\,\sigma^2}{\textit{sensitivity to}\,\bar{x}}\leqslant\frac{.5\sigma^2 Cbe^{-m\bar{x}}}{\bar{x}Ce^{-m\bar{x}}}$.

Therefore,

$$\frac{\textit{sensitivity to}\,\sigma^2}{\textit{sensitivity to}\,\bar{x}} \leqslant \frac{.5\,m\,\sigma^2}{\bar{x}}. \tag{5}$$

Both Equations 4 and 5 show that $\frac{\textit{sensitivity to}\,\sigma^2}{\textit{sensitivity to}\,\bar{x}} \to 0$ as $\bar{x} \to \infty$, implying that the numerator is much smaller in size than the denominator for large values of $\bar{x}$. Sensitivity to mean is greater than sensitivity to variance for sufficiently large $\bar{x}$, regardless of the saturating function used to model the precipitation-ANPP relationship. In the case of $f(x) = a - b/x$, Equation 4 indicates that sensitivity to mean will be greater than sensitivity to variance whenever $\bar{x}$ is greater than σ, which is always the case when looking at interannual time series of precipitation and ANPP.

Literature Cited

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Appendix C

Chapter Three Tables[1]

Table C-1. Data set description.

Data set	Reference	Years	Location	Site	Ecosystem	Dom. species	MAT (°C)	Precip. data	Mean annual precip. (mm)	Std. dev. precip.	Mean ANPP (g/m^2)	Std. dev. ANPP
Andales	Andales et al. 2006	17	Cheyenne, Wyoming, United States	High Plains Grasslands Research Station	mixed prairie	unknown	7.6	April-Aug.	384	64	144	48
Badkhzy	ORNL	25	Badkyz, Mary, Turkmenistan	Badkhzy Nature Reserve Station	desert steppe	Poa bulbosa	14.8	Jan.-May	266	69	61	29
Bai1	Bai et al. 2001	12	Ewenke Qi, Inner Mongolia, China	Ewenke Grassland Management Station	meadow steppe	Stipa baica-lensis	-1.9	Jan.-Dec.	330	83	243	53
Bentley	Bentley and Talbot 1951	13	Oneals, California, United States	San Joaquin Experimental Range	annual grassland	Hordeum marinum	15.8	Sept.-Aug.	527	155	184	41
CC 1927	Cedar Creek LTER	11	Bethel, Minnesota, United States	Cedar Creek Ecosystem Science Reserve	old field	Poa pratensis	6.7	Jan.-Dec.	803	199	116	27
Dzhany-bek	ORNL	21	Dzhanybek, West Kazakhstan, Kazakhstan	Dzhanybek Research Station	semi-arid steppe	Agro-pyron deser-torum	6.6	Jan.-May	274	36	140	39
Hulett	Hulett and Tomanek 1969	24	Hays, Kansas, United States	near Fort Hays Experiment Station	mixed prairie	Boute-loua gracilis, Buchloe dacty-loides	12	Jan.-Dec.	580	171	291	114
JOR BASN	Jornada LTER	19	Las Cruces, New Mexico, United States	Jornada LTER	desert grassland	Boute-loua eriopoda	14.7	Jan.-Dec.	138	65	242	76
JOR IBPE	Jornada LTER	19	Las Cruces, New Mexico, United States	Jornada LTER	desert grassland	Boute-loua eriopoda	14.7	Jan.-Dec.	106	57	242	95
JOR SUMM	Jornada LTER	19	Las Cruces, New Mexico, United States	Jornada LTER	desert grassland	Boute-loua eriopoda	14.7	Jan.-Dec.	146	114	263	89
KNZ 001d	Konza Prairie LTER	34	Manhattan, Kansas, United States	Konza Prairie Biological Station	tallgrass prairie	unknown	12.5	Jan.-Dec.	810	188	457	93
KNZ 004b	Konza Prairie LTER	24	Manhattan, Kansas, United States	Konza Prairie Biological Station	tallgrass prairie	unknown	12.5	Jan.-Dec.	810	187	400	91
Kursk	ORNL	30	Kursk, Kursk Oblast, Russia	Kursk long-term ecological study site	meadow steppe	Bromus riparius	5.6	April-Oct.	560	92	367	126

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Data set	Reference	Years	Location	Site	Ecosystem	Dom. species	MAT (°C)	Precip. data	Mean annual precip. (mm)	Std. dev. precip.	Mean ANPP (g/m^2)	Std. dev. ANPP
Ma 2010	Ma et al. 2010	13	Xilinhot, Inner Mongolia, China	Inner Mongolia Grassland Ecosystem Research Station	typical steppe	Leymus chinensis, Stipa grandis	0.6	Jan.-Dec.	342	67	208	35
O'Con-nor	O'Connor et al. 2001	19	Bloemfontein, Free State, South Africa	Sydenham farm, Univ. of Orange Free State	semi-arid grassland	Themeda triandra, Cymbo-pogon pluri-nodes	15.6	Jan.-Dec.	560	194	125	76
Patton silty	Patton et al. 2007	21	Streeter, North Dakota, United States	Central Grasslands Research Extension Center	old field	Poa pratensis, Nassella viridula, Carex inops spp. heliophila	5	Nov.-Oct.	454	138	283	56
Rogler Haas	Rogler and Haas 1946	12	Mandan, North Dakota, United States	Northern Great Plains grassland Station	mixed prairie	Bouteloua gracilis, Hesperostipa comata	5.6	April-July	406	81	42	27
SGS ESA1	Shortgrass Steppe LTER	16	Nunn, Colorado, United States	Shortgrass Steppe LTER	short-grass steppe	Boute-loua gracilis	9.5	Jan.-Dec.	332	83	88	30
SGS forage	Shortgrass Steppe LTER	39	Nunn, Colorado, United States	Shortgrass Steppe LTER	short-grass steppe	Boute-loua gracilis	9.5	Jan.-Dec.	332	93	68	25
SGS mid-slope	Shortgrass Steppe LTER	25	Nunn, Colorado, United States	Shortgrass Steppe LTER	short-grass steppe	Boute-loua gracilis	9.5	Jan.-Dec.	332	84	65	23
SGS OC	Shortgrass Steppe LTER	17	Nunn, Colorado, United States	Shortgrass Steppe LTER	short-grass steppe	Boute-loua gracilis	9.5	Jan.-Dec.	332	97	108	43
SGS ridge	Shortgrass Steppe LTER	25	Nunn, Colorado, United States	Shortgrass Steppe LTER	shortg-rass steppe	Bouteloua gracilis	9.5	Jan.-Dec.	332	84	58	20
SGS sec25	Shortgrass Steppe LTER	17	Nunn, Colorado, United States	Shortgrass Steppe LTER	short-grass steppe	Bouteloua gracilis	9.5	Jan.-Dec.	332	97	62	30
SGS swale	Shortgrass Steppe LTER	25	Nunn, Colorado, United States	Shortgrass Steppe LTER	short-grass steppe	Bouteloua gracilis	9.5	Jan.-Dec.	332	84	103	48
Smoliak 1986	Smoliak 1986	37	Manyberries, Alberta, Canada	Agriculture Canada Research Substation	mixed prairie	Hespero-stipa comata, Pascopyrum smithii	4.7	April-July	327	65	39	16

Data set	Reference	Years	Location	Site	Ecosystem	Dom. species	MAT (°C)	Precip. data	Mean annual precip. (mm)	Std. dev. precip.	Mean ANPP (g/m^2)	Std. dev. ANPP
Towne	Towne and Owensby 1984	13	Manhattan, Kansas, United States	Kansas Flint Hills	tallgrass prairie	Schizachyrium scoparium, Koeleria macrantha	12.9	Jan.-Dec.	828	192	327	70
To-woomba	ORNL	26	Bela-Bela, Limpopo, South Africa	Towoomba Research Station	mesic grassland	Cymbopogon pospischilii	18.7	Sept.-April	645	145	132	72

TABLE C-2. Fitted model parameters.

Data set	Linear model slope	Linear model intercept	Linear model r^2	Nonlin. model parameter a	Nonlin. model parameter b	Nonlin. model r^2	Lag model intercept	Lag model precip. parameter	Lag model lag parameter	Lag model r^2	Linear model AICc weight	Nonlinear model AICc weight	Lag model AICc weight
Andales	0.47	9	0.41	255	30445	0.34	-23	0.51	0.16	0.43	0.62	0.25	0.14
Badkhzy	0.13	25	0.09	96	8966	0.2	46	0.09	-0.23	0.14	0.17	0.76	0.08
Bai1	0.28	152	0.19	331	26684	0.24	1	0.34	0.54	0.51	0.29	0.39	0.32
Bentley	0.14	113	0.32	268	37758	0.37	192	0.11	-0.32	0.39	0.37	0.56	0.06
CC 1927	0.01	114	0	127	4025	0	166	0.02	-0.5	0.4	0.38	0.38	0.24
Dzhany-bek	0.73	64	0.52	186	4130	0.41	52	0.76	0.07	0.53	0.75	0.09	0.17
Hulett	0.38	51	0.34	437	84347	0.25	19	0.37	0.13	0.36	0.65	0.15	0.21
JOR BASN	0.54	168	0.22	340	11494	0.24	137	0.5	0.15	0.24	0.4	0.51	0.09
JOR IBPE	0.89	146	0.28	298	4451	0.15	186	0.92	-0.19	0.31	0.65	0.16	0.19
JOR SUMM	0.48	191	0.39	331	6007	0.28	187	0.48	0.02	0.39	0.71	0.15	0.13
KNZ 001d	0.3	216	0.38	690	177656	0.35	230	0.3	-0.03	0.38	0.56	0.29	0.16
KNZ 004b	0.17	263	0.13	546	107791	0.15	223	0.16	0.12	0.15	0.38	0.51	0.1
Kursk	0.28	256	0.04	430	23923	0.02	54	0.37	0.46	0.22	0.14	0.11	0.75
Ma 2010	0.22	125	0.15	301	33949	0.21	214	0.13	-0.28	0.23	0.38	0.56	0.06
O'Con-nor	0.28	-20	0.53	314	88221	0.66	-85	0.3	0.44	0.68	0.04	0.73	0.24
Patton silty	0.2	204	0.25	360	26340	0.36	248	0.2	-0.16	0.28	0.16	0.79	0.05
Rogler Haas	0.3	-35	0.5	101	14149	0.54	-28	0.33	-0.39	0.63	0.34	0.52	0.14
SGS ESA1	0.19	13	0.41	143	20821	0.33	20	0.2	-0.11	0.43	0.64	0.24	0.12
SGS forage	0.16	16	0.35	98	9211	0.3	-17	0.17	0.42	0.52	0.01	0	0.99
SGS	0.21	-7	0.59	134	22629	0.61	-10	0.2	0.07	0.59	0.31	0.61	0.08

Data set	Linear model slope	Linear model intercept	Linear model r^2	Nonlin. model parameter a	Nonlin. model parameter b	Nonlin. model r^2	Lag model intercept	Lag model precip. parameter	Lag model lag parameter	Lag model r^2	Linear model AICc weight	Nonlinear model AICc weight	Lag model AICc weight
mids-lope													
SGS OC	0.26	15	0.37	198	29969	0.43	15	0.26	0	0.37	0.29	0.67	0.05
SGS ridge	0.17	-3	0.55	118	19797	0.62	-10	0.17	0.13	0.57	0.12	0.83	0.05
SGS sec25	0.25	-27	0.72	146	27284	0.74	-27	0.25	0.02	0.72	0.33	0.61	0.05
SGS swale	0.41	-37	0.52	243	45465	0.57	-41	0.4	0.08	0.52	0.21	0.73	0.06
Smoliak 1986	0.17	11	0.48	74	5168	0.44	-6	0.17	0.44	0.67	0	0	1
Towne	0.23	84	0.43	438	127269	0.44	52	0.16	0.34	0.51	0.41	0.49	0.1
To-woomba	0.24	-18	0.3	264	79059	0.29	-26	0.24	0.06	0.3	0.49	0.39	0.13

Table C-3. Relative increases in the standard deviation of annual ANPP with a 5% increase in the standard deviation of annual precipitation. Standard deviations shown are those from the “predicted” ANPP time series based on the observed, not the perturbed, ANPP time series.

Data set	Linear model std. dev. (g/m^2)	Linear model inc. in std. dev. (g/m^2)	Linear model increase in std. dev. (%)	Nonlin. model std. dev. (g/m^2)	Nonlin. model increase in std. dev. (g/m^2)	Nonlin. model increase in std. dev. (%)	Nonlin. model increase in std. dev., dry years (%)	Nonlin. model increase in std. dev., wet years (%)	Lag model std. dev. (g/m^2)	Lag model increase in std. dev. (g/m^2)	Lag model increase in std. dev. (%)	Weigh-ted model increase in std. dev (%)	Weigh-ted model increase in std. dev., dry years (%)	Weigh-ted model increase in std. dev., wet years (%)
Andales	31	1.5	5	28	1.7	6.1	7.7	3.3	31	1.5	5	5.3	5.8	4.5
Badkhzy	9	0.4	5	13	0.9	7.4	10	3	6	0.3	5	7	9.1	3.4
Bai1	23	1.2	5	26	2.2	8.4	10.3	3.3	37	1.8	4.9	7	8.1	4
Bentley	23	1.2	5	25	1.5	5.9	7.9	2.5	17	0.9	5	5.6	6.8	3.5
CC 1927	2	0.1	5	1	0.1	5.7	7.6	3.2	3	0.2	5	5.4	6.3	4.1
Dzhany-bek	29	1.4	5	25	3.6	14.1	18.1	2.4	29	1.5	5	5.9	6.3	4.7
Hulett	67	3.3	5	57	6.4	11.2	13.6	2.5	62	3.1	5	6.2	6.6	4.5
JOR BASN	35	1.8	5	37	3.2	8.5	13.3	1.7	35	1.8	5	7	9.6	3.1
JOR IBPE	50	2.5	5	37	7.4	20	24.4	1.8	50	2.5	5	7.9	8.8	4.4
JOR SUMM	56	2.8	5	47	9.1	19.5	24.8	0.6	55	2.8	5	7.6	8.5	4.2
KNZ 001d	57	2.9	5	55	3.5	6.3	8.9	3.2	56	2.8	5	5.4	6.3	4.4
KNZ 004b	33	1.6	5	35	2.2	6.3	8.8	3	31	1.5	5	5.8	7.2	3.9
Kursk	26	1.3	5	20	1.7	8.7	11	3.5	34	1.7	5	6.6	7.6	4.3
Ma 2010	14	0.7	5	16	0.8	4.9	6.5	3.6	8	0.4	5	5	5.9	4.2
O'Con-nor	55	2.8	5	62	4.1	6.6	9.3	2.1	62	3.1	5	6.5	9.1	2.3

Data set	Linear model std. dev. (g/m²)	Linear model inc. in std. dev. (g/m²)	Linear model increase in std. dev. (%)	Nonlin. model std. dev. (g/m²)	Nonlin. model increase in std. dev. (g/m²)	Nonlin. model increase in std. dev. (%)	Nonlin. model increase in std. dev., dry years (%)	Nonlin. model increase in std. dev., wet years (%)	Lag model std. dev. (g/m²)	Lag model increase in std. dev. (g/m²)	Lag model increase in std. dev. (%)	Weigh-ted model increase in std. dev (%)	Weigh-ted model increase in std. dev., dry years (%)	Weigh-ted model increase in std. dev., wet years (%)
Patton silty	28	1.4	5	34	4	11.9	14.7	3	29	1.4	5	10.7	13.1	3.4
Rogler Haas	19	1	5	20	1.3	6.3	8.7	3.1	21	1.1	5	5.8	7.3	3.8
SGS ESA1	19	1	5	17	0.9	5.6	7.6	2.5	20	1	5	5.2	5.7	4.3
SGS forage	15	0.7	5	14	1.8	12.8	15.6	2.8	16	0.8	5	6.6	7.2	4.5
SGS mids-lope	18	0.9	5	18	1.3	7.1	9.4	2.9	17	0.8	5	6.4	7.9	3.6
SGS OC	26	1.3	5	28	2.1	7.3	10.1	2.8	26	1.3	5	6.6	8.6	3.5
SGS ridge	15	0.7	5	16	1.1	7.1	9.4	2.9	14	0.7	5	6.8	8.9	3.2
SGS sec25	25	1.3	5	26	1.9	7.3	10.1	2.8	25	1.3	5	6.5	8.3	3.6
SGS swale	34	1.7	5	36	2.5	7.1	9.4	2.9	33	1.7	5	6.6	8.4	3.4
Smoliak1986	11	0.6	5	11	0.8	7.5	10.7	1.9	12	0.6	5	5.6	6.3	4.3
Towne	46	2.3	5	47	3.4	7.2	8.9	3.3	32	1.6	5	6.2	7.1	4.1
To-woomba	40	2	5	39	2.5	6.5	8.6	2.8	39	1.9	5	5.6	6.6	4

APPENDIX D

INTERPRETING THE PRODUCTION TO RAINFALL VARIABILITY RATIO

An easy, common way to compare variability in precipitation and production is to directly compare the CV of production (CV_{PROD}) with the CV of precipitation (CV_{PPT}). Previous studies have attempted to explain why the ratio CV_{PROD}:CV_{PPT} (Production to Rain Variability Ratio, PRVR) is greater or less than 1 at different sites. PRVR greater than 1 has interested ecologists because it seems to suggest that production somehow amplifies variability in precipitation, which could have climate change implications. However, PRVR does not account for the fact that production is often a linear function of precipitation. In this appendix, I recast PRVR in a linear regression framework that reveals that PRVR is largely controlled by the y-intercept of the regression line that predicts production from precipitation. The y-intercept of a temporal precipitation-production model is typically an extrapolation of the data and does not accurately represent production in years of no rainfall. In other words, PRVR is very sensitive to an estimated statistical parameter that is not very informative about ecological processes.

Background: Using PRVR to compare rainfall and production variability

To characterize production variability relative to precipitation variability, Noy-Meir and Walker (1984) compared the coefficient of variation (CV) of production with the CV of precipitation. Le Houerou et al. (1988) introduced the production to rain variability ratio (PRVR), the CV of production (CV_{PROD}) divided by the CV of precipitation (CV_{PPT}):

$$PRVR = \frac{CV_{PROD}}{CV_{PPT}} = \frac{SD_{PROD}\overline{PPT}}{SD_{PPT}\overline{PROD}} \tag{1}$$

In Equation 1, $\overline{PROD}$ and SD_{PROD} are the mean and standard deviation of production, and $\overline{PPT}$ and SD_{PPT} are the mean and standard deviation of precipitation.

PRVR has been widely used to compare production variability with rainfall variability: sites with PRVR greater than 1 have more variable production than rainfall. PRVR greater than 1 is commonly documented (Lehouerou et al. 1988, Lauenroth and Sala 1992, Xiao et al. 1996, Guevara et al. 1997, Veron et al. 2002, Wiegand et al. 2004, Hu et al. 2007, Yang et al. 2008a), but PRVR can also be less than 1 (Guevara et al. 1997, Prince et al. 1998, Paruelo and Lauenroth 1998, Diouf and Lambin 2001, Veron et al. 2002, Wessels et al. 2007, Yang et al. 2008b).

PRVR greater or less than 1 seems to suggest that production variability could be amplifying or buffering variability in precipitation. Previous studies have sought explanations for high or low PRVR. For example, Lauenroth and Sala (1992) propose that high PRVR is related to the fact that years with the same annual precipitation may still differ in intraseasonal water availability. Wiegand et al. (2004) suggest that PRVR greater than 1 can be attributed to lag effects. LeHouerou et al. (1988) suggest that PRVR is indirectly linked to topography and that low PRVR in arid or semi-arid sites is only an artifact of short data sets. Hu et al. (2007) reason that PRVR is affected by vegetation type and condition. I argue that high or low PRVR does not need to be attributed to any of these factors, but has a much simpler explanation.

Analysis: Predicting PRVR from a site's precipitation-production relationship

Production is a linear or mostly linear function of precipitation at most water-limited sites (Chapter 2). However, PRVR does not account for this relationship, which has an influence on the variability of production. To demonstrate how this is the case, I re-write PRVR in terms of a linear regression between the two variables.

I begin by considering a time series in which production is a linear function of precipitation. Recall that in least squares regression, the slope of the fitted regression line, b, is related to the correlation coefficient r and the standard deviations of the two variables (SD_x, SD_y):

$b = r\frac{SD_y}{SD_x}$. I can rewrite the equation above in terms of our variables of interest:

$$SD_{PROD} = \frac{b\,SD_{PPT}}{r} \tag{2}$$

Next, recall also that the intercept *a* of a least squares regression line can also be calculated:

$a = \bar{Y} - b\,\bar{X}$, where $\bar{X}$ and $\bar{Y}$ are the means of the predictor and response variables, respectively. Rearranging the equation and plugging in our variables of interest, I obtain the following expression for mean primary production:

$$\overline{PROD} = a + b\,\overline{PPT} \tag{3}$$

Equation 3 indicates that mean production depends on the slope and the intercept of the precipitation-production relationship. If I substitute Equations 2 and 3 into Equation 1, we obtain the following equation for PRVR:

$$PRVR = \frac{b\,\overline{PPT}}{(a + b\,\overline{PPT})\,r} \tag{4}$$

Equation 4 shows that PRVR depends on the correlation *r* and on each site's unique precipitation-production relationship. When $r = 1$, all of the variability in ANPP can be attributed to variability in precipitation. It is important to notice that even in this case, when SD_{PROD} is perfectly proportional to SD_{PPT}, PRVR is only 1 when the y-intercept is 0.

I fit a linear model to each of the 58 data sets of annual precipitation and primary production that I collected (Chapter 2) and then regressed PRVR on each of the variables in Equation 4 (Fig. D-1). Equation 4 successfully predicts PRVR at all sites.

Solving Equation 4 for the conditions when the numerator is greater than the denominator indicates that PRVR is greater than 1 whenever $a < b\,\overline{PPT}\left(\frac{1}{r} - 1\right)$.

Conclusions: PRVR is not informative about ecological processes

The y-intercept in temporal precipitation-production relationships is seldom zero and not necessarily an indicator of production in a year of no rain. Yet it explains over a third of the variability in PRVR. It is possible that positive y-intercepts reflect lag effects in production and that negative intercepts reflect minimum precipitation thresholds for production (Veron et al. 2005), However, at wetter sites especially, the y-intercept fitted in a precipitation-production regression is an extrapolation from the data that makes assumptions about how production responds to precipitation in extremely dry years. If we compare two sites that produce the same amount of biomass per unit precipitation (same slope) and have the same *r*, the site with a lower y-intercept will have a lower mean ANPP (Equation 4) and therefore a higher CV_{PROD} and higher PRVR. Veron et al. (2005) demonstrated the importance of y-intercepts in determining interannual variation in rain use efficiency.

Solving Equation 4 for the conditions when the numerator is greater than the denominator indicates that PRVR is greater than 1 whenever $a < b\,\overline{PPT}\,(\frac{1}{r} - 1)$. PRVR greater or less than 1 does not necessarily reflect lag effects, vegetation characteristics, or lack of appropriate data. Instead, it captures the correlation of two variables and their linear dependence upon each other. In most cases, high PRVR may simply indicate that a site's precipitation-production relationship has a low y-intercept.

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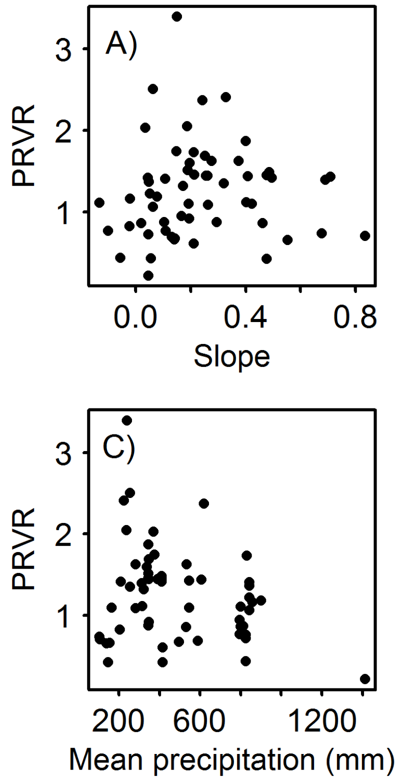

FIG. D-1. PRVR is strongly controlled by the y-intercept fitted to a linear regression model of precipitation and production (B). The y-intercept explains 30.5% of the variation in PRVR across sites. The other variables that determine PRVR - the slope of the regression relationship (A), mean precipitation (D), and the correlation coefficient between precipitation and production (D) - do not contribute significantly to explaining variation in PRVR. The data shown is from 58 long-term data sets of precipitation and primary production from around the globe.

Appendix E

Co-author permission

August 8, 2011

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Dear James Powell,

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Signed ___________________________

Date ____________