GLOBAL CHANGE ECOLOGY - ORIGINAL PAPER

Elevated carbon dioxide alters impacts of precipitation pulses on ecosystem photosynthesis and respiration in a semi-arid grassland

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Abstract Predicting net C balance under future global change scenarios requires a comprehensive understanding of how ecosystem photosynthesis (gross primary production; GPP) and respiration (Re) respond to elevated atmospheric $[CO_2]$ and altered water availability. We measured net ecosystem exchange of CO_2 (NEE), GPP and Re under ambient and elevated $[CO_2]$ in a northern mixed-grass prairie (Wyoming, USA) during dry intervals and in response to simulated precipitation pulse events. Elevated $[CO_2]$ resulted in higher rates of both GPP and Re across the 2006 growing season, and the balance of these two fluxes (NEE) accounted for cumulative growing season C uptake (-14.4 ± 8.3 g C m^{-2}). Despite lower GPP and Re, experimental plots under ambient $[CO_2]$ had greater cumulative uptake (-36.2 ± 8.2 g C m^{-2}) than plots under elevated $[CO_2]$. Non-irrigated control plots received 50% of average precipitation during the drought of 2006, and had near-zero NEE (1.9 ± 6.4 g C m^{-2}) for the growing season. Elevated $[CO_2]$ extended the magnitude and duration of pulse-related increases in GPP, resulting in a significant $[CO_2]$ treatment by pulse day interaction, demonstrating the potential for elevated $[CO_2]$ to increase the capacity of this ecosystem to respond to late-season precipitation. However, stimulation of Re throughout the growing season under elevated $[CO_2]$ reduced net C uptake compared to plots under ambient $[CO_2]$. These results indicate that although elevated $[CO_2]$ stimulates gross rates of ecosystem C fluxes, it does not necessarily enhance net C uptake, and that C cycle responses in semi-arid grasslands are likely to be more sensitive to changes in precipitation than atmospheric $[CO_2]$.

Keywords Climate change · Prairie ·
Net ecosystem carbon dioxide exchange · Carbon cycle ·
Carbon dioxide flux

Introduction

A primary focus of much research in the biogeosciences is the net C balance of ecosystems (Running et al. 1999; Geider et al. 2001) and how ongoing global changes will impact gross primary production (GPP) and ecosystem respiration (Re) and their sum, net ecosystem CO_2 exchange (NEE). Ecosystem C dynamics are sensitive to both climatic variability and rising concentrations of atmospheric CO_2 because of their tight link to biological activity and biogeochemistry. Elevated $[CO_2]$ may increase GPP and C uptake by directly stimulating leaf-level photosynthesis; however, concurrent increases in Re [due to increasing root respiration and enhanced priming of soil organic matter (SOM)] may result in ecosystem C losses (e.g., Carney et al. 2007). These effects of elevated $[CO_2]$ on ecosystem structure and function will occur against a

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backdrop of changes in precipitation and temperature regimes, which will similarly influence daily and seasonal rates of biogeochemical transformations at the ecosystem scale (Rustad et al. 2001; Knapp et al. 2002; Verburg et al. 2005; Chou et al. 2008).

Responses of mesic ecosystems to increasing [CO_2] are relatively well understood, but considerably less is known about the effects of elevated [CO_2] on arid and semiarid ecosystems, where annual, seasonal, and event-driven precipitation patterns interact with elevated [CO_2] to determine plant and microbial processes (Nelson et al. 2004; Jasoni et al. 2005). In general, elevated [CO_2] enhances photosynthesis in C_3 species, and decreases both stomatal conductance and transpiration in both C_3 and C_4 plants (Ainsworth et al. 2004; Long et al. 2004). Decreased stomatal conductance is an important direct effect of elevated [CO_2] that indirectly improves soil moisture, particularly in arid and semiarid ecosystems (Owensby et al. 1997; Niklaus et al. 1998; Volk et al. 2000; Morgan et al. 2004). Enhanced soil moisture with elevated [CO_2] is especially important during drought (Owensby et al. 1993) in these water-limited ecosystems, where increased plant productivity, water-use efficiency, and soil respiration have been observed (Morgan et al. 2001; LeCain et al. 2003; Nelson et al. 2004; Pendall et al. 2003). While temperature is often considered the most important abiotic factor controlling Re, soil moisture may be of even greater importance in water-limited ecosystems (Davidson et al. 1998; Conant et al. 2004; Borken et al. 2006).

Because of the key role that water plays in semiarid regions, the amount, location, and duration of soil water availability drive the temporal dynamics of C exchange processes (Lauenroth and Sala 1992; Singh et al. 1998; Heisler-White et al. 2008). For semiarid ecosystems such as the northern mixed-grass prairie, changes in precipitation patterns (frequency, magnitude, and timing of events) and subsequent soil moisture availability are predicted to have a greater effect on future C balance than increases in [CO_2] alone (Huxman et al. 2004b; Weltzin et al. 2003). In water-limited ecosystems, episodic rainfall events trigger pulses of biological activity (Noy-Meir 1973), and differential responses of plant and soil processes to variability in resource supply may result in temporally variable rates of ecosystem C exchange (Potts et al. 2006; Huxman et al. 2004a). Ecosystem response to episodic moisture availability is a function of the ability of organisms to up-regulate metabolic processes (Huxman et al. 2004b). Soil microbiota may respond to changes in soil water availability within hours, whereas grasses respond on the order of hours to days (Sala and Lauenroth 1982; Schwinning et al. 2002; Potts et al. 2006). Both antecedent soil moisture conditions and microbial activity may influence the magnitude and time delay of these responses. Given the

sensitivity of these ecosystems to pulses in water availability, it is critical to characterize the responses of ecosystem C fluxes to transient conditions imposed by soil wetting and drying.

Intensification of the hydrologic cycle under global climate change may shift precipitation patterns in ways that impact ecological structure and function (Weltzin et al. 2003; Weltzin and Tissue 2003; International Panel on Climate Change 2007). Increases in extreme precipitation regimes (more intense rain events or severe drought) are predicted for arid and semiarid regions (Easterling et al. 2000; Groisman et al. 1999; International Panel on Climate Change 2007), and increased inter-rainfall dry intervals can significantly impact grassland productivity even when precipitation event size is increased to maintain total rainfall amount (Fay et al. 2003; Heisler-White et al. 2008). Moreover, water-limited ecosystems are hypothesized to have the greatest physiological responses to elevated atmospheric [CO_2] (Jin and Evans 2007; Morgan et al. 2004; Mellilo et al.1993; Volk et al. 2000), potentially leading to non-additive interactions between moisture regime and [CO_2].

The influence of water pulses on ecosystem processes can be examined in a number of ways (Schwinning and Sala 2004), including seasonality, relative event size or the duration of the dry interval between events (Huxman et al. 2004b; Potts et al. 2006; Heisler-White et al. 2008). In the semiarid prairies of North America, available soil moisture and physiological activity are generally highest during the early growing season, gradually decline through July and August, and sometimes increase in response to monsoon-like rain events in late summer (LeCain et al. 2002). We therefore expected that the responses of GPP and Re to elevated [CO_2] and moisture pulses would be seasonally dependent.

The objectives of this paper were to: (1) characterize seasonal patterns of Re, GPP, and NEE in response to elevated [CO_2]; (2) evaluate the influence of individual water pulses on ecosystem C exchange at ambient and elevated [CO_2]; and (3) quantify the response of ecosystem C exchange during a natural drought (growing season precipitation 50% of long-term mean) to near-average moisture conditions resulting from regular irrigation. We compared net and gross ecosystem CO_2 exchange rates taken within dry intervals between rainfall events to those during early (May) and late-season (August) moisture pulses. We hypothesized that: (1) elevated atmospheric [CO_2] would stimulate GPP and Re, and that net C gain over the growing season would be greatest under elevated [CO_2] due to greater enhancement of GPP; (2) elevated [CO_2] would increase the magnitude and duration to which Re and GPP were stimulated following precipitation beyond the response at ambient [CO_2]; and (3) the effect of adding precipitation would be greater than the effect of elevated [CO_2] on gross and net CO_2 fluxes.

Materials and methods

Study site

The Prairie Heating and CO_2 Enrichment experiment was established in 2006 at the USDA-ARS High Plains Grassland Research Station (HPGRS) in Cheyenne, Wyoming. The ecosystem is a high-elevation (1,930 m) native northern mixed-grass prairie with approximately 55% C_3 grasses [*Pascopyrum smithii* (Rybd.) A. Love and *Hesperostipa comata* (Trin. & Rupr.) Barkworth], 25% C_4 grasses [*Bouteloua gracilis* (H.B.K.) Lag], and the remaining vegetation a mixture of C_3 forbs, sedges, and subshrubs (Schuman et al. 1999); total cover averages 50–60%. *Artemesia frigida* (Willd.), a small tap-rooted subshrub, is common. The soils are in the Ascalon series (fine-loamy, mixed mesic Aridic Argiustolls), and biological soil crusts are not present. Mean air temperature is −2.5°C in January and 17.5°C in July, and on average there are 127 frost-free days per year. Mean annual precipitation is 384 mm, and mean growing season precipitation is 275 mm (1 April–31 August for 1973–2005; HPGRS data). Growing season precipitation is characterized by episodic rainfall inputs and dry inter-rainfall periods of variable length. The majority (ca. 40%) of daily precipitation events during the growing season are <5 mm, while events ≥20 mm represent 34% of total inputs (HPGRS data). The site is characterized by high winds (mean wind velocity 6 m s^{-1} with gusts to 35 m s^{-1}), low relative humidity, and high incident radiation, which together cause rapid desiccation between rainfall events.

Experimental design

The experimental design was a randomized complete block layout (blocked by soil gravel content with two replications of each treatment in the first block and three in the second block). Utilizing free-air CO_2 enrichment technology, pure CO_2 was delivered to the perimeter of experimental plots to maintain mean atmospheric [CO_2] of 600 ± 30 p.p.m. CO_2 in elevated plots (Miglietta et al. 2001).

Experimental plots ($n = 5$ per treatment) were rings 3.4 m in diameter and isolated from surrounding soil by steel flange buried to 60 cm installed over the summer 2005. Within each experimental plot, a single 46 × 46-cm square frame constructed of aluminum angle riveted to 7.5-cm-deep aluminum sheeting and sealed with silicone was buried to near surface level. Installation of frames occurred in April 2006.

Treatments for this study included present ambient (A; 380 p.p.m.) and elevated atmospheric [CO_2] (E;

600 p.p.m.). These treatments received eight simulated precipitation pulses of 20 mm from late May up to and including early August delivered manually at ca. weekly intervals. Ambient [CO_2] non-watered areas (treatment C) were designated in each soil block with a total of five experimental measurement frames split between the soil blocks. These plots served as the control treatment and represented ecosystem response to ambient moisture and [CO_2] conditions. The experimental ring infrastructure did not surround treatment C plots, but we believe this had little effect on the results we obtained. A natural precipitation event added 5 mm of moisture to our site during watering for the May pulse (total 25 mm for treatments A and E, 5 mm for treatment C).

Ecosystem-level CO_2 exchange

CO_2 exchange was measured diurnally 5 times during the growing season (30 May, 22 June, 11 July, 3 August, and 23 August) at ca. 20-day intervals. For each diurnal, NEE and Re were measured 5 times over the course of 24 h (at ca. 0400, 0900, 1300, 1600, and 2100 hours). To evaluate pulse-related responses, we measured CO_2 exchange at 1300 hours both 1 day prior to and at days 1, 3, 5, and 7 following two simulated precipitation pulses (31 May, and 4 August 2006).

We used a Lexan polycarbonate (GE Plastics, Pittsfield, Mass.) static chamber (height × length × width: 50 × 45 × 45 cm) fitted with two circulating fans, a Q190 photosynthetically active radiation sensor (LI-COR, Lincoln, Neb.), and an open-path LI-7500 infrared gas analyzer (LI-COR) for measuring [CO_2]. The bottom of the chamber was fitted with L-shaped aluminum and lined with closed-cell rubber stripping to seal the chamber to the buried aluminum frames (chamber volume: surface area ratio = 0.53 m). Light attenuation by the Lexan chamber material was approximately 21%. This approach was similar to those used in previous studies to measure ecosystem gas exchange (Patrick et al. 2007; Huxman et al. 2004a; Jasoni et al. 2005). Temperature in the chamber increased by ≤1°C during sunny conditions, and conditions remained well within the range of accurate density measurements of CO_2 for the LI-7500 (Li-Cor 2001). The change in chamber [CO_2] was recorded at 1-s intervals over 2 min, and fluxes (NEE and Re) were calculated over the last 90 s of each measurement period. Re was measured after NEE data were recorded by placing an opaque cover over the chamber to block light and eliminate photosynthesis. GPP was calculated from the relationship: NEE = GPP + Re. A correction factor for water vapor dilution was applied to the [CO_2] data

before the fluxes (F; either NEE or Re, μmol m^{-2} s^{-1}) were calculated (Jasoni et al. 2005):

$$F = \frac{\left[\frac{dC'}{dt} \times P(1,000 - W_i) \times V\right]}{8.314 \times TA}$$

where dC'/dt was the rate of change in the dry-air mole fraction of C over 90 s. Ambient air pressure (P; kPa), was recorded on the LI-7500 internal pressure transducer, W_i was the initial water vapor mole fraction, V was chamber volume (m^3), T (Kelvin) was recorded inside the instrument box and A was the ground area covered by the chamber (m^2). We developed Microsoft Excel macros to efficiently process the data and assess their quality (code available on request). We adopted the standard sign convention for NEE used for eddy covariance (Baldocchi 2003), with negative values indicating CO_2 uptake by the ecosystem and positive values indicating flux to the atmosphere.

Soil temperature at 5 cm (9053 probe; HANNA Instruments 1998, Woonsocket, R.I.) and volumetric soil water content at 0–6 cm (HH2 moisture meter; Delta-T Devices 2005) were recorded when CO_2 fluxes were measured, and a species cover index was estimated visually within the experimental frames using plastic reference squares that were 1, 5, 10, and 20% of the frame area.

Data and statistical analyses

Integrations of daily NEE, Re, and GPP were calculated using linear interpolation between measurement points to calculate the hourly C balance. These values were then summed over 24 h and are presented as g C m^{-2} day^{-1}. Missing data points were accounted for by averaging the values of the remaining replicate plots for that time point. This enabled us to calculate a daily-integrated value for that plot, with approximately 6% out of 450 values filled in this way.

Integrated daily NEE, GPP, and Re values were linearly interpolated between diurnals to estimate C uptake and release over the growing season for each treatment. Treatment differences for cumulative fluxes during both diurnals and pulses were assessed using ANOVA (PROC GLM). Exploration of scaling relationships between midday Re and GPP and whole-day CO_2 release or uptake, respectively, were also performed using simple linear regression. Because daily NEE cannot be estimated from midday NEE, we used the following equation to estimate this net flux: $NEE_{daily} = GPP_{daily} + Re_{daily}$ (where GPP_{daily} and Re_{daily} were first estimated by linear regression).

We used a linear mixed-effects model (PROC MIXED) to test for the significance of treatment and treatment $\times$ day interaction among NEE, Re, and GPP across the five diurnal sampling dates that occurred in the 2006 growing season. The REPEATED statement was used to model variation within experimental units, and an autoregressive order one covariance structure was selected based on Akaike's information criterion. The pre-planned comparisons of treatment differences within a given sampling period were conducted using least squared means and a Tukey adjustment. Patterns of volumetric soil water content were also investigated in this way. ANOVA was used to compare changes in vegetation cover among treatments between May and August.

We used a linear mixed-effects model (PROC MIXED) to test for the significance of CO_2, pulse, and the $CO_2 \times$ pulse interaction among NEE, Re, and GPP for the May and August simulated precipitation pulses. Because our goal with this analysis was to identify CO_2 effects and the $CO_2 \times$ pulse interaction, we limited this analysis to the ambient and elevated CO_2 plots, which both received simulated precipitation pulses during the 2006 growing season. We considered the pre-pulse measurement to be the "control" and post-pulse measurements made on individual dates to be the "pulse effect". The $CO_2 \times$ pulse interaction term could therefore be evaluated directly. Treatments for the CO_2 main effect included "ambient" and "elevated" and treatments for the pulse main effect included "pre-pulse" and "post-pulse". Separate analyses were run to compare the pre-pulse with post-pulse days 1, 3, 5, and 7. We used the repeated statement with a mixed-effects model to examine the dynamics of the response after the pulse.

We used the non-linear curve fitting function within SigmaPlot version 10.0 (Systat Software) to explore relationships between GPP and Re, and between these fluxes and soil moisture content. All other statistical analyses were conducted in SAS version 9.1. For all tests, significance was determined at the $\alpha = 0.05$ level unless noted otherwise.

Results

Climate and vegetation

Ambient precipitation at the study area during the 2006 growing season (1 April–31 August) was 139 mm, 51% of the long-term mean of 274 mm (strong drought conditions; Fig. 1). An additional 160 mm was distributed as eight 20-mm events in irrigated treatments (A and E; total inputs 299 mm, 9% above the long-term mean).

Soil moisture in the 0- to 6-cm layer during the 2006 growing season varied between 5 and 30%, with significant effects of treatment, date, and treatment $\times$ date interaction ($P < 0.01$; Fig. 2). Soil water content in treatment C was
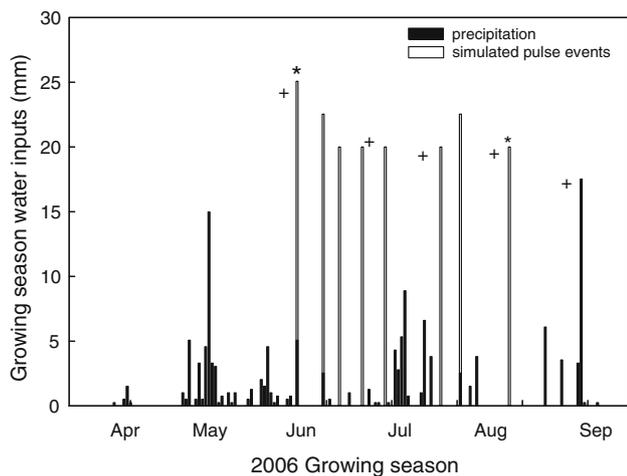
Fig. 1 Growing season water inputs for experimental plots at the Prairie Heating and CO_2 Enrichment (PHACE) site. Data are expressed as precipitation from ambient rainfall (*black bars*) and water applied via simulated pulse events (*white bars*). Precipitation data are from the High Plains Grassland Research Station meteorological station located <1 km from the PHACE site. The five diurnal measurements are indicated by a *plus sign*. Pre- and post-pulse response measurements were conducted on the first and final simulated precipitation events, on 31 May and 4 August, respectively. Post-pulse measurements were taken over a 7-day period, and the first day of each measurement period is indicated by *asterisks*

Fig. 2 Daily integrated **a** net ecosystem exchange (*NEE*), **b** gross primary production (*GPP*), and **c** ecosystem respiration (*Re*) for diurnal measurements taken at ca. 2-week intervals throughout the 2006 growing season. *Positive values* indicate net efflux to the atmosphere, while *negative values* indicate net C uptake. The *vertical gray bars* denote the time frame in which C exchange measurements were taken in response to the May and August simulated precipitation events. **d** Volumetric soil moisture (%) is provided for all treatments as a reference. All data points represent treatment mean ± 1 SE. *A* Ambient [CO_2] (380 p.p.m.), watered; *E* elevated atmospheric [CO_2] (600 p.p.m.), watered; *C* ambient [CO_2], not watered

considerably lower than in treatments A and E in June due to low ambient rainfall and the absence of experimental irrigation in control plots. Later in the summer following natural rainfall events, soil moisture in treatment C increased to similar values as treatments A and E. Average soil moisture was greatest in treatment E (11.1 ± 0.4%) compared to A (9.8 ± 0.3%) and C (7.7 ± 0.3%), but was significantly higher in treatment E than A on 12 July (Fig. 2). In response to simulated precipitation pulses, soil moisture in irrigated treatments A and E increased from <10 to 28% in May and to 23% in August (Fig. 3); no CO_2 treatment effects on soil moisture were detected during either pulse.

Total green vegetation cover was greatest within treatment E during both pulse events; the proportion of *P. smithii* was highest within treatment A, but the proportion of *B. gracilis* did not differ among treatments (Table 1).

CO_2 exchange responses

Positive NEE (net CO_2 efflux) was observed in treatment E in May, prior to the first water application (Fig. 2a), while negative NEE (CO_2 uptake) of ca. the same magnitude was observed in treatments A and C. Significant uptake was observed for treatments E and A in late June (following four simulated rainfall events), whereas net efflux was measured within treatment C. NEE was not significantly
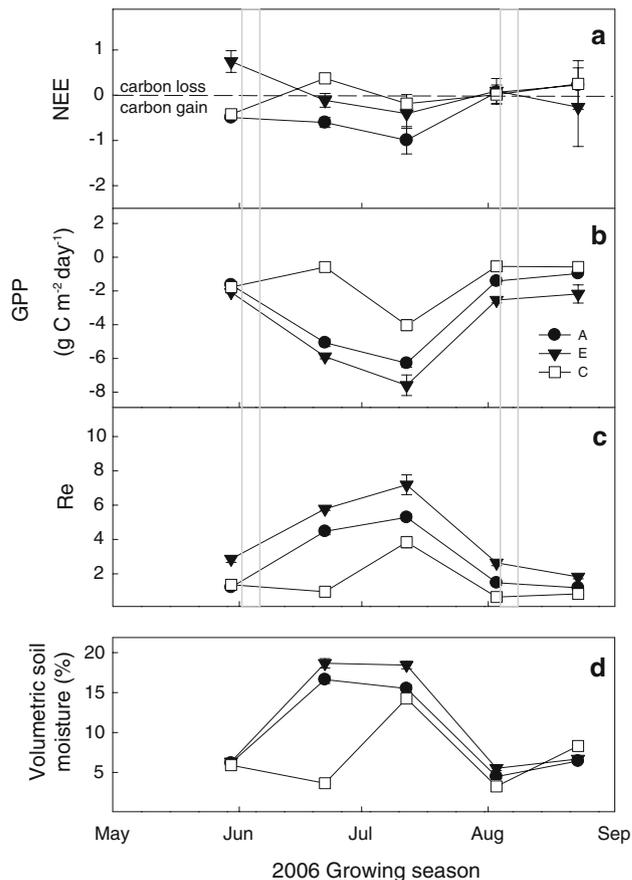
altered by either simulated rainfall or [CO_2] treatment during the inter-pulse measurements for the remainder of the growing season. Cumulative growing season C gain was greater in treatment A (−36.2 ± 8.2 g C m^{-2}) than in treatment E (−14.4 ± 8.3 g C m^{-2}; Table 2). While an average net C loss was observed in treatment C (1.9 ± 6.4 g C m^{-2}), it was not statistically different than zero.

GPP was similar among all treatments during the first diurnal in May (Fig. 2b; $P > 0.05$), but was enhanced in treatment E during all remaining diurnals, peaking in early July at −7.6 ± 0.6 g C m^{-2} day^{-1}. Water additions also increased GPP rates, evidenced by greater GPP in treatment A than treatment C during all diurnals ($P < 0.05$) except for the final diurnal in late August (which occurred
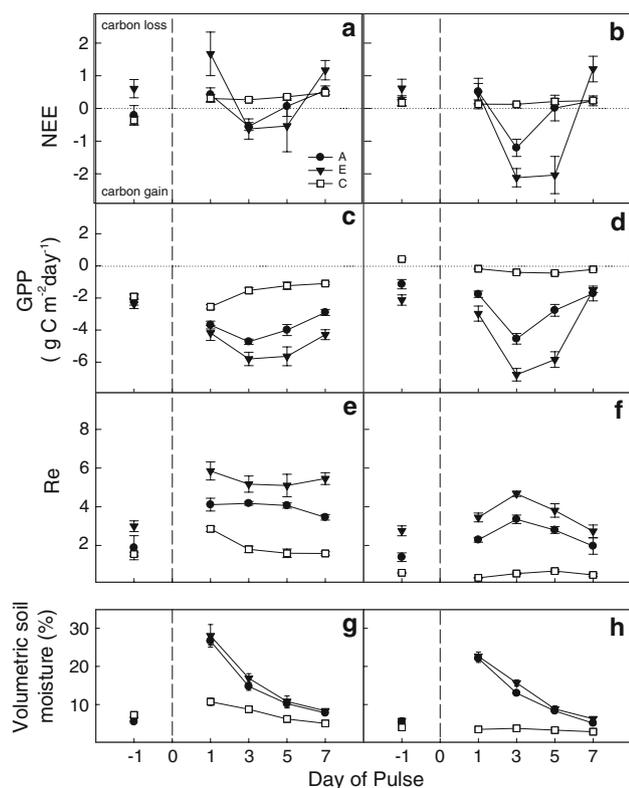
Fig. 3 Daily integrated **a**, **b** NEE, **c**, **d** GPP, and **e**, **f** Re in response to early (May) and late season (August) simulated precipitation events. Volumetric soil moisture (%) for the May (**g**) and August (**h**) pulse is included as a reference. Measurement dates are referenced to the day of the pulse and reflect pre- (−1 day) and post-pulse (days 1, 3, 5, and 7) responses. All data points are treatment means ± 1 SE. For abbreviations, see Fig. 2

Table 1 Mean green vegetation cover (SE) and percent cover blue grama [*Bouteloua gracilis* (H.B.K.) Lag. Ex Steud] and western wheatgrass [*Pascopyrum smithii* (Rybd.) A. Love] expressed as a percent of total vegetation (SE). *Different letters* indicate statistically significant treatment differences during the May or August sampling period

Pulse	Cover class	Treatment		
		A	E (%)	C
May	Vegetation	27 (3.7) ab	35 (5.8) a	16 (3.6) b
	B. gracilis	26 (11.4) a	27 (11.6) a	48 (10.2) a
	P. smithii	42 (11.3) a	20 (5.6) b	11 (2.6) b
August	Vegetation	22 (3.5) b	42 (10.9) a	16 (2.1) b
	B. gracilis	28 (9.0) a	36 (8.3) a	19 (1.4) a
	P. smithii	2 (4.0) a	9 (2.6) b	6 (2.2) b

A Ambient [CO_2] (380 p.p.m.), watered; *E* elevated atmospheric [CO_2] (600 p.p.m.), watered; *C* ambient [CO_2], not watered

after an ambient rainfall event; Fig. 2b). Re fluxes were higher in treatment E than A throughout the growing season (Fig. 2c). Re was similar between treatments A and C during the first and last diurnals ($P > 0.05$), but greater in

treatment A than C in June, July, and early August, suggesting that water additions increased Re even during inter-pulse intervals (Fig. 2c). Summed over the growing season, GPP and Re were highest in treatment E and lowest in treatment C (Table 2).

Regression analysis between midday rates and daily integrated values of GPP and Re (from the five diurnal measurements) revealed significant positive linear relationships (Fig. 4):

$$GPP_{daily} \left(g\ C\ m^{-2}\ day^{-1}\right) = 0.4654$$
$$\times\ GPP_{mid\text{-}day} \left(\mu mol\ C\ m^{-2}\ s^{-1}\right) \left[r^2 = 0.94, P < 0.01\right]$$

$$Re_{daily} \left(g\ C\ m^{-2}\ day^{-1}\right) = 0.6404$$
$$\times\ Re_{mid\text{-}day} \left(\mu mol\ C\ m^{-2}\ s^{-1}\right) \left[r^2 = 0.96, P < 0.01\right]$$

These linear relationships were used to estimate daily rates of GPP and Re from the midday measurements taken in response to the May and August simulated precipitation pulses.

Pulse-driven responses of ecosystem CO_2 exchange

Both the May and August watering pulses stimulated biological activity, altering NEE and its component CO_2 fluxes Re and GPP (Fig. 3a–f). Significant treatment effects on NEE (summed over 7 days) were observed only in August, but Re and GPP were both stimulated by irrigation during both pulses (Table 2). The May pulse resulted in net CO_2 efflux, whereas the August pulse resulted in net uptake in both irrigated treatments. In the dry conditions of treatment C, net CO_2 efflux was observed in both May and August. The ratio of A/C (Table 2) indicated that irrigation stimulated GPP by 2.5 times in May and 8 times in August, and stimulated Re by 2 times in May and 5 times in August, relative to the non-irrigated treatment. The response of C cycling to irrigation was clearly greater than to elevated CO_2; the ratios of E/A (Table 2) were always lower than for A/C.

Elevated CO_2 altered the influence of irrigation on GPP especially during the August pulse. In May, GPP did not differ in treatments A and E prior to the pulse, and a similar increase in GPP was observed on post-pulse day 1. In August, however, GPP was significantly higher in treatment E than A both before (40% higher) and after (68% higher) water was applied to the plots, with a significant $CO_2 \times$ pulse interaction (comparing pre- vs. post-pulse day 3, $P < 0.05$). Thus, irrigation stimulated GPP to a greater extent in treatment E than A; this effect was similarly observed on post-pulse day 5. Summed over the week, GPP was 1.3 and 1.7 times greater in treatment E than A in May and August, respectively (Table 2). Re was greater in treatment E than A prior to both May and August pulses,

Table 2 Cumulative estimates[a] for C uptake (gross primary production; *GPP*) and release (*Re*) and the net C balance (net ecosystem exchange of CO_2; *NEE*)[b]. *Letters* indicate statistically significant differences between treatments at $P \leq 0.05$ (one-way ANOVA). *A/C* Flux response to watering, *E/A* additional response to elevated CO_2 for watered plots; *Pulse 1/GS avg., Pulse 2/GS avg.* responses to water inputs of each flux within each treatment, relative to growing season average; for other abbreviations, see Table 1
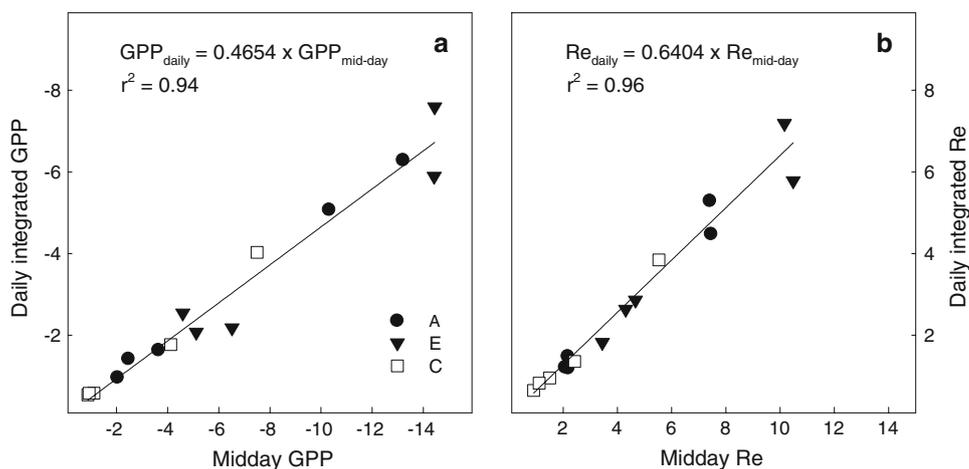
Treatments						
Time interval	Parameter	A	E	C	A/C	E/A
Growing season	NEE	-36.2 ± 8.2 a	-14.4 ± 8.3† b	1.9 ± 6.4 c		
	GPP	-300.0 ± 7.6 b	-393.2 ± 23.8 a	-135.8 ± 6.3 c		
	Re	265.4 ± 5.7 b	375.9 ± 16.7 a	139.8 ± 10.0 c		
7-day GS average	NEE	-3.0	-1.2	0.2		
	GPP	-24.7	-24.1	-11.1	2.2	1.3
	Re	21.8	31.0	11.5	1.9	1.4
Pulse 1	NEE	0.9 ± 0.4 a	3.5 ± 2.5 a	2.4 ± 0.4 a		
	GPP	-27.7 ± 0.4 b	-35.4 ± 2.7 a	-11.0 ± 0.9 c	2.5	1.3
	Re	28.6 ± 0.5 b	38.9 ± 1.8 a	13.4 ± 0.7 c	2.1	1.4
Pulse 2	NEE	-1.2 ± 1.5 ab	-5.8 ± 2.0 a	1.2 ± 0.2 b		
	GPP	-19.3 ± 1.3 b	-32.0 ± 2.3 a	-2.4 ± 0.3 c	8.0	1.7
	Re	18.1 ± 0.9 b	26.2 ± 1.0 a	3.6 ± 0.3 c	5.0	1.4
Pulse 1/GS avg.	GPP	1.1	1.5	1.0		
	Re	1.3	1.3	1.2		
Pulse 2/GS avg.	GPP	0.8	1.3	0.2		
	Re	0.8	0.8	0.3		

† $P \leq 0.1$

[a] Cumulative estimates are in g C m^{-2} for the 2006 growing season and the periods (7-day) following simulated pulse precipitation events. Estimates are based on linear interpolation

[b] *Negative values* of NEE indicate ecosystem uptake of CO_2

Fig. 4 Linear relationship between midday and daily integrated rates of **a** GPP and **b** Re for the 2006 growing season. Data points reflect treatment means for individual diurnal measurements. Units for midday rates are μmol m^2 s^{-1}. Units for daily integrated rates are g C m^2 s^{-1}. Both regression lines are significant at $P < 0.01$. For abbreviations, see Fig. 2

Panel a: $GPP_{daily} = 0.4654 \times GPP_{mid-day}$, $r^2 = 0.94$

Panel b: $Re_{daily} = 0.6404 \times Re_{mid-day}$, $r^2 = 0.96$

and for seven of the ten post-pulse measurements ($P < 0.01$), but no $CO_2 \times$ pulse interaction was observed. Summed over both pulse weeks, Re was 1.4 times greater in treatment E than A (Table 2).

The relationship between Re and GPP observed during the inter-pulse periods was strongly linear ($r^2 = 0.91$) with the highest values for both Re and GPP observed in treatment E (Fig. 5a). During the May pulse, the relationship

was also linear with highest fluxes (and greatest variance) in treatment E (Fig. 5b). In contrast, the relationship between Re and GPP was non-linear in August (Fig. 5c), as Re leveled off relative to GPP in both treatments A and E.

Hysteretic responses to pulse-related changes in soil moisture content were observed for both Re and GPP fluxes (Fig. 6). Peak fluxes of Re and GPP did not generally coincide with the wettest soil moisture conditions

Fig. 5 Relationship between daily integrated GPP and Re for diurnal measurements (**a**) and the 9-day pre- and post-pulse sampling intervals of the early (**b**) and late season (**c**) simulated precipitation events. **a–c** *Equations* describe the best-fit line, significant at $P \leq 0.01$. For abbreviations, see Fig. 2
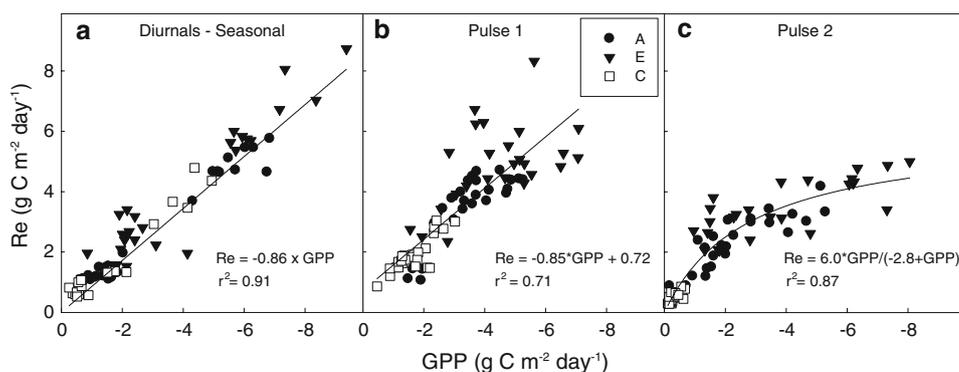

Fig. 6 Relationship between Re of CO_2 and volumetric soil water content during pulse 1 (**a**) and pulse 2 (**b**). Relationship between GPP and volumetric soil water content during pulse 1 (**c**) and pulse 2 (**d**). *Circles* indicate treatment A and *triangles* indicate treatment E for individual days before and after the pulse. Pre-pulse measurements are indicated by *white symbols* containing *plus* symbols. Post-pulse day 1 is indicated by *black symbols*, days 3 and 5 are indicated by *symbols* in *shades* of *gray* in decreasing intensity, and day 7 is indicated by *white symbols*. Log-normal curve fits are shown for GPP for pulse 2 where parameters did not overlap between treatments. *Dashed line* Curve fit for treatment E, *solid line* curve fit for treatment A. For abbreviations, see Fig. 2
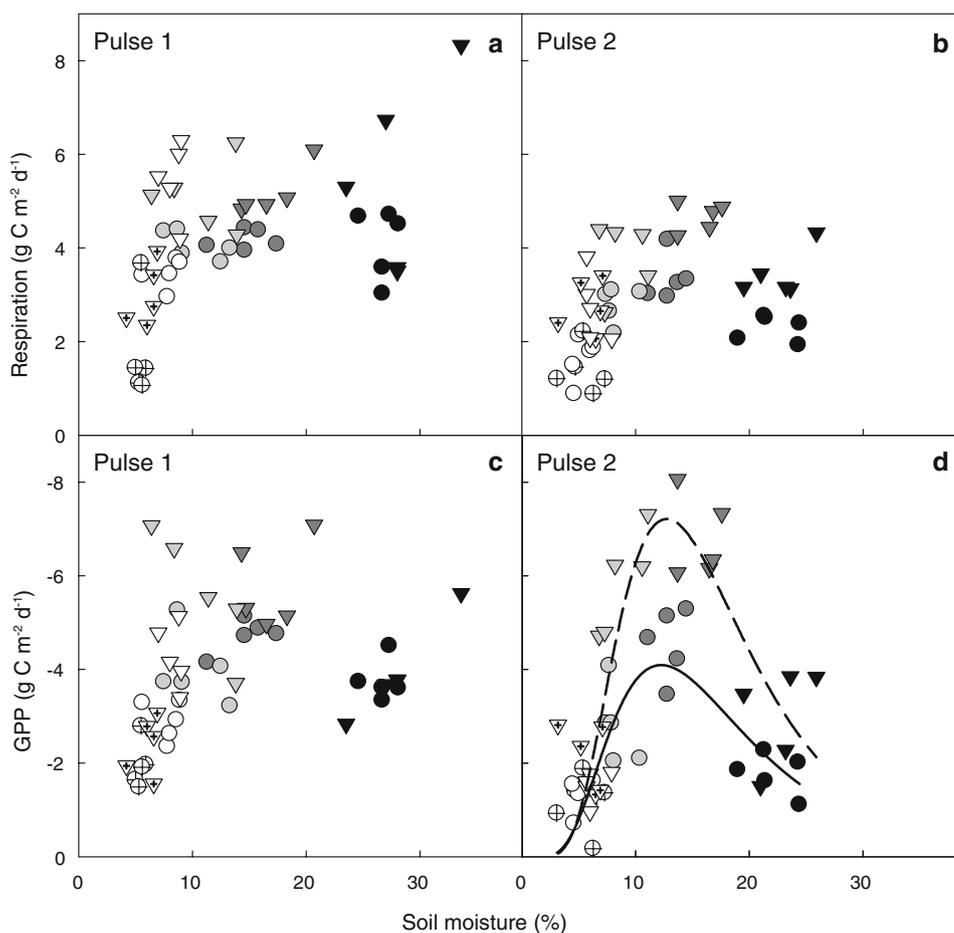
(post-pulse day 1), but rather occurred about 3 days following the pulse. The response of both fluxes to soil moisture tended to be greater in treatment E than A, with the largest difference for GPP during pulse 2, visualized with log-normal curves fit through the data (Fig. 6).

Discussion

This study provides evidence that elevated atmospheric [CO_2] can reduce net ecosystem CO_2 uptake from the atmosphere during both dry intervals and following precipitation events in a semiarid grassland ecosystem. Despite enhancing GPP in response to a precipitation pulse late in the growing season, elevated [CO_2] stimulated Re consistently throughout the season, leading to reduced seasonal uptake relative to ambient [CO_2] plots. Our results also demonstrate that during years of drought, semiarid ecosystems can be a net source of CO_2 to the atmosphere. These results have important implications within arid and semiarid regions, where episodic precipitation events interspersed with long dry periods govern C dynamics

(e.g., Huxman et al. 2004a) and regulate ecosystem structure and function (Weltzin et al. 2003). We suggest that the increased duration and magnitude of Re and GPP under elevated compared to ambient $[CO_2]$ following precipitation events were driven by soil moisture that accumulated in response to reduced transpiration rates (Morgan et al. 2004). The enhanced response of GPP to soil moisture under elevated compared to ambient $[CO_2]$, together with the interactive effects of $[CO_2]$ treatment and pulse on ecosystem CO_2 exchange, demonstrate that elevated $[CO_2]$ stimulates physiological responses to soil moisture at the ecosystem scale.

Semiarid rangeland ecosystems are frequently water-limited (Burke et al. 1998; Sims and Singh 1978), thus it was not surprising that the greatest effects on CO_2 fluxes and net C gain were due to moisture availability. Watering treatments increased growing season precipitation inputs from 50% below average to 9% above average, enhanced average GPP by 220% and Re by 190%, and changed the ecosystem from a small source to a sink of C (Table 2). NEE and its components were most strongly enhanced by watering in late June, when differences in soil moisture were greatest, but were still stimulated later in the season when soil moisture was similar among treatments. Seasonal NEE in ambient $[CO_2]$ plots was 36 g m^{-2}, lower than growing season NEE of 75 g m^{-2} averaged over 3 years in mixed-grass prairie in Alberta Canada (Flanagan et al. 2002), and lower than annual NEE of 53 g m^{-2} averaged over 5 years in mixed-grass prairie in North Dakota (Svejcar et al. 2008). Although grasslands are commonly net C sources during drought years, a comparison of eight temperate grasslands totaling 49 site-years found no simple relationships between precipitation and NEE (Svejcar et al. 2008).

GPP responses

In Canadian mixed-grass prairie GPP was most strongly controlled by green leaf area, which in turn was correlated with soil moisture (Flanagan et al. 2002). In this experiment, simulated precipitation enhanced GPP by 250% in May and 800% in August (treatment A compared to C; Table 2), but vegetative cover did not change between May and August (Table 1). Lower relative *B. gracilis* cover on control plots in August than May could partly explain low GPP in August on those plots, because this shallow-rooted species is sensitive to summer drought (LeCain et al. 2002). GPP within treatment E was 130 and 170% greater than within treatment A for early and late season pulses, respectively. This could partly be attributed to 150% higher vegetation cover on treatment E than A in August. Additionally, photosynthesis rates were probably enhanced directly via CO_2 fertilization and/or indirectly via improved plant-soil water relations (Morgan et al. 2004). Elevated $[CO_2]$ appears to have increased the duration of plant activity within the growing season.

Re responses

In this study, simulated precipitation increased Re by 210% during pulse 1 and 510% during pulse 2 in treatment A compared with C (Table 2), demonstrating the importance of C losses following rewetting in this semiarid grassland. The loss of C following rewetting is thought to result from rapid mineralization of cell solutes (Fierer and Schimel 2003), and somewhat slower mineralization of plant residues (Norton et al. 2008). Rewetting C loss has been implicated in reduced net C uptake in Mediterranean ecosystems (Jarvis et al. 2007), although long-term variability in soil moisture may reduce soil C mineralization (Fierer and Schimel 2002). Our results suggest that continued water applications on treatments A and E did reduce weekly average Re, which was stimulated 130% by pulse 1 relative to the growing season average for each treatment, but was only 80% of the respective growing season averages by pulse 2 (Table 2). This reduced sensitivity of Re to repeated wetting may result from reduction in the labile C pool and/or alteration of the microbial community (Fierer and Schimel 2002).

Our study confirms other reports that elevated $[CO_2]$ elicits higher rates of soil respiration, which has been explained by increased belowground C inputs resulting from greater plant growth, enhanced turnover of fine roots, root hairs, mycorrhizas and rhizosphere-associated microbial biomass, priming of existing SOM, and sometimes increased overall root production (Arnone et al. 2000; Milchunas et al. 2005; Pendall et al. 2003; Pendall et al. 2004; Carney et al. 2007). Enhanced decomposition of older SOM under elevated CO_2 in semiarid grassland was partly explained by interactions with soil moisture (Pendall et al. 2003). Increased Re was responsible for lower net CO_2 uptake under elevated than ambient $[CO_2]$ during the 2006 growing season, although the source of the C loss (older SOM vs. recent substrates) was not established by this experiment.

Relationships between Re, GPP and soil moisture

The ratio of respiration to GPP for both whole plants and ecosystems has been found by some to be consistent over a variety of plant sizes, growth rates, growth $[CO_2]$ and temperatures, which is useful for models that incorporate parameters of plant productivity (e.g., Gifford 1995; Waring et al. 1998). However, a recent meta-analysis by DeLucia et al. (2007) reported that the relationship is actually quite variable in forest ecosystems, with a mean

C-use efficiency (defined as the ratio of net primary production to GPP) of 0.53 that ranged from 0.23 to 0.83. In response to precipitation pulses, we did not find a consistent relationship between GPP and Re, with a linear relationship in May and a non-linear relationship in August. Flanagan et al. (2002) found that maximum Re lagged peak GPP in Canadian prairie, suggesting that if high rates of GPP continued for longer periods of time, Re may increase again as C substrates become available to microbes. Alternatively, repeated wetting events may have depleted labile C pools by August, leading to the lower rate of Re relative to GPP (Fierer and Schimel 2002; Birch 1958; Jarvis et al. 2007). Thus, while utilization of a constant ratio of Re:GPP for this ecosystem may be appropriate at a growing season timescale (e.g., Chimner and Welker 2005; Gilmanov et al. 2007), it fails to capture the dynamics that follow individual precipitation events as well as the cumulative response to frequent wetting and drying.

This study demonstrated that net ecosystem CO_2 uptake in mixed-grass prairie depends on adequate soil moisture, and that moisture availability can interact with elevated $[CO_2]$ to limit C storage. Under ambient $[CO_2]$, water additions stimulated GPP substantially more than Re, but under elevated $[CO_2]$, water additions stimulated Re nearly as much as GPP. Strong, short-term stimulation of GPP by elevated $[CO_2]$ in response to an August moisture pulse did not compensate for season-long CO_2 losses, leading to lower net uptake than under ambient $[CO_2]$ conditions. In addition to soil moisture, responses of NEE and component fluxes are likely to be influenced by differences in antecedent conditions (Ogle and Reynolds 2004; Potts et al. 2006), vegetative cover (Flanagan et al. 2002) and the availability of labile substrates for soil respiration (Fierer and Schimel 2002), all of which vary within and between seasons. Longer-term study is required to determine whether net ecosystem production is stimulated by elevated $[CO_2]$ in this grassland.

References

Ainsworth EA, Rogers A, Blum H, Nosberger J, Long SP (2004) Testing the "source-sink" hypothesis of down-regulation of photosynthesis in elevated $[CO_2]$ in the field with single gene substitutions in Glycine max. Agric For Meteorol 122:85–94

Arnone JA III, Zaller JG, Spehn EM, Niklaus PA, Wells CE, Körner C (2000) Dynamics of root systems in native grasslands: effects of elevated atmospheric CO_2. New Phytol 147:73–85

Baldocchi DD (2003) Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present, and future. Glob Chang Biol 9:479–492

Birch HF (1958) The effect of soil drying on humus decomposition and nitrogen availability. Plant Soil 10:9–31

Borken W, Savage K, Davidson EA, Trumbore SE (2006) Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil. Glob Chang Biol 12:177–193

Burke IC, Lauenroth WK, Vinton MA, Hook PB, Kelly RH, Epstein HE, Aguilar MR, Robles MD, Aguilera MO, Murphy KL, Gill RA (1998) Plant-soil interactions in temperate grasslands. Biogeochemistry 42:121–143

Carney KM, Hungate BA, Drake BG, Megonigal JP (2007) Altered soil microbial community at elevated CO_2 leads to loss of soil carbon. Proc Natl Acad Sci USA 104:4990–4995

Chimner RA, Welker JM (2005) Ecosystem respiration responses to experimental manipulations of winter and summer precipitation in a mixed grass prairie, WY, USA. Biogeochemistry 73:257–270

Chou WW, Silver WL, Jackson RD, Thompson AW, Allen-Diaz B (2008) The sensitivity of annual grassland carbon cycling to the quantity and timing of rainfall. Glob Chang Biol 14:1382–1394

Conant RT, Dalla-Betta J, Klopatek CC, Klopatek JM (2004) Controls on soil respiration in semiarid soils. Soil Biol Biochem 36:945–951

Davidson EA, Belk E, Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Glob Chang Biol 4:217–227

DeLucia EH, Drake JE, Thomas RB, Gonzales-Melers M (2007) Forest carbon use efficiency: is respiration a constant fraction of gross primary production? Glob Chang Biol 13:1157–1167

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. Science 289:2068–2074

Fay PA, Carlisle JD, Knapp AK, Blair JM, Collins SL (2003) Productivity responses to altered rainfall patterns in a C4-dominated grassland. Oecologia 137:245–251

Fierer N, Schimel JP (2002) Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. Soil Biol Biochem 34:777–787

Fierer N, Schimel JP (2003) A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. Soil Sci Soc Am J 67:798–805

Flanagan LB, Wever LA, Carlson PJ (2002) Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. Glob Chang Biol 8:599–615

Geider RJ, Delucia EH, Falkowski PG et al (2001) Primary productivity of planet earth: biological determinants and physical constraints in terrestrial and aquatic habitats. Glob Chang Biol 7:849–882

Gifford RM (1995) Whole plant respiration and photosynthesis of wheat under elevated CO_2 concentration and temperature: long-term vs. short-term distinctions for modeling. Glob Change Biology 1:385–396

Gilmanov TG et al (2007) Partitioning European grassland net ecosystem CO_2 exchange into gross primary productivity and ecosystem respiration using light response function analysis. Agric Ecosyst Environ 121:93–120

Groisman PY, Karl TR, Easterling DR, Knight RW, Jamason PB, Hennessy KJ, Suppiah R, Page CM, Wibig J, Fortuniak K,

Razuvaev VN, Douglas A, Førland E, Zhai PM (1999) Changes in the probability of heavy precipitation: important indicators of climatic change. Clim Change 42:243–283

Heisler-White JL, Knapp AK, Kelly EF (2008) Increasing precipitation event size increases aboveground net primary production in a semi-arid grassland. Oecologia 158:129–140

Huxman TE, Cable JM, Ignace DD, Eilts J, English NB, Weltzin J, Williams DG (2004a) Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: the role of native versus non-native grasses and soil texture. Oecologia 141:295–305

Huxman TE, Snyder KA, Tissue D, Leffler JA, Ogle K, Pockman WT, Sandquist DR, Potts DL, Schwinning S (2004b) Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. Oecologia 141:254–268

International Panel on Climate Change (2007) Climate Change 2007: the physical science basis, summary for policy makers. IPCC WGI fourth assessment report

Jarvis PG, Rey A, Petsikos C, Wingate L, Rayment M, Pereira JS, Banza J, David JS, Miglietta F, Borgetti M, Manca G, Valentini R (2007) Dying and wetting of Mediteranean soils stimulates decomposition and carbon dioxide emission: the "Birch effect". Tree Physiol 27:929–940

Jasoni RL, Smith SD, Arnone JA (2005) Net ecosystem exchange in Mojave Desert shrublands during the eighth year of exposure to elevated CO_2. Glob Chang Biol 11:749–756

Jin VL, Evans RD (2007) Elevated CO_2 increases microbial carbon substrate use and nitrogen cycling in Mojave Desert soils. Glob Chang Biol 13:452–465

Knapp AK, Fay PA, Blair JM, Blair JM, Collins SL, Smith MD, Carlisle JD, Harper CW, Danner BT, Lett MS, McCarron JK (2002) Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298:2202–2205

Lauenroth WK, Sala OE (1992) Long-term forage production of North-American shortgrass steppe. Ecol Appl 2:397–403

LeCain DR, Morgan JA, Schuman GE, Reeder JD, Hart RH (2002) Carbon exchange and species composition of grazed pastures and exclosures in the shortgrass steppe of Colorado. Agric Ecosyst Environ 93:421–435

LeCain DR, Morgan JA, Mosier AR, Nelson JA (2003) Soil and plant water relations determine photosynthetic responses of C_3 and C_4 grasses in a semiarid ecosystem under elevated CO_2. Ann Bot 91:41–52

LI-COR (2001) LI-7500 CO_2/H_2O analyzer, instruction manual, section 2–11. LI-COR, Lincoln

Long SP, Ainsworth EA, Rogers A, Ort DR (2004) Rising atmospheric carbon dioxide: plants FACE the future. Annu Rev Plant Biol 55:591–628

Mellilo JM, McGuire AD, Kicklighter DW, Moore BI, Vorosmarty CJ, Schloss AL (1993) Climate change and terrestrial net primary production. Nature 363:234–240

Miglietta F, Hoosbeek MR, Foot J, Gigon F, Hassinen A, Heijmans M, Peressotti A, Saarinen T, van Breemen N, Wallén B (2001) Spatial and temporal performance of the MiniFACE (free air CO_2 enrichment) system on bog ecosystems in northern and central Europe. Environ Monit Assess 66:107–127

Milchunas DG, Mosier AR, Morgan JA, LeCain DR, King JY, Nelson JA (2005) Root production and tissue quality in a shortgrass steppe exposed to elevated CO_2: using a new ingrowth method. Plant Soil 268:111–122

Morgan JA, LeCain DR, Mosier AR, Milchunas DG (2001) Elevated CO_2 changes water relations and productivity and affects gas exchange in C_3 and C_4 grasses of the Colorado shortgrass steppe. Glob Chang Biol 7:451–466

Morgan JA, Pataki DE, Körner C, Clark H, Del Grosso SJ, Grünzweig JM, Knapp AK, Mosier AR, Newton PCD, Niklaus PA, Nippert JP, Nowak RS, Parton WJ, Polley HW, Shaw MR (2004) Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO_2. Oecologia 140:11–25

Nelson JA, Morgan JA, LeCain DR, Mosier AR, Milchunas DG, Parton BA (2004) Elevated CO_2 increases soil moisture and enhances plant water relations in a long-term field study in semiarid shortgrass steppe of Colorado. Plant Soil 259:169–179

Niklaus PA, Spinnler D, Körner C (1998) Soil moisture dynamics of calcareous grassland under elevated CO_2. Oecologia 117:201–208

Norton U, Mosier AR, Derner JD, Morgan JA, Ingram LJ, Stahl PD (2008) Moisture pulses, trace gas emissions and soil C and N in cheatgrass and native grass-dominated sagebrush steppe. Soil Biol Biochem 40:1421–1431

Noy-Meir I (1973) Desert ecosystems: environment and producers. Annu Rev Ecol Syst 4:51–58

Ogle K, Reynolds JF (2004) Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. Oecologia 141:282–294

Owensby CE, Coyne PI, Ham JM, Auen LM, Knapp AK (1993) Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO_2. Ecol Appl 3:644–653

Owensby CE, Ham JM, Knapp AK, Bremer D, Auen LM (1997) Water vapour fluxes and their impact under elevated CO_2 in a C_4-tallgrass prairie. Glob Chang Biol 3:189–195

Patrick L, Cable JM, Potts D, Ignace D, Barron-Gafford G, Griffith A, Alpert H, Van Gesterl N, Robertson T, Huxman TE, Zak J, Loik ME, Tissue D (2007) Effects of an increase in summer precipitation on leaf, soil, and ecosystem fluxes of CO_2 and H_2O in a sotol grassland in Big Bend National Park, Texas. Oecologia 151:704–718

Pendall E, Del Grosso S, King JY, LeCain DR, Milchunas DG, Morgan JA, Mosier AR, Ojima DS, Parton WA, Tans PP, White JWC (2003) Elevated atmospheric CO_2 effects and soil water feedbacks on soil respiration components in a Colorado grassland. Glob Biogeochem Cycl 17(2):15-1 to 15-13. doi:10.1029/2001GB001821

Pendall E, Mosier AR, Morgan JA (2004) Rhizodeposition stimulated by elevated CO_2 in a semiarid grassland. New Phytol 162:447–458

Potts DL, Huxman TE, Cable JM, English NB, Ignace DD, Eilts JA, Mason MJ, Weltzin JF, Williams DG (2006) Antecedent moisture and seasonal precipitation influence the response of canopy-scale carbon and water exchange to rainfall pulses in a semiarid grassland. New Phytol 170:849–860

Running SW, Baldocchi DD, Turner D et al (1999) A global terrestrial monitoring network, scaling tower fluxes with ecosystem modeling and EOS satellite data. Remote Sens Environ 70:108–127

Rustad LE, Campbell J, Marion GM et al (2001) A meta-analysis of the responses of soil respiration, net N mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543–562

Sala OE, Lauenroth WK (1982) Small rainfall events: an ecological role in semiarid regions. Oecologia 53:301–304

Schwinning S, Sala OE (2004) Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141:211–220

Schwinning S, Davis K, Richardson L, Ehleringer JR (2002) Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. Oecologia 130:345–355

Sims PL, Singh JS (1978) The structure and function of ten western North American grasslands. III. Net primary production, turnover and efficiencies of energy capture and water use. Ecology 66:573–597

Singh JS, Milchunas DG, Lauenroth WK (1998) Soil water dynamics and vegetation patterns in a semi-arid grassland. Plant Ecol 134:77–89

Svejcar T et al (2008) Carbon fluxes on North American rangelands. Rangel Ecol Manage 61:465–474

Verburg PSJ, Larsen J, Johnson DW, Schorran DE, Arnone JA (2005) Impacts of an anomalously warm year on soil CO_2 efflux in experimentally manipulated tallgrass prairie ecosystems. Glob Chang Biol 11:1720–1732

Volk M, Niklaus PA, Körner C (2000) Soil moisture effects determine CO_2 response of grassland species. Oecologia 125:380–388

Waring RH, Landseberg JJ, Williams M (1998) Net primary production of forests: a constant fraction of gross primary production? Tree Physiol 18:129–134

Weltzin JF, Tissue DT (2003) Resource pulses in arid environments—patterns of rain, patterns of life. New Phytol 157:171–173

Weltzin JF, Loik ME, Schwinning S, Williams DG, Fay PA, Haddad BM, Harte J, Huxman TE, Knapp AK, Lin G, Pockman WT, Shaw R, Small EE, Smith MD, Smith SD, Tissue DT, Zak JC (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. Bioscience 53:941–952