Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change

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Abstract

Climate change is causing measurable changes in rainfall patterns, and will likely cause increases in extreme rainfall events, with uncertain implications for key processes in ecosystem function and carbon cycling. We examined how variation in rainfall total quantity (Q), the interval between rainfall events (I), and individual event size (S_E) affected soil water content (SWC) and three aspects of ecosystem function: leaf photosynthetic carbon gain (A_{CO_2}), aboveground net primary productivity (ANPP), and soil respiration (J_{CO_2}). We utilized rainout shelter-covered mesocosms (2.6 m³) containing assemblages of tallgrass prairie grasses and forbs. These were hand watered with 16 $I \times Q$ treatment combinations, using event sizes from 4 to 53 mm. Increasing Q by 250% (400–1000 mm yr⁻¹) increased mean soil moisture and all three processes as expected, but only by 20–55% ($P \leq 0.004$), suggesting diminishing returns in ecosystem function as Q increased. Increasing I (from 3 to 15 days between rainfall inputs) caused both positive (A_{CO_2}) and negative (J_{CO_2}) changes in ecosystem processes (20–70%, $P \leq 0.01$), within and across levels of Q, indicating that I strongly influenced the effects of Q, and shifted the system towards increased net carbon uptake. Variation in S_E at shorter I produced greater response in soil moisture and ecosystem processes than did variation in S_E at longer I, suggesting greater stability in ecosystem function at longer I and a priming effect at shorter I. Significant differences in ANPP and J_{CO_2} between treatments differing in I and Q but sharing the same S_E showed that the prevailing pattern of rainfall influenced the responses to a given event size. Grassland ecosystem responses to extreme rainfall patterns expected with climate change are, therefore, likely to be variable, depending on how I, Q, and S_E combine, but will likely result in changes in ecosystem carbon cycling.

Keywords: carbon cycle, climate change, mesocosm, photosynthesis, productivity, rainout shelter, soil moisture, soil respiration, tallgrass prairie

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Introduction

The impacts of climate change on terrestrial ecosystems are the focus of considerable scientific and public interest because of the potential impacts on ecosystem function, as well as concern over the maintenance of ecosystem services (Parson *et al.*, 2003; Bennett *et al.*, 2005; Groisman *et al.*, 2005). Most climate change scenarios forecast an increasing occurrence of extreme precipitation events (Christensen & Hewitson, 2007), which will likely result in increased intra-annual rainfall variability. Indeed, increases in both total rainfall amounts and in the frequency of extreme events have been documented and are likely to continue during the 21st century (Karl & Knight, 1998; Easterling *et al.*, 2000; Groisman *et al.*, 2005; Alley *et al.*, 2007).

Intra-annual variability in rainfall is one level in a hierarchy that describes the rainfall regimes at time scales ranging from seasons to decades (Greenland,

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1999; Goodin *et al.*, 2002). Each level plays an important role in ecosystem function, and interannual variability in total rainfall quantity, Q, has been the most extensively studied (Weltzin & McPherson, 2003). However, intra-annual variation in individual event size, S_E, and the interval between individual events, I, more closely matches the time scales (days to weeks) most relevant to the plant and microbial processes regulating productivity and carbon cycling (Schwinning & Sala, 2004). Variation at this scale is considerably less well understood. For example, many studies demonstrated the importance of pulsed events for photosynthesis, soil respiration, decomposition, and other ecosystem processes (Ogle & Reynolds, 2004), but only recently have field experiments begun to show that a pattern of increased intra-seasonal variability alters rates of ecosystem processes compared with less variable conditions (Knapp *et al.*, 2002; Fay *et al.*, 2003; Loik, 2007; Maestre & Reynolds, 2007).

The magnitude and direction of responses to variation in I and S_E may depend on several factors, including the threshold event size for different ecosystem processes (Ogle & Reynolds, 2004), total rainfall (i.e. Q; Weltzin & McPherson, 2003), topoedaphic factors (Swemmer *et al.*, 2007), the abundance and variability of other limiting resources (e.g. N; Maestre & Reynolds, 2007), and species and life stage (Lundholm & Larson, 2004; Swemmer *et al.*, 2006). In addition, antecedent patterns in rainfall and soil moisture may either prime or inhibit responses of ecosystem processes (Loik, 2007; Sponseller, 2007), potentially leading to differential responses among key ecosystem processes controlling C cycling (Schwinning & Sala, 2004; Potts *et al.*, 2006). However, general models of these responses have not yet emerged.

We conducted an experiment to examine the possible impacts of extreme rainfall events on key aspects of carbon cycling in experimental grasslands composed of C_4 grasses and C_3 forbs and legumes in a novel rainfall manipulation facility in NE Kansas, USA (Fig. 1). The experiment focused on three primary questions. (1) How does the effect of variation in I differ with Q? This question addresses the hierarchical relationship between intra- and interannual rainfall variability. (2) Do ecosystem processes respond similarly to variation in I, Q, and S_E? This question addresses the effects of rainfall variability on the balance among pools and fluxes of carbon. (3) How do ecosystem processes respond to the same S_E produced by different I/Q combinations? This question addresses how ecosystem function may be primed, or inhibited, by the overall pattern of variability. To answer these questions, we measured the responses in soil water content (SWC) and three key processes involved in ecosystem function and C cycling:

Fig. 1 The Rainfall Mesocosm facility at the Konza Prairie Biological Station in NE Kansas, USA, showing a $400\,\mathrm{mm\,yr^{-1}}$ mesocosm (left) and an adjacent $1000\,\mathrm{mm\,yr^{-1}}$ mesocosm (right).

(1) leaf-level photosynthesis (A_{CO_2}) in the dominant C_4 grass, *Andropogon gerardii*, (2) aboveground net primary production (ANPP), and (3) soil CO_2 efflux from autotrophic + heterotrophic respiration (J_{CO_2}) to varying I at four levels of Q, using a range of modest to extreme S_E. These ecosystem processes represent the primary flux of CO_2 into the system (A_{CO_2}), the annual flux of C through the vegetation as represented by current year aboveground plant biomass (ANPP), and the primary flux of CO_2 out of the system and into the atmosphere (J_{CO_2}). Our primary hypothesis was that more extreme events (longer I and/or larger S_E) would cause declines in A_{CO_2}, ANPP, and J_{CO_2} due to the inhibitory effects of amplified soil moisture variability on biological activity (Fay *et al.*, 2003). Grassland systems are ideal for this research because they respond rapidly to resource manipulations, are often highly productive and species-rich, cover 40% of US land area, and are a globally important agroecological resource. Extreme rainfall events may be especially important drivers of ecosystem function in grasslands, where in most years evapotranspiration exceeds rainfall.

Methods

This study was conducted in the Rainfall Mesocosm facility at the Konza Prairie Biological Station, a Long-Term Ecological Research site in Kansas, USA (39.1°N, 96.9°W). The facility contains $64–2.6\,\mathrm{m^3}$ mesocosms; for this study, each mesocosm was assigned to one of the 16 watering treatments: $I = 3$, 6, 10, or 15-day dry

Table 1 Summary statistics describing the 16 watering treatments and temporal variability in the soil water content (SWC)

| Quantity (Q, mm yr^{-1}) | Interval (I, days) | Water applications | | | | Soil water content* | |
		Event size (S_E, mm)	No. of water events	$\sum$ Water input (mm)†	CV (%)‡	Amplitude (%)§	CV (%)¶
400	3	4.3	50	214.4	141.2	3.86	13.63
400	6	8.6	25	214.7	223.5	9.25	13.89
400	10	14.3	15	215.8	300.3	16.31	16.55
400	15	21.4	10	214.6	374.1	24.15	21.94
600	3	6.4	50	325.6	141.9	4.12	15.94
600	6	12.9	25	322.3	223.5	13.69	13.33
600	10	21.4	15	325.5	300.9	20.23	18.00
600	15	32.1	10	321.7	374.1	27.34	20.15
800	3	8.6	50	428.9	141.2	5.53	11.22
800	6	17.1	25	427.0	223.7	12.38	13.17
800	10	28.6	15	428.9	299.9	24.17	16.66
800	15	42.9	10	428.6	374.1	25.86	18.23
1000	3	10.7	50	537.0	141.2	5.04	12.40
1000	6	21.4	25	537.1	223.5	12.45	12.00
1000	10	35.7	15	536.7	299.9	26.50	17.03
1000	15	53.6	10	536.0	374.1	29.40	17.65
Konza growing season mean 1983–2001 (April–August)							
835	6.4	17.8	27.7	493.3	300.2		

*SWC values are for the complete watering cycles between 6 June and 3 September, the months of most rapid growth and biomass accumulation.

†Total water input is for the beginning of the growing season through peak aboveground biomass (April 7 through September 3, 2004).

‡Calculated using a value of 0 mm for days without water inputs.

§Mean percent decrease in SWC per watering cycle.

¶Calculated from daily mean SWC values.

periods crossed with $Q = 400$, 600, 800, or 1000 mm yr^{-1} in a randomized complete block design ($n = 4$ mesocosms trt^{-1}). S_E ranged from 4 to 53 mm per water application. The association between I, Q, and S_E is presented in Table 1. These levels of I, Q, and S_E bracketed current rainfall regimes in grasslands of the US Central Plains, likely encompassed most future rainfall scenarios (Alley *et al.*, 2007), and created a realistic pattern and range of variability in soil moisture (Fig. 2a and b; Porporato *et al.*, 2006). The rainfall treatments were initiated in April 2004, and applied with a metered hand sprayer, using water from an onsite well. Water was applied at the soil surface, so there were no losses to canopy interception or runoff. Seventy-five percent of the assigned Q were applied during the growing season (April–October), reflecting the typical seasonal distribution of rainfall in this region.

The mesocosms were constructed of plastic-lined wood, and arranged in two, 2×16 arrays underneath an 11×25 m rainout shelter (Rainbow Plus, Stuppy Greenhouse Manufacturing Inc., North Kansas City, MO, USA). The shelter had open walls and ends, eaves 2.4 m high to maximize air movement and heat dissipa-

tion, and a roof of clear corrugated polycarbonate (DynaGlas Plus, SPS International, San Jose, CA, USA) that allowed > 90% light transmission. Each mesocosm housed a $1.44 \text{ m}^2 \times 1.8$ m deep reconstructed soil profile that was planted in April 2003 with seeds of three C_4 perennial warm season grasses, *A. gerardii*, *Schizachyrium scoparium*, and *Sorghastrum nutans*; greenhouse propagated seedlings of seven forbs, *Asclepias tuberosa*, *Aster ericoides*, *Echinacea angustifolia*, and *Liatris punctata*; and legumes, *Amorpha canescens*, *Lespedeza capitata*, and *Psoralea tenuiflora*. The species were planted in an identical spatial arrangement to minimize initial differences in species interactions across treatments. The mesocosms were watered as needed during plant establishment.

SWC was determined in the top 30 cm of the soil profile in each mesocosm every 2 h during the study using three-rod waveguides connected to an automated time domain reflectometry system (TDR 100, Campbell Scientific, Logan, UT, USA).

A_{CO_2} of *A. gerardii* was measured in mid-July (2004), a critical period in the growing season when this species achieves maximum vegetative growth. *A. gerardii*
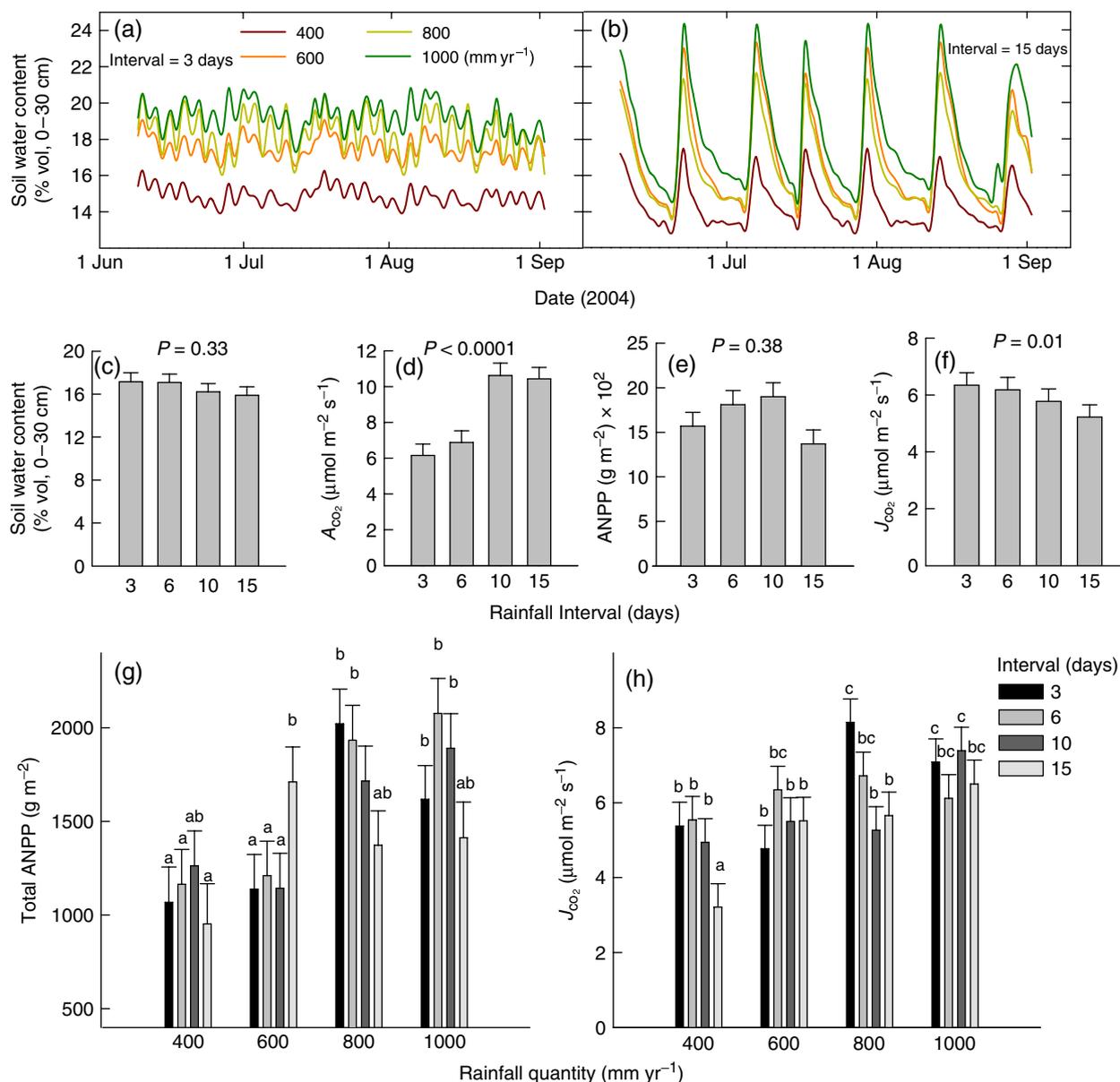
Fig. 2 Soil water content and ecosystem processes. (a, b) Growing season time courses of mean soil water content for the four Q treatments in mesocosms watered at 3 or 15-day intervals. (c–f) Means of soil water content, A_{CO_2}, ANPP, and J_{CO_2} by I averaged over the four Q treatments. (g, h) Means of ANPP and J_{CO_2} for the 16 $I \times Q$ treatments. Error bars denote ±1 SE of the mean.

accounts for a large fraction of the biomass in tallgrass prairie and in the mesocosm species assemblages. Leaves were measured under wet (1 day after watering) and dry (1 day before the next watering) conditions for each interval treatment with an infrared gas analyzer (LiCor 6400, Li-COR Biosciences, Lincoln, NE, USA) using a blue-red (85:15) light source providing 1500 μmol m^{-2} s^{-1} illumination. Each measurement used two to three fully expanded upper canopy leaves from two different tillers of typical size and vigor, with two soil measurements per mesocosm per day con-

ducted between 1000 and 1400 CDT. Data presented here are the average of the wet and dry measurements.

ANPP was quantified at peak growing season biomass (late summer 2004) by clipping aboveground plant biomass from three 0.1 m^2 quadrats per mesocosm, sorting to species, and weighing after drying to constant mass. All previous year aboveground standing dead biomass was removed just before the beginning of the growing season (April 2004), so ANPP could be directly determined from the aboveground biomass.

J_{CO_2} was measured eight times during May–September 2004 with a portable infrared gas analyzer (LI-6200, Li-COR Inc.) and an $850 \, cm^3$ soil chamber with sampling area of $40.7 \, cm^2$. The chamber was placed on PVC collars (1.7 cm height, 8 cm diameter) to reduce disturbance and spatial variation in J_{CO_2} between sample dates. For a measurement, chamber $[CO_2]$ was reduced below ambient (< 360 ppm) before placing the chamber, and once the rate of $[CO_2]$ increase stabilized (usually ≤ 1 min), J_{CO_2} was sampled over a 20 s interval. Measurements were taken from two collars per mesocosm on each sample date.

Statistical analyses of soil moisture and the ecosystem processes were conducted in SAS v 9.1 (SAS Institute, Cary, NC, USA), using the PROC MIXED method of maximum likelihood estimation (Littell *et al.*, 1996). The analyses were conducted using a randomized complete blocks model to examine the main effects and interactions of I and Q, and using an analysis of covariance model with unequal slopes (I as main effect, S_E as covariate) to examine how the sensitivity of ecosystem processes to changing S_E differed among the I treatments. ANOVA results are presented in Table 2.

Results

The watering treatments caused large effects on soil moisture dynamics. Increasing I from 3 to 15 days caused a sixfold increase in the mean amplitude of change in SWC between watering events and a 50% increase in the CV of SWC ($P < 0.0001$; Fig. 2a and b, Table 1), indicating that longer I strongly increased the variability in 0–30 cm SWC. In addition, longer I caused a small, statistically nonsignificant decrease in mean growing season SWC (7% $P = 0.33$; Fig. 2c). In contrast, Q set the overall level of SWC, but had much less effect on temporal variability. As Q increased from 400 to $1000 \, mm \, yr^{-1}$ (a 250% change), the mean growing season SWC increased by only 20% ($P < 0.0043$; Table 3), accompanied by only a modest increase in the amplitude of SWC ($P = 0.0007$) and no effect on the CV of SWC ($P = 0.12$). No significant $I \times Q$ effects on SWC means or variability were detected ($P = 0.41–0.98$).

The watering treatments caused substantial, and sometimes opposing, effects on ecosystem processes. With longer I, A_{CO_2} at peak growth in *A. gerardii* increased $> 70\%$ ($P < 0.0001$), ANPP showed no statistically significant response ($P = 0.38$), whereas growing

Table 2 Analysis of variance (ANOVA) and analysis of covariance (ANCOVA) statistics for the effects of rainfall interval (I) and total annual quantity (Q) on soil water content means and variability, and the ecosystem function metrics in grassland mesocosms

ANOVA				ANCOVA			
Effect	df	F	P-value	Effect	df	F	P-value
Amplitude (% of maximum SWC)							
I	3,43	77.82	<0.0001				
Q	3,43	6.84	0.0007				
$I \times Q$	9,43	1.06	0.4118				
SWC CV							
I	3,43	13.30	<0.0001				
Q	3,43	2.09	0.1162				
$I \times Q$	9,43	0.60	0.7904				
SWC (volumetric, %)							
I	3,40	5.13	0.3298	I	4,32.6	42.95	<0.0001
Q	3,40	1.18	0.0043	$I \times S_E$	4,48.1	4.84	0.0023
$I \times Q$	9,40	0.23	0.9881				
A_{CO_2} ($\mu mol \, m^{-2} \, s^{-1}$)							
I	3,42	13.35	<0.0001	I	4,36.1	1.68	0.1750
Q	3,42	6.64	0.0009	$I \times S_E$	4,46.1	34.52	<0.0001
$I \times Q$	9,42	0.61	0.7845				
ANPP ($g \, m^{-2}$)							
I	3,47	0.88	0.4597	I	4,47	2.11	0.0940
Q	3,47	12.20	<0.0001	$I \times S_E$	4,47	26.49	<0.0001
$I \times Q$	9,47	2.00	0.0602				
J_{CO_2} ($\mu mol \, m^{-2} \, s^{-1}$)							
I	3,45	4.08	0.0120	I	4,48	1.51	0.2145
Q	3,45	11.93	<0.0001	$I \times S_E$	4,48	40.62	<0.0001
$I \times Q$	9,45	3.02	0.0066				

Table 3 Effects of total annual quantity of rainfall, averaged across rainfall intervals, on mean $\pm$ SE of soil water content, its amplitude and CV, and carbon cycling metrics

Q (mm yr^{-1})	SWC (%)	Amplitude (%)	CV (%)	A_{CO_2} (μmol m^{-2} s^{-1})	ANPP (g m^{-2})	J_{CO_2} (μmol m^{-2} s^{-1})
400	14.93 $\pm$ 0.78	0.026 $\pm$ 0.003	16.50 $\pm$ 1.72	6.92 $\pm$ 0.67	1059.9 $\pm$ 81.9	4.79 $\pm$ 0.42
600	16.55 $\pm$ 0.86	0.036 $\pm$ 0.004	16.98 $\pm$ 1.75	7.31 $\pm$ 0.62	1251.6 $\pm$ 78.7	5.61 $\pm$ 0.42
800	16.98 $\pm$ 0.80	0.037 $\pm$ 0.003	14.82 $\pm$ 1.72	9.50 $\pm$ 0.62	1571.7 $\pm$ 78.7	6.47 $\pm$ 0.42
1000	17.86 $\pm$ 0.78	0.041 $\pm$ 0.003	14.77 $\pm$ 1.72	10.35 $\pm$ 0.64	1661.7 $\pm$ 78.7	6.89 $\pm$ 0.42

season meant J_{CO_2} decreased 19% ($P = 0.01$; Fig. 2d–f), suggesting that variation in I caused differential changes among these processes. In contrast, variation in Q did not cause differential changes among these parameters. All three measures of carbon cycling increased to a similar extent as Q increased (44–56%, $P \leq 0.0009$; Table 3), suggesting faster overall C cycling, but not changes in the balance among them as seen with varying I. There were also significant $I \times Q$ interaction terms for ANPP ($P = 0.06$) and J_{CO_2} ($P = 0.006$; Fig. 2g and h) because I varied more strongly at some levels of Q than at others. For example, I had stronger effects on ANPP at $Q = 1000$ mm yr^{-1} than at $Q = 400$ mm yr^{-1}, again suggesting that the effects of I depended both on Q and on the process in question.

The effects of S_E on SWC and ecosystem processes also depended strongly on I. Analysis of covariance of SWC vs. S_E demonstrated that when $I = 15$ days, the slope of SWC vs. S_E was less than one-third of that for $I = 3$ days ($P = 0.0023$; Fig. 3a), signifying that variation in S_E had much less effect on soil moisture at longer I than at shorter I. Similarly, all three ecosystem processes showed the same pattern of interaction between I and S_E; the slopes of A_{CO_2}, ANPP, and J_{CO_2} vs. S_E at $I = 15$ days were only $\sim 20\%$ of that when $I = 3$ days ($P \leq 0.001$; Fig. 3b–d), indicating that the effects of S_E depended on I in the same manner for all the three processes.

There were three treatments, $I/Q = 15$ days/400 mm, 10 days/600 mm, and 6 days/1000 mm, that required the same S_E (21.4 mm; Fig. 3). SWC, ANPP, and J_{CO_2} differed significantly among them ($P = 0.01$), and were always highest in the 6 days/1000 mm treatment. This signified that this S_E could have different effects on soil moisture and some ecosystem processes when produced by different I/Q combinations.

Discussion

Our results show that each of the elements of rainfall variability we considered caused significant effects on soil moisture and ecosystem function. The responses to

longer I and accompanying larger S_E were indeed extreme events in terms of their effects on soil moisture variability in the top 30 cm of the soil profile, where the majority of biological activity occurs (Jackson et al., 1996; Nippert & Knapp, 2007). After the first growing season of rainfall treatments, the primary hypothesis that longer I and/or larger S_E would negatively impact ecosystem function proved partially correct, but too simplistic as shown by the interactions we found among I, Q, and S_E in their effects on soil moisture and ecosystem function.

Interactions between I and Q

Not surprisingly, larger Q increased mean soil moisture, A_{CO_2}, ANPP, and J_{CO_2}. The range of Q was large, 250% (400–1000 mm), but the increases in each of these response variables were modest, 20–56%, suggesting that increasing Q increased the rate at which carbon moved through the system, but with diminishing returns, especially in mean soil moisture, as overall water limitation was relieved and other limiting factors came into play.

Variation in I (averaged across Q; Fig. 2d–f) caused responses of similar magnitude as variation in Q (averaged across I, Table 3) in ecosystem function (20–70%), indicating that more extreme rainfall patterns could have as large an effect on ecosystem function as the total amount of rainfall. This is consistent with the findings of previous rainfall manipulation experiments in this system (Fay et al., 2003). In addition, significant $I \times Q$ interactions revealed the presence of strong (up to 70%) variation in ANPP and J_{CO_2} among the I treatments within levels of Q (Fig. 2g and h). Thus, the responses of ANPP and J_{CO_2} to a given annual quantity of rainfall greatly varied depending on the frequency with which the individual events were provided, indicating that variation in I affected the water use efficiency of ANPP and J_{CO_2}, and modulated the responses of these ecosystem processes to rainfall quantity, as was suggested from analysis of long-term ANPP trends in tallgrass prairie (Nippert et al., 2006).
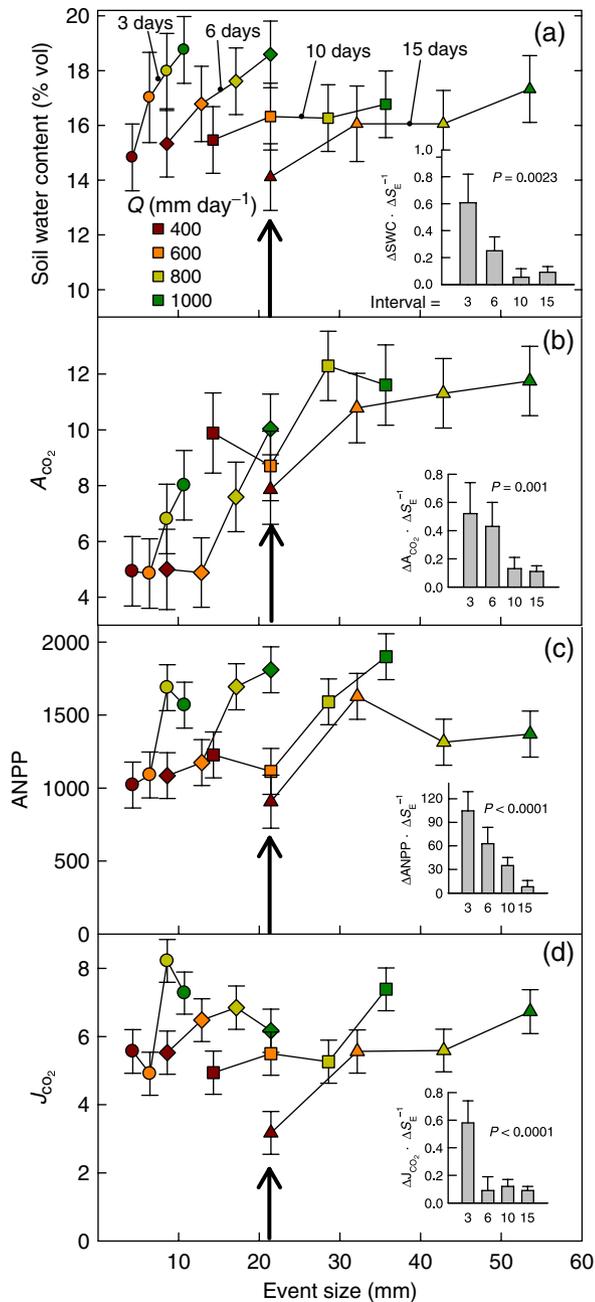
Fig. 3 Mean soil water content and ecosystem processes for the sixteen $I \times Q$ treatments, plotted by the associated S_E. *Insets*: the slopes of these variables, per mm change in S_E for the four I treatments. Error bars denote ± 1 SE. Arrows mark the three treatments sharing the same event size (21.4 mm).

Responses to I

Variation in I caused both increases and decreases in ecosystem function (Fig. 2d–f), with longer I increasing leaf-level carbon uptake (A_{CO_2}) while simultaneously reducing the carbon efflux from the soil. Previous

studies have also reported mixed ($+/-$) responses in ecosystem processes to changes in rainfall frequency or pattern (Ogle & Reynolds, 2004), sometimes modulated by N availability (Maestre & Reynolds, 2007) or topoedaphic factors (Swemmer *et al.*, 2006). The strong increase with longer I was seen in the process (A_{CO_2}) that is most strongly coupled to water stress. The larger events associated with longer I were clearly more effective events from the perspective of leaf carbon gain, likely because longer I shifted soil moisture deeper in the profile and thus reduced temporal variability compared with the surface layer, stabilizing plant water supplies against increased variability in the surface layer. Increased N availability may also have contributed to higher A_{CO_2} (Maestre & Reynolds, 2007). The reduction in J_{CO_2} at longer I was expected (Harper *et al.*, 2005) and is primarily due to longer periods of soil moisture deficit in the surface layer where roots and microbes are concentrated. The smaller response to I in J_{CO_2} compared with A_{CO_2} likely reflects the co-limitation of J_{CO_2} by water and temperature (Luo & Zhou, 2006). The lack of response to I in ANPP may reflect a greater fraction of assimilated C allocated belowground and hence not accounted for by an estimate of aboveground productivity. The lack of response in ANPP also suggests that the threshold dry interval required to suppress ANPP was >15 days for this experimental system.

The change we observed in the balance between carbon uptake (via A_{CO_2}) and carbon loss (via J_{CO_2}) suggests that longer I resulted in greater net ecosystem uptake of C, and that more extreme rainfall patterns could have important implications for carbon cycling via an increase in C uptake relative to loss. Potts *et al.* (2006) reported shifts in the balance between carbon uptake and output after a rainfall pulse; our findings extend their results to repeated pulses during an entire growing season. This change in balance may increase the sink strength of the system with respect to C (Sponseller, 2007) and, therefore, increase C sequestration, especially if accompanied by downward shifts in root depth distributions, which would be expected with longer dry intervals between rainfall events (Luo *et al.*, 2001; Bonan, 2002). Recent models and field evidence suggest that North American terrestrial ecosystems will gain C (Schimel *et al.*, 2000; Jastrow *et al.*, 2005) due to anthropogenic increases in atmospheric [CO_2] (Bonan, 2002). Greater net uptake of C, as our results suggest could happen with more extreme rainfall events (longer I, larger S_E), could reinforce the effects of CO_2 on carbon sequestration.

Interactions between I and S_E

Another major effect was the interaction between longer I and the responses of SWC and the three ecosystem

processes to varying S_E (Fig. 3). In all cases, the variation in S_E within each I caused less change in soil moisture and ecosystem function when I was long (and events less frequent) than when I was short. The increased sensitivity to variation in S_E at short I suggests that the frequent inputs of water primed the system to respond to subsequent events, as Loik (2007) found, and that this priming effect was lost at longer I. A more extreme rainfall regime in I and S_E could, therefore, result in both a shift in the balance among ecosystem processes and increased resistance to variation in event size, even though longer I and larger S_E were associated with greater short-term (days, weeks) temporal variation in SWC (Fig. 2). Potts et al. (2006) also reported that increased rainfall variability was capable of causing independent responses in different ecosystem components, leading to alternative functional states with respect to carbon cycling in semiarid grassland. We suggest that the changes in carbon balance and stability that we found may make mesic grassland more resistant to some effects of increased [CO_2]. For example, longer I could offset the enhanced plant water status associated with CO_2 enrichment (Anderson et al., 2001), lowering C uptake and productivity. In a shortgrass steppe, drought offset the effects of CO_2 enrichment on aboveground biomass seen in wetter years (Morgan et al., 2001; Nelson et al., 2004).

Different treatments, same S_E

A useful feature of the treatment structure in this experiment was that three of the I/Q combinations shared the same event size (21.4 mm), affording a test of the effects of different overall patterns of variation while controlling for event size. The three treatments varied in both Q (400, 600, and 1000 mm yr^{-1}) and the CV of soil moisture (12%, 18%, and 22%, respectively; Table 1). The significant differences in soil moisture, ANPP, and J_{CO_2} among these treatments meant that a given event size was of different value, in terms of ecosystem response, depending on both the quantity of rainfall and the variability in soil moisture of the rainfall regime that spawned that event size (White et al., 2000).

Conclusions

The impacts of variation in Q, I, and S_E on ecosystem function have resisted simple characterization, in part because of the hierarchical structure of rainfall variability and complex interactions among these three elements, which are difficult to separate in field studies experiencing natural rainfall regimes. These results

suggest that ecosystem responses to future extreme rainfall patterns are likely to be variable and dependant on the specific ways that I, Q, and S_E combine during each growing season. A practical implication of these results is that the increases in extreme events that have already been documented (Groisman et al., 2005) and are forecasted to continue (Christensen & Hewitson, 2007) have the potential to substantially alter ecosystem function and carbon sequestration in grasslands under future climates. We need better predictions of rainfall event sizes, the intervals between events, and annual totals, as well as further field data from experiments that manipulate CO_2, temperature, and rainfall events in order to correctly characterize ecosystem functional responses to climate change. With this information, ecosystem models will then be able to more effectively forecast carbon dynamics under the combined effects of extreme rainfall, warming, and CO_2 regimes (Norby & Luo, 2004).

Acknowledgements

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