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# Relative effects of precipitation variability and warming on tallgrass prairie ecosystem function

**P. A. Fay**[1], **J. M. Blair**[2], **M. D. Smith**[3], **J. B. Nippert**[2], **J. D. Carlisle**[4], **and A. K. Knapp**[5]

[1]USDA ARS Grassland Soil and Water Research Laboratory, 808 E Blackland Rd., Temple, Texas 76502, USA
[2]Division of Biology, Kansas State University, Manhattan, Kansas 66506, USA
[3]Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06520, USA
[4]Utah Climate Center, Utah State University, Logan, Utah 84322, USA
[5]Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado 80523, USA

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**Abstract.** Precipitation and temperature drive many aspects of terrestrial ecosystem function. Climate change scenarios predict increasing precipitation variability and temperature, and long term experiments are required to evaluate the ecosystem consequences of interannual climate variation, increased growing season (intra-annual) rainfall variability, and warming. We present results from an experiment applying increased growing season rainfall variability and year round warming in native tallgrass prairie. During ten years of study, total growing season rainfall varied 2-fold, and we found ∼50–200 % interannual variability in plant growth and aboveground net primary productivity (ANPP), leaf carbon assimilation ($A_{CO_2}$), and soil $CO_2$ efflux ($J_{CO_2}$) despite only ∼40 % variation in mean volumetric soil water content (0–15 cm, $\Theta_{15}$). Interannual variation in soil moisture was thus amplified in most measures of ecosystem response. Differences between years in $\Theta_{15}$ explained the greatest portion (14–52 %) of the variation in these processes. Experimentally increased intra-annual season rainfall variability doubled the amplitude of intra-annual soil moisture variation and reduced $\Theta_{15}$ by 15 %, causing most ecosystem processes to decrease 8–40 % in some or all years with increased rainfall variability compared to ambient rainfall timing, suggesting reduced ecosystem rainfall use efficiency. Warming treatments increased soil temperature at 5 cm depth, particularly during spring, fall, and winter. Warming advanced canopy green up in spring, increased winter $J_{CO_2}$, and reduced summer $J_{CO_2}$ and forb ANPP, suggesting that the effects of warming differed in cooler versus warmer parts of the year. We conclude that (1) major ecosystem processes in this grassland may be substantially altered by predicted changes in interannual climate variability, intra-annual rainfall variability, and temperature, (2) interannual climate variation was a larger source of variation in ecosystem function than intra-annual rainfall variability and warming, and (3) effects of increased growing season rainfall variability and warming were small, but ecologically important. The relative effects of these climate drivers are likely to vary for different ecosystem processes and in wetter or drier ecosystems.

## 1 Introduction

Terrestrial ecosystems account for large exchanges of carbon (C) with the atmosphere (Denman et al., 2007), but the control of these fluxes by climate remains poorly understood. Precipitation and temperature are two primary elements of climate regulating ecosystem function. Important variation in precipitation and temperature, from an ecosystem perspective, occurs on daily to decadal time scales (Bonan, 2002; Goodin et al., 2002). Recent analyses of long-term weather records show that temperatures are warming at a rate not seen in the last century (Trenberth et al., 2007), and that areas of the Northern Hemisphere have experienced increased total annual precipitation, a greater proportion of precipitation in large events, and longer periods of drought (Groisman et al., 2005; Groisman and Knight, 2008). Projected increases in atmospheric $CO_2$ and other greenhouse gases are expected to reinforce these trends (Karl et al., 2009). These observed and expected changes in the means and variability of precipitation and temperature on inter- and intra-annual time scales will likely have important impacts on terrestrial ecosystem

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*Correspondence to:* P. A. Fay
(philip.fay@ars.usda.gov)

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structure and function, but these have been largely unexplored.

The conceptual framework for understanding ecosystem responses to precipitation variability originates in research on arid ecosystems showing that ecosystem responses to rainfall patterns depend on the temporal separation of rainfall pulses and the extent of inactivity between pulses (Noy-Meir, 1973). Soils play a crucial role by capturing discontinuous inputs of precipitation, and making it available for plant and microbial function in amounts and durations determined, in part, by soil physical properties, vegetation, and disturbance (Reynolds et al., 2004; Rodriguez-Iturbe and Porporato, 2004). Ecosystem responses to altered precipitation variability may differ among wet or dry systems or years, depending on how often thresholds of too little or too much soil moisture are exceeded (Knapp et al., 2008). For example, Heisler-White et al. (2009) found that increased growing season rainfall variability resulted in increased net primary productivity in semiarid grasslands, but decreased it in more mesic grasslands.

Previous studies in tallgrass prairie suggest that variation in precipitation at different temporal scales affects different aspects of ecosystem structure and function (Schwinning and Sala, 2004). For example, several studies have linked 2-fold or more interannual variation in aboveground net primary productivity (ANPP) to interannual variability in precipitation (Briggs and Knapp, 1995; Knapp et al., 2001; Huxman et al., 2004). Variation in the size and spacing of precipitation events within a growing season also affects numerous processes. A pattern of larger growing season rainfall events separated by longer dry intervals caused increased soil moisture variation and reduced ANPP, leaf carbon assimilation, and soil $CO_2$ efflux compared to the same total rainfall quantity distributed in smaller more frequent events (Mielnick and Dugas, 2000; Knapp et al., 2002; Fay et al., 2003a; Harper et al., 2005; Nippert et al., 2009).

Previous studies have found varying ecosystem responses to warming. Earlier spring greenup and flowering was reported in several studies (Badeck et al., 2004; Cleland et al., 2006; Sherry et al., 2007). Increased soil respiration is generally the most commonly found response to warming (Rustad et al., 2001), but both increases (Zhou et al., 2006), decreases (Liu et al., 2009), and soil moisture-dependent responses (Almagro et al., 2009) have been reported in grasslands. Similarly, warming generally increased aboveground biomass in a cross-biome meta-analysis (Rustad et al., 2001), but studies in grassland have reported no response (de Valpine and Harte, 2001; Dukes et al., 2005; Xia et al., 2009) or decreased aboveground productivity (De Boeck et al., 2008). Varying responses to warming in grassland likely reflect complex interactions among temperature, soil water availability and the temperature and moisture sensitivities of key plant and microbial physiological processes.

The influence of interannual variability in rainfall and temperature can make it difficult to assess the effects of intra-annual climatic variation (Nippert et al., 2006b). Interactions between warming and intra-annual rainfall variability may amplify interannual variation and create threshold changes in ecosystem structure (CCSP, 2010). An understanding of these interactions and their consequences for ecosystems requires long-term field experiments. Although there are long-term warming experiments (e.g. Saleska et al., 1999; An et al., 2005; Sherry et al., 2009), we know of no experiments in perennial grasslands that have manipulated growing season rainfall variability and warming for long enough to compare their effects to those of interannual climate variation. Grasslands are important and experimentally tractable systems for examining these issues because they cover approximately 40 % of the land surface, are rich and dynamic in biodiversity, are a globally important agricultural resource, and are at risk from degradation and habitat conversion. Understanding the basic functional responses of grasslands to multiple climate drivers over different time scales is critical for predicting impacts of future climate regimes on grasslands and their ability to sustainably provide ecosystem goods and services, such as food, fiber, and clean water, while maintaining biological diversity (Hoekstra et al., 2005).

Here we report results from the first 10 yr (1998–2007) of an ongoing experiment in a water-limited perennial tallgrass prairie in Kansas, in the middle of the North American Central Plains. In 1998, we began an experiment featuring an altered rainfall timing treatment that increased growing season rainfall variability, relative to ambient rainfall patterns, without changing total rainfall amount. In 2003, the increased rainfall variability regime was combined with a warming treatment. Here we extend previous studies (Knapp et al., 2002; Fay et al., 2003a; Harper et al., 2005; Nippert et al., 2009) by evaluating (1) the responsiveness of ecosystem processes to interannual climate variability vs. the responsiveness to increased within-growing season (intra-annual) rainfall variability, and (2) how the effects of increased inter- and intra-annual rainfall variability on ecosystem processes interact with and compare to those of experimental warming.

These objectives were addressed through measurements of the timing of plant growth and senescence, rates of plant biomass accumulation and flowering, leaf photosynthesis, and soil $CO_2$ efflux. We hypothesized that interannual climate variability would be the primary driver of interannual variability in ANPP, while increased intra-annual rainfall variability would be the primary driver of average rates of leaf photosynthesis and soil $CO_2$ efflux. We also hypothesized that interannual climate variability and increased intra-annual rainfall variability would have stronger effects on most ecosystem processes than warming in this grassland, which is in the center of the thermal range of the dominant species.

## 2 Methods

This study was conducted in the Rainfall Manipulation Plots (RaMPs) facility at the Konza Prairie Biological Station (KPBS) in northeastern Kansas, USA (39°05′ N, 96°35′ W). The vegetation of the site is dominated by $C_4$ grasses, primarily *Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, and *Sporobolus asper*, plus a number of $C_3$ forbs, primarily *Solidago canadensis*, *Aster ericoides*, and *S. missouriensis*. The climate is temperate midcontinental. Mean annual temperature is 13 °C, mid-growing season (July) mean temperature is 27 °C (range 20 to 33 °C), and mean annual precipitation is 835 mm. Total rainfall during the biologically most active portion of the growing season (1 May through 30 September) averages 635 mm, with the driest period during July and August. The RaMPs are located on Irwin silty clay loam soils, typical of lowland prairie in this region. The plots were burned each spring in late March, prior to green-up. Frequent fire was historically common in this grassland and today is a typical management practice (Knapp et al., 1998).

The RaMPs facility consists of twelve 14 × 9 m fixed-location rainout shelters covered from 1 May through 31 October by a clear polyethylene roof. The shelters exclude natural rainfall from the plots and divert the excluded rainfall to storage tanks for application to the plots using overhead sprinklers. Each shelter covers a hydrologically isolated 6 × 6 m sampling plot. See Fay et al. (2000) for additional details on the rainout shelter design.

### 2.1 Treatments

During Phase I, 1998–2001, four experimental rainfall treatments were applied in three replicates. The treatments were factorial combinations of two growing season rainfall quantities combined with two growing season rainfall patterns, as follows:

- Ambient: each time a natural rainfall event occurred, the quantity of rain that fell was applied to the plots within 24 h, replicating the naturally occurring rainfall regime in number and sizes of rainfall events, length of dry intervals between events, and total growing season amount.

- Reduced quantity: as in ambient, except 70 % of each rainfall event was applied.

- Altered pattern: intra-annual rainfall variability was increased by accumulating the collected rainfall until the dry interval was 50 % longer than the ambient dry interval. Then the accumulated rainfall was applied as a single large event, at a rate that insured all rainfall entered the soil profile. The total growing season amount of rainfall applied in this treatment was identical to ambient, while the number of rain events was reduced and the size of rain events and length of dry intervals were increased.

- Reduced quantity and altered pattern: as in altered pattern, except only 70 % of the accumulated rainfall was applied, which imposed both drought and increased rainfall variability.

All rainfall application amounts were reduced by 10 % from the nominal ambient amount to offset slight increases in soil moisture underneath the rainout shelters compared to the adjacent unsheltered control plots. In 2002, the reduced quantity treatment was discontinued as a transition to prepare for Phase II. All plots continued to receive their assigned rainfall timing treatment (ambient vs. altered) but all now received growing season rainfall amounts equivalent to 100 % of ambient, $n = 6$ per rainfall treatment.

Phase II began in 2003 with the initiation of a warming treatment. Infrared heating lamps (HS-2420, Kalglo Electronics Co, Bethlehem, PA, USA) were installed in two randomly chosen 2 × 2 m subplots within the 6 × 6 m rainfall treatment plots. The lamps were operated continuously year round, and emitted a constant 20–25 $\mathrm{W\,m^{-2}}$ of downward infrared radiation. Lamps were placed 1.2 m above the soil surface at the beginning of each growing season and raised periodically to maintain that height above the plant canopy. The lamps are identical to those of other grassland warming experiments (Luo et al., 2001), and here increased day (0.4–0.6 °C) and night (1.0–1.5 °C) canopy temperatures of a 2 × 2 m area during May through August. Two additional 2 × 2 m subplots were unwarmed and thus experienced ambient temperatures. One unwarmed subplot contained a dummy lamp to control for effects from the physical presence of the lamps and associated infrastructure.

### 2.2 Microclimate and ecosystem function measurements

Sensors were installed to measure rainfall, soil temperature, and soil water content. Natural rainfall quantities were measured with six manual rain gauges. Soil temperature was measured with thermocouples at 5 cm depth ($T_{\mathrm{soil}_{05}}$) in two ambient and two altered rainfall plots during 1998–2003, and in the center of each of the four subplots in three ambient and three altered plots during 2004–2007. $T_{\mathrm{soil}_{05}}$ was logged every 30 min and stored as 1 h averages on data loggers (CR10X, Campbell Scientific, Logan, UT, USA).

Soil volumetric water content at 0–15 cm depth ($\Theta_{15}$) was measured using time domain reflectometry methods. Probes consisting of a pair of 15 cm long stainless steel rods were inserted vertically at the soil surface at four locations per plot (Phase I), or in the center of each subplot (Phase II). During 1998–2004, these probes were read weekly using a Tektronix cable tester. Beginning in 2005, $\Theta_{15}$ was measured with 30 cm long probes (CS616, Campbell Scientific, Logan, UT, USA) inserted at 30°. $\Theta_{15}$ was logged every 10 min and stored as 30 min averages on data loggers. We used the daily average $\Theta_{15}$ of one day per week from the continuous data to match the sampling frequency of the pre-2005 $\Theta_{15}$ data.

## 2.3 Plant growth measurements

### 2.3.1 Canopy greenness

Spring canopy green up and fall canopy senescence was quantified in the 2005–2007 growing seasons by measuring percent green cover with a digital canopy camera (First Growth, Decagon Devices Inc., Pullman, WA, USA). Each subplot was imaged between 09:00 and 12:00 LT every four to seven days following the first appearance of new spring growth (∼late April) until canopy closure (mid–late June), and from the onset of canopy decline until frost (∼late August–October). Percent green cover was estimated by a proprietary algorithm in the camera processor, which estimated the ratio of green pixels to total pixels in the image. The camera was calibrated with a white card prior to each sampling, to control for variation in illumination among sample dates.

### 2.3.2 Canopy light penetration

Light interception by the canopy was determined at midseason as a proxy of accumulated midseason aboveground biomass. Vertical profiles of photosynthetic photon flux density (PPFD) were measured with a ceptometer (Decagon Devices Inc., Pullman, WA, USA) at 10 cm increments to the maximum canopy height (<1 m). Profiles were measured between 12:00 and 14:00 at two locations per plot during 1999–2002, and one location per subplot during 2003–2007 on 2–4 clear days each July. Light profiles were fit with a sigmoid equation:

$$\mathrm{PPFD} = a/(1-e^{(x-x_0)/b}) \qquad (1)$$

where $a$ = maximum PPFD, $x_0$ = height of 50 % PPFD and $b$ = slope of PPFD decrease. Smaller $x_0$ values indicate that the height of interception of 50 % of the light is closer to the ground, and deeper penetration of light into the canopy means less aboveground biomass. Seven out of 300 profiles did not fit this equation at $p < 0.0001$, and were omitted from analysis.

### 2.3.3 Aboveground net primary productivity

ANPP was estimated annually from harvests of aboveground biomass at the end of the growing season (mid October). All aboveground biomass was clipped at ground level from $20 \times 50$ cm sampling quadrats. Ten quadrats per plot were harvested during 1998–2002, and four quadrats per subplot (16 per plot) were harvested during 2003–2007. The plots were burned each spring and ungrazed, so accumulated aboveground biomass represented current year production. Harvested samples were sorted into grasses and forbs, and weighed after drying at 65 °C for at least 48 h. One plot differed markedly in plant species composition from the others and was omitted from the biomass analyses. Data from 1998–2002 were reported in Knapp et al. (2002) and Fay et al. (2003a).

### 2.3.4 Flowering

Flowering culms of *Andropogon gerardii* and *Sorghastrum nutans* were counted each September in two locations per plot during 1999–2002, and once per subplot during 2003–2007.

## 2.4 Measurements of $CO_2$ fluxes

### 2.4.1 Leaf photosynthesis

Leaf net photosynthesis ($A_{CO_2}$) was measured weekly from June through September in 1998 and 1999, and one to three times per month in June, July, and August in 2000, 2002, and 2005–2006 on *A. gerardii*. *Solidago canadensis* was also measured during 1998–2000, and *S. nutans* was measured in 2002, 2005 and 2006. Sampling dates were chosen to capture the full range of growing season soil moisture variability.

$A_{CO_2}$ during 1998–2002 was measured with two annually calibrated closed path infrared gas analyzers (LI-6200, LI-Cor Biosciences, Lincoln, NE, USA). $A_{CO_2}$ was measured on four plants per plot, using fully expanded, recently matured upper canopy leaves, and was completed between 10:00 h–15:00 h. The 1998–1999 weekly measurements usually were conducted on cloud-free days. Measurements were omitted from analysis if PPFD was <500 µmol m$^{-2}$ s$^{-1}$, and entire plots were omitted from analysis when plot mean PPFD was <1000 µmol m$^{-2}$ s$^{-1}$. This data filtering resulted eliminated 7 % (244 out of 3488) measurements. All measurements during 2000 and 2002 were conducted on clear days.

$A_{CO_2}$ during 2005–2006 was measured with two open path infrared gas analyzers (LI-6400, LI-Cor, Biosciences, Lincoln, NE, USA) with red/blue LED light sources and $CO_2$ injectors. Measurements were conducted in one warmed subplot and one unwarmed subplot per plot. Each measurement used one recently matured leaf per tiller from two tillers per species. Cuvette conditions were 1500 µmol m$^{-2}$ s$^{-1}$ PPFD, 370 µmol mol$^{-1}$ ($CO_2$), and near ambient relative humidity. This PPFD is adequate for light saturation and comparable to light levels in the 1998–2002 data. Measurements were logged when stability (the coefficient of variation of $A_{CO_2}$) was <1 % over 15 s. Measurements usually stabilized in 5–10 min. Data from 1999 were reported in Fay et al. (2002), and from 2005–2006 in Nippert et al. (2009).

### 2.4.2 Soil $CO_2$ *fluxes*

Soil $CO_2$ efflux ($J_{CO_2}$) was measured with an infrared gas analyzer (LI-6200, LI-Cor Biosciences Inc., Lincoln, NE). During the growing season, $J_{CO_2}$ was measured weekly each May through October. Winter $J_{CO_2}$ was measured on 7–9 snow-free dates during November through March in 2005/2006 and 2006/2007. $J_{CO_2}$ was measured at two permanently installed PVC collars (8 cm diam, 1.7 cm height inserted to 1.2 cm) at four locations per plot during 1998–2002, and at two collars per subplot from 2003–2007. Data from 1998–2001 were reported in Harper et al. (2005). $J_{CO_2}$ rates were estimated from the linear rise in $CO_2$ concentration over 1 to 3 min.

### 2.5 Data analysis

Intra-annual rainfall variability was quantified by computing the coefficient of variation (CV) from the daily rainfall amounts applied to the RaMPs during the growing season (1 May–30 September). Mean growing season $\Theta_{15}$ was computed by averaging the weekly measurements for each year. Variability during the growing season in $\Theta_{15}$ was quantified by computing two variability metrics: (1) the CV of $\Theta_{15}$, which expresses temporal variability in mean $\Theta_{15}$ as a percentage of $\Theta_{15}$; (2) the mean change in soil moisture between successive individual rainfall events ($\Delta\Theta_{15}$), which describes the absolute amplitude of variation in $\Theta_{15}$.

Statistical analyses of soil moisture and ecosystem process responses to treatments and year were conducted using linear mixed models procedures in SAS 9.1 (SAS Institute Inc, 2003) in two steps. First, a repeated measures model was fit to data from all ten years with rainfall pattern (ambient vs. altered) as a fixed effect in a randomized complete block design (RCB), year as the repeated effect, and plot as the experimental unit. Type III sums of squares were used to orthogonally compare the effect of interannual climate variability versus effects of increased intra-annual rainfall variability.

Second, separate repeated measures models were fit to the two phases of the experiment. The model for Phase I (1998–2002) contained rainfall pattern and quantity and their interaction as fixed effects in RCB, year as the repeated effect, and plot as the experimental unit. Type III sums of squares were again used to compare effects of interannual climate variation against effects of intra-annual variability and quantity treatments. The model for Phase II (2003–2007) contained rainfall pattern as a whole-plot fixed effect in RCB, warming as a subplot fixed effect, and year as the repeated effect. This model compared interannual climate variation to increased rainfall variability and warming effects. For responses measured multiple times during the growing season (i.e. soil moisture means and variability, midseason biomass, $A_{CO_2}$, $J_{CO_2}$), the growing season mean was used for analysis, calculated by averaging values from individual sample dates in each year. Transformations were applied to response variables where needed to meet assumptions of normality and/or equal variances. Means separations were performed using the LSMEANS statement with the DIFF option. Full ANOVA results are presented in the Appendix (Tables A1, A2).

We used multiple regression (MR) analysis to determine which among mean $\Theta_{15}$, $CV_{\Theta_{15}}$, or $T_{soil_{05}}$ explained more variation in key ecosystem responses. Grass and forb ANPP, $A_{CO_2}$, and $J_{CO_2}$ were analyzed with a stepwise procedure with $p = 0.10$ required for variable retention. Variance inflation factors for the predictor variables ranged from 1.2 ($T_{soil_{05}}$) to 1.7 ($CV_{\Theta_{15}}$), suggesting that multicollinearity among the predictor variables was low. Univariate regression analyses of these variables were also conducted.

## 3 Results

### 3.1 Microclimate

#### 3.1.1 Rainfall

Total growing season rainfall inputs (May–September) varied 1.8–fold between years, from 334 mm in 2005 to 600 mm in 1998 (Fig. 1a). The altered rainfall treatment dramatically changed growing season rainfall regimes. Event sizes were larger, small events became infrequent, and dry intervals increased compared to the ambient rainfall pattern (Fig. 1b). As a result, the CV of individual rainfall events was significantly greater in 9 out of 10 yr in the altered treatment compared to ambient (Fig. 1c, $p < 0.0001$, Table A1). The reduced quantity treatment during Phase I caused only minor though significant ($p = 0.01$) variation in rainfall CV.

#### 3.1.2 Mean soil moisture

There were significant differences among years in growing season mean soil moisture. Under ambient rainfall, $\Theta_{15}$ ranged from 27 % in 2002 to 38 % in 1999 (Fig. 1d, $p < 0.0001$, Table A1). Altered rainfall patterns reduced $\Theta_{15}$ to about 86 % of ambient values for the 10 yr combined ($p = 0.0025$), even though the treatments received the same total rainfall amounts. The reduced quantity treatment reduced $\Theta_{15}$ to 90 % of ambient values ($p = 0.01$), similar to the magnitude of the altered rainfall effect. $\Theta_{15}$ was marginally reduced ($p = 0.094$) in warmed compared to unwarmed subplots, due to significant differences in 2006 (1.9 %, $p = 0.009$) and 2007 (1.8 %, $p = 0.01$).

#### 3.1.3 Soil moisture variability

Altered rainfall patterns increased $CV_{\Theta_{15}}$ (16 %) and $\Delta\Theta_{15}$ (2-fold) (Fig. 1e, $p < 0.01$, Table A1), indicating greater soil moisture variability during the growing season and a greater amplitude of soil moisture change between sequential rainfall events. $CV_{\Theta_{15}}$ was a decreasing function of $\Theta_{15}$ (Fig. 2, $R^2 = 0.38$, $p < 0.0001$), indicating that lower mean soil moisture was often accompanied by greater growing season soil moisture variability. $\Delta\Theta_{15}$ was weakly correlated with $\Theta_{15}$ ($R^2 = 0.07$, $p < 0.0001$), indicating that the amplitude of soil moisture change between events was only loosely associated

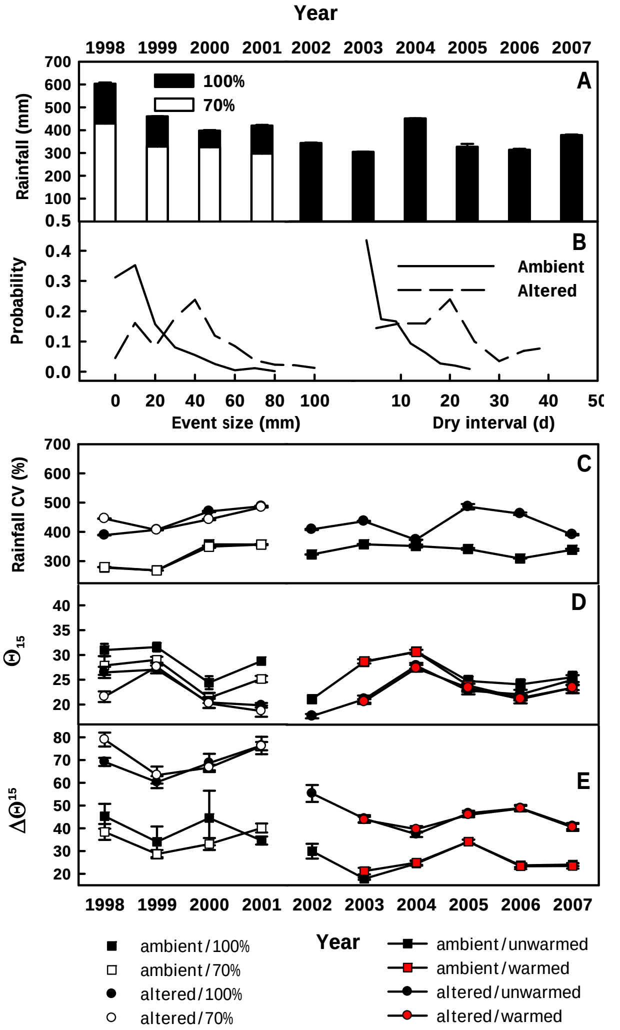

**Fig. 1.** Annual rainfall inputs and soil moisture means and variability in the RaMPs experiment during the rainfall pattern $x$ quantity treatments (Phase I, 1998–2001) and the rainfall pattern $x$ warming treatments (Phase II, 2003–2007). **(A)** Total growing season rainfall. **(B)** Probability density functions of individual rainfall event size (100 % treatments) and dry interval length. **(C)** Coefficient of variation (CV) of daily rainfall inputs during the growing season. **(D)** Mean volumetric soil water content for 0–15 cm ($\Theta_{15}$). **(E)** Mean change in $\Theta_{15}$ between successive rainfall events ($\Delta\Theta_{15}$). Error bars denote one SE.

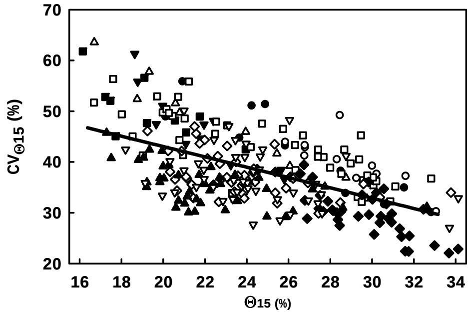

**Fig. 2.** Association between growing season mean volumetric soil water content for 0–15 cm ($\Theta_{15}$) and its coefficient of variation ($\mathrm{CV}_{\Theta_{15}}$). Each point represents a plot, and symbols denote different years.

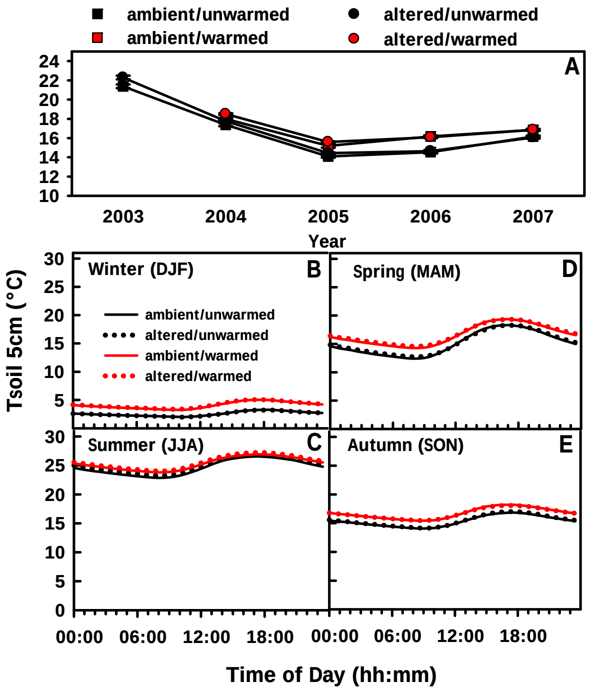

**Fig. 3.** Soil temperature at 5 cm depth ($T_{\mathrm{soil}_{05}}$) by rainfall pattern and warming treatment during 2003–2007. **(A)** Mean annual soil temperature, error bars denote 1 SE. **(B–E)** Diurnal variation in $T_{\mathrm{soil}_{05}}$ for each season.

with mean soil moisture, and likely more dependent on rain event size. $\Delta\Theta_{15}$ and $\mathrm{CV}_{\Theta_{15}}$ were unaffected by reduced rainfall quantity ($0.06 < p < 0.19$, Table A1) and $\Delta\Theta_{15}$ was unaffected by warming ($p = 0.23$).

### 3.1.4 Soil temperature

$T_{\mathrm{soil}_{05}}$ differed significantly among years (Fig. 3a, $p < 0.0001$, Table A1), varying by 3 °C during 2004–2007. However, $T_{\mathrm{soil}_{05}}$ varied considerably more among seasons than among years. Winter $T_{\mathrm{soil}_{05}}$ averaged 2–4 °C, increasing to 15–17 °C during spring and fall, and 24–26 °C during summer (Fig. 3b–e). $T_{\mathrm{soil}_{05}}$ differed 2–3 °C between day and night, regardless of season.

The warming treatment caused a 1 °C overall increase in mean annual $T_{\mathrm{soil}_{05}}$ during 2004–2007 (Fig. 3a, $p < 0.0001$, Table A1), with the increase varying from 0.7 °C in 2004 to 1.5 °C in 2006 ($p < 0.0001$). Warming caused larger increases in $T_{\mathrm{soil}_{05}}$ during fall, winter and spring (1.3–1.6 °C) compared to summer (0.7 °C, all $p < 0.0001$, Fig. 3b–e). Warming effects on $T_{\mathrm{soil}_{05}}$ were similar day and night.

## 3.2 Plant growth responses

### 3.2.1 Canopy greenness

Warming was the largest factor affecting canopy green up during spring. During late April and May (weeks 15–20) when green up was most rapid, warming increased greenness by 13–96 % compared to unwarmed subplots (Fig. 4, $p < 0.0001$, Table A2). Differences among years in canopy greenness were highly significant ($p < 0.0001$) but much smaller (3 %, data not shown) than the effect of warming. Altered rainfall patterns caused no significant effects on greenness during weeks 15–20 ($p = 0.34$). However, as the season progressed (early June, weeks 20–22), the warming effect diminished and altered rainfall patterns reduced greenness ~8 % compared to ambient rainfall ($p = 0.0079$). Canopy senescence in the late summer/fall showed small but significant ($p < 0.0001$) differences among years, but no significant warming or rainfall effects (Table A2).

### 3.2.2 Midseason aboveground biomass

There were large differences among years in canopy light levels at midseason ($x_0$, height of interception of 50 % of the light), a direct measure of canopy structure and a proxy for aboveground biomass. Across all years, $x_0$ varied almost 2-fold (Fig. 5a, $p < 0.0001$, Table A2), while altered rainfall patterns reduced $x_0$ 17 % ($p = 0.016$), indicating less aboveground biomass at midseason. Altered rainfall reduced $x_0$ in all years during Phase I ($p = 0.04$), while during Phase II $x_0$ was significantly reduced in 2004 and 2005 ($p < 0.001$). Warming only affected $x_0$ in 2007, increasing it by 15 % ($p = 0.0002$).

### 3.2.3 Aboveground net primary productivity

For all years combined, total ANPP varied 2-fold among years (Fig. 5b, $p < 0.0001$, Table A2), while altered rainfall reduced total ANPP by an average of 10 % compared to ambient rainfall ($p = 0.0098$, Table A2). During Phase I, altered pattern and reduced quantity treatments both reduced total ANPP by 15 % compared to ambient ($0.004 < p < 0.03$, Table A2). However, total ANPP was not affected by altered rainfall patterns during Phase II ($p \geq 0.12$). Warming caused a ~5 % reduction in Phase II ANPP ($p < 0.039$).

Grass ANPP accounted for 80 % of total ANPP and varied to a similar degree among years ($p < 0.0001$, Fig. 5c). Grass ANPP was not affected by altered rainfall patterns, but increased in 2007 in response to warming ($p = 0.017$, Table A2). Forb ANPP showed little variation among years except for an increase in 2007 (Fig. 5d, $p < 0.0001$, Table A2). Warming had the strongest effects on forb ANPP, reducing it 23 % compared to unwarmed subplots ($p = 0.04$), with no significant difference in warming effects among years ($p = 0.91$). There were no significant effects of rainfall treatments on forb ANPP ($p > 0.40$).

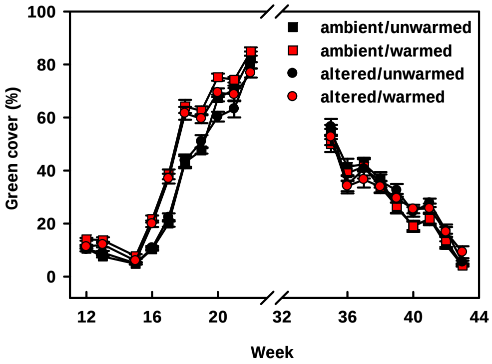

**Fig. 4.** Cover of green vegetation (%) during spring and fall, by rainfall pattern and warming treatment during 2005–2007. Error bars denote 1 SE.

### 3.2.4 Flowering

Flowering culm production in *A. gerardii* and *S. nutans* was low in most years but was abundant in 1999 and 2004 (Fig. 5e–f, $p < 0.0001$, Table A2). *A. gerardii* flowering did not differ between rainfall or warming treatments ($0.16 < p < 0.70$, Table A2). In contrast, altered rainfall patterns reduced *S. nutans* flowering by 50 % for all years combined ($p = 0.0036$), as well as in both Phase I and II ($0.006 < p < 0.04$, Table A2). Warming treatments had no effects on flowering culm production for *S. nutans*.

## 3.3 Plant and soil $CO_2$ flux responses

### 3.3.1 Leaf carbon assimilation

There were large differences among years in $A_{CO_2}$ for the codominant grasses *A. gerardii* and *S. nutans*. Mean $A_{CO_2}$ in *A. gerardii* varied 3-fold among years (Fig. 6a, $p < 0.0001$, Table A1), and was reduced 8 % by altered rainfall patterns for all years combined ($p = 0.03$) because of significant effects in 1998, 2000, and 2002. During Phase I, *A. gerardii* $A_{CO_2}$ was unaffected by the reduced quantity treatment (data not shown, $p > 0.46$, Table A1). For *S. nutans*, $A_{CO_2}$ varied 80 % among years (Fig. 6b, $p < 0.0001$), and was reduced by altered rainfall patterns in 2002 ($p = 0.007$). Warming had no effect on $A_{CO_2}$ for either grass. In contrast, *S. canadensis* showed little interannual variation in $A_{CO_2}$ and no response to altered rainfall patterns. However, the reduced quantity treatment decreased *S. canadensis* $A_{CO_2}$ by 10 % compared to ambient quantity ($p < 0.05$, Table A1), mainly because of a large decrease in 2000 (Fig. 6b). For all three species, $\Theta_{15}$ was reduced by 8 to 38 % ($0.07 > p > 0.0001$) in years when alterations in rainfall timing and/or quantity caused significant reductions in $A_{CO_2}$.

### 3.3.2 Soil $CO_2$ *fluxes*

Mean growing season $J_{CO_2}$ varied by 46 % among years, ($p < 0.0001$, Fig. 7a, Table A1). Altered rainfall patterns

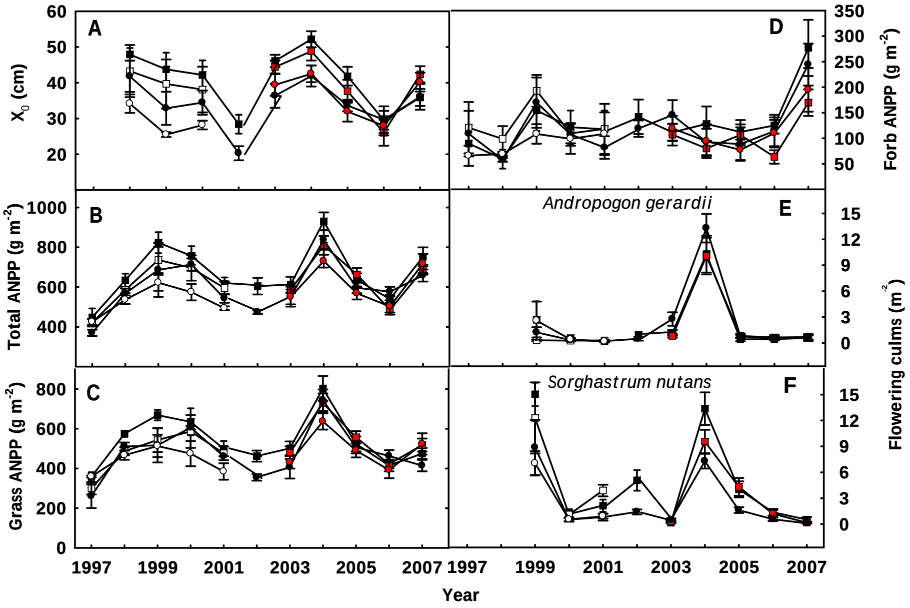

**Fig. 5.** Plant growth by year in the rainfall pattern and warming treatments, error bars denote 1 SE. Symbols as in Fig. 1. **(A)** Canopy light interception ($x_0$), the height in the canopy receiving 50 % of incoming light, a proxy for aboveground biomass. **(B)** Total, **(C)** grass and **(D)** forb ANPP. Flowering culm production in the dominant $C_4$ grasses **(E)** *Andropogon gerardii* and **(F)** *Sorghastrum nutans*.

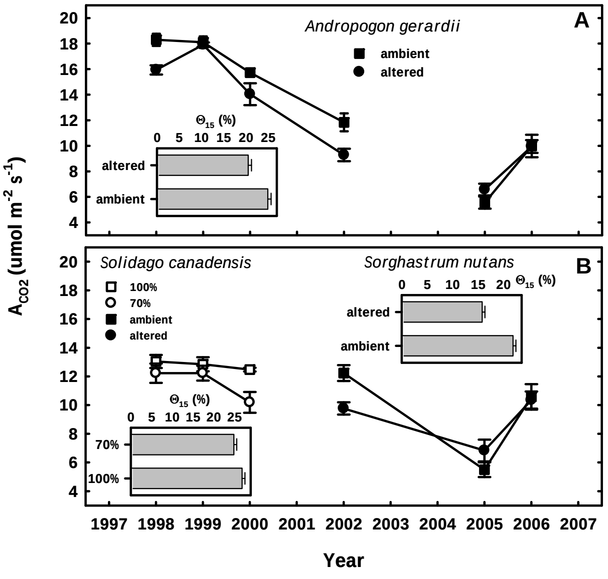

**Fig. 6.** Leaf photosynthesis ($A_{CO_2}$) by rainfall treatment for **(A)** *Andropogon gerardii* ($C_4$) and **(B)** *Sorghastrum nutans* ($C_4$), and *Solidago canadensis* ($C_3$). Insets: mean 0–15 cm volumetric soil water content ($\Theta_{15}$) for years when altered rainfall caused significant reductions in $A_{CO_2}$. Error bars denote 1 SE of the mean.

reduced $J_{CO_2}$ by 8 % ($p = 0.0005$), with similar reductions each year ($p = 0.18$). During Phase I, altered rainfall reduced $J_{CO_2}$ by 13 % (Fig. 7b, $p < 0.0001$), while the reduced quantity treatment caused a 7 % decrease ($p = 0.032$). During Phase II, altered rainfall patterns marginally reduced $J_{CO_2}$ compared to ambient rainfall (Fig. 7c, $p = 0.08$), and warming reduced $J_{CO_2}$ by 5 % compared to ambient ($p = 0.04$). $J_{CO_2}$ was much lower during winter than during the growing season, and increased 11 % with warming ($p = 0.003$, Fig. 7d). Winter $J_{CO_2}$ was unaffected by altered growing season rainfall patterns.

### 3.3.3 Correlations with soil moisture and temperature

Total and grass ANPP, $J_{CO_2}$, and $A_{CO_2}$ for all three species increased with $\Theta_{15}$ ($0.14 < R^2 < 0.52$, $0.0001 < p < 0.003$, Fig. 8a–c, Table 1), while forb ANPP was not correlated with $\Theta_{15}$ ($p = 0.48$). Grass ANPP and $J_{CO_2}$ decreased with $CV_{\Theta_{15}}$, ($R^2 = 0.04 - 0.22$, $0.0001 < p < 0.01$ Fig. 8d–e). $A_{CO_2}$ was not correlated with $CV_{\Theta_{15}}$ for any of the species, although the variability in $A_{CO_2}$ decreased with $CV_{\Theta_{15}}$ (Fig. 8f). $A_{CO_2}$ in *A. gerardii* and *S. nutans* were increasing functions of $T_{soil_{05}}$ ($R^2 = 0.04 - 0.12$, $0.007 < p < 0.04$, data not shown).

$\Theta_{15}$ was the first variable to enter multiple regression models for total ANPP, grass ANPP, and $A_{CO_2}$, accounting for 18–52 % of the variation ($0.0001 < p < 0.009$, Table 1). $CV_{\Theta_{15}}$ was the second variable to enter the MR model for grass and forb ANPP, and *A. gerardii* $A_{CO_2}$, explaining an additional 2–7 % of variation in these variables ($0.0001 < p < 0.003$). $CV_{\Theta_{15}}$ did not enter models for $A_{CO_2}$ of *S. canadensis* or *S. nutans*. Thus, $\Theta_{15}$ consistently explained more of the variation in these ecosystem processes. $J_{CO_2}$ followed a different pattern. $CV_{\Theta_{15}}$ was first to enter the MR model ($R^2 = 0.27$, $p < 0.0001$) followed by $\Theta_{15}$ ($R^2 = 0.11$, $p < 0.0001$). $T_{soil_{05}}$ entered the MR models last or not at all, accounting for only 1–6 % of

**Table 1.** Regression parameters and statistics for mean soil moisture at 15 cm depth ($\Theta_{15}$), intra-annual season soil moisture variability at 15 cm depth ($\mathrm{CV}_{\Theta_{15}}$), and soil temperature at 5 cm depth ($T_{\mathrm{soil}_{05}}$) from univariate and multivariate regression models for ANPP, leaf photosynthesis, and soil $CO_2$ efflux.

| | | | Univariate Regression | | | | | Multiple Regression | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Intercept | Slope | $R^2$ | $p$ | | Partial $R^2$ | Model $R^2$ | $F$ | $p$ |
| ANPP | Total | $\Theta_{15}$ | 279.0 | 1480.0 | 0.16 | <0.0001 | $\Theta_{15}$ | 0.19 | 0.19 | 44.9 | <0.0001 |
| | | $\mathrm{CV}_{\Theta_{15}}$ | 890.0 | −6.4 | 0.10 | <0.0001 | $\mathrm{CV}_{\Theta_{15}}$ | – | – | – | |
| | | $T_{\mathrm{soil}_{05}}$ | – | – | – | <0.11 | $T_{\mathrm{soil}_{05}}$ | 0.02 | 0.21 | – | 0.0192 |
| | Grass | $\Theta_{15}$ | 118.0 | 1621.0 | 0.18 | <0.0001 | $\Theta_{15}$ | 0.18 | 0.18 | 41.6 | <0.0001 |
| | | $\mathrm{CV}_{\Theta_{15}}$ | 831.0 | −8.1 | 0.15 | <0.0001 | $\mathrm{CV}_{\Theta_{15}}$ | – | – | – | |
| | | $T_{\mathrm{soil}_{05}}$ | – | – | – | 0.15 | $T_{\mathrm{soil}_{05}}$ | 0.105 | 0.20 | 3.6 | 0.0576 |
| | Forb | $\Theta_{15}$ | – | – | – | 0.32 | $\Theta_{15}$ | – | – | – | – |
| | | $\mathrm{CV}_{\Theta_{15}}$ | 59.5 | 1.7 | 0.01 | 0.02 | $\mathrm{CV}_{\Theta_{15}}$ | 0.02 | 0.02 | 4.4 | 0.0125 |
| | | $T_{\mathrm{soil}_{05}}$ | – | – | – | 0.80 | $T_{\mathrm{soil}_{05}}$ | 0.02 | 0.04 | 3.2 | 0.0049 |
| Leaf photosynthesis | *A. gerardii* | $\Theta_{15}$ | 0.011 | 57.9 | 0.52 | <0.0001 | $\Theta_{15}$ | 0.52 | 0.52 | 103.8 | <0.0001 |
| | | $\mathrm{CV}_{\Theta_{15}}$ | – | – | – | 0.11 | $\mathrm{CV}_{\Theta_{15}}$ | 0.08 | 0.61 | 20.4 | <0.0001 |
| | | $T_{\mathrm{soil}_{05}}$ | 28.75 | 0.66 | 0.04 | 0.04 | $T_{\mathrm{soil}_{05}}$ | 0.02 | 0.63 | 5.8 | 0.018 |
| | *S. nutans* | $\Theta_{15}$ | 3.05 | 36.74 | 0.19 | 0.005 | $\Theta_{15}$ | 0.19 | 0.19 | 13.6 | 0.003 |
| | | $\mathrm{CV}_{\Theta_{15}}$ | – | – | – | 0.38 | $\mathrm{CV}_{\Theta_{15}}$ | – | – | – | – |
| | | $T_{\mathrm{soil}_{05}}$ | −14.48 | 0.95 | 0.12 | 0.007 | $T_{\mathrm{soil}_{05}}$ | 0.08 | 0.27 | 6.1 | 0.019 |
| | *Grasses combined* | $\Theta_{15}$ | 0.40 | 54.34 | 0.44 | <0.0001 | $\Theta_{15}$ | 0.44 | 0.44 | 122.9 | <0.0001 |
| | | $\mathrm{CV}_{\Theta_{15}}$ | 7.19 | 0.10 | 0.02 | 0.03 | $\mathrm{CV}_{\Theta_{15}}$ | 0.08 | 0.52 | 26.8 | <0.0001 |
| | | $T_{\mathrm{soil}_{05}}$ | – | – | – | 0.46 | $T_{\mathrm{soil}_{05}}$ | 0.01 | 0.54 | 3.5 | <0.0001 |
| | *S. canadensis* | $\Theta_{15}$ | 7.04 | 19.8 | 0.19 | 0.004 | $\Theta_{15}$ | 0.22 | 0.22 | 9.4 | 0.009 |
| | | $\mathrm{CV}_{\Theta_{15}}$ | – | – | – | 0.14 | $\mathrm{CV}_{\Theta_{15}}$ | 0.10 | 0.32 | 5.0 | 0.0322 |
| | | $T_{\mathrm{soil}_{05}}$ | – | – | – | 0.22 | $T_{\mathrm{soil}_{05}}$ | – | – | – | – |
| Soil $CO_2$ flux | | $\Theta_{15}$ | 5.19 | 12.04 | 0.18 | <0.0001 | $\mathrm{CV}_{\Theta_{15}}$ | 0.27 | 0.27 | 60.3 | <0.0001 |
| | | $\mathrm{CV}_{\Theta_{15}}$ | 11.65 | −0.09 | 0.28 | <0.0001 | $T_{\mathrm{soil}_{05}}$ | 0.06 | 0.33 | 15.5 | 0.0001 |
| | | $T_{\mathrm{soil}_{05}}$ | – | – | – | 0.90 | $\Theta_{15}$ | 0.11 | 0.44 | 31.2 | <0.0001 |

variation in total ANPP, forb ANPP, $J_{CO_2}$, and *S. nutans* $A_{CO_2}$ ($0.0001 < p < 0.02$), and not entering models for grass ANPP or $A_{CO_2}$ of *A. gerardii* or *S. canadensis*.

## 4 Discussion

Results from ten years of experimental rainfall manipulation and five years of warming treatments encompassing a wide range of natural climatic variability show that interannual climate variation, increased intra-annual (growing season) rainfall variability, and warming all affected key ecosystem processes. There was more interannual variation in ecosystem function than there was from intra-annual rainfall variability and warming. However the relatively smaller effects of intra-annual rainfall variability and warming still caused significant effects on some processes.

### 4.1 Interannual variability caused greater effects than increased intra-annual rainfall variability on most ecosystem processes

Our analyses demonstrated that large (nearly 2-fold) interannual variation in total (May–September) rainfall resulted in ∼40 % interannual variation in growing season mean soil moisture ($\Theta_{15}$). The magnitude of interannual rainfall variability was greater than that of interannual mean soil moisture variability because of the limited capacity for soil to store rainfall (Brady and Weil, 2002; Rodriguez-Iturbe and Porporato, 2004). Nonetheless, variation in $\Theta_{15}$ was associated with 50 to 300 % variation in rates of key ecosystem processes. High interannual variation in total ANPP resulted from high variation in grass ANPP (Fig. 5a, b), which is consistent with previous studies (Briggs and Knapp, 1995; Knapp et al., 2001). In contrast, forb ANPP was relatively constant among years (Fig. 5d), as reported in previous studies (Knapp et al., 2001). Interannual variation in flowering of the codominant grasses was also high, but qualitatively different from that of total ANPP. Flowering was high only during the two years with the highest $\Theta_{15}$ (1999 and 2004), and was consistently low in other years, suggesting there is a threshold total rainfall requirement for flowering in these grasses. Craine et al. (2010) also found a threshold requirement for grass flowering in this grassland. A rainfall regime with more frequent drought years could result in fewer flowering events, potentially lowering future inputs to the seed bank from these grasses.

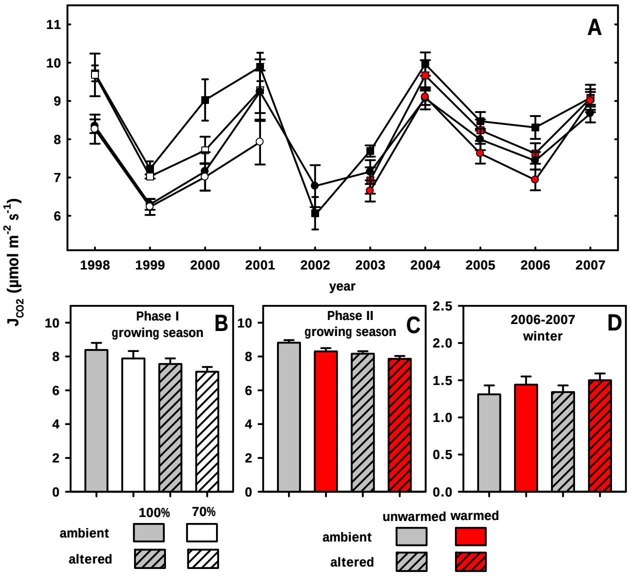

**Fig. 7.** Soil CO$_2$ efflux ($J_{CO_2}$) by rainfall and warming treatments. **(A)** Mean growing season $J_{CO_2}$ by year, symbols as in Fig. 1. Growing season mean $J_{CO_2}$ during **(B)** Phase I and **(C)** Phase II. **(D)** Winter $J_{CO_2}$ by rainfall pattern and warming during 2006–2007. Note that scaling for **(D)** differs from that for **(B–C)**. Error bars denote 1 SE of the mean.

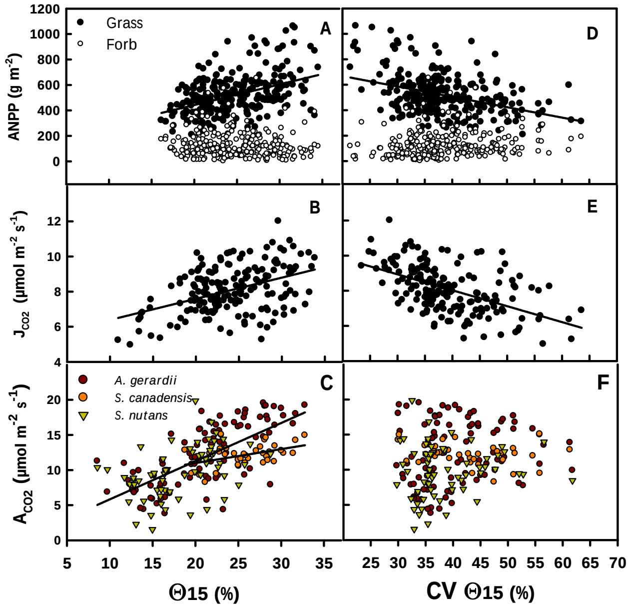

**Fig. 8.** Correlations of grass and forb aboveground net primary productivity (ANPP), growing season means of leaf photosynthesis ($A_{CO_2}$) and soil CO$_2$ flux ($J_{CO_2}$) with 0–15 cm volumetric soil water content ($\Theta_{15}$) and the coefficient of variation of $\Theta_{15}$ ($CV_{\Theta_{15}}$). Regression statistics are shown in Table 1.

Interannual variability in $A_{CO_2}$ of the grasses was of comparable magnitude to that of total ANPP. We expected interannual variability to have a smaller effect on $A_{CO_2}$ relative to that of intra-annual rainfall variability, because $A_{CO_2}$ in these grasses decreases strongly with soil moisture depletion, and recovery is often slow when soil moisture is restored, especially after extended drought (Knapp, 1985; Heckathorn et al., 1997). Leaf level photosynthesis has been associated with long-term plant success in this grassland (McAllister et al., 1998), and the ability to track soil moisture variability is crucial to the success of the grasses (Swemmer et al., 2006; Nippert et al., 2006a). The finding that $A_{CO_2}$ was strongly correlated with $\Theta_{15}$ (Table 1) suggests that on average, $A_{CO_2}$ was strongly coupled to interannual climate variation and associated interannual differences in soil water supply.

High responsiveness in grass $A_{CO_2}$ to interannual variation was consistent with grass growth responses. For example, grass ANPP and $A_{CO_2}$ was more highly correlated with $\Theta_{15}$ than was forb ANPP and $A_{CO_2}$ (Table 1). C$_4$ grasses such as *A. gerardii* and *S. nutans* typically have higher photosynthetic rates and experience greater variation in plant water status than forbs (Knapp, 1984; Turner et al., 1995; McAllister et al., 1998; Nippert et al., 2006a). Stable isotope studies of soil water use by C$_4$ grasses at the Konza site shows that they rely on surface soil water regardless of landscape location, soil water availability, or time of year, while forbs increase their dependence on deeper soil moisture as surface soils dry (Nippert and Knapp, 2007a, b). Such differential access to soil moisture among species and functional groups could provide a mechanism for increased temporal variability in community structure under more variable rainfall regimes.

### 4.2 Increased intra-annual rainfall variability reduced rates of ecosystem processes, other things being equal

The altered rainfall timing treatment markedly changed the probability distributions of rainfall inputs (Fig. 1b), increasing the variability in rainfall by creating longer dry periods and larger rainfall events. This translated directly to increased soil moisture variability and reduced mean $\Theta_{15}$ in some or all years, caused by the prolonged periods of low soil moisture during the longer dry periods. This confirms and extends our previous findings of the effects of increased rainfall variability on soil moisture dynamics in this grassland (Knapp et al., 2002; Fay et al., 2003a, 2008). Since total rainfall inputs were unchanged, increased rainfall variability reduced the effective storage of rainfall in the upper part of the soil profile.

We found that soil moisture variability was a decreasing function of mean soil moisture (Fig. 2). In contrast, we previously reported that soil moisture variability was independent of mean soil moisture in our experiment (Knapp et al., 2002; Fay et al., 2003a). However, the current finding is based on a longer data set, emphasizing the need for long-term manipulations that capture enough natural rainfall variability to correctly show the relationship of interannual variation in soil moisture (Davidowitz, 2002).

Increased intra-annual rainfall variability significantly affected most ecosystem processes when compared to an equal amount of rainfall at ambient variability. However, the effects of interannual variation for soil moisture and most ecosystem processes were considerably larger than the effect of increased intra-annual variability (Fig. 9a inset) and most ecosystem processes. Increased rainfall variability reduced plant growth and leaf and soil $CO_2$ fluxes only 8–17 % despite the large increase in the amplitude of soil moisture variability ($\Delta\Theta_{15}$). This confirms and extends our earlier findings (Knapp et al., 2002). The reduction in rates of ecosystem processes with altered rainfall timing suggest that increased rainfall variability increased water limitation in this grassland. The result of increased water limitation may be a grassland that is more sensitive to interannual climate variation (Huxman et al., 2004).

The magnitude of interannual variation in $J_{CO_2}$ (∼46 %) was less than interannual variation in leaf carbon assimilation or total ANPP. A similar magnitude of interannual variation in $J_{CO_2}$ was reported in a semiarid grassland by Liu et al. (2009) and in an annual grassland by Chou et al. (2009). However, in the multiple regression analysis, $CV_{\Theta_{15}}$ explained more variation in $J_{CO_2}$ than did $\Theta_{15}$, suggesting that $J_{CO_2}$ was actually more strongly associated with intra-annual rainfall variability. This result could be explained if soil moisture variability disproportionately affected belowground processes such as allocation of current photosynthate to roots, root biomass, litter decomposition, or microbial biomass or substrate availability (Luo and Zhou, 2006), resulting in greater reductions in overall belowground metabolic activity compared to those from mean soil moisture.

### 4.3 Warming effects occur at different times of year than intra-annual rainfall effects

The warming treatment raised soil temperature, especially during spring, fall, and winter. The most apparent effects of warming were found in canopy greenness, soil respiration, and forb ANPP. The marked increase in spring canopy greenness indicates that warming advanced ecosystem phenology. This result is consistent with findings from larger spatial scales (Badeck et al., 2004). Warming effects on canopy greenness diminished and were replaced by altered rainfall effects from late spring through the remainder of the growing season. This result suggests a transition from temperature control of early spring canopy greenness to control by rainfall variability. The lack of late season response to warming contrasts with some studies, where warming led to earlier senescence in annual grassland (Zavaleta et al., 2003) and increased fall green aboveground biomass (Wan et al., 2005). In this system, the lack of late warming response could be explained by several mechanisms, such as acclimation to warming over the growing season, possibly combined with inadequate late season soil moisture (Gielen et al., 2005).

The warming treatment reduced mean growing season $J_{CO_2}$ by about 5 %. Liu et al. (2009) also found reduced $J_{CO_2}$ with experimental warming in semiarid grassland, while warming increased annual $J_{CO_2}$ in Oklahoma tallgrass prairie (Zhou et al., 2006). An increase in soil respiration of about 20 % with warming was typical across grassland, forest, and desert ecosystems (Rustad et al., 2001). $J_{CO_2}$ is an increasing function of soil temperature and a quadratic function of soil moisture in our experiment (Harper et al., 2005). Our finding of lower $J_{CO_2}$ despite warmed soil may mean that lower soil moisture offset the stimulatory effect of warming. The quadratic response of $J_{CO_2}$ to soil moisture may explain why warming may cause lower $J_{CO_2}$ with reduced soil moisture in some cases (Liu et al., 2009) or higher $J_{CO_2}$ with reduced soil moisture in others (Zhou et al., 2006).

In contrast, warming caused a marked increase in $J_{CO_2}$ during winter. This suggests that winter soil respiration was primarily limited by soil temperature. Similarly, Almagro et al. (2009) found that soil respiration increased with soil temperature during moist, cool conditions. The increase in winter $CO_2$ efflux, while small in absolute terms, would still affect total annual soil $CO_2$ efflux. As a result, annual responses in soil respiration to global changes cannot be inferred from short-term or growing season measurements, but the entire year must be accounted for.

Reduced forb ANPP was the most consistent effect of the warming treatment on plant growth. Specific mechanisms for this response cannot be deduced from the present dataset, but may include altered aboveground or belowground competitive interactions with grasses, based on, for example, differences in growth rates, allocation patterns or photosynthetic efficiencies. Because forbs contribute much of the plant diversity in these grasslands, warming may be a stronger driver of biodiversity change over time than increased rainfall variability. However, reduced forb ANPP only translated into reduced total ANPP in two out of five years. This overall lack of strong warming responses in ANPP indicated that following spring green up, rainfall variability was the main driver of biomass accumulation. Warming did not affect biomass production in annual grassland (Dukes et al., 2005), forb biomass in alpine meadow (de Valpine and Harte, 2001), or grass and forb biomass in semiarid Mongolian steppe (Xia et al., 2009). However warming reduced aboveground biomass in experimental grassland assemblages grown in a cool temperate climate, due to lower soil moisture (De Boeck et al., 2008). The weak effect of the warming treatment on total ANPP was consistent with the MR finding that $T_{soil_{05}}$ explained little variation in these processes. Wan et al. (2005) and Klein et al. (2005) reported similar results in grasslands.

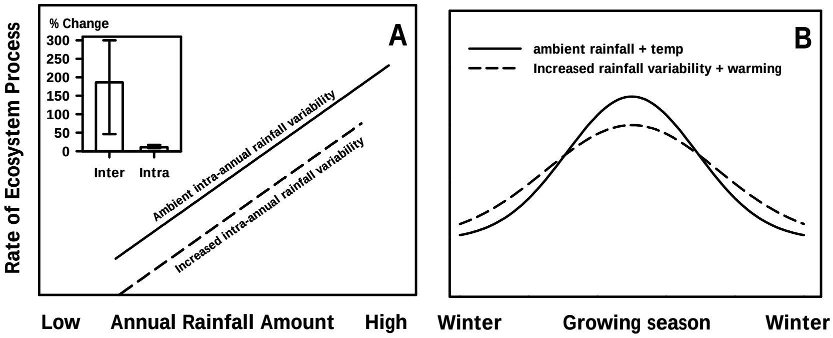

**Fig. 9.** Conceptual model of the coupled effects of **(A)** Annual rainfall amount and increased intra-annual rainfall variability, showing here the simplest case of a linear relationship of ecosystem function with rainfall amount for this ecosystem, and **(B)** increased intra-annual rainfall variability and warming on ecosystem processes. The inset shows the mean and range of the % change in four primary ecosystem processes (aboveground net primary productivity, midseason aboveground biomass, $A_{CO_2}$ of *A. gerardii*, and $J_{CO_2}$) to interannual and intra-annual (increased rainfall variability) effects.

### 4.4 A conceptual model of the coupling of rainfall variability and warming

The findings from the first ten years of this experiment suggest that interannual climate variation, increased growing season rainfall variability, and warming can be hypothesized to exert effects on this grassland ecosystem in the following ways.

1. Interannual climate variation, mainly in growing season rainfall total, drives interannual variation in average soil moisture and rates of key ecosystem processes (Fig. 9a).
2. Increased intra-annual (growing season) rainfall variability reduces rates of most ecosystem processes compared to ambient rainfall patterns with the same total amount of rainfall. This reduction in ecosystem function (*sensu* Hui et al., 2003) is an indicator of lower ecosystem rainfall use efficiency resulting from greater temporal variability in growing season soil moisture.
3. Within a growing season (Fig. 9b), warming likely stimulates ecosystem processes during cooler parts of the growing season (e.g. spring canopy development, winter $CO_2$ efflux), but during the middle, warmer and water-limited portion of the growing season, increased rainfall variability and warming effects where they occur likely reduce rates of ecosystem processes. This sequential difference in the effects of warming and increased intra-annual rainfall variability changes the seasonal dynamics of ecosystem processes, compared to ambient temperature and variability.

This framework reveals several gaps in our understanding of the effects of rainfall and temperature variability on this grassland, indicating important areas for further research.

1. For the ranges of rainfall amounts and ecosystem responses in this study, we suggest a linear relationship between rainfall amount and average rates of ecosystem processes (Fig. 9a). However over a larger range of rainfall, asymptotic or threshold responses could occur.
2. In the simplest, linear case, increased intra-annual rainfall variability will decrease ecosystem processes equally at all rainfall amounts (Fig. 9a). However if ecosystem responses to rainfall amount prove to be nonlinear, we would expect greater effects of increased rainfall variability at intermediate rainfall amounts. Variability effects will decrease at high rainfall amounts because of less frequent soil moisture deficit, and at low rainfall amounts because of lower overall soil moisture.
3. The interactive effects of rainfall amount and intra-annual variability (Fig. 9a), and the transitions between effects of rainfall variability and warming (Fig. 9b) will likely differ among processes.

## 5 Conclusions

For several major ecosystem processes in this grassland interannual variability was the strongest driver, followed by intra-annual rainfall variability and warming. The nature of the relationship between intra-annual rainfall variability and warming has important implications for understanding the effects of climate change on this grassland, and its ability to sustainably provide food and fiber while supporting biological diversity and other ecosystem goods and services. Future research should seek explanation for how the interactive effects of these drivers may change in wetter or drier ecosystems (Knapp et al., 2008; Heisler-White et al., 2009), and examine daily to weekly variability, which strongly affects soil moisture and $CO_2$ fluxes (Fay et al., 2003b; Ogle and Reynolds, 2004; Harper et al., 2005).

## Appendix A

**Table A1.** Analysis of variance *F* statistics for rainfall and soil moisture variation responses to pattern, quantity, and warming treatments in RaMPs.

| | Rainfall CV | $\Theta_{15}$ | $\Delta\Theta_{15}$ | $CV_{\Theta_{15}}$ | $T_{\mathrm{soil}_{05}}$ | Soil $CO_2$ *flux* | Leaf photosynthesis | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | *A. gerardii* | *S. canadensis* | *S. nutans* |
| 1998–2007 | | | | | | | | | |
| Pattern | $2907.8^{c}$ | $15.5^{b}$ | $819.0^{c}$ | $9.1^{a}$ | $11.1^{a}$ | $25.2^{c}$ | $4.1^{a}$ | – | 0.1 |
| Year | $87.0^{c}$ | $44.9^{c}$ | $127.2^{c}$ | $69.3^{c}$ | $352.2^{c}$ | $21.8^{c}$ | $95.0^{c}$ | – | $31.4^{c}$ |
| Year * Pattern | $52.0^{c}$ | $11.2^{c}$ | $26.3^{c}$ | $7.6^{c}$ | 1.2 | 1.4 | $4.2^{b}$ | – | $5.9^{b}$ |
| 1998–2001 | | | | | | | | | |
| Pattern | $26809.0^{c}$ | $60.0^{c}$ | $95.5^{c}$ | $40.5^{c}$ | – | $30.4^{c}$ | $7.4^{a}$ | 0.8 | – |
| Quantity | $8.2^{a}$ | $14.2^{a}$ | 0.1 | 5.2 | – | $5.0^{a}$ | 0.0 | $8.2^{a}$ | – |
| Pattern * Quantity | $24.6^{c}$ | $1.9^{c}$ | 1.2 | 1.8 | – | 0.1 | 0.9 | 2.0 | – |
| Year | $234.5^{c}$ | $65.4^{c}$ | $8.3^{b}$ | $11.2^{c}$ | – | $31.6^{c}$ | $32.5^{c}$ | 3.3 | – |
| Year * Pattern | $88.7^{c}$ | $8.7^{b}$ | 1.6 | $7.5^{b}$ | – | 0.2 | $8.1^{b}$ | 1.0 | – |
| Year * Quantity | $126.8^{c}$ | 2.6 | 1.4 | 1.6 | – | 1.0 | 0.8 | 1.4 | – |
| Year * Pattern * Quantity | $83.8^{c}$ | 2.1 | 2.0 | 1.1 | – | 0.8 | 2.4 | 1.1 | – |
| 2003–2007 | | | | | | | | | |
| Pattern | $1542.0^{c}$ | $13.0^{b}$ | $787.4^{c}$ | $20.1^{b}$ | $8.0^{a}$ | 3.8 | 0.7 | – | 1.0 |
| Warming | – | 2.9 | 0.3 | 0.0 | $219.8^{c}$ | $4.4^{a}$ | 3.3 | – | 1.6 |
| Pattern * Warming | – | 0.3 | 0.2 | 1.1 | 0.0 | 0.4 | 0.1 | – | 0.3 |
| Year | $52.4^{c}$ | $115.0^{c}$ | $53.1^{c}$ | $98.9^{c}$ | $731.5^{c}$ | $62.6^{c}$ | $45.0^{c}$ | – | $50.9^{c}$ |
| Year * Pattern | $97.9^{c}$ | $24.6^{c}$ | $39.5^{c}$ | $5.6^{c}$ | $6.1^{c}$ | 1.0 | 0.4 | – | 1.4 |
| Year * Warming | – | 2.0 | 0.7 | $3.1^{a}$ | $15.5^{c}$ | 2.0 | 0.0 | – | 0.1 |
| Year * Pattern * Warming | – | 0.9 | 1.2 | 0.4 | 2.5 | 0.2 | 0.3 | – | 0.2 |

[a] $p < 0.05$; [b] $p < 0.01$; [c] $p < 0.001$

**Table A2.** Analysis of variance *F* statistics for vegetation responses to pattern, quantity, and warming treatments in RaMPs.

| | Canopy greenness | | | Canopy light penetration | Aboveground net primary productivity | | | Plant reproduction | |
|---|---|---|---|---|---|---|---|---|---|
| | Weeks 15–20 | Weeks 20–22 | Weeks 35–43 | $x_0$ | Total | Grass | Forb | *A. gerardii* | *S. nutans* |
| 1998–2007 | | | | | | | | | |
| Pattern | – | – | – | $6.0^{a}$ | $8.9^{b}$ | 2.1 | 0.8 | 0.3 | $14.3^{b}$ |
| Year | – | – | – | $65.6^{c}$ | $28.3^{c}$ | $26.2^{c}$ | $10.5^{c}$ | $45.8^{c}$ | $76.5^{c}$ |
| Year * Pattern | – | – | – | $2.2^{a}$ | 1.4 | 0.9 | 0.4 | 0.9 | $3.4^{b}$ |
| 1998–2001 | | | | | | | | | |
| Pattern | – | – | – | $5.7^{a}$ | $12.2^{b}$ | 3.8 | 0.4 | 0.1 | $13.6^{b}$ |
| Quantity | – | – | – | 2.0 | $5.9^{a}$ | 4.1 | 0.1 | 0.2 | 0.1 |
| Pattern * Quantity | – | – | – | 0.1 | 0.2 | 0.0 | 0.2 | 1.0 | 0.0 |
| Year | – | – | – | $11.2^{c}$ | $12.4^{c}$ | $9.1^{c}$ | $14.8^{c}$ | 2.0 | $40.8^{c}$ |
| Year * Pattern | – | – | – | 2.5 | 0.4 | 0.3 | 0.2 | 0.2 | 1.5 |
| Year * Quantity | – | – | – | 0.0 | 0.4 | 0.4 | 1.2 | 0.6 | 3.8 |
| Year * Pattern * Quantity | – | – | – | 0.0 | 0.3 | 1.6 | 0.8 | 1.6 | 1.7 |
| 2003–2007 | | | | | | | | | |
| Pattern | 1.0 | $10.8^{c}$ | 2.4 | 3.5 | 2.7 | 0.7 | 0.1 | 0.6 | $5.1^{a}$ |
| Warming | $161.5^{c}$ | $17.3^{c}$ | 0.7 | 0.0 | $4.7^{a}$ | 0.0 | $4.8^{a}$ | 2.1 | 1.3 |
| Pattern * Warming | 3.5 | 0.3 | 0.0 | 0.3 | 0.1 | 0.1 | 0.7 | 1.0 | 0.5 |
| Year | $240.6^{c}$ | $50.5^{c}$ | $69.3^{c}$ | $80.4^{c}$ | $49.8^{c}$ | $51.6^{c}$ | $18.4^{c}$ | $209.4^{c}$ | $275.1^{c}$ |
| Year * Pattern | 0.3 | 0.4 | 1.7 | $8.1^{c}$ | 1.9 | 1.4 | 0.8 | $2.9^{a}$ | $9.8^{c}$ |
| Year * Warming | $22.8^{c}$ | 0.5 | 1.4 | $5.9^{c}$ | 2.0 | $3.1^{a}$ | 0.2 | 0.4 | 0.8 |
| Year * Pattern * Warming | 1.8 | 0.1 | 0.0 | 0.8 | 0.9 | 1.6 | 0.4 | 1.0 | 2.4 |

[a] $p < 0.05$; [b] $p < 0.01$; [c] $p < 0.001$

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