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Increased rainfall variability and reduced rainfall amount decreases soil CO_2 flux in a grassland ecosystem

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Abstract

Predicted climate changes in the US Central Plains include altered precipitation regimes with increased occurrence of growing season droughts and higher frequencies of extreme rainfall events. Changes in the amounts and timing of rainfall events will likely affect ecosystem processes, including those that control C cycling and storage. Soil carbon dioxide (CO_2) flux is an important component of C cycling in terrestrial ecosystems, and is strongly influenced by climate. While many studies have assessed the influence of soil water content on soil CO_2 flux, few have included experimental manipulation of rainfall amounts in intact ecosystems, and we know of no studies that have explicitly addressed the influence of the timing of rainfall events. In order to determine the responses of soil CO_2 flux to altered rainfall timing and amounts, we manipulated rainfall inputs to plots of native tallgrass prairie (Konza Prairie, Kansas, USA) over four growing seasons (1998–2001). Specifically, we altered the amounts and/or timing of growing season rainfall in a factorial combination that included two levels of rainfall amount (100% or 70% of naturally occurring rainfall quantity) and two temporal patterns of rain events (ambient timing or a 50% increase in length of dry intervals between events). The size of individual rain events in the altered timing treatment was adjusted so that the quantity of total growing season rainfall in the ambient and altered timing treatments was the same (i.e. fewer, but larger rainfall events characterized the altered timing treatment). Seasonal mean soil CO_2 flux decreased by 8% under reduced rainfall amounts, by 13% under altered rainfall timing, and by 20% when both were combined ($P < 0.01$). These changes in soil CO_2 flux were consistent with observed changes in plant productivity, which was also reduced by both reduced rainfall quantity and altered rainfall timing. Soil CO_2 flux was related to both soil temperature and soil water content in regression analyses; together they explained as much as 64% of the variability in CO_2 flux across dates under ambient rainfall timing, but only 38–48% of the variability under altered rainfall timing, suggesting that other factors (e.g. substrate availability, plant or microbial stress) may limit CO_2 flux under a climate regime that includes fewer, larger rainfall events. An analysis of the temperature sensitivity of soil CO_2 flux indicated that temperature had a reduced effect (lower correlation and lower Q_{10} values) under the reduced quantity and altered timing treatments. Recognition that changes in the timing of rainfall events may be as, or more, important than changes in rainfall amount in affecting soil CO_2 flux and other components of the carbon cycle highlights the complex nature of ecosystem responses to climate change in North American grasslands.

Keywords: climate change, precipitation variability, rainfall manipulation, rainout shelters, soil moisture, soil respiration, tallgrass prairie

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Introduction

Increased atmospheric concentrations of carbon dioxide (CO_2) and other greenhouse gases are expected to increase global surface temperatures and alter precipitation patterns (Trenberth, 1998, 1999). Many climate change predictions suggest that periodic droughts will become more common and extreme rainfall events more frequent (Mearns *et al*., 1995; Frederick & Major, 1997; Easterling *et al*., 2000). Climate records suggest that precipitation patterns have already shifted over the 20th century; Karl & Knight (1998) reported a 10% increase in total precipitation for the United States, with about half of this increase because of very heavy rainfall events ($>50\,\mathrm{mm\,day^{-1}}$). The combination of increased dry periods interspersed with larger individual rainfall events will result in extended periods of soil moisture deficit and greater variability in soil water content (Giorgi *et al*., 1998; Jackson *et al*., 2001), with important consequences for many terrestrial ecosystems (Austin *et al*., 2004), and for grasslands in particular (Knapp *et al*., 2002; Fay *et al*., 2003). Climate constrains the regional extent, productivity, and composition of grasslands (Borchert, 1950; Sala *et al*., 1988; Briggs & Knapp, 1995; Knapp *et al*., 2001) and cross-biome comparisons indicate that aboveground net primary productivity (ANPP) is more responsive to climatic variability in grasslands than in other terrestrial ecosystems (Knapp & Smith, 2001). Indeed, the capacity to respond to transient pulses of resource availability is a key characteristic of grasslands, especially tallgrass prairie ecosystems (Seastedt & Knapp, 1993; Blair, 1997). Recent studies have shown that an experimental increase in rainfall variability can reduce ANPP to the same degree as a 30% reduction in total rainfall quantity (Knapp *et al*., 2002; Fay *et al*., 2003). A crucial, but unresolved question, is the extent to which altered rainfall patterns may impact soil CO_2 flux, an important process affecting carbon cycling and storage in terrestrial ecosystems.

Soil CO_2 flux is the release of CO_2 produced by autotrophic (plant roots) and heterotrophic (microbes and soil fauna) respiration, and is thus, an integrative indicator of belowground production and metabolic activity. Soil CO_2 flux is positively correlated with root biomass (Schlesinger & Andrews, 2000), and estimates of the proportion of soil CO_2 flux contributed by root-associated processes range from 20% to 90% globally (Boone *et al*., 1998) and are about 40% for tallgrass prairie ecosystems (Kucera & Kirkham, 1971). In addition to root biomass and activity, soil CO_2 flux is strongly influenced by soil temperature, soil water content, and substrate availability (Linn & Doran, 1984; Craine *et al*., 1999; Zak *et al*., 1999). The dependence of both plant and microbial processes on soil water availability suggests that soil CO_2 flux will be sensitive to increased temporal variability in soil water content resulting from altered rainfall patterns. Predictions with regard to a simple reduction in rainfall amount are straightforward (i.e. lower CO_2 efflux with increased water stress). However, predicting responses to increased variability in soil water content resulting from fewer, larger rainfall events is more challenging. On one hand, prolonged water deficits during inter-rainfall periods may reduce soil CO_2 efflux (Bremer *et al*., 1998), as a result of increased plant and microbial stress. Alternatively, higher root mortality during dry periods could increase substrate availability via belowground litter inputs in the short term, although reduced new root production under dry conditions may result in lower root mass in the long term (Hayes & Seastedt, 1987). In addition, periodic large rainfall events may increase the magnitude of wetting–drying cycles, which have been shown to result in pulses of high microbial activity (Birch, 1958; Denef *et al*., 2001), although this response may not be sustainable (Fierer & Schimel, 2002). A further complication is that large rainfall events may temporarily suppress soil respiration and CO_2 efflux because of reduced diffusion in fine-textured soil with a high water-filled pore space (Bouma & Bryla, 2000). As a result of these complex, and potentially opposing responses, it is difficult to predict *a priori* the responses of soil CO_2 flux to a change in the timing of rainfall events, with no change in the total amount of growing season rainfall, although an understanding of these responses is essential for predicting how altered rainfall regimes are likely to influence ecosystem C dynamics and net CO_2 exchange by terrestrial ecosystems under potential future climates.

The goals of this study were to evaluate (1) the independent and interactive effects of reduced rainfall amounts and an altered growing season rainfall pattern on soil CO_2 flux, and (2) the relationship of soil CO_2 flux with soil water content and soil temperature. Because photosynthesis and plant productivity influence belowground C allocation and, consequently, soil respiration (Ekblad & Hogberg, 2001), we also present data on ANPP to evaluate potential relationships between aboveground plant responses and soil CO_2 flux. Our specific hypotheses were that: (1) reduced rainfall quantity alone would decrease soil CO_2 flux; (2) altering rainfall timing and increasing temporal variability in soil moisture would result in an overall reduction in CO_2 flux, although potentially of lesser magnitude than that caused by reduced rainfall quantity; (3) the combined effect of reduced rainfall amount and altered timing would be additive; (4) both reduced rainfall quantity and altered rainfall timing would increase soil moisture limitation of soil CO_2 flux, and consequently decrease its temperature sensitivity; and (5) decreased soil water availability in both the reduced rainfall quantity and altered rainfall timing would reduce ANPP, consistent with responses in soil CO_2 flux.

Materials and methods

Study site

This study was conducted at the Konza Prairie Biological Station (KPBS) near Manhattan, Kansas, USA (39°05′ N, 96°35′W). Vegetation at KPBS is representative of native grasslands in the region; plant communities are dominated by warm-season C_4 grasses, which can contribute $\geq$80% of ANPP in annually burned prairie (Knapp *et al.*, 1998a), while a speciose assemblage of forbs and C_3 grasses contributes much of the floristic diversity (Towne, 2002). The regional climate is characterized as temperate continental and is extremely variable both among and within years (Knapp & Seastedt, 1998; Goodin *et al.*, 2003). Mean monthly air temperature varies from -3 °C in January to 27 °C in July (Hayden, 1998). Annual precipitation averages 834 mm yr^{-1} (1891–2002), with high interannual variability (coefficient of variation = 24%); about 75% of annual precipitation (approx. 635 mm) falls as rain during the April through October growing season (Sophocleous, 1998).

Rainfall manipulations

This study utilized the Rainfall Manipulation Plots (RaMPs) experimental facility at KPBS. The RaMPs facility was constructed in 1997 in an annually burned native prairie on 1–2 m deep Irwin silty clay loam soils (Pachic Argiustolls; Jantz *et al.*, 1975). The facility consists of 12 fixed-location rainout shelters, which exclude ambient rainfall inputs from plots of intact, native grasslands, and three unsheltered reference plots (Fay *et al.*, 2000). Each 9 m × 14 m shelter covers a 7.6 m × 7.6 m plot surrounded by a 1.1 m deep metal barrier, which reduces lateral exchange of surface and soil water with the surroundings. Data were collected from the central 6 m × 6 m area of each plot. The shelters have open sides to minimize microclimate changes, and are covered with a clear polyethylene (6 mil, UV-transparent) roof during the growing season (with target dates of April 1–October 1). Natural rainfall is collected from the roofs and diverted into storage tanks (7570 L capacity) for later reapplication through an overhead sprinkler system. The roofs are removed each winter and replaced with new plastic each spring.

Four experimental rainfall regimes were implemented in the sheltered plots during the growing seasons of 1998–2001 ($n = 3$ shelters per treatment). The treatments were factorial combinations of two growing season rainfall amounts (100% or 70% of ambient rainfall amounts) and two temporal patterns of rain events (ambient timing or a 50% increase in length of dry intervals between events). This resulted in four treatments: (1) Ambient rainfall quantity and timing; (2) Reduced rainfall quantity with no change in timing of rainfall events; (3) Altered rainfall timing with no change in total growing season rainfall amounts; and (4) Altered timing with reduced quantity. The ambient treatment was designed to match the natural precipitation inputs of each growing season. The altered timing treatment applied all accumulated rainfall at the end of each increased dry interval as a single large event; thus, there was no change in total rainfall quantity, only a change in its temporal distribution. As a result, temporal variability in rainfall was altered while controlling the total quantity of rainfall added during the growing season. Ambient rainfall quantities were determined using six rain gauges around the perimeter of the site. In 2001, all rainfall quantities applied to the sheltered plots were adjusted downward by 30% (based on data from previous seasons) to offset increased soil moisture caused by reductions in evapotranspiration beneath the shelters. Collected rainfall in the ambient and reduced quantity treatments, was applied within 12 h of natural rain events, replicating the temporal pattern of rainfall inputs for each growing season. In the altered timing treatments, dry intervals were defined as the interval between the most recent rain events of 5 mm or larger, because smaller amounts are mostly intercepted by the plant canopy (Seastedt, 1985). Rainfall manipulations were based on ambient rainfall patterns rather than long-term means in order to incorporate realistic seasonal and interannual variability into the treatments.

Soil responses

Soil CO_2 flux was measured weekly between 10:00 and 15:00 h during the 1998–2000 growing seasons and twice weekly during 2001. We used a portable infrared gas analyzer (LI-6200, Li-COR Inc., Lincoln, NE, USA) with an 850 cm^3 soil respiration chamber that sampled a soil surface area of 40.7 cm^2 (Knapp *et al.*, 1998b); chamber design was similar to Norman *et al.* (1992). The chamber was placed on bare soil (1998–1999) or on polyvinyl chloride (PVC) collars (1.7 cm height, 8 cm diameter, 2000–2001), which minimized disturbance and variability because of spatial heterogeneity during repeated sampling. Chamber [CO_2] was reduced below ambient (<360 ppm) prior to placing the chamber, and once the rate of [CO$_2$] increase stabilized (usually ≤ 1 min) flux was sampled over a 20 s interval. Five spatially separate measurements were collected from each plot on each sample date. We avoided taking measurements when soils were saturated (i.e. immediately after large rainfall events), as preliminary data indicated that soil CO$_2$ flux remains close to zero for 1–2 days following a large rain event, reflecting reduced diffusion in soils with a high percentage of water filled soil pore space. Instead, if weekly sampling coincided with large rain events, we delayed sampling to capture periods of high CO$_2$ flux that typically occurred within a few days after large events.

Volumetric soil water content (θ_v) in the 0–15 cm soil layer was measured approximately weekly using time domain reflectometry (TDR; $n = 4$ TDR probe pairs per plot). When soil CO$_2$ flux measurements fell between dates on which soil water content was measured, soil water content was estimated from empirically derived wetting and drying functions based on antecedent soil water content and days since rainfall (Fay *et al.*, 2002). Soil temperature at 5 and 15 cm depths was measured continuously in one plot per treatment.

ANPP was estimated annually by harvesting all aboveground biomass from ten 0.1 m^2 samples per plot at the end of the growing season (mid-October). Because the plots were burned each spring and not grazed, accumulated aboveground biomass represented the current year's ANPP. Samples were sorted into grasses and forbs. Woody species made up <2% of the aboveground biomass and were omitted from the analysis. All plant biomass samples were dried at 65 °C for at least 48 h prior to weighing.

Data analysis

Each sheltered plot was an experimental unit, so replicate measurements were averaged by plot for analysis. Individual sample date and growing season treatment means for soil water content and CO$_2$ flux were analyzed by mixed model ANOVA (Littell *et al.*, 1996). Rainfall treatments were treated as fixed effects and sample dates, or years, were treated as repeated measures. Mean growing season soil CO$_2$ fluxes for individual treatments and years were compared with the mean and variability of soil water content by linear regression. Variability of soil water content for a treatment and year was estimated using the corrected sum of squares, which was not correlated with mean soil water content ($P = 0.41$).

We assessed the sensitivity of soil CO$_2$ flux to temperature by fitting exponential models of mean soil CO$_2$ flux, by sample date and treatment, to mean values of soil temperature at 5 cm depth, and calculating temperature sensitivity coefficients (Q_{10}), which describe the change in flux over a 10 °C change in soil temperature. We assessed the relationship between soil water content and soil CO$_2$ flux by fitting quadratic equations to the data from individual treatments, and from all treatments combined. A response surface relating soil water content, soil temperature, and CO$_2$ flux was calculated using Mielnick & Dugas' (2000) equation (1),

$$J_{\mathrm{CO_2}} = (a \times \mathrm{e}^{bT_s}) \times [2.12 \times (\theta_v - \min\theta_v) \times (\max\theta_v - \theta_v)^c], \tag{1}$$

where $J_{\mathrm{CO_2}}$ is the soil CO$_2$ flux, T_s the soil temperature at 5 cm (°C), and θ_v the volumetric soil water content at 0–15 cm. The model was fit to our complete data set (all years, all treatments) to determine appropriate coefficients for the temperature and soil moisture components of the model ($a = 9.65$, $b = 0.068$, $c = 0.622$). Soil water content was bounded to the minimum (0.10) and maximum (0.50) θ_v values in our data set to exclude situations when soil CO$_2$ flux is limited by extremely dry and wet conditions. Predicted soil CO$_2$ flux values for each treatment were then computed using the full data set model and compared with observed flux values by linear regression.

Results

The experimental treatments effectively altered the timing and amounts of precipitation inputs (Fig. 1a, b). Mean growing season rainfall amount over the 4 years was 7% above average, but the study period included years with above and below average rainfall and was representative of longer-term climate patterns for this area (Hayden, 1998). The protocol for creating the altered timing treatment resulted in a mean rainfall event size 2.3 times larger than ambient rain events, with a 2.5 fold greater mean dry interval between events (Table 1).

Soil water content was influenced by both the quantity and timing of rainfall events. Soil water content from the ambient and altered treatments in the 2000–2001 growing seasons (Fig. 1c) was representative of the range of variation in soil water content during the four study years. In typical years, soil water content is high in May and June, and decreases from July to September as temperatures and transpirational demand increase while rainfall decreases, and the ambient treatment produced this general pattern in most years (e.g. 2000; Fig. 1c). The reduced quantity treatment resulted in lower soil water content than in the ambient treatment but with the same temporal dynamics ($r^2 = 0.93$; data not shown). The altered

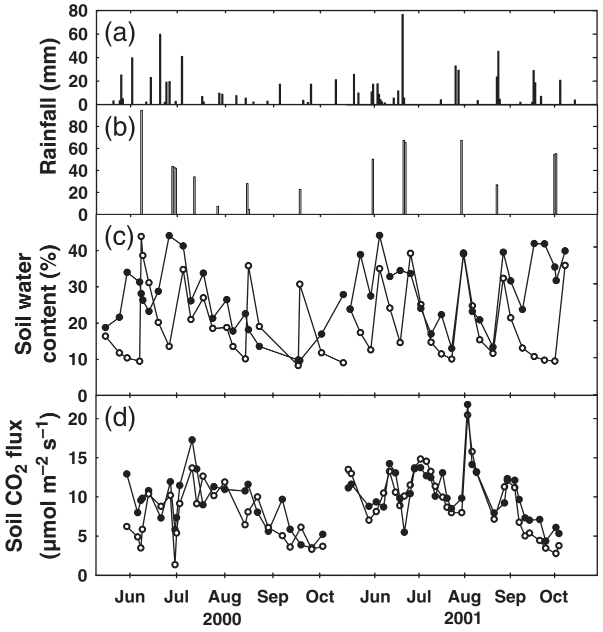

Fig. 1 Growing season rainfall patterns in 2000 and 2001 for ambient rainfall timing (a) and altered rainfall timing (b) treatments. Seasonal patterns in soil water content (c); error bars omitted for clarity – standard errors averaged <20% of the mean. Seasonal patterns of soil CO_2 flux (d); error bars omitted for clarity – standard errors averaged <13% of the mean. Ambient treatment (filled circles and bars) and altered timing treatment (open circles and bars). Years 1998 and 1999 followed trends similar to the years shown.

timing treatment produced pulsed soil wetting events separated by periods of soil water depletion, most notably during dry periods in August and September (e.g. 2000; Fig. 1c). Averaged across all 4 years, the mean absolute change in soil water content between consecutive measurements in the altered rainfall timing treatment was 11% volumetric water content, which was 1.3 times greater than the difference between consecutive measurements in the ambient treatment, reflecting the greater variability in soil water availability in the altered rainfall timing treatment. The increased temporal variability in soil water content in the altered rainfall timing treatment was especially pronounced during July and August in most years, although the timing of ambient rainfall inputs occasionally resulted in similar soil water content patterns in both treatments (e.g. August and September 2001; Fig. 1c). When averaged over the four growing seasons, mean soil water content was reduced by 11% in the reduced quantity treatment, by 19% in the altered timing treatment, and by 23% in the altered timing + reduced quantity treatments compared with the ambient rainfall treatment [Fig. 2a; (quantity $F(1,8) = 11.84$, $P < 0.01$); (timing $F(1,8) = 51.81$, $P < 0.01$); (quantity × timing NS)].

Table 1 Summary of rainfall applications in the ambient and altered rainfall timing treatments in the Rainfall Manipulation Plot experiment (1998–2001)

Year	Total rain applied (mm)	Number of events (≥ 5 mm)	Mean rain event size (mm)	Mean dry interval (days)
Ambient (natural rainfall timing and full rainfall quantity)				
1998	611	16	33.6	8.3
1999	478	15	29.5	8.8
2000	368	15	22.9	11.6
2001	445	14	30.8	11.4
Mean	476	15	29.2	10.0
Altered (altered rainfall timing and full rainfall quantity)				
1998	610	7	87.1	20.8
1999	474	7	67.7	24.2
2000	379	8	47.4	24.4
2001	445	7	63.6	30.3
Mean	477	7	68	24.9

Number of rain events, mean event quantity, and mean dry interval are based only on rain events ≥ 5 mm (see text).

Soil CO_2 fluxes broadly tracked the temporal variability in soil water content (Fig. 1d). Peak fluxes generally occurred in July and August in all treatments, which were the hottest months with intermediate soil water contents. The temporal dynamics of soil CO_2 flux in 2000 and 2001 showed that individual rainfall events usually increased CO_2 flux, and the extended dry intervals typically decreased CO_2 flux (Fig. 1d). Occasional large pulses of CO_2 flux occurred following large rain events (e.g. August 2001); in other cases CO_2 flux temporarily decreased after large events (e.g. July 1, 2000). When averaged over the four study years, soil CO_2 flux was affected by both rainfall quantity and timing [(quantity $F(1,8) = 4.62$, $P = 0.06$); (timing $F(1,8) = 16.29$, $P < 0.01$); (quantity × timing NS)], and was significantly lower in the reduced quantity (by 8%), altered timing (13%) and reduced quantity + altered timing (20%) treatments compared with the ambient treatment (Fig. 2b). ANPP responded similarly to the rainfall treatments [(quantity $F(1,8) = 14.26$, $P < 0.01$); (timing $F(1,8) = 14.58$, $P < 0.01$); (quantity × timing NS)], and was reduced by an average of 9% in the reduced quantity treatment, by 9% in the altered timing treatment, and by 18% in the reduced quantity + altered timing treatment, compared with the ambient rainfall treatment (Fig. 2c). The response of soil CO_2 flux to the rainfall treatments (Fig. 2b) mirrored the treatment differences in soil moisture (Fig. 2a) and in ANPP (Fig. 2c), suggesting a link between soil water dynamics, aboveground productivity, and rates of root and microbial respiratory activity over multiple years. However, mean CO_2 flux

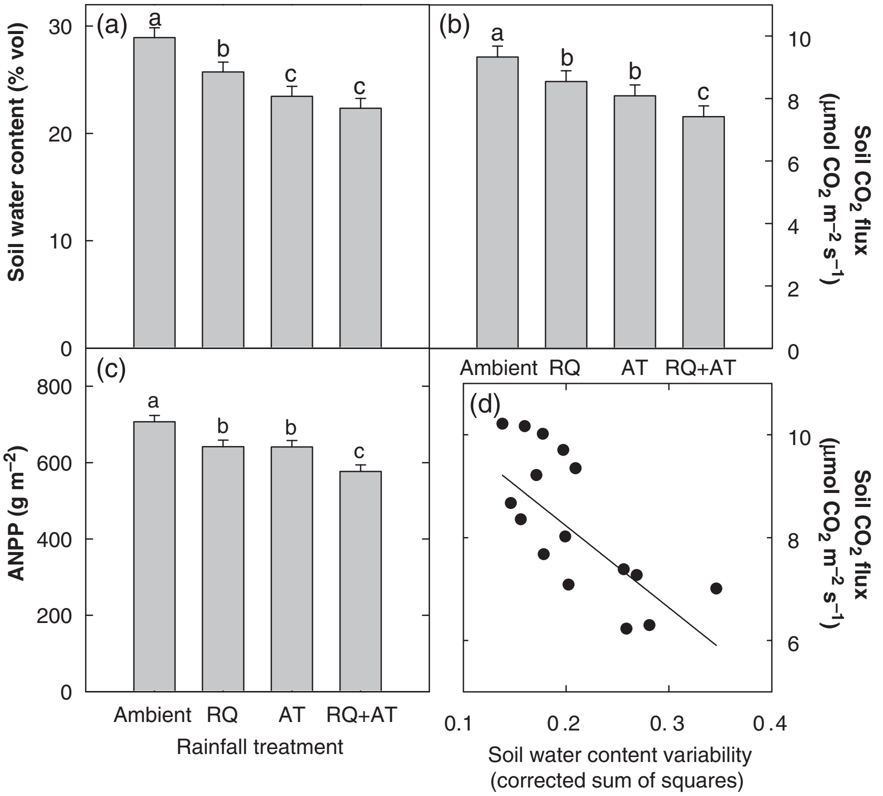

Fig. 2 Mean (±1 SE) volumetric soil water content (a: 0–15 cm), growing season soil CO_2 flux (b: µmol CO_2 m^{-2} s^{-1}), and aboveground net primary productivity (c: ANPP g m^{-2}) for each experimental treatment across the 4 years of this study. The treatments are abbreviated as follows: ambient rainfall (Ambient), reduced rainfall quantity (RQ), altered rainfall timing (AT), and reduced quantity + altered timing (RQ + AT). Unique letters represent significantly different means as determined using repeated measures analysis of variance ($P<0.05$). Seasonal mean soil CO_2 flux was negatively related to variability in soil water content (d); each point represents a single treatment seasonal mean.

was not related to mean soil water content when the treatment means from individual years were compared by regression ($P = 0.81$, data not shown). Instead, mean CO_2 flux was significantly reduced in years and treatments that produced higher variability in soil water content (Fig. 2d; $r^2 = 0.49$, $P<0.01$), suggesting that intra-annual variability in soil water content may be a more important regulator of annual soil CO_2 flux than is mean soil water content within individual years.

Comparisons of the relationship between soil CO_2 flux and soil temperature and soil moisture across all treatments and years suggested that temperature was a better predictor of soil CO_2 flux ($r^2 = 0.38$) than was soil moisture ($r^2 = 0.16$; Table 2a). When regressions were performed by treatment, temperature was more strongly correlated with CO_2 flux, and Q_{10} values were larger indicating greater temperature sensitivity, in the ambient rainfall timing treatments ($r^2 = 0.50-0.53$, $Q_{10} = 2.1-2.2$) compared with altered rainfall timing treatments ($r^2 = 0.31-0.33$, $Q_{10} = 2.0$; Table 2a). In contrast, soil water content was more strongly correlated with CO_2 flux in the reduced rainfall quantity ($r^2 = 0.18-0.23$) compared with ambient quantity treatment ($r^2 = 0.07-0.13$; Table 2a). When soil moisture and soil temperature were combined in the Mielnick–Dugas model with coefficients adjusted for our site, soil moisture and temperature together explained 49% of the variance in observed soil CO_2 flux for all treatments combined (Table 2a), and the combined model improved the prediction of flux in the reduced quantity and reduced quantity + altered timing treatments over predictions based on temperature alone (Tables 2a and 2b). The response surface formed by the soil CO_2 flux values predicted from the Mielnick–Dugas model (Fig. 3) revealed the combined responses of soil CO_2 flux to soil temperature and moisture, and indicated that the highest soil CO_2 fluxes occurred at high soil temperatures and intermediate soil water contents. Both low and very high soil water content strongly suppressed the temperature response, while cool soil temperatures suppressed the soil moisture response.

We also assessed temporal trajectories of monthly mean soil CO_2 flux in relation to seasonal trajectories of

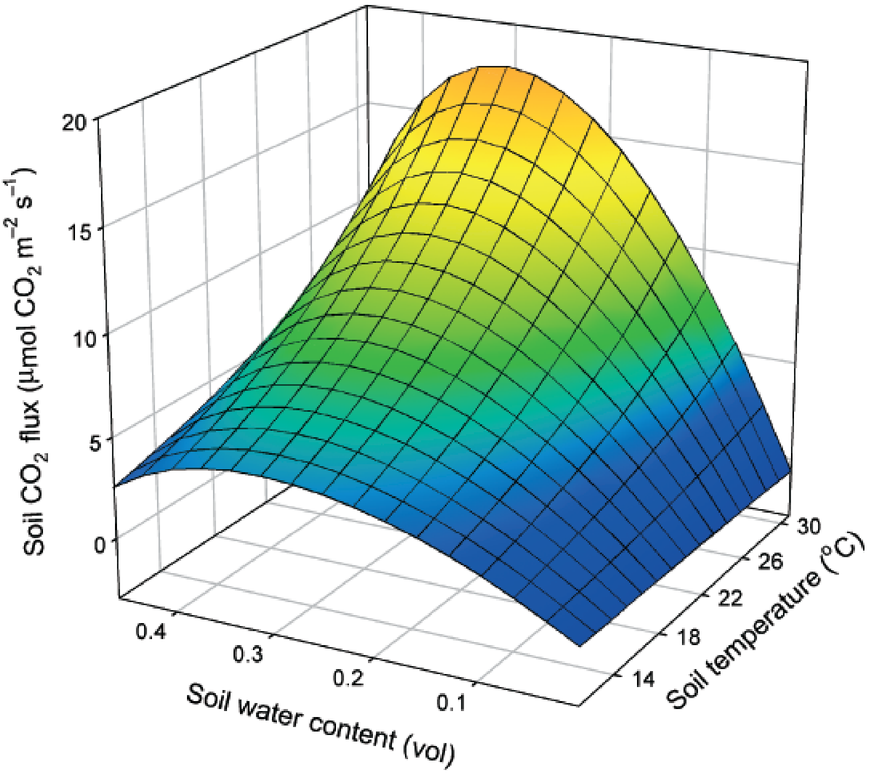

Fig. 3 Response surface generated using output from the Mielnick–Dugas model, which describes soil CO_2 flux as a function of combined exponential soil temperature and quadratic soil water content equations. Volumetric soil water content data are based on time domain reflectometry measurements (0–15 cm) and soil temperature data were collected at 5 cm deep.

soil temperature and soil water content (Fig. 4). Combined seasonal trajectories of monthly soil CO_2 flux and temperature were similar in all four treatments (Fig. 4a–d), while combined seasonal trajectories of monthly soil CO_2 flux and soil water content were more strongly affected by both rainfall timing and rainfall quantity (Fig. 4e-h). The trajectories of monthly mean CO_2 flux were in general agreement with the Mielnick–Dugas response surface. For example, the ambient and reduced quantity treatments started the season with similar soil temperatures (Fig. 4a–d) but higher soil water content (Fig. 4e, f) than the altered rainfall timing treatments (Fig. 4g, h), and hence had higher soil CO_2 flux compared with the altered timing and reduced quantity + altered timing treatments. Soil CO_2 fluxes in all treatments were generally greatest in July and August, a time of similar high soil temperatures and intermediate soil water contents. However, the peak fluxes were generally lower in the altered rainfall timing treatments. September fluxes decreased in concert with decreasing soil temperature (Fig. 4a–d) and soil moisture (Fig. 4e-h), and fluxes in all treatments converged at their minima in October in association with lower temperatures at the end of the growing season.

Discussion

Potential changes in both the amounts and timing of rainfall events are important aspects of regional climate change, which can alter the distribution and dynamics of water content and biological processes in soils, with significant ecosystem-level consequences. Soil water content is a key driver of biological processes in many terrestrial ecosystems, and plays a prominent role in grasslands through its influence on plant productivity (Sala *et al.*, 1988; Lauenroth & Sala, 1992; Knapp & Smith, 2001) and soil processes (Burke *et al.*, 1997; Epstein *et al.*, 2002). Our results, and others (Noy-Meir, 1973; Sala & Lauenroth, 1982), indicate that both the size and timing of rainfall events are important in arid to semi-arid ecosystems. Large events may penetrate deeper into the soil profile, recharging deep soils or potentially moving beneath the rooting zone, while small rain events replenish only surface soil horizons. Increasing both the size of individual rainfall events and the length of inter-rainfall intervals should result in greater recharge of deep soils, but extended drought conditions in the upper soil layers. Although many plant species in these grasslands have roots that extend to depths of 1 m or more, the majority of root biomass

Table 2a Relationship of soil CO_2 flux to soil temperature [regression coefficients ($y = ae^{bx}$) and temperature sensitivity coefficient ($Q_{10} = e^{10b}$)] and soil water content [quadratic ($J_{CO_2} = y_0 + ax + bx^2$)]

Soil temperature	*a*	*b*	r^2	*P*	Q_{10}
Ambient rainfall timing					
Full quantity	1.373 (0.319)	0.0797 (0.009)	0.53	<0.01	2.218
Reduced quantity	1.322 (0.318)	0.0751 (0.009)	0.51	<0.01	2.120
Altered rainfall timing					
Full quantity	1.531 (0.467)	0.0691 (0.012)	0.33	<0.01	1.995
Reduced quantity	1.263 (0.423)	0.0721 (0.013)	0.31	<0.01	2.057
All treatments combined	1.485 (0.209)	0.0708 (0.005)	0.38	<0.01	2.030

Soil water content	y_0	*a*	*b*	r^2	*P*
Ambient rainfall timing					
Full quantity	3.282 (2.49)	49.68 (19.64)	−94.51 (36.20)	0.08	0.04
Reduced quantity	2.461 (1.44)	55.20 (13.15)	−106.5 (27.38)	0.18	<0.01
Altered rainfall timing					
Full quantity	0.891 (2.01)	64.91 (18.04)	−112.0 (35.67)	0.14	<0.01
Reduced quantity	0.038 (1.48)	67.56 (14.05)	−112.6 (29.31)	0.24	<0.01
All treatments combined	1.338 (0.86)	61.09 (7.66)	−113.6 (15.36)	0.16	<0.01

Standard errors for coefficients are reported in parentheses.

Table 2b Correlation of CO_2 fluxes predicted using the Mielnick–Dugas model (*y*) with measured soil CO_2 fluxes (*x*, independent variable) ($y = ax + b$)

Treatment	*a*	*b*	r^2	*P*
Ambient rainfall timing				
Full quantity	3.97 (0.58)	0.61 (0.06)	0.53	<0.01
Reduced quantity	2.24 (0.63)	0.85 (0.07)	0.64	<0.01
Altered rainfall timing				
Full quantity	4.57 (0.68)	0.57 (0.08)	0.38	<0.01
Reduced quantity	3.64 (0.65)	0.73 (0.08)	0.48	<0.01
All treatments combined	3.75 (0.32)	0.67 (0.04)	0.49	<0.01

Standard errors for coefficients are reported in parentheses.

(70–80%) occurs in the upper 30 cm of the soil (Kucera & Dahlman, 1968; Rice *et al.*, 1998), making soil water dynamics in this zone especially important for predicting and understanding plant and soil responses to different rainfall regimes. For example, previous results from the RaMPs experiment have indicated a strong negative correlation between variability in soil water content at 0–30 cm and ANPP (Knapp *et al.*, 2002).

In our study, mean surface (0–15 cm) soil water content was reduced by 11% with a 30% reduction in rainfall amounts and no change in intra-growing season rainfall timing. The temporal dynamics of soil water content were not significantly affected by this treatment. However, a change in the timing of rainfall to longer inter-rainfall periods and commensurately larger rain events altered the temporal dynamics of soil water content and resulted in an even greater reduction in mean surface soil water content (19% lower than ambient) despite no reduction in total growing season rainfall amounts. The combination of altered rainfall timing and reduced rainfall amounts reduced mean soil water content even further (23% lower than ambient). These changes in soil water dynamics affected mean annual ANPP over the 4 years of this study. Mean ANPP was greatest in the ambient rainfall treatment, and was reduced by an equivalent amount (9%) in response to either a 30% reduction in rainfall quantity or a change in the timing of rainfall events with no change in growing season amount. The combination of reduced rainfall quantity + altered timing resulted in an 18% reduction in ANPP compared with the ambient rainfall treatment. These changes in plant productivity have important consequences for soil CO_2 flux, since plants contribute both directly (root respiration) and

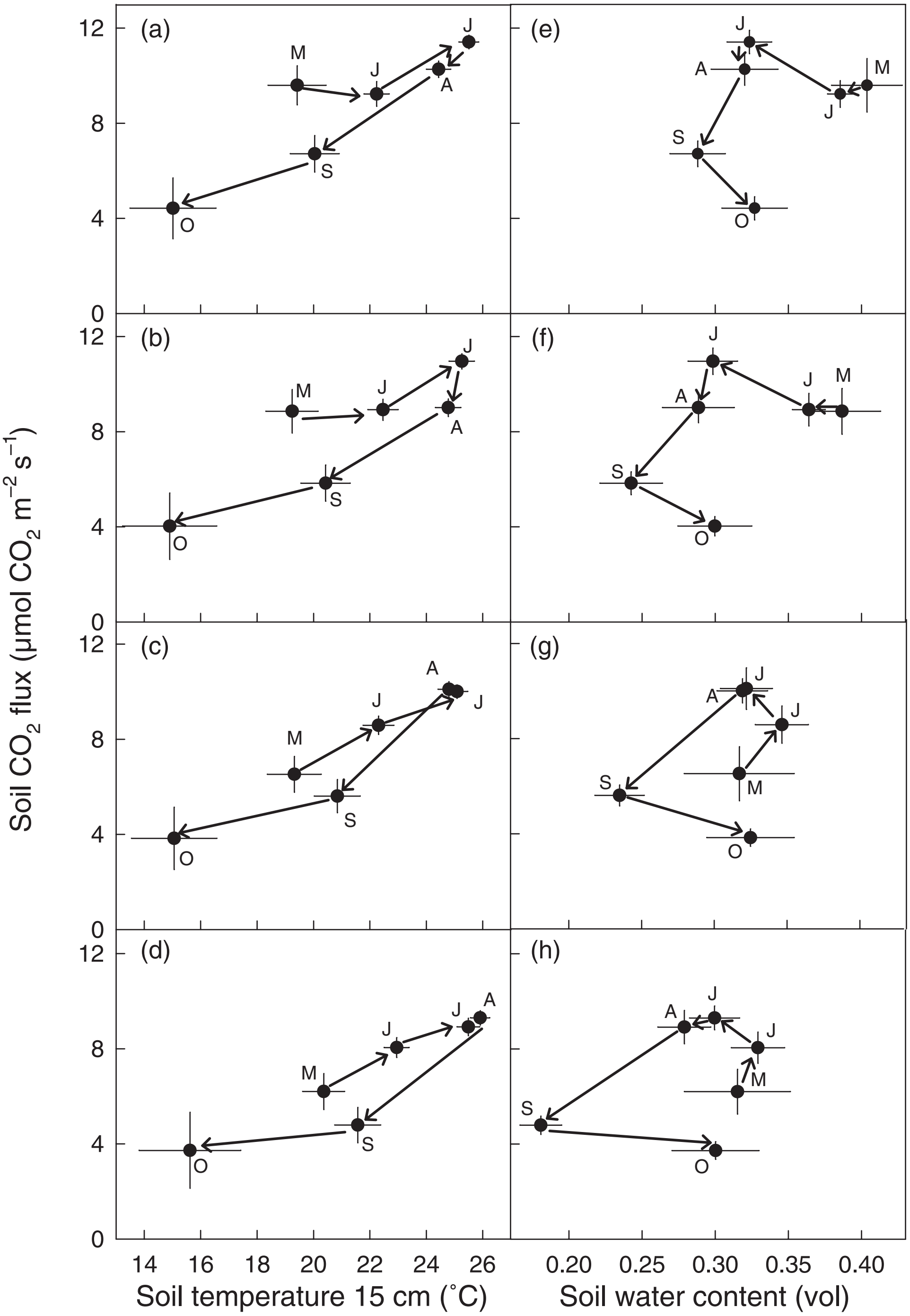

Fig. 4 Seasonal trajectories of monthly mean soil CO_2 flux with soil temperature and soil water content. First point in the arrow sequence is the monthly mean for May, second is June, then July, August, September, and October. Relationships of soil CO_2 flux to soil temperature (panels on left, a–d) and to soil water content (panels on right, e–h) are arranged by treatment, from top to bottom, as ambient rainfall, reduced rainfall quantity, altered rainfall timing, and reduced quantity + altered timing.

indirectly (root exudation and root litter inputs) to CO_2 production belowground.

Mean soil CO_2 flux was significantly affected by both a reduction in the quantity of rainfall events and a change in the timing of rainfall inputs. Surprisingly, soil CO_2 flux was reduced as much by a shift in the timing of rain events as by a 30% reduction in rainfall quantity (Fig. 2b), with the effects of changes in these two aspects of rainfall patterns being additive (i.e. the greatest reduction occurred in the reduced amount

+ altered timing treatment). Low soil water content can limit soil CO_2 flux, and the lower soil CO_2 flux observed in response to our rainfall treatments may be explained, in part, as a response to the overall reduction in mean soil water content caused by the rainfall manipulations. However, our results also indicate that lower CO_2 flux was correlated with increased temporal variability in soil water content, independent of changes in mean soil water content (Fig. 2d), suggesting that changes in the temporal variability of rainfall and the resulting changes in soil water dynamics may be as, or more, important than changes in rainfall amount in affecting soil CO_2 flux.

The responses of soil CO_2 flux to variability in rainfall inputs and soil water content occurred over multiple time frames. First, soil CO_2 flux generally fell to low levels during extended dry periods within a growing season, and soil CO_2 flux was often enhanced for a few days after a rain event ended a prolonged dry period (Fig. 1). This observation is consistent with studies of the effects of wetting and drying on C mineralization in soils (Birch, 1958, 1964; van Gestel *et al.*, 1993). The drying and rapid rewetting of soils can increase availability of labile organic substrates through microbial death and cell lysis (van Gestel *et al.*, 1993; Halverson *et al.*, 2000) or by destabilizing soil aggregates, making physically protected soil organic matter accessible to microbes (Denef *et al.*, 2001). Thus, the occasional pulses of high soil CO_2 fluxes following large rain events in the altered rainfall timing treatment may be because of rapid mineralization of organic constituents made available by the prolonged dry conditions and rapid rewetting events. However, the repeated wet-dry cycles of our altered rainfall timing treatment led to decreased soil CO_2 flux when averaged over the growing season (Fig. 2b), possibly because of the effects of prolonged soil moisture deficit on substrate supply and/or microbial populations. Fierer & Schimel (2002) suggested that the enhanced C mineralization associated with drying/rewetting events is short-lived and that repeated wet–dry cycles may lead to reduced mineralization rates over time because of increased substrate limitation.

At longer time scales, altered rainfall timing reduced mean growing season soil CO_2 flux, and led to changes in the seasonal trajectory of soil CO_2 flux. The seasonal trajectory of soil CO_2 flux in temperate grasslands is influenced by both climate (seasonal patterns of temperature and soil water content) and plant phenology. In most years, soil CO_2 flux is high early in the growing season when soils are moist, increases to a peak in mid growing season (coincident with high temperatures, maximal plant growth and adequate soil water), and decreases late in the season as a result of decreased plant activity, lower temperatures, and/or depleted soil water reserves (Knapp *et al.*, 1998b). Generally, the altered timing treatment interrupted the typical pattern of high CO_2 flux early in the growing season and reduced flux late in the growing season. For example, altered rainfall timing resulted in lower early season (May) soil CO_2 fluxes compared with ambient rainfall timing. Interactive effects also were apparent in the seasonal trajectories of soil CO_2 flux (Fig. 4), where the same temperature or soil water content at different times of the season resulted in different fluxes of soil CO_2. These shifts in temporal patterns of soil CO_2 flux are likely because of interactions among temperature, soil moisture variation, and plant phenology. For example, Knapp *et al.* (1998b) reported a hysteresis in the seasonal trajectory of soil CO_2 flux and temperature, with higher fluxes in the spring and early summer for any given temperature, relative to fluxes late in the growing season. We observed a similar pattern in this study (Fig. 4a–d), which may be related to both plant phenology and increased soil water deficits late in the growing season (Fig. 4e–h). Decreased soil CO_2 flux at the end of the growing season also coincides with the onset of flowering and subsequent senescence of the C_4 grasses (Knapp *et al.*, 1998b), at which time less substrate is presumed to be available for root and root-associated respiration.

Lower mean annual soil CO_2 flux in both the reduced rainfall quantity and altered rainfall timing treatments is likely mediated, at least in part, by plant responses to the rainfall treatments, including a reduction in C assimilation (Fay *et al.*, 2002; Knapp *et al.*, 2002) and potential reductions in root-associated respiration. Reduced soil CO_2 flux can be related to decreased root mass (Johnson & Matchett, 2001), lower root respiration in drought-stressed plants (Burton *et al.*, 1998; Rochette *et al.*, 1991), and possible changes in root exudation and associated microbial respiration in the rhizosphere. Root-associated respiration is partially derived from newly fixed carbon (Ekblad & Hogberg, 2001), which accounted for up to 40% of soil CO_2 flux from a Minnesota grassland (Craine *et al.*, 1999). Therefore, patterns in photosynthetic gains may provide insights to patterns in soil CO_2 fluxes. Leaf-level photosynthesis in the dominant C_4 grasses strongly decreases during extended soil moisture deficits and periods of high temperature (Knapp, 1984, 1985; Long, 1999; Fay *et al.*, 2002). These reductions in photosynthesis may reduce C supply to the rhizosphere and lead to reduced soil CO_2 flux. An observation consistent with this hypothesis is that photosynthetic rates in the dominant grass, *Andropogon gerardii*, remain depressed even in wet soil following an extended dry period (Fay unpublished data). Thus, a change in rainfall timing that results in longer inter-rainfall periods may have a greater effect on plant and soil responses than would be expected based on total quantity of rainfall inputs. At the seasonal scale, substrate limitation for soil heterotrophic respiration would likely be most pronounced late in the growing season, as plant productivity declines and prior to organic matter inputs following plant senescence. At an annual scale, aboveground productivity was reduced by both reductions in rainfall amounts and by shifts in rainfall timing (Fig. 2c), and the responses of ANPP to changes in the mean and variability of soil water content (Knapp *et al.*, 2002; Fay *et al.*, 2003) were similar to the responses observed for soil CO_2 flux in this study, suggesting that a similar relationship exists between above- and belowground carbon flux in response to altered rainfall variability.

Temperature, water, and substrate availability are the basic underlying controls on soil CO_2 fluxes. Soil temperature was a strong predictor of CO_2 flux for individual date × treatment combinations, consistent with the direct effects of temperature on root and microbial metabolism (Metting, 1993; McMichael & Burke, 1996; Lambers *et al.*, 1996) and earlier results from this grassland (Knapp *et al.*, 1998b). With increased variability in soil water content in the altered rainfall timing treatment, soil temperature explained less of the variance in soil CO_2 flux than under ambient rainfall timing. This may be due, in part, to the lower average soil water content associated with altered rainfall timing treatment. The response surface analysis (Fig. 3) indicated that both low soil water content and very high soil water content – conditions that occurred more frequently in the altered rainfall timing treatment – should decrease the temperature sensitivity of soil CO_2 flux. Bremer *et al.* (1998) also found that soil CO_2 flux was more sensitive to soil water content than to soil temperature during prolonged drying cycles in tallgrass prairie. This shift in the relative sensitivity of soil CO_2 flux is important because it indicates that altered rainfall patterns have the potential to modify soil CO_2 flux responses to future warming (Luo *et al.*, 2001). The lower Q_{10} values we observed in the altered rainfall timing treatments (2.00 and 2.06), relative to ambient rainfall timing and quantity (2.22), provides additional evidence that the sensitivity of soil CO_2 flux to warming may be modulated by changes in the timing of rainfall events. In total, these results suggest that predictions regarding climate driven changes in soil CO_2 flux need to consider the interactive effects of changes in precipitation and temperature, and in particular the potential influence of rainfall timing on the relationship between temperature and soil CO_2 flux.

Conclusions

Grassland ecosystems are highly sensitive to variability in rainfall and soil water content, thus these ecosystems will be especially responsive to any change in climatic regime that increases variability. Changes in the frequency and magnitude of rainfall events, and subsequent changes in the variability of soil water content, could interact with or offset the effects of other aspects of climate change on carbon cycling (i.e. enhanced CO_2 concentrations and increased temperature). The present study demonstrated reduced soil CO_2 flux under both reduced rainfall quantity and altered rainfall timing. This suggests that rates of carbon cycling are slowed by increased variability in soil water content; a factor that may offset predicted losses of soil carbon under future climatic scenarios. An additional complication is that plant community composition varies in mesic grasslands with the degree of water limitation and changes in soil water content associated with enhanced variability in precipitation may lead to subsequent changes in vegetation composition (Knapp *et al.*, 2001), with additional consequences for carbon cycling and other ecosystem processes. Clearly, changes in temporal variability of soil moisture associated with altered precipitation regimes are an important factor that will need to be considered when forecasting the responses of grassland ecosystems to future climates.

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