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Decreasing Precipitation Variability Does Not Elicit Major Aboveground Biomass or Plant Diversity Responses in a Mesic Rangeland

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Abstract

Inter- (between years) and intra- (within year) annual variability of precipitation are high on rangelands. We used replicated rainout shelters in a southern tallgrass prairie ecosystem to decrease precipitation variability for 3 yr (1999–2001). We removed interannual variability in total precipitation plus either 1) interannual variability in the seasonal distribution of precipitation (seasonal distribution) or 2) all additional variability in precipitation, including within-year differences in precipitation (even distribution). Our objective was to determine if decreasing variability in precipitation elicits aboveground biomass and plant diversity responses. Aboveground biomass was harvested in June (peak biomass) and December (end of growing season). Plant species diversity, richness, and evenness were determined each June. Reducing precipitation variability had limited effects on total aboveground biomass, grass and forb biomass, and biomass of key species across the 3 yr of investigation. Species richness, species diversity, species evenness, and functional group richness and diversity all were similar across the precipitation treatments across years. Total aboveground biomass and biomass of the dominant C4 perennial grasses little bluestem (*Schizachyrium scoparium*) and Indiangrass (*Sorghastrum nutans*) generally were not responsive to the precipitation treatments. However, one species-specific response did occur with the annual forb firewheel (*Gaillardia pulchella* Foug.) displaying consistent increases in biomass in the seasonal distribution precipitation treatment across all 3 yr. This suggests that increased predictability of precipitation at a given stage of this species's growth can elicit changes in productivity of a single species that are not manifest at the community level due to constraints of the dominant species. These findings indicate that the southern tallgrass prairie ecosystem is adaptable to changes in precipitation to result in relatively stable production that facilitates simpler predictions in response to altered precipitation regimes.

Resumen

La variación de la precipitación entre (entre años) y dentro (en años) es sumamente alta en los pastizales. Utilizamos un protector de lluvia en forma replicada en la parte sur en un ecosistema de los pastizales altos para disminuir la variabilidad de la precipitación durante tres años (1999–2001). Eliminamos la variabilidad interanual en la precipitación total además 1) la variabilidad interanual en la distribución estacional de la precipitación (distribución estacional) o 2) toda la variabilidad adicional de la precipitación, incluyendo las diferencias dentro del año de la precipitación (distribución igual). Nuestro objetivo fue determinar si el disminuir la variabilidad de la precipitación produciría una respuesta en la biomasa aérea y en la diversidad de plantas. La biomasa aérea fue cosechada en junio (máxima producción de biomasa) y Diciembre (final de la época de crecimiento). La diversidad de las especies de plantas, riqueza y uniformidad se determinaron cada junio. El reducir la variabilidad de la precipitación tuvo efectos limitados en la total biomasa aérea, biomasa de las gramíneas y herbáceas y la biomasa de las especies claves en los tres años de la investigación. La biomasa aérea total y la biomasa de las gramíneas dominantes perenes C4 como little bluestem (*Schizachyrium scoparium*) e Indiangrass (*Sorghastrum nutans*) generalmente no respondieron a los tratamientos de la precipitación. Sin embargo, una respuesta específica ocurrió en la herbácea anual firewheel (*Gaillardia pulchella* Foug.) mostrando un sólido incremento en la biomasa con los tratamientos de la distribución de la precipitación estacional a través de los tres años. Esto sugiere que un aumento en la predictibilidad de la precipitación en determinada etapa de crecimiento de esta especie puede provocar cambios en la productividad de una sola especie que no se manifiesta en el nivel de la comunidad debido a las limitaciones de la especie dominante. Estos resultados indican que los ecosistemas del sur de los pastizales altos son adaptables a los cambios de precipitación a originar una producción relativamente estable que facilita las predicciones más simples en respuesta a los regímenes de precipitación modificada.

Key Words: altered precipitation regime, climate change, ecosystem stability, Southern tallgrass prairie, species richness, rainout shelter

INTRODUCTION

Precipitation influences the distribution and productive capacity of rangelands in the Great Plains region of North America, as well as species and functional group composition (Teeri and Stowe 1976; Sala et al. 1988; Briggs and Knapp 1995; Paruelo

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and Lauenroth 1996; Epstein et al. 1997; Tieszen et al. 1997). Consequently, predicted changes in inter- and intra-annual variability of precipitation (Easterling et al. 2000; Groisman et al. 2005; Christensen et al. 2007) may influence production, composition, and diversity of these ecosystems (Knapp et al. 2002; Adler et al. 2006). Functioning of rangelands should be more responsive to changes in precipitation variability when species or groups of species respond similarly to changes (Chapin et al. 1997).

Inter- and intra-annual variability of precipitation are high on rangelands (Lauenroth et al. 1999; Harmel et al. 2003; Derner and Hart 2007; Derner et al. 2008). Aboveground biomass is more sensitive to interannual variability in precipitation in Great Plains rangelands than in other biomes in North America (Knapp and Smith 2001), and carbon cycling and net ecosystem exchange are influenced by interannual variability in precipitation (Chou et al. 2008; Polley et al. 2010; Zhang et al. 2010). In addition, within-year patterns of precipitation influence production and composition of Great Plains rangelands (Knapp et al. 2001, 2002; Fay et al. 2003; Harper et al. 2005; Derner et al. 2008; Heisler-Smith et al. 2009), as well as of other rangelands in the western United States (Bates et al. 2006) and around the world (e.g., Swemmer et al. 2007). The influence of precipitation variability on the length of dry periods is an important determinant of production (Knapp et al. 2002; Heisler-Smith et al. 2009). Great Plains rangelands are characterized by having more small precipitation events (< 5 mm) and short intervals (< 10 d) between events compared to Intermountain areas (Lauenroth and Bradford 2009), further showcasing the pulse behavior of the Great Plains ecosystems to precipitation. Dry intervals of short duration are more prevalent at wet than drier sites, but the importance of these dry periods for ecosystem processes increases with increasing mean annual precipitation and temperature (Lauenroth and Bradford 2009).

Rangeland responses to variability in precipitation have been studied mostly by experimentally altering timing and amounts (e.g., Fay et al. 2002, 2003; Heisler-White et al. 2009), and by evaluating responses to variability in precipitation across seasons/years (Derner and Hart 2007; Derner et al. 2008). In contrast, here we decreased the high variability in precipitation that characterizes southern tallgrass prairie ecosystem (Harmel et al. 2003) on prairie plots for a period of 3 yr (1999–2001). Prior experimentation has shown that aboveground biomass responses to increased variability in precipitation are often constrained by dominant species (Smith and Knapp 2003; Polley et al. 2007). These dominant species acquire a disproportionate share of the available resources such that ecosystem responses are largely influenced by these species. Therefore, our primary objective was to determine if decreasing variability in precipitation elicits similar results in which the dominant species of southern tallgrass prairie, little bluestem (*Schizachyrium scoparium* [Michx.] Nash), and Indiangrass (*Sorghastrum nutans* [L.]), constrain effects on aboveground biomass, and secondarily on plant diversity. We evaluated effects of decreasing precipitation variability by comparing rangeland exposed to current inter- and intra-annual variability in precipitation to rangeland on which we removed interannual variation in total precipitation plus either 1) interannual variation in the seasonal distribution of precipitation (seasonal distribution) or 2) all additional variability in precipitation, including within-year differences in precipitation (even distribution).

MATERIALS AND METHODS

Site Description

Research was conducted on a 3-ha remnant tallgrass prairie located on the United States Department of Agriculture-Agricultural Research Service (USDA-ARS) Grassland, Soil and Water Research Laboratory near Riesel, Texas (31°28′N; 96°52′W). This remnant has been managed for annual haying in mid-June since 1936. Soils on the study site are the Heiden series (fine, smectitic thermic Udic Hapulsterts) that are well drained and slowly permeable with 1–3% slope. Clay content of the soil is 40–60%. Little bluestem and Indiangrass, both C4 perennial grasses, are the dominant species.

Precipitation Treatments

Both inter- and intra-annual variability in precipitation are high at this site (Harmel et al. 2003). Long-term (1939–1999) mean annual precipitation is 871 (± 228, 1 SD) mm with wet springs (April–June) and drier summer and winter months (Harmel et al. 2003). Twice-replicated 9 × 10 m rainout shelters (Stuppy Greenhouse Manufacturing, Kansas City, MO; Fay et al. 2000) were constructed in late 1998 to manipulate precipitation amounts and distribution beginning January 1999. Effects of these rainout shelters on photosynthetic photon flux density (−22%), net radiation during the day (−22%), daytime maximum and nighttime minimum soil temperatures (+1.2 to 1.8°C), mean day or nighttime air temperatures (no effect), and midday vapor pressure deficits (no effect) have been previously reported (Fay et al. 2000). Within each rainout shelter, the 90-m^2 area was divided into three 30-m^2 areas, each 3 × 10 m; areas were separated by landscape edging to prevent any lateral water flow. Each of these 30-m^2 areas was randomly assigned one of three treatments: 1) mimic ambient precipitation with its inter- and intra-annual variability, 2) remove interannual variability in both the total and seasonal distribution of precipitation by irrigating to match the mean total and seasonal precipitation pattern for the site (seasonal distribution), or 3) remove interannual variability in total precipitation and within-year variability in the distribution of precipitation by applying equal amounts of irrigation water to plots each week (even distribution). Mimicking current inter- and intra-annual variability was achieved by manually applying water weekly from a ground water source to match ambient conditions. Water that ran off rainout shelters was not collected. The seasonal-distribution treatment was implemented by irrigating weekly to match the mean and seasonal distribution of precipitation at the site (60-yr pattern), resulting in spring-dominated precipitation and an annual total of 871 mm (see Fig. 1). The even-distribution treatment was implemented by applying equal amounts of water each week to cumulatively sum to the 60-yr annual mean of 871 mm (72.6 $mm \cdot mo^{-1}$). Water was applied at a rate of 25 $mm \cdot h^{-1}$ using a manual sprinkler irrigation system with three sprinklers for each 30-m^2 area. Weekly applications of the water were necessary given the amounts being applied and the permeability of this soil with

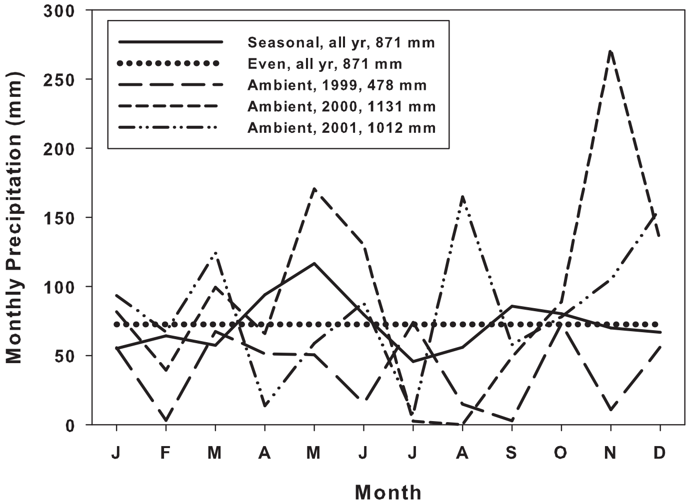

Figure 1. Monthly precipitation (mm) added to rainout shelter plots for three precipitation treatments for 1999 to 2001.

high clay content, and the desire to reduce dry periods by decreasing precipitation variability. This likely further kept soil moisture levels more constant than would naturally occur and reduced the pulse responses of this system to precipitation event-driven variability. Soil water measurements were not conducted. Annual totals of 478, 1 131, and 1012 mm were applied in 1999, 2000, and 2001, respectively, to the areas for which we mimicked ambient conditions, whereas the other two treatments received the annual total of 871 mm each year (Fig. 1). Two automated weather stations were installed in July 2000: one in the center of one of the rainout shelters and the other approximately 25 m away in the prevailing upwind direction.

Vegetation Sampling

Within each 30-m^2 area, eight 1×1m plots were permanently established for vegetation sampling. Plant species composition in all plots was nondestructively quantified in mid-June of 1999, 2000, and 2001. Plants within plots were identified to species (if possible) or genus and assigned to a functional group: C4 perennial grass, C3 perennial grass, perennial forb, annual forb, or subshrub. Species composition was determined by visually estimating each plant species's foliar cover using seven cover categories modified from Daubenmire (1959): $1 = < 1\%$ cover; 2 = 1–5%; 3 = 6–25%; 4 = 26–50%; 5 = 51–75%; 6 = 76–95; 7 = 96–100%. Midpoints of cover classes were used in data analysis for each species (Towne et al. 2005; Hickman and Derner 2007). Plant species diversity [Shannon index, $H' = -\sum (\rho_i \cdot \ln \rho_i)$, where ρ_i = proportional cover of species i within the 1-m^2 plot, Magurran 1988], richness (S = number of species sampled per plot), and evenness of species cover (Pielou's index $J' = H'/\ln S$) were calculated. To assess changes in functional group composition, cover of each functional group was used to calculate functional group diversity using Shannon diversity, where ρ_i = the proportional contribution of functional group i cover to the plant community (Magurran 1988).

Aboveground biomass was harvested in each plot to a height of 5 cm in mid-June each year following sampling of plant species composition. This timing coincided with typical prior management of this prairie for hay harvest. Biomass harvested in June was sorted to species in even-numbered plots for each shelter ($n = 4$) and assigned to perennial grass, forb (annual and perennial combined), or other groups. Biomass harvested that was prior year's growth was classified as dead. All plots were again harvested to a height of 5 cm in December each year, but biomass was not sorted to species or group. Total annual aboveground biomass per plot was obtained by adding June and December harvest values. Coefficients of variation (CV) of total aboveground biomass and plant groups (perennial grasses, forbs) were also calculated across the three study years for each precipitation treatment.

Each 3×10 m area was considered an experimental unit, resulting in low replication of $n = 2$ for each precipitation treatment. For analyses, values from the individual 1×1 m plots within each 3×10 m area were averaged to give one replicate value. June, December, and total annual biomass were analyzed using mixed-model analysis of variance (ANOVA) with year as a random factor and treatment a fixed factor. Plant diversity metrics were analyzed using mixed-model multivariate ANOVA (MANOVA) with year as a random factor and treatment as a fixed factor. A probability level of $\leq 10\%$ was considered significant given the limited replication of the precipitation treatments in this experiment.

RESULTS

Average (July 2000–December 2001) air temperature inside rainout shelters was similar compared to outside (19.9°C inside vs. 19.5°C outside), whereas average wind speeds were reduced by 70%.

June ($P = 0.0260$), December ($P = 0.0104$), and total annual ($P = 0.0159$) aboveground biomass all exhibited year × precipitation treatment differences (Table 1). Annual total biomass did not respond as expected; total annual biomass in the ambient plots differed by a maximum of 21% between the high (2001) and low (1999) mean values, despite the twofold difference in annual precipitation amounts. June biomass was similar between 1999 and 2000, but less for all treatments in 2001. In contrast, December biomass was generally similar between 1999 and 2000, but greater for 2001. Total annual biomass was similar among years for the decreased precipitation variability treatments, with ambient plots having similar values in 1999 and 2000, but greater in 2001.

June biomass was less for the ambient precipitation treatment in 1999 ($P = 0.0767$), with differences not observed between the treatments, which reduced precipitation variability (Table 1). No differences among treatments occurred for June biomass in either 2000 ($P = 0.5280$) or 2001 ($P = 0.1527$). The contribution of June biomass to total annual biomass was consistent (70–79%) across treatments for the first 2 yr (1999 and 2000), but represented only 52–53% across treatments in the final year (2001). December biomass was less for the ambient treatment in 1999 ($P = 0.0696$) compared to the seasonal distribution treatment, but did not differ from the even distribution treatment. In 2000 December biomass was less for the ambient treatment ($P = 0.0271$) compared to both treatments with reduced precipitation variability. No differ-

Table 1. Mean (± 1 SE, $n = 2$) June and December aboveground biomass (g · m^{-2}) from rainout shelters with three precipitation treatments from 1999 to 2001. Different lowercase letters among precipitation treatments indicate significant ($P < 0.10$) differences within years. Different uppercase letters among years indicate significant ($P < 0.10$) differences within precipitation treatments for June, December, and annual total biomass.

Group/species	Precipitation treatment: Mimic ambient	Seasonal	Even
	1999		
Perennial grass	185.8 (40.5)	206.0 (49.5)	210.4 (19.1)
Schizachryrium scoparium	127.3 (48.1) a	75.8 (12.4) b	134.2 (33.8) a
Sorghastrum nutans	30.3 (15.0)	31.7 (1.5)	41.1 (10.0)
Forbs	101.6 (21.9)	137.1 (32.2)	128.7 (19.9)
Gaillardia pulchella	57.5 (21.9) b	118.0 (13.4) a	89.1 (41.8) b
Dead	113.7 (1.1)	105.9 (18.5)	109.6 (27.3)
June total	410.1 (26.4) bA	465.7 (2.2) aA	487.1 (1.1) aA
December total	141.6 (9.0) bC	190.4 (2.4) aB	176.7 (13.1) abB
Annual total	551.7 (35.3) bB	656.1 (2.7) aA	663.8 (14.2) aA
	2000		
Perennial grass	223.1 (42.7)	249.5 (43.2)	245.5 (46.0)
Schizachryrium scoparium	122.0 (48.6)	138.5 (6.5)	137.3 (2.9)
Sorghastrum nutans	81.5 (54.1)	90.7 (21.6)	90.2 (22.5)
Forbs	165.6 (28.8)	150.0 (8.8)	142.5 (37.5)
Gaillardia pulchella	68.1 (16.5) b	112.9 (5.6) a	83.5 (38.4) b
Dead	55.5 (4.7)	48.9 (18.6)	48.2 (7.9)
June total	460.9 (2.7) A	448.5 (15.0) A	436.2 (30.6) A
December total	119.9 (4.9) bB	188.5 (4.4) aB	160.4 (13.9) aB
Annual total	580.8 (7.5) B	637.0 (19.4) A	596.6 (16.7) A
	2001		
Perennial grass	154.1 (6.9)	173.4 (38.3)	156.6 (14.5)
Schizachryrium scoparium	97.8 (22.2)	77.5 (7.5)	84.5 (7.2)
Sorghastrum nutans	36.9 (21.1)	56.5 (21.3)	65.1 (16.6)
Forbs	80.0 (10.3)	79.0 (13.1)	104.2 (7.5)
Gaillardia pulchella	23.6 (3.4)b	46.9 (15.7) a	22.0 (6.5) b
Dead	89.6 (19.3)	53.6 (14.7)	54.9 (5.2)
June total	364.4 (30.2) B	329.0 (29.7) B	319.6 (6.6) B
December total	337.6 (30.8) A	285.2 (18.0) A	275.2 (6.9) A
Annual total	702.0 (60.9) A	614.2 (47.7) A	594.8 (13.0) A

ences among treatments occurred for December biomass in 2001 ($P = 0.2250$). Total biomass (June + December) was less for the ambient treatment only in 1999 ($P = 0.0620$), with no differences observed in 2000 ($P = 0.1405$) or 2001 ($P = 0.1858$).

Coefficient of variation (CV) was smaller in the treatments with reduced precipitation variability for both the December and annual total biomass values (Table 2). The CV of perennial grass biomass was less with the precipitation treatments that reduced precipitation variability, whereas CV for forb and June total biomass was greater (Table 2). Species richness, species diversity, species evenness, and functional group richness and diversity all were similar across the precipitation treatments across years (Table 3).

Precipitation treatment did not influence perennial grass ($P = 0.4437$ in 1999, $P = 0.8743$ in 2000, and $P = 0.1464$ in 2001) or forb ($P = 0.1130$ in 1999, $P = 0.2525$ in 2000, and $P = 0.3030$ in 2001) biomass in any year (Table 1). Biomass of the dominant C4 perennial grass little bluestem decreased in the seasonal precipitation treatment, but only in the first year of the study (1999, $P = 0.0513$). Biomass of the other main C4 perennial grass Indiangrass was not affected by precipitation treatments ($P = 0.6305$) but was greater in 2000 compared to the other 2 yr ($P = 0.0654$). Biomass of the annual forb firewheel (*Gaillardia pulchella* Foug.) was consistently greater for all years in the seasonal distribution precipitation treatment ($P = 0.0180$).

DISCUSSION

Reducing precipitation variability by removing interannual variability in total precipitation and either maintaining the mean seasonal distribution or eliminating within-season variation in precipitation had limited effects on total aboveground biomass, grass and forb biomass, biomass of key species, and plant diversity across the 3 yr of investigation in this mesic rangeland. We did observe that reducing precipitation variability decreased coefficients of variation in total aboveground biomass compared to the ambient treatment. Our

Table 2. Coefficient of variation in aboveground biomass for June and December harvests with three precipitation treatments across the three study years (1999–2001).

Harvest	Precipitation treatment		
	Mimic ambient	Seasonal	Even
June total	11.7	18.0	28.5
Grass	68.1	31.0	33.1
Forbs	18.4	57.5	34.5
December total	60.0	25.0	30.4
Annual total	13.0	3.3	10.1

Table 3. Mean (± 1 SE, $n = 6$) richness and diversity values across three precipitation treatments from 1999 to 2001.

Variable	Precipitation treatment		
	Mimic ambient	Seasonal	Even
Species richness	22.4 (0.4)	23.1 (0.5)	22.2 (0.5)
Species diversity	2.72 (0.02)	2.70 (0.02)	2.70 (0.03)
Species evenness	0.87 (0.01)	0.86 (0.01)	0.86 (0.01)
Functional group richness	2.4 (0.1)	2.5 (0.01)	2.4 (0.01)
Functional group diversity	0.78 (0.06)	0.77 (0.06)	0.67 (0.05)

biomass findings are in agreement with a prior study demonstrating that dominant species of the southern tallgrass prairie (little bluestem and Indiangrass) constrained effects on aboveground biomass (Polley et al. 2007). Similar constraints have been observed with dominant species in northern tallgrass prairie (Smith and Knapp 2003). Ecosystem responses are largely influenced by these dominant species, which acquire a disproportionate share of the available resources. Novel here is that reducing intra- and interannual variability in precipitation not only had limited effects on aboveground biomass, but it also did not influence any of the plant diversity metrics (species diversity, species richness, species evenness, functional group richness, and diversity).

Our finding that total aboveground biomass did not respond to the reduced precipitation variability is consistent with a previous 5-yr study in remnant and restored mesic rangelands in this tallgrass prairie area where dominant C4 perennial grasses limited biomass response to variability in precipitation (Polley et al. 2007). Similarly, biomass of the C4 grass red grass (*Themeda triandra* Forssk) in the Serengeti was insensitive to a range of temporal variances in precipitation in a growth chamber experiment, provided the total amount remained unchanged (Williams et al. 1998). Also, physiological processes and biomass of the dominant C4 grass big bluestem (*Andropogon gerardii* Vitman) in northern tallgrass prairie were largely nonresponsive to long-term water manipulations over 3 yr (Silletti and Knapp 2001; Fay et al. 2002, 2003). Collectively, these findings suggest that responses of dominant C4 grasses constrain the effects of altered precipitation on aboveground biomass in mesic rangelands through disproportionate resource uptake (Smith and Knapp 2003; Polley et al. 2007).

Uncertainty regarding predictions for amounts, distributions and variability of precipitation in global change models (Christensen et al. 2007) makes it difficult to accurately forecast production and diversity responses for most rangeland ecosystems. For this rangeland ecosystem, however, extreme modifications in precipitation variability (e.g., protracted drought) may be needed to elicit aboveground biomass (e.g., Heisler-White et al. 2009) and plant diversity responses due to intrinsic high inter- and intra-annual precipitation variability (Harmel et al. 2003). Mitchell and Csillag (2001) proposed that stability of vegetation composition may be more important than simple changes in aboveground biomass for answering questions related to impacts regarding global change. Compensation among species and/or within functional groups likely reduced effects of species responses on community biomass in this study, although we did observe that one species, the annual forb firewheel, responded to reduced precipitation variability. Compensatory interactions among major components at both species and functional group levels led to community-level stability in biomass for an Inner Mongolia grassland (Bai et al. 2004).

MANAGEMENT IMPLICATIONS

Decreasing precipitation variability in this mesic rangeland did not elicit major aboveground biomass or plant diversity responses. Therefore, these simple responses regarding limited effects on total aboveground biomass, grass and forb biomass, and biomass of key species (C4 perennial grasses little bluestem and Indiangrass) and plant diversity metrics (species richness, species diversity, species evenness, and functional group richness and diversity) can assist land mangers with predicting effects of potential changes in precipitation for this rangeland. Ecosystem function will likely be little affected due to the lack of biomass and diversity responses. Ecosystem stability should be greater with less variation of biomass across years; for example, annual biomass differed by only about 20% even with a twofold difference in annual precipitation. Collectively, our findings indicate that constraints of the dominant grass species through resource uptake result in relatively stable biomass production and plant diversity in this southern tallgrass prairie ecosystem despite altered precipitation regimes, suggesting that this ecosystem is adaptable to changes in precipitation.

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