Sensitivity of mean annual primary production to precipitation

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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 determines the sensitivity of mean ANPP to changes in mean precipitation, whereas 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.

Keywords: aboveground net primary production, climate change, Jensen’s inequality, precipitation, primary production

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Introduction

Primary production is 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 production (ANPP) is positively correlated with mean annual precipitation (MAP) at regional scales (Lieth, 1973; Parton 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 & Sala, 1992; O’Connor et al., 2001; Khumalo & Holechek, 2005; Knapp et al., 2006; Patton et al., 2007). Thus, changes in precipitation regimes associated with anthropogenic climate change may have large impacts on ANPP.

General circulation models (GCMs) project latitude-dependent changes in MAP due to climate forcing (Giorgi & Francisco, 2000; Zhang et al., 2007). 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 & Soden, 2008; Wetherald, 2009). However, although 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. Both observational studies and experimental manipulations demonstrate 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), suggesting that increases in precipitation variance will affect ANPP. Therefore, 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 MAP 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. 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 & 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 were 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 analysed for other rainfall and production patterns by Knapp & Smith (2001) and by Lehouerou et al. (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 where they were available. The Lehouerou data sets are from semi-arid and arid sites. In a few cases, updated data from these sites were 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 articles by using the published tabular data or by digitizing figures. Finally, we used net primary productivity data sets from the Oak Ridge National Laboratory (ORNl) 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 were 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 = \(a - \frac{b}{\text{precipitation}}\)) 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 relatively 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 & Balling, 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 ($\sigma^2$) 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:

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

(1)

In Eqn (1), $f$ is the linear or nonlinear model describing the precipitation-ANPP relationship, $a$ and $b$ are the fitted parameters of the precipitation-ANPP model, and ($\bar{x}$) and ($\sigma^2$) are the mean and variance of the precipitation time series. The second term in Eqn (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. Eqn (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 Eqn (1) with respect to the mean and variance of precipitation. Details of the sensitivity analysis are given in Appendix S1. 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 (Bai et al., 2008; Paruelo et al., 1999). To the best of our knowledge, cross-system studies of primary production sensitivity to changes in precipitation variance based on long-term data have been limited to comparing different measures of variability, such as coefficient of variation (Lehouerou et al., 1988; Fang et al., 2001; Knapp and Smith, 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 MAP, precipitation seasonality (summer or winter), mean annual 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 1; Table S2 in Appendix S2). 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 6 data sets from herbaceous alpine ecosystems, 3 from forested ecosystems, 46 from grasslands, and 3 from shrub-dominated ecosystems. 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 of the 58 data sets. Figure 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 nonlinear precipitation-ANPP relationship best described 5 of 6 data sets from herbaceous alpine ecosystems, 2 of 3 data sets from forests, 22 of 46 data sets from grasslands, and 2 of 3 data sets from shrublands. A chi-square goodness of fit test indicated that the probability of having a nonlinear precipitation-ANPP relationship was not different across these biomes ($\chi^2 = 1.68, df = 3, P = 0.69$).

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
Table 1  Sensitivity of ANPP mean to precipitation mean and variance

<table>
<thead>
<tr>
<th>Data sets</th>
<th>Reference</th>
<th>Years</th>
<th>Location</th>
<th>Study site</th>
<th>Biome</th>
<th>Mean annual precip. (mm)</th>
<th>Mean annual temp. (°C)</th>
<th>Mean annual ANPP (g/m²)</th>
<th>Sensitivity to mean</th>
<th>Sensitivity to variance</th>
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<td>291</td>
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<td>near Rio Mayo</td>
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<td>Data sets</td>
<td>Reference</td>
<td>Years</td>
<td>Location</td>
<td>Study site</td>
<td>Biome</td>
<td>Mean annual precip. (mm)</td>
<td>Mean annual temp. (°C)</td>
<td>Mean annual ANPP (g/m²)</td>
<td>Sensitivity to mean</td>
<td>Sensitivity to variance</td>
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<td>132</td>
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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 four cases and for a lognormal distribution in eight 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 $-0.18$ 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 (Table 1). Mixed prairie in North Dakota had the highest sensitivity (1.81), but seven other sites also had sensitivities greater than one: Bloemfontein, South Africa (1.71); Sevilleta LTER, New Mexico (1.2); Shortgrass Steppe LTER, Colorado (1.1); Towoomba Research Station, South Africa (1.1); and three different grassland sites in Inner Mongolia, China (1.3, 1.3, 1.2). Two sites, alpine tundra at Niwot Ridge and annually tilled grassland at Kellogg Biological Station, had negative sensitivities ($-0.2$ and $-0.05$ respectively).

In almost all data sets, mean ANPP exhibited negative sensitivities to precipitation variance due to concave down precipitation-ANPP relationships (Table 1).
ANPP to changes in precipitation variance was smaller than the sensitivity to changes in precipitation mean (Fig. 3). 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 = $0.20 + 0.002$\text{MAP} − $2.23\times10^{-6}$\text{MAP}²) fit the relationship between MAP and ANPP sensitivity to precipitation mean better than a linear regression model, according to AICc (Fig. 4). In this model, which explains 16% of the variation in sensitivities to precipitation mean, sensitivity to mean peaks at sites with 507 mm MAP. Sensitivities to precipitation mean were very low or even negative at the four wettest sites, Hubbard Brook LTER, Kellogg Biological Station LTER, Niwot Ridge LTER, and Hopland Field Station.

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 26% of the variation in sensitivity to precipitation mean and had stronger AICc support (AICc weight = 0.76) 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. T-tests indicated no significant difference ($P > 0.1$) between sensitivities calculated from sites with growing season precipitation data and sensitivities from sites with total annual precipitation data.

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 precipitation (Raaisänen, 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 CO₂, almost all GCMs project changes in interannual precipitation that fall within this range (Raaisänen, 2002). Second, although ANPP sensitivities to interannual precipitation variability were small, primary production could be more sensitive to intraannual precipitation variability (Lázaro et al., 2001; Fay et al., 2003; Snyder & Tartowski, 2006; Swemmer et al., 2007; Heisler-White et al., 2009; Medvigy et al., 2010). Time series analyses and precipitation manipulation experiments both indicate that ANPP is affected by the timing and size of individual precipitation events (Lázaro et al., 2001; Fay et al., 2003; Swemmer et al., 2007; Heisler-White et al., 2009), which alter water availability throughout the growing season.

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 & Knapp, 2005). Our analyses use historical data to estimate how precipitation changes could impact one important ecosystem function in the short term. Over the longer term, as species assemblages shift, the precipitation-ANPP relationship may also change, but predicting the direction and rate of such changes remains a challenge. Because our analyses are based on temporal precipitation-ANPP relationships, which are usually less steep than spatial precipitation-ANPP relationships (Lauenroth & Sala, 1992; Huxman et al., 2004), our conclusion that ANPP is far more sensitive to changes in precipitation means than variances is conservative.

Cross-system patterns in sensitivities

We demonstrated, not surprisingly, that the wettest sites are largely insensitive to changes in mean precipitation. However, 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, all grasslands and shrublands, sensitivities to precipitation mean are greater than one. 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 475–500 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 and 600 mm such as mixed prairie or shortgrass steppe in the United States 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 (Paruelo et al., 1999; Bai et al., 2008; Noy-Meir, 1973). 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 & 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 come 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.

Conclusions

Climate change will alter both the mean and variance of interannual precipitation. This analysis quantifies the sensitivity of mean ANPP to these changes. Our analysis indicates that the impact of increases in interannual precipitation variability on mean 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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Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Sensitivity analysis.

**Appendix S2.** Sensitivity of ANPP mean to precipitation mean and variance (detailed version).

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