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Intra-annual rainfall variability and grassland productivity: can the past predict the future?

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Abstract

Precipitation quantity has been shown to influence grassland aboveground net primary productivity (ANPP) positively whereas experimental increases in of temporal variability in water availability commonly exhibit a negative relationship with ANPP. We evaluated long term ANPP datasets from the Konza Prairie Long Term Ecological Research (LTER) program (1984–1999) to determine if similar relationships could be identified based on patterns of natural variability (magnitude and timing) in precipitation. ANPP data were analyzed from annually burned sites in native mesic grassland and productivity was partitioned into graminoid (principally C_4 grasses) and forb (C_3 herbaceous) components. Although growing season precipitation amount was the best single predictor of total and grass ANPP ($r^2=0.62$), several measures of precipitation variability were also significantly and positively correlated with productivity, independent of precipitation amount. These included soil moisture variability, expressed as CV, for June ($r^2=0.45$) and the mean change in soil moisture between weekly sampling periods in June and August (%wv) ($r^2=0.27$ and 0.32). In contrast, no significant relationships were found between forb productivity and any of the precipitation variables ($p>0.05$). A multiple regression model combining precipitation amount and both measures of soil moisture variability substantially increased the fit with productivity ($r^2=0.82$). These results were not entirely consistent with those of short-term manipulative experiments in the same grassland, however, because soil moisture variability was often positively, not negatively related to ANPP. Differences in results between long and short term experiments may be due to low variability in the historic precipitation record compared to that imposed experimentally as experimental levels of variability exceeded the natural variability of this dataset by a factor of two. Thus, forecasts of ecosystem responses to climate change (i.e. increased climatic variability), based on data constrained by natural and recent historical rainfall patterns may be inadequate for assessing climate change scenarios if precipitation variability in the future is expected to exceed current levels.

Introduction

Climate change models differ with regard to projected changes in annual precipitation amounts in the central US, but they are in agreement with predictions that the dynamics of event distribution will become more variable (Groisman et al. 1999; Easterling et al. 2000; Houghton et al. 2001).

General circulation models predict precipitation events of a greater magnitude, but with longer intervening dry periods and reduced frequency. The longer dry periods between storms will generally lead to reduced soil moisture levels (Knapp et al. 2002). Predictions by the Canadian Model Scenario (VEMAP) suggest that the Great Plains region of North America will experience an approximate 30% decrease in annual precipitation over the next century (USGCRP 2003). Perhaps more importantly, similar model predictions for soil moisture forecast a 50% decline during June–August over the next century (USGCRP 2003). Substantial changes in moisture availability and temporal variability will undoubtedly impact ecosystems in which productivity is limited by water availability (Sala et al. 1988; Weltzin et al. 2003). The mesic grasslands (tallgrass prairie) ecosystem of the Central Great Plains is one such region sensitive to dynamic changes in precipitation timing (Fay et al. 2003). Thus, a better understanding of the relationship between productivity and precipitation amount and variability is warranted.

The importance of precipitation amount vs. precipitation pattern on grassland productivity has been assessed using experimental rainfall manipulation plots (RaMPs) at the Konza Prairie Biological Station (KPBS) (Fay et al. 2000). Results of this research indicate that when temporal variability in soil moisture was increased independent of rainfall quantity, carbon cycling processes and plant community composition were altered (Knapp et al. 2002; Fay et al. 2003). Specifically, greater precipitation variability (changes in rainfall pattern, independent of seasonal amount), increased soil moisture variability and reduced mean soil water content, which resulted in increased plant water stress and decreased productivity (Fay et al. 2002; Knapp et al. 2002; Fay et al. 2003). Thus, based on experimental approaches, both precipitation amount (Knapp et al. 2001) and temporal pattern have been shown to be important in determining productivity within this grassland.

An alternative approach to assessing potential changes in climate on grassland ecosystems is to use long term ecological data and climate records to identify those aspects of climate to which ecological processes are most likely to be sensitive (Sala et al. 1988; Burke et al. 1991; Lauenroth and Sala 1992; Sala et al. 1992; Paruelo et al. 1999; Jobbágy and Sala 2000). For example, Briggs and Knapp (1995, 2001) used regression analysis to assess the responsiveness of aboveground net primary productivity (ANPP) in tallgrass prairie to interannual variation in precipitation based on long term data. Subsequent experimental manipulation of precipitation events confirmed and further defined this relationship (Knapp et al. 2001).

The objective of this research was to compare the results of manipulative experiments, which have focused primarily on intra-annual precipitation alterations, to those derived from analyses of long term natural precipitation variability recorded at the Konza Prairie LTER site. The Konza LTER site has archived biological and climatological data since its inception in 1981, and this dataset was used as a proxy for assessing decadal-scale changes in this grassland. The overarching question that guided this analysis was: 'do the patterns of variability present in long term Konza datasets mimic the results found in short term experimental manipulations?' To answer this question, we used 16 years of precipitation and ANPP data from an annually burned watershed on site. Annually-burned sites are both the most productive and water limited of all burn frequencies in the tallgrass prairie (Knapp et al. 1998, 2001). We analyzed patterns of natural precipitation and soil moisture variability (inter- and intra-annually) to assess their influence on ANPP of both common growth forms (C_4 grasses and C_3 forbs) in this grassland. Specifically, we sought evidence for the importance of intra-annual variability on ANPP independent of precipitation amount using these long term datasets. We predicted that the productivity response to precipitation and/or soil moisture variability would be consistent with patterns identified through experimental manipulations in annually burned prairie.

Methods

Analyses were based on long term ecological data collected at KPBS, in northeastern Kansas, USA (39°05′ N, 96°35′ W). KPBS is a 3487 ha unplowed tallgrass prairie dominated by a few warm-season C_4 grasses, yet supporting a species-rich pool of herbaceous C_3 forbs (Freeman 1998). KPBS experiences a temperate mid-continental climate of cold, dry winters and warm wet summers with the majority of the annual precipitation occurring between April and September (835 mm mean annual precipitation).

Total aboveground productivity is estimated by quantifying the current years' biomass in the annually burned watersheds (Briggs and Knapp 1995). Plant biomass is harvested during late August/early September, the time of peak biomass. Total ANPP is measured using four transects with five 0.1 m^2 subplots therein. This protocol is repeated for each soil type – watershed combination. The clipped subplots are marked so as to avoid subsequent re-sampling for at least 4 years. This method ensures independence in productivity data between consecutive years. For comparisons in this study, measurements of ANPP come from a single annually-burned watershed on KPBS which has historically been the most representative of all the annually-burned watersheds on site. For the data we compared, each transect in this watershed was located on the same soil type. Biomass was separated into multiple components that included graminoid and forb biomass, current year's dead, and a minor woody plant component (if present). Following sorting, biomass was oven-dried at 60 °C for 48 h and weighed to the nearest 0.01 g (Abrams et al. 1986). Total ANPP can vary widely across years, but this response is largely driven by the grass component (Figure 1).

As part of the LTER program, soil moisture is measured at bi-weekly intervals across many sites on KPBS. Because these estimates are too coarse temporally to quantify variability, we estimated daily values in soil moisture. These estimates were derived using a soil hydrology model (WaterMod 2.0.9, Greenhat Software, 1998). This mechanistic model is described in detail in Johnson et al. (2003), but briefly, the model is driven by the relationship between biomass productivity and agents of soil moisture change, particularly soil water infiltration and drainage, run-off, soil characteristics, precipitation amount, and estimates of potential evapotranspiration (PET) (calculated using the Penman-Monteith equation). Soil water infiltration is calculated using a capacitance model, which is parameterized using saturated water content, drainage point, and saturated hydraulic conductivity of the soil (Johnson et al. 2002, 2003). Measured input variables included end of season ANPP, daily precipitation, and daily PET, and they were used to derive daily model estimates of soil moisture for each year. The model was sensitive to annual biomass changes, and was parameterized

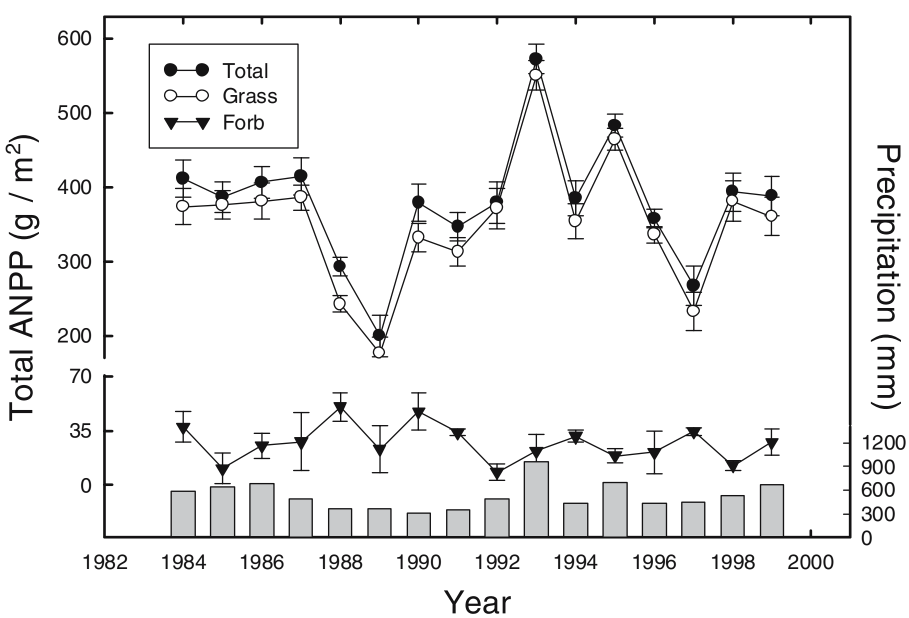

Figure 1. Long term record of aboveground net primary production (ANPP) plus SE ($n = 20$) for grass (primarily C_4 species) and forb (C_3 herbaceous plants) with corresponding growing season precipitation amount in annually burned mesic grassland in NE Kansas (Konza Prairie LTER site). Typically, grass productivity accounts for approximately 95% of total ANPP with variations in timing and amount of precipitation shifting this percentage between 90 and 99% (Briggs and Knapp 1995).

with dates for emergence (5/1), maximum growth (7/15), date of harvest (9/30) and water use coefficienct (209 mm precipitation per kg dry weight, which equates to the average total biomass multiplied by the growing season precipitation, Briggs and Knapp 1995). To assess the accuracy of the model, estimates of soil moisture from the 20 to 30 cm soil depth were compared to bi-weekly neutron probe measurements available from the site at a 25 cm depth. We calculated the percent difference between the measured soil moisture value and the modeled estimate and then noted the average monthly difference across the entire dataset for each month of the growing season. The largest difference between measured and modeled values occurred in the month of April ($\mu = 16.7\%$, SE = 1.4%). However, as the growing season advanced, predictions of soil moisture were ≥90% similar to measured values for July, August, and September ($\mu = 8.6$, 10.5, and 10.8%, and SE = 1.2, 1.6, 1.9%, respectively). Model estimates were consistently lower than measured values in April, but for the subsequent 5 months, no consistent bias between measured and modeled predictions occurred, and the model followed the temporal dynamics of soil moisture following wetting and drying events. The linear relationship between measured and modeled soil moisture is portrayed graphically in the inset panel of Figure 2.

Statistical analyses were focused on several abiotic parameters that could potentially influence productivity. Variables analyzed included timing of precipitation events, length of dry-periods, the magnitude of the precipitation-event, mean monthly pan evaporation, indices of rainfall evenness during the growing season (Bronikowski and Webb 1996), and consecutive differences in precipitation amount between events, months, and years (Oesterheld et al. 2001). Simple and multiple linear regression (SLR, MLR) comparisons were made between ANPP and these abiotic parameters using the GLM functions of SAS (SAS 2001). Multiple linear regression procedures were performed using a stepwise model selection method to identify significant reduced models containing non-correlated variables. The appropriate model to use was identified from the pool of candidate models by Akaike's Information Criterion.

Analyses of colinearity were performed to ensure independence among the predictor variables used. Yearly measurements of ANPP were independent from consecutive years due to the aforementioned biomass harvesting protocol. Point estimates in the analyses refer to an average growing season value for each year, unless otherwise specified. Due to the time-series nature of the data, a test of autocorrelation among residuals was performed to identify any first-order serial correlation between year-to-year ANPP or precipitation data. Based on the Durbin–Watson test statistic, errors between years were uncorrelated for either variable (DW = 1.728 and 1.719 for precipitation and ANPP, respectively).

Results

The majority of predictor variables we used exhibited no relationship with grass productivity, and of those that did, many lacked independence from precipitation amount. However, two parameters describing soil moisture variability were significantly related to ANPP independent of precipitation amount. The first variable was an absolute difference index expressing the mean change in soil moisture between weekly sample periods. This index has been previously used as an indicator of soil moisture variability (Knapp et al. 2002). The second index of variability was the coefficient of variation (CV) of mean monthly soil moisture. CV has also been used as a representative index of variability (Le Houérou et al. 1988; Fay et al. 2003). Both parameters were calculated for each of the growing season months (April–September) for all 16 years.

Precipitation and soil moisture amount were significantly and positively related to grass ANPP in this annually burned grassland (Figure 2). Growing season precipitation amount best explained the variation of grass ANPP ($r^2 = 0.62$). However, none of the abiotic predictor variables analyzed were significantly related to forb ANPP during this 16-year-period. Neither index of soil moisture variability was significantly related to productivity across the entire growing season, but when analyses were conducted with monthly timesteps, relationships were significant for portions of the growing season (Table 1). For the absolute difference index, variability and productivity were significantly correlated for the months of June and August, but the nature of the relationship differed. For this index, variability

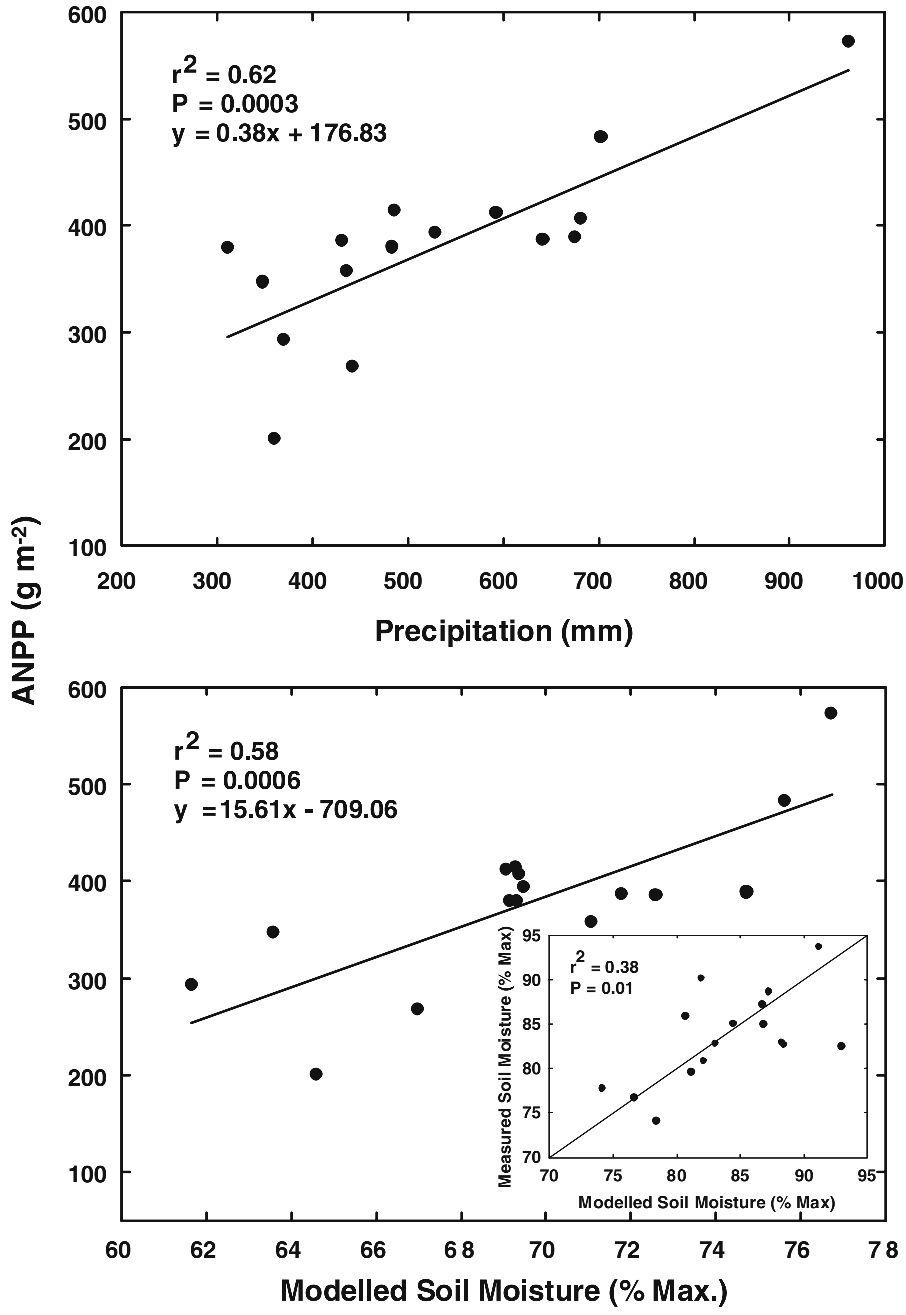

Figure 2. Grass aboveground net primary production vs. growing season (April–Sept.) precipitation (mm) and mean growing season soil moisture (modeled) at 30 cm depth. Inset figure shows model predictions vs. measured soil moisture (neutron probes at 25 cm) averaged over the entire season for each year of the study. The solid line is a 1:1 line between measured vs. modeled soil moisture.

and productivity were positively correlated in June, but negatively correlated in August (Table 1). The remaining months had positive trends, albeit extremely weak correlations. The CV index had similar seasonal trends to the absolute difference index with significant positive trends in June, and subsequent negative trends for the remainder of the season (Table 1). Although non-significant, the CV index exhibited a negative trend across the entire growing season.

Table 1. Correlation coefficient matrix depicting the relationships between grass ANPP (end of season) and two indices of soil moisture variability (an absolute difference index vs. the CV, see text) partitioned by the six growing season months and for the entire season.

Index by month		Soil moisture variability index vs. grass ANPP						
		Apr.	May	June	July	Aug.	Sept.	Entire season
Absolute difference	r^2	0.14	0.02	**0.27**	0.01	**0.32**	0.01	0.05
	Pearson's	0.37	0.13	**0.52**	0.09	**-0.57**	0.12	0.23
CV	r^2	0.15	0.06	**0.45**	0.01	0.15	0.02	0.03
	Pearson's	−0.38	0.26	**0.67**	−0.32	−0.38	−0.14	−0.17

Both the coefficient of determination and the Pearson correlation coefficient are given to describe the proportional reduction in error and nature (positive or negative) of the linear relation, respectively. Values for significant associations ($p < 0.05$) are in bold.

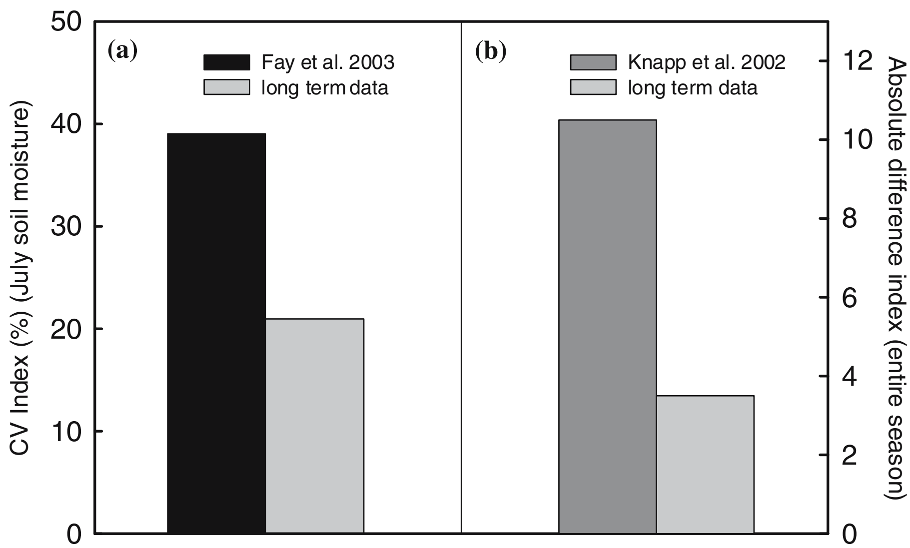

Figure 3. Comparison of the magnitude of soil water variability imposed experimentally vs. estimated from the long term record of precipitation variability. Bars correspond to the magnitude of variability experienced for CV of July soil water content (A) and mean variability in soil water content over the growing season (B). The different time periods of variability compared between A and B (July vs. entire season, respectively) were chosen to match those reported from experimental studies (Knapp et al. 2002; Fay et al. 2003).

The magnitude of the natural variability noted in the two soil moisture indices using long term datasets was considerably lower than that imposed experimentally in the rainfall manipulation plots (RaMPs) study (Figure 3). The maximum CV of soil water content in July for the long term data (16 years) was only 54% of the variability reported in the RaMPs experiment (3 years) (CV = 21 vs. 39%; Figure 3a). Similarly, the maximum variability in soil water content (absolute difference index) reported in the long term datasets was only 33% of the maximum variability imposed in the RaMPs experiment (variability = 3.5 vs. 10.5; Figure 3b).

A multiple linear regression (MLR) model was used to determine if multiple factors could explain more variation than the analysis of precipitation amount alone (Figure 2). Predictor variables included in the full model MLR analysis included five variables added in this order: annual precipitation amount, average annual soil moisture, the mean difference in weekly soil water contents (for May and June only), CV of June soil moisture, and the average length of consecutive dry-periods between rain occurring during the growing season. The analysis identified three variables to be significant for predicting ANPP: precipitation amount and the two soil moisture variability

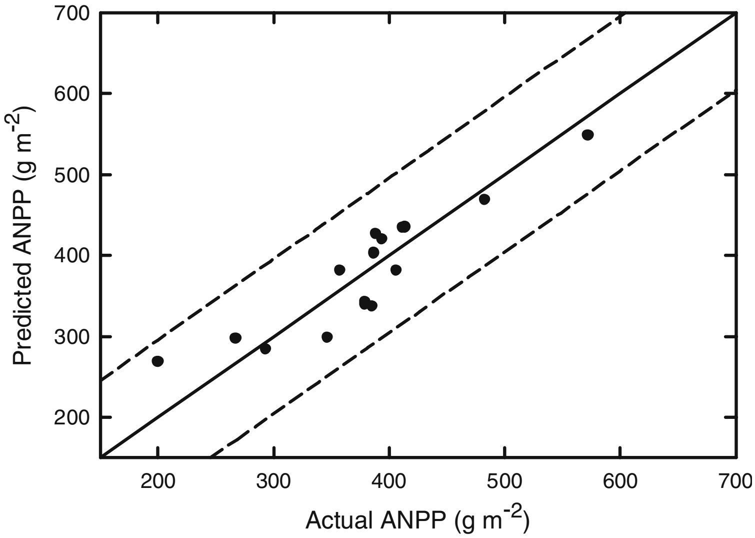

Figure 4. Actual vs. predicted ANPP based on a multivariate regression model incorporating three independent variables (precipitation amount, CV of June soil moisture, and mean variability in soil water content for May and June combined, $r^2 = 0.82$). The proportion of explained variance for the three variables is 0.62, 0.04, and 0.16, respectively. The solid line is a 1:1 relationship and the dashed line represents the 95% C.I. for the multivariate model. Filled circles represent values predicted from the multivariate regression model.

parameters ($r^2 = 0.82$, Figure 4). Each of these variables exhibited a positive correlation with ANPP.

Discussion

Analyses of long term datasets or natural climatic gradients have been used to predict ecosystem responses to future climates (Burke et al. 1991; Paustain et al. 1995; Alward et al. 1999; Rastetter et al. 2003; Dunne et al. 2004). These methods provide a long term alternative to experimental approaches to climate change research that rely on highly manipulative experiments. Long term data sets are expected to reveal patterns of ecosystem responses to climate variability similar to those identified by short-term manipulation. However, this assumes that predicted changes for future climates are of a similar magnitude to that recorded in the historic data. A key question addressed by this study is: can the past predict the future for this grassland?

Assessing the impact of precipitation variability on ecosystem productivity and function is inherently difficult due to spatial and temporal differences within a site as well as across an entire region. Grasslands exhibit higher inter-annual variation in productivity and may require longer time periods to reveal trends in variability compared to forested biomes (Lauenroth and Sala 1992; Frank and Inouye 1994). Within grassland biomes, the influence of precipitation variability on ANPP depends on the ecosystem structure and whether the constraint is biological or biogeochemical (Paruelo et al. 1999). Inter-annual variation in ANPP within the shortgrass steppe of Colorado, USA resulted from both current year precipitation amount and ANPP of the previous year (Oesterheld et al. 2001). However, in this tallgrass ecosystem, within-season variability in rainfall patterns are more likely to contribute to the large variation in annual ANPP reported (Frank and Inouye 1994; Knapp and Smith 2001). Tallgrass prairie ANPP can respond quickly to changes in precipitation due to the inherently high RGR of the dominant vegetation resulting in LAI adjustments during the growing season (Paruelo et al. 1999). This leads to high temporal plant and soil water dynamics (James et al. 2003). Within the tallgrass prairie, the dynamics of rainfall distribution are characterized by the majority of events being small (< 10 mm) and not contributing largely to the annual sum, interspersed with a small number of large events (> 25 mm) that constitute the majority of the total annual amount of precipitation. Because of the relative contribution and frequency of small vs. large events, the variance of precipitation patterns can potentially be as important as the overall annual amount and serve as a key driver of biomass production (Lauenroth and Sala 1992; Williams et al. 1998).

In order to compare the long term data archived at KPBS to short-term manipulative experiments, we required soil moisture data at a finer temporal scale (daily) than available from the long term data (bi-weekly). Modeling soil moisture on a daily timestep allowed for comparisons of identical measures of precipitation variability, as manifested through changes in soil moisture between both datasets (long term and experimental). Without this daily timestep, the central theme of the manuscript comparing experimental manipulations and long term data would be impossible. As an alternate approach to determining the influence of abiotic variability, models can be used heuristically to explore how varying amounts of precipitation translate into different levels of soil moisture by progressively changing the values of other influential abiotic variables used in the correlative analysis. This technique would provide mechanistic support for conclusions derived from studies of correlative patterns between abiotic parameters and ANPP without reliance upon daily estimates of modeled soil moisture.

Analyzing the natural variability in precipitation patterns from the LTER data sets at KPBS, several similarities and differences were evident when compared to the reported findings of the rainfall manipulation plots (RaMPs). Perhaps the most prominent result of the RaMPs experiment was the negative relationship between ANPP and soil moisture variability; a relationship stronger than that between productivity and soil water amount (Knapp et al. 2002; Fay et al. 2003). While a significant relationship between productivity and soil moisture variability was present in the long term datasets (Table 1), the relationship between ANPP and average soil moisture amount was much stronger (Figure 2; $r^2 = 0.58$). The differing results between studies using long vs. short-term data was likely due to differences in the magnitude of variability being compared. Both indices of soil moisture variability calculated from the historical record were of a magnitude that was less than half of that imposed in RaMPs studies (Figure 3; Knapp et al. 2002; Fay et al. 2003). Indeed, if the results of Knapp et al. (2002) or Fay et al. (2003) were constrained to the range of values reported in the long term dataset, the patterns, significance, and implications would be altered markedly.

The nature of the relationship between variability and productivity also differed between the RaMPs experiment and the long term datasets. Results from both the site and biome level have shown that precipitation variability and precipitation amount are inversely correlated (Knapp and Smith 2001; Knapp et al. 2002; Fay et al. 2003). In this study, indices of soil moisture variability were not significantly correlated with productivity when averaged across the entire growing season (Table 1). However, the relationship between productivity and variability were significant when analyzed as a monthly response (Table 1). The response differed during the growing season, with generally positive trends for April, May, and June, and negative trends during July, August, and September. The change in slope from positive to negative may reflect the seasonal pattern of shifting limitations within the tallgrass prairie community (Seastedt and Knapp 1993; Blair 1997). The positive relationship early in the growing season suggests that productivity was limited by variables other than precipitation and soil moisture (i.e., light and temperature). For example, because soil moisture is high in the spring, extended warm dry periods with high irradiance that would increase soil water variability would almost certainly increase growth in the dominant C_4 grasses. This transition from a positive to negative relationship between ANPP and soil moisture variability illustrates the time periods for which precipitation exerts the greatest control over growth. Little influence of soil moisture is noted during the cool spring season, but variability exerts a greater impact following the summer dry-down of soil moisture. Changing seasonal relationships between productivity and precipitation have been reported for other grasslands. Jobbágy and Sala (2000) found that cumulative precipitation was a non-significant predictor of grass productivity in the Patagonian Steppe when expressed annually, but a significant relationship between ANPP and precipitation amount arose when the analysis was divided into seasons. Similarly, Jobbágy et al. (2002) have reported that in space and time, temperature, not precipitation, is the primary variable initiating growth.

Using space for time substitutions, Sala et al. (1988) explained a significant amount of grassland ANPP ($r^2 = 0.90$) using a single predictor variable: precipitation amount. However, using 19 years of productivity and meteorological data at a single site (KPBS), the explanatory power of this relationship was reduced substantially (Briggs and Knapp 1995). Because the relationship between productivity and a single variable weakens at the site level as Sala et al. (1988) predicted, we included other variables in this analysis in an attempt to improve the model. We found a substantial increase in the amount of variability explained ($r^2 = 0.82$) using a MLR model that incorporated variability indices compared with a single predictor variable ($r^2 = 0.62$ for precipitation amount alone). The substantial increase in explanatory power reported here contradicts the results of Briggs and Knapp (1995), who found that the inclusion of multiple meteorological variables resulted in $< 10\%$ increase in explanatory power. The increase we report may result from the inclusion of parameters reflecting variability rather than means of additional variables (soil moisture, evaporation, etc.). The increased fit of this MLR model does support the contention of Sala et al. (1988), that at an individual site, the inclusion of multiple variables will be required to explain the dynamics of inter-annual ANPP.

Increased precipitation variability in an altered global climate will likely contribute to wider inter-annual ANPP fluctuations in the grassland regions of North America (Knapp et al. 2002; Fay et al. 2003). Previous results from experimental studies suggest that increased variability will negatively influence productivity in the tallgrass prairie (Knapp et al. 2002; Fay et al. 2003). The relationship between ANPP and moisture variability in this long term data set differed across the growing season with positive relationships early, and negative relationships later. Despite these differences, results from both short and long term studies illustrate the importance of temporal patterns of precipitation, not just seasonal means, on grassland ANPP. These results also indicate that long term datasets may not capture the range of variability forecast under altered climate scenarios, and thus analyses based solely on these historic data may not be sufficient to predict future ecosystem responses.

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