

The sensitivity of annual grassland carbon cycling to the quantity and timing of rainfall

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Abstract

Global climate models predict significant changes to the rainfall regimes of the grassland biome, where C cycling is particularly sensitive to the amount and timing of precipitation. We explored the effects of both natural interannual rainfall variability and experimental rainfall additions on net C storage and loss in annual grasslands. Soil respiration and net primary productivity (NPP) were measured in treatment and control plots over four growing seasons (water years, or WYs) that varied in wet-season length and the quantity of rainfall. In treatment plots, we increased total rainfall by 50% above ambient levels and simulated one early- and one late-season storm. The early- and late-season rain events significantly increased soil respiration for 2–4 weeks after wetting, while augmentation of wet-season rainfall had no significant effect. Interannual variability in precipitation had large and significant effects on C cycling. We observed a significant positive relationship between annual rainfall and aboveground NPP across the study ($P = 0.01$, $r^2 = 0.69$). Changes in the seasonal timing of rainfall significantly affected soil respiration. Abundant rainfall late in the wet season in WY 2004, a year with average total rainfall, led to greater net ecosystem C losses due to a $\sim 50\%$ increase in soil respiration relative to other years. Our results suggest that C cycling in annual grasslands will be less sensitive to changes in rainfall quantity and more affected by altered seasonal timing of rainfall, with a longer or later wet season resulting in significant C losses from annual grasslands.

Abbreviations:

WY = water year
 R_h = heterotrophic respiration
 R_s = soil respiration
 R_r = root respiration
NPP = net primary productivity
NEP = net ecosystem production
RC = root contribution

Keywords: climate change, grassland, heterotrophic, Mediterranean climate, net ecosystem production, productivity, rainfall manipulation, root, soil carbon, soil respiration

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Introduction

Global climate changes are expected to alter precipitation regimes in the grassland biome, influencing ecosystem C gain and loss (NAST, 2001; Karl & Trenberth,

2003). Particularly important are potential changes to soil C storage, given the immensity of the soil C pool relative to the biotic and atmospheric compartments (Schimel *et al.*, 1994; Rees *et al.*, 2005). Grassland soils contain significant amounts of C because grasses shunt a large proportion of their photosynthate belowground (Jackson *et al.*, 1997). Globally, grassland soils store 28–37% of the terrestrial soil organic C (SOC) pool (Lal, 2004).

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Carbon dynamics in grassland ecosystems are tightly coupled with the magnitude and timing of precipitation (Knapp & Smith, 2001; Knapp *et al.*, 2002). In general, the effects of precipitation change are not as well studied as those of increased temperature or elevated CO₂ (Weltzin *et al.*, 2003). Mean annual precipitation is well established as a critical driver of grassland productivity (Leith, 1975; Lauenroth & Sala, 1992). In mesic systems, variability in rainfall timing (not total precipitation) has more recently been proposed as an important control on both plant productivity (Knapp *et al.*, 2002) and soil respiration in grassland systems (Harper *et al.*, 2005). Nevertheless, most climate manipulation studies have focused on the response of grassland aboveground C dynamics to rainfall change or variability, as opposed to belowground dynamics (Briggs & Knapp, 1995; Knapp *et al.*, 2001; Shaw *et al.*, 2002; Fay *et al.*, 2003; Zavaleta *et al.*, 2003; Nippert *et al.*, 2006).

Annual grasslands are excellent model systems for exploring the effects of changes in precipitation regimes on C dynamics because plant productivity and decomposition are largely confined to an annual cycle. In California alone, annual grasslands cover over 4.4 million ha, or roughly 20% of state area (Huntsinger *et al.*, 2007). In annual grasslands, plant growth and most microbial activity is restricted to the fall–winter–spring wet season, with a cessation of plant life during summer drought months (Chiariello, 1989; Heady *et al.*, 1992). Because their life-history strategy is intimately linked with the timing of rainfall, annual grasslands are likely to be particularly sensitive to altered precipitation regimes. Most global climate models predict changes to winter rainfall and/or the seasonal timing of rainfall in the Mediterranean biome, where annual grasslands are prevalent, although considerable uncertainty exists regarding regional patterns (Knowles & Cayan, 2002; Lenihan *et al.*, 2003; Hayhoe *et al.*, 2004; Ramos & Martinez-Casasnovas, 2006). Prior manipulation studies in annual grassland have shown a positive link between increased precipitation inputs and net primary productivity (NPP) (Dukes *et al.*, 2005), although nitrogen (N) is thought to be a strong co-limiting factor to grassland NPP (Dukes *et al.*, 2005).

In this study, we investigated the above- and belowground responses of ecosystem C cycling to interannual variation in the amount and timing of rainfall. Coupled with this natural experiment, we used simulated rainfall additions to increase the intensity of wet-season storms (50% increase over ambient rainfall), and lengthen the wet season. Wet-season extension was accomplished by adding two distinct rainfall events per year, referred to as ‘wet-up events,’ which bracketed (i.e. occurred just before and immediately following) the natural wet season. The goal of this field-based rainfall

manipulation experiment was to identify potential feedbacks to elevated atmospheric CO₂ and climate change through responses in ecosystem C storage and loss resulting from altered rainfall regimes.

Materials and methods

Study site

The study was conducted at the Sierra Foothill Research and Extension Center (SFREC) located in Browns Valley, Yuba County, CA (39°15'N, 121°17'W), where historical land use is cattle grazing. The terrain ranges from 90 to 600 m a.s.l. with moderate to steep slopes. Mean rainfall is 750 mm yr⁻¹ with high interannual variability (565–1130 mm over the period from 1989 to 2006, <http://www.cimis.water.ca.gov/cimis/data.jsp>). Rainfall varied significantly across the study years (Fig. 1a). Summer maximum air temperature can exceed 40 °C while winter minimum temperature drops to 2–5 °C; mean annual temperature is 16 °C. Soils are xeric shallow clay loams of the Auburn (loamy, Oxidic, Thermic, Ruptic-Lithic Xerochrepts) and Argonaut (fine, mixed, Thermic Mollic Haploxeralfs) series (Herbert & Begg, 1969; Dahlgren *et al.*, 1997). Plants are dominantly annual grasses (e.g. *Avena* spp., *Bromus* spp., *Lolium* spp. and *Hordeum* spp.) with forbs (e.g. *Erodium* spp.) and legumes (e.g. *Trifolium* spp.) frequently present (Allen-Diaz & Jackson, 2000; Jackson *et al.*, 2006). Mediterranean annual grasslands generally experience a fall–winter–spring rainfall regime. The growing season for annual plants at this site is typically from late October to May, with most rapid growth in spring (Jackson *et al.*, 1988; Jackson, 1989; Heady *et al.*, 1992) and peak flowering occurring for most grasses in April and May (Heady, 1988).

Experimental design

In the spring of 2003, we established three experimental blocks in annual grassland. Two blocks were located in the eastern region of the field station (‘Campbell’ pastures), while the third was located on the western side of the property (‘Porter’ pasture). Each experimental block consisted of a treatment plot with added rainfall and an unmanipulated control plot, separated by a buffer strip 15 m wide. Plots were 15 m × 30 m each and contained only herbaceous vegetation. Control plots received ambient rainfall without alteration. We define the water year (WY) as the 12-month period between September 1 and August 31 and refer to each WY according to the calendar year in which each WY begins; for instance, WY 2003 begins in September 2003 and ends in August 2004. Each WY, treatment plots

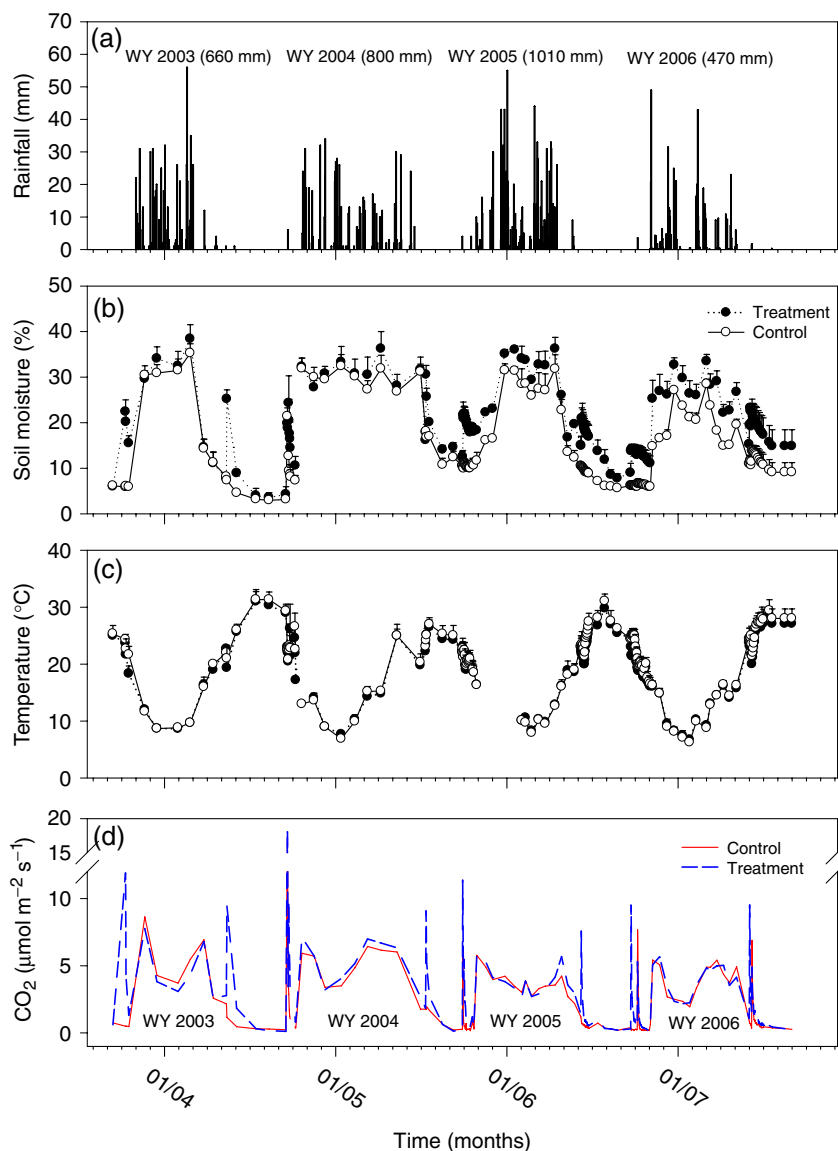


Fig. 1 (a) Daily ambient precipitation data from September 2003 to August 2005, measured at Browns Valley (Station #84) by the California Irrigation Management Information System, publicly available at <http://www.cimis.water.ca.gov/cimis/data.jsp>. All precipitation at this site falls as rain (note: experimental water additions are not shown in this panel). (b) Volumetric soil water content from 0 to 10 cm depth from September 2003 to August 2005 measured in treatment (filled circles) and control (open circles) plots. Error bars represent standard errors ($n = 3$). (c) Soil temperature data measured in treatment and control plots from September 2003 to August 2005. (d) Carbon dioxide efflux in treatment and control plots measured instantaneously with an IRGA system at a bi-weekly frequency, with the exception of daily sampling during early- and late-season simulated rain events. Over the four water years, rainfall amounts in millimeters were 660, 1030; 800, 1240; 1010, 1555; and 470, 740 (control plots, treatment plots, respectively).

received one simulated rainfall event in early fall and a second simulated rainfall event in late spring. These early- and late-season wet-up events each delivered approximately 20 mm rainfall over ~ 7 h via 28 microsprinklers (Model MS VI, Toro, Bloomington, MN, USA). The amount of water added was chosen to reflect the long-term average for the first significant rainfall event of a given WY. Fall wet-up events took place approximately 1–3 weeks before the start of

the rainy season, and were substantial enough to trigger seedling germination 3–4 days after wet-up. Late-season wet-ups took place approximately 4 weeks after the end of the rainy season. Microsprinklers were mounted on 4 ft tall poles and arrayed in a grid throughout the plot. The microsprinklers irrigated in a 360° pattern.

During the wet season, automated sprinklers increased hourly rainfall in treatment plots by 50%. This

rainfall augmentation was intended to increase individual storm intensity and significantly increase the total annual rainfall the plots received relative to the long-term average. Ambient rainfall in each treatment plot was measured using a tipping-bucket rain gauge (Forestry Suppliers, Jackson, MI, USA) installed above sprinkler height and wired to a CR10X datalogger (Campbell Scientific, Logan, UT, USA). An electrical signal sent by the CR10X to a 12 VDC-operated valve (Superior Controls, Valencia, CA, USA) upstream of the sprinklers opened the valve for a time interval proportional to hourly rainfall. Irrigation water was supplied from a nearby lake and filtered before entering the irrigation system. Sprinkler flow rate was approximately 62.8 L h^{-1} . Analysis of irrigation water by colorimetric methods following persulfate digest (Cabrera & Beare, 1993) showed that it contained $<0.3 \text{ ppm N}$ from the source water and $<0.01 \text{ ppm N}$ from the sprinkler outflow. The maximum delivery rate of the automated system was 1749 L h^{-1} , so during heavy storms ($>5.3 \text{ mm h}^{-1}$ of precipitation) any deficit in irrigation was fulfilled by operating sprinklers manually.

Soil moisture, temperature, and bulk density

Soil moisture was measured during all study years. We sampled soils (0–10 cm depth) bi-weekly for gravimetric moisture content for WYs 2003 and 2004. In April 2004, we installed automated, real-time, TDR-based probes at 0–10 cm depth to measure volumetric water content (Campbell Scientific CS616, three probes per plot). Bi-weekly gravimetric measurements were continued from April 2004 to August 2005 to calibrate probe output; additional gravimetric samples were collected periodically thereafter for quality control. Volumetric water content obtained by gravimetric methods was linearly correlated with probe measurements, ($r^2 = 0.8$). Soil temperature was obtained hourly in the 0–10 cm depth using automated probes (Campbell Scientific, one probe per plot) beginning in May 2005. Before that, soil temperature was recorded during each respiration measurement using a temperature probe connected to a portable infrared gas analyzer (IRGA). Soil bulk density was $1.13 \pm 0.05 \text{ g cm}^{-3}$, measured using volumetric soil cores to 10 cm depth. We measured total percent C four times per year in air-dried, ground soils (also to 10 cm depth, roots removed) using a Carlo Erba Elantech elemental analyzer (Lakewood, NJ) and converted C concentrations to C contents using the calculated bulk density for each plot.

Soil respiration

Soil respiration was measured using a Li-6400 IRGA (Li-Cor Biosciences, Lincoln, NE, USA) fitted with a soil

efflux chamber. Measurements were made bi-weekly between 07:00 and 16:00 hours; the chamber was used in conjunction with thin-walled polyvinyl chloride collars (five per plot) driven 2.5 cm into the soil. We sampled daily or every 2–3 days following wet-up events until soil respiration was not significantly different between treatment and control plots. Methane fluxes were measured monthly in 2003–2004 from gas samples collected from vented static gas flux chambers (Keller & Reiners, 1994) at 0, 5, 15, 25, and 40 min timepoints. Gas samples were analyzed on a gas chromatograph using a flame ionization detector. Methane fluxes were indistinguishable from zero and are not presented here.

Plant dynamics

The grasslands at the study site are strongly dominated by annual plant species. These plants die at the end of the wet season and dead aboveground tissues remain upright and mostly intact throughout the summer drought. The lack of physical contact with soil decomposers (Dukes & Field, 2000), coupled with severe moisture stress, strongly inhibits decomposition during summer. Aboveground NPP (ANPP) measurements were determined by harvesting peak standing biomass at the end of the growing season (cf. Dukes *et al.*, 2005; Harper *et al.*, 2005), typically in July. All aboveground vegetation was harvested to the ground surface in six $30 \times 30 \text{ cm}$ quadrats per plot, dried at 65°C , and weighed. To obtain belowground NPP (BNPP), root biomass was estimated once annually also at peak biomass by harvesting soil cores (eight per plot, 0–15 cm depth) in late spring, washing roots free of soil, drying roots at 65°C , and weighing. The majority of roots are located in the top 10 cm of soil in this ecosystem (Jackson *et al.*, 1988). These sites have been historically grazed (~ 130 years), but cattle were removed for our experiment. After biomass harvests, we trimmed the litter buildup in all plots to conform to standard grazing management practices for the region and minimize thatch accumulation (Heady, 1956; Bartolome, 1979). Species composition was estimated annually by a point-intercept method (100 points per plot). We grouped plants into the functional types of annual grasses, perennial grasses, or forbs, which captured all plant species present during the experiment.

Data analysis

Statistical analyses were performed using JMPIN 5.1 (SAS Institute) and SYSTAT 10 (SSI, Richmond, CA, USA), and curve-fitting was performed using SIGMAPLOT 10 (Richmond). Data were transformed as needed to meet the assumptions for ANOVA. Soil moisture and temperature

were compared across treatment, experimental block, and WY using repeated measures ANOVA followed by the Tukey HSD test. We interpolated CO₂ flux measurements to daily rates and summed to estimate R_s , the mass of C per unit area respired annually (Silver *et al.*, 2005). We used ANOVA followed by the Tukey HSD test to explore effects of treatment and WY for R_s and annual NPP. Linear least-squares regressions were performed to explore patterns in log-transformed soil CO₂ fluxes, with soil temperature, soil moisture, and year as explanatory variables. Unless otherwise noted, we report mean values followed by standard errors ($n = 3$), and results were considered to be statistically significant at or above the 95% level unless otherwise noted.

Modeling net ecosystem production (NEP)

We follow the general approach of Hanson *et al.* (2000) to quantify the annual incremental change in C content for the annual grassland ecosystem, using the following equation:

$$\begin{aligned} \text{Net ecosystem production} \\ = \text{ANPP} + \text{BNPP} - (R_s - R_r) - \text{DOC}, \end{aligned} \quad (1)$$

where R_r is the root plus rhizosphere respiration, R_s the soil respiration [the sum of soil heterotrophic respiration (R_h) and root/rhizosphere respiration], and DOC is the dissolved organic C losses. All units are expressed as the mass of C per unit area. The sum ANPP + BNPP, at the end of the growing season, equals total litter inputs to soil. Root exudates were not directly measured and thus not included in this approximation; therefore, our BNPP values may be low estimates. We assume complete turnover of senescent plant biomass within a 12-month period (Heady *et al.*, 1992). Because intra-annual root turnover was not measurable with the soil core sampling technique, we calculated NEP using our direct field measurements of BNPP and also after adjusting for a 50% increase in BNPP, in accordance with results from a cross-comparison of root estimation methods in a nearby California annual grassland site (Higgins *et al.*, 2002).

Shoots were clipped before measuring soil CO₂ effluxes so R_s excludes shoot respiration. Root respiration is zero outside the growing season in annual grasslands (Xu & Baldocchi, 2004). Finally, we assume that DOC fluxes were negligible relative to the larger fluxes of respiration and production, cf. Dahlgren & Singer (1994), who reported DOC concentrations attenuating to $0 \mu\text{mol L}^{-1}$ in the B horizon of annual grassland soils at the study site. Thus, NEP is estimated as the difference between NPP and ($R_s - R_r$). Quantifying the component fluxes of R_h and R_r is difficult in annual

grassland systems, and methodology represents a matter of ongoing debate. Few studies have directly estimated field rates of R_r and R_h for California annual grassland and such measurements were outside the scope of this study. We test two alternative scenarios based on the recent literature. Under the first scenario, we estimate the root contribution (RC) to soil respiration at 35% of total R_s , based on estimates from root exclusion plots in perennial grasslands (Zhou *et al.*, 2007). Under the second scenario, we estimate RC at 70% of R_s , from a study in Southern California annual grassland dominated by similar grasses as SFREC (*Bromus*, *Avena*, *Vulpia*) (Hooper, 2003). We refer to these scenarios as 'low-RC' (35%) and 'high-RC' (70%). We applied similar RC values for treatment and control plots during the growing season. Partitioning of soil respiration may not be equal under different rainfall treatments. To address this, we calculated NEP using a longer growing season in treatment plots than in the controls to reflect the earlier germination date of grasses. This had no significant effect on NEP.

Results

Responses to rainfall manipulation

Rainfall treatments significantly raised soil volumetric water content in all years (Fig. 1b). Rainfall additions increased soil moisture by 7–8% in WYs 2005 and 2006 ($P < 0.001$): soil moisture was 23% vs. 15% (WY 2005) and 18% vs. 11% (WY 2006) in treatment and controls, respectively. Soil moisture was 18% vs. 14% in WY 2003 ($P = 0.06$), and 23% vs. 20% in WY 2004 ($P = 0.05$) in treatment and control plots, respectively.

Soil moisture following wet-ups remained significantly elevated for 27 and 25 days, respectively, in the falls of WY 2003 and WY 2005. In WY 2004, an early fall storm coincided with the timing of the wet-up event (September 19), and soil moisture was elevated for 16 days in treatment plots relative to controls (Fig. 1a and b). In WY 2006, treatment plots had higher soil moisture than controls throughout the year (Fig. 1b). Spring wet-up events, conducted after the conclusion of late spring rains, significantly increased soil moisture for approximately 23, 20, and 14 days in WYs 2003, 2004, and 2005, respectively (Fig. 1b). There were no significant effects of rainfall treatment on soil temperatures (Fig. 1c).

The wet-up events resulted in large pulses of soil CO₂ across the soil–atmosphere interface. Early- and late-season wet-up events increased soil respiration to two to four times that of the controls. During early season events, plots lost an average of $31 \pm 2 \text{ g C m}^{-2}$ more than controls, while late-season events resulted in the additional loss of $27 \pm 4 \text{ g C m}^{-2}$ (Table 1). The greatest

Table 1 Soil respiration response to wet-up events over 4 water years

Water year	C respired (g C m^{-2}) per wet-up	
	Rainfall treatment	
	Control	Treatment*
<i>Early-season wet-up</i>		
2003	13.2 (1.6)	50.1 (7.4)
2004	46.0 (11.0)	74.9 (5.9)
2005	14.1 (1.9)	45.3 (1.1)
2006	19.2 (1.2)	45.1 (2.6)
<i>Late-season wet-up</i>		
2003	26.4 (4.5)	66.7 (3.3)
2004	37.8 (3.8)	63.5 (3.1)
2005	9.4 (0.5)	29.6 (3.3)
2006	29.5 (5.0)	52.7 (9.9)

*Rainfall treatment increased natural rainfall events by 50% and also added approximately 40 mm rainfall per year via distinct early- and late-season wet-up events. The mass of carbon respired differed significantly between treatment and controls for all wet-up events. The duration of each wet-up varied according to how long treatment CO_2 fluxes remained elevated above controls (see text). IRGA measurements were made daily or near-daily following wet-ups.

C losses from wet-up events and the largest relative differences between treatment and controls occurred in WY 2003.

Soil CO_2 fluxes declined exponentially after the wet-up events and significantly exceeded control plot fluxes for 3–4 weeks (Fig. 2). Both early- and late-season wet-up events increased soil respiration relative to controls although late-season events resulted in lower maximum fluxes compared with early-season events (Fig. 2). Individual wet-up events differed slightly in their coefficients of the fitted exponential curves (Appendix A1). Total annual soil respiration was greater in treatment plots than in controls over all 4 years of the study ($P = 0.1$, Fig. 3). This effect was largely due to wet-up events, and not to increased soil respiration in treatment plots during the rainy season. The exception was in WY 2005 when wet season soil respiration was significantly greater in treatment plots than in controls ($P = 0.06$).

Total soil C content in the 0–10 cm depth averaged $2697 \pm 84 \text{ g C m}^{-2}$ in treatment plots and $2587 \pm 45 \text{ g C m}^{-2}$ in the controls, with no statistically significant difference between treatments. Soil C pools declined over the course of the study in both treatments and controls. In treatment plots, soil C pools decreased at a rate of approximately $200 \text{ g C m}^{-2} \text{ yr}^{-1}$ ($r^2 = 0.35$, $P = 0.05$). In controls, soil C pools declined by $150 \text{ g C m}^{-2} \text{ yr}^{-1}$ ($r^2 = 0.37$, $P = 0.05$) (Fig. 4).

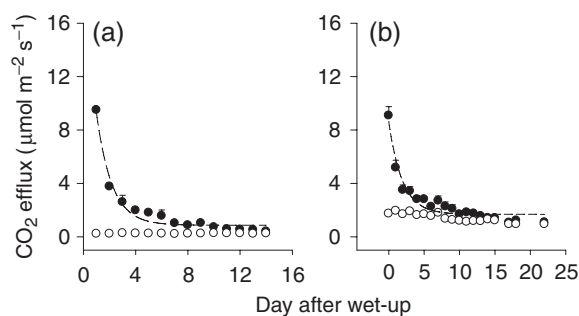


Fig. 2 Fluxes of CO_2 following two representative wet-up events: (a) fall wet-up, September 21, 2006 and (b) spring wet-up, July 12, 2005. Filled circles represent augmented rainfall treatment; unfilled circles signify control treatment. Symbols represent means and error bars are standard errors ($n = 3$). Exponential decay curve fits are shown for treatment data (no significant change observed in control plots), where the functional form is $Y = Y_0 + a \times e^{-bx}$. Curve fits were (a) $Y = 0.867 + 19.7 \times e^{-0.847x}$ and (b) $Y = 1.68 + 6.97 \times e^{-0.521x}$ and the respective r^2 values for these fits were 0.97 and 0.94.

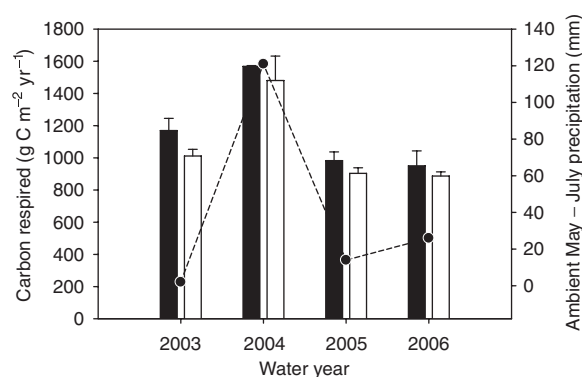


Fig. 3 Soil respiration (R_s) and rainfall for 4 water years (WYs). The dark bars represent treatment plot data, and light bars represent control plots. Instantaneous fluxes were interpolated and integrated to obtain mass of C per unit area per year. Circles connected by dashed lines indicate the amount of natural warm-season precipitation (defined as millimeters of May and June rainfall) for each WY. Warm-season precipitation was greatest in WY 2004, coinciding with the highest C respired ($P < 0.001$), although the rainfall total was highest in WY 2005.

Effects of seasonal timing of rainfall on soil respiration

In control plots, we observed large and significant differences in annual respiration rates across years. Soil respiration was approximately 50% greater in WY 2004 compared with all other years (Fig. 3). Increases in soil respiration were not simply linked to a greater total amount of rainfall in the WY. The greatest ambient rainfall total was 1010 mm yr^{-1} (approximately 30% above the long-term mean) and occurred in WY 2005,

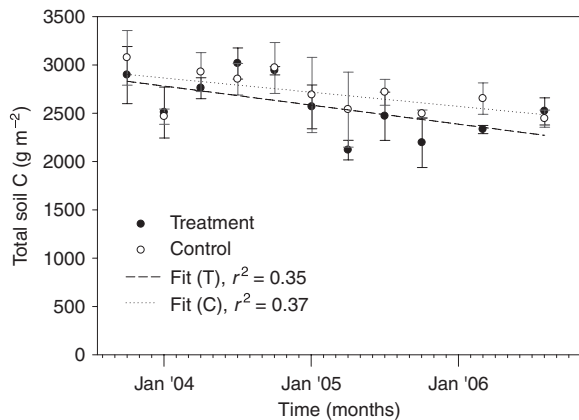


Fig. 4 Total soil C content, 0–10 cm depth, in treatment and control plots over 3 years.

but respiration was higher in WY 2004. Although WY 2004 rainfall was similar to the long-term mean (800 mm), rains lasted into June in an unusual 2-month extension to the wet season (Fig. 1a). Soil moisture was higher in the control plots during the summer of 2005 relative to other years (Fig. 1b). In May, June, and July of WY 2004, control plots respired $318 \pm 24 \text{ g C m}^{-2}$, compared with $122 \pm 11 \text{ g C m}^{-2} \text{ yr}^{-1}$ in WY 2005. Rainfall between May and July was quite low in WY 2005 (14 mm) compared with 121 mm in WY 2004 (Fig. 3).

A combination of soil moisture and temperature explained approximately 50% of the variability in soil CO_2 effluxes using data from all months (data not shown). However, separation of the data set into growing-season months (November–March, when soils are moist and grasses are most active) or intense drought months (July–August, with no live plants) resulted in two contrasting models. Soil temperature was the best predictor of soil CO_2 efflux during growing-season months, characterized by a quadratic relationship ($r^2 = 0.45$; Fig. 5a), while soil moisture was the best predictor (with linear fit) during summer drought months ($r^2 = 0.84$; Fig. 5b), when effluxes of soil CO_2 were low ($0\text{--}0.2 \mu\text{mol m}^{-2} \text{ s}^{-1}$).

Plant dynamics, net ecosystem production, and soil C pools

Using data from all years, ANPP increased significantly with increasing precipitation, including rainfall manipulations (Fig. 6, $r^2 = 0.75$, $P < 0.03$) but no consistent relationship with rainfall was observed for BNPP. Trends in total NPP were mixed and there was no significant effect of rainfall treatment (Table 2). Mean unadjusted BNPP was $180 \pm 87 \text{ g m}^{-2}$ over the study. In years with higher rainfall in control plots, the ratio of

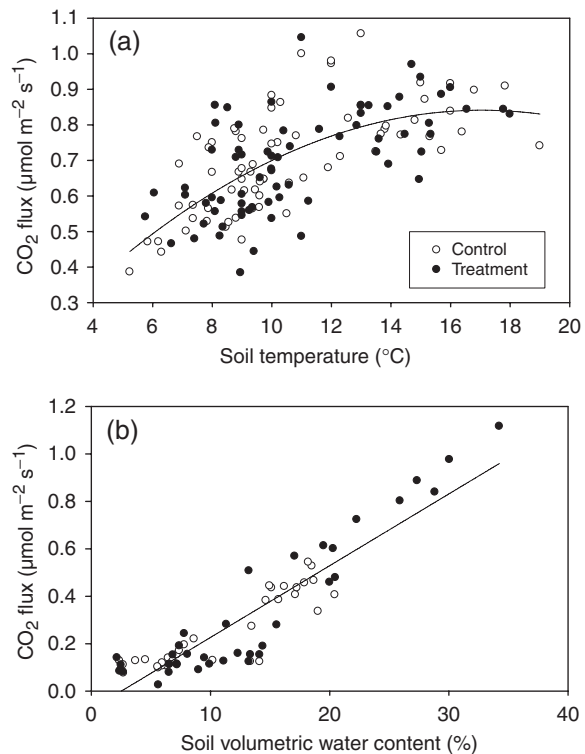


Fig. 5 Modeled relationships between soil CO_2 efflux and (a) soil temperature, during growing-season months, characterized by a quadratic relationship ($r^2 = 0.45$); and (b) soil moisture during summer drought months, with linear fit ($r^2 = 0.84$). Soil CO_2 fluxes were initially log-transformed.

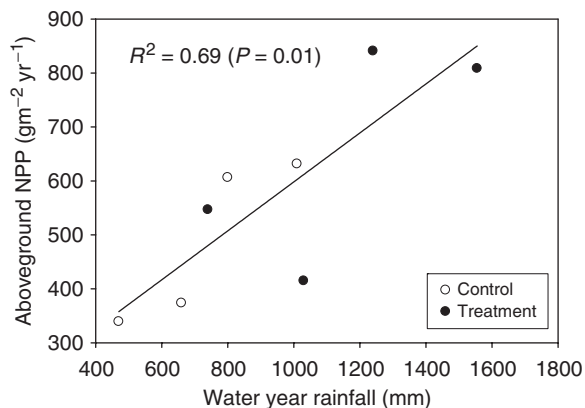


Fig. 6 Annual aboveground net primary production (NPP, in grams of dry biomass) in control and rainfall addition plots.

belowground to aboveground biomass decreased, reflecting substantial shifts in plant allocation (Fig. 7). The root:shoot ratio in control plots was significantly smaller ($P = 0.04$) in the wetter WYs 2004 or 2005 (0.11 and 0.18, respectively) compared with the drier WYs 2003 and 2006 (0.3 and 1.5, respectively). We did not observe

a difference in senescence date between rainfall treatments and there were no statistically significant changes in plant functional types with rainfall treatments (data not shown).

Our simple model of NEP yielded C gains or losses depending upon the assumed RC value. Using the field-measured NPP data and the low-RC scenario, modeled NEP consistently indicated C loss to the atmosphere (negative values) regardless of rainfall treatment, averaging -432 and -438 $\text{g C m}^{-2} \text{yr}^{-1}$ (control and treatment plots, respectively). Modeled NEP tended to be relatively less negative (less C loss) under the high-RC scenario, averaging -126 and -116 $\text{g C m}^{-2} \text{yr}^{-1}$ (control and treatment, respectively). Under the high-RC scenario, C gains occurred in WY 2005 and WY 2006. For both RC scenarios, the largest C losses occurred in WY 2004, the year with an unusually long wet season (Table 2). Augmented rainfall treatment did not alter NEP values significantly. Adjusting BNPP upward by 50% to account for turnover did not affect the sign of NEP for the low-RC scenario in any study year; and in only one of the four study years (WY 2005), NEP in control plots changed from a small positive number to a small negative number under the high-RC scenario (Table 2).

Discussion

Effects of rainfall timing on soil respiration

We observed very large and rapid increases in CO_2 effluxes (up to ~ 20 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) following early-season wet-up events. As these high flux rates occurred before the germination of annual grasses, they were due to heterotrophic respiration (Schimel *et al.*, 1989). Microbes have the capacity to respond rapidly to wetting events in semiarid and Mediterranean ecosystems (Liu *et al.*, 2002; Austin *et al.*, 2004; Huxman *et al.*, 2004a, b). Short-term increases in microbial respiration can be fueled by a sudden change in soil water potential, which causes microbes to either accept a rapid influx of soil water (which can lead to cell wall collapse), or to release intracellular solutes to maintain osmotic pressure, which in extreme cases can lead to complete cell lysis. The surviving soil microbes undergo a 'feeding frenzy' by capitalizing on the greater resource supply. This activity takes place in the span of a few hours to 2 days and despite elevated respiration rates, does not necessarily alter the microbial biomass (Kieft *et al.*, 1987).

We found that CO_2 fluxes were not very responsive to rainfall augmentation during the wet season, with only

Table 2 Net ecosystem production (NEP) [see Eqn (1)] for different rainfall treatments and two root contribution (RC) values with standard errors indicated in parentheses

Water year	Treatment	NPP (g C m^{-2})	R_s (g C m^{-2})	RC* (%)	NEP (g C m^{-2})	
					Field	Adjusted†
2003	Control	241 (23)	1011 (42)	35	-417 (36)	-445 (34)
				70	-92 (29)	-119 (26)
	Treatment	294 (43)	1170 (76)	35	-485 (50)	-529 (45)
				70	-138 (61)	-182 (52)
2004	Control	334 (46)	1480 (152)	35	-748 (62)	-764 (62)
				70	-365 (19)	-381 (20)
	Treatment	456 (85)	1568 (6)	35	-700 (107)	-718 (103)
				70	-306 (126)	-324 (122)
2005	Control	371 (56)	918 (73)	35	-249 (102)	-277 (100)
				70	21 (82)	-7 (80)
	Treatment	454 (48)	1012 (71)	35	-257 (28)	-282 (33)
				70	20 (22)	-5 (25)
2006	Control	396 (44)	887 (26)	35	-132 (48)	-245 (32)
				70	115 (61)	2 (43)
	Treatment	455 (24)	950 (93)	35	-133 (81)	-224 (90)
				70	139 (61)	48 (69)

*During the growing season, soil respiration was assumed to be either 35% or 70% from root respiration (see text), and entirely due to heterotrophic microbial respiration during the drought season. An earlier start to the growing season was assumed for treatment plots but the timing of senescence was assumed to be equivalent between treatments.

†The adjusted NEP value includes upward adjustment of belowground NPP by 50% (cf. Higgins *et al.*, 2002).

R_s , soil respiration (measured by IRGA); NPP, net primary production in C mass units; RC, root contribution (to soil respiration).

one of four study years (WY 2005) showing a significant difference. Our treatment increased the intensity of individual storms, supplying additional water when soils were already moist from ambient rainfall. Even in control plots, soils reached a maximum field capacity (35–40% volumetric water content) each year, beyond which additional water input was not likely to be retained (Fig. 1b). During these periods, soil respiration is not likely to be limited by water availability. The primary effect of increased rainfall on soil CO₂ fluxes occurred following the early- and late-season wet-up events when ambient moisture content was relatively low. Our multi-year data set documents the potential sensitivity of soil respiration in these ecosystems to relatively small changes in the seasonal timing of rainfall. A shift in the timing of rainfall can trigger significant increases in soil respiration, even if the total amount of rainfall does not increase. The high soil CO₂ fluxes in the spring of WY 2004 were driven by late-season rainfall co-occurring with warm temperatures.

Globally, soil respiration tends to increase with increasing moisture and temperature (Schlesinger, 1977). In California's Mediterranean grasslands, rainfall and temperature affect soil respiration differently by season. We observed a strong relationship between soil CO₂ fluxes and summer soil moisture (Fig. 5b), similar to observations in some semiarid grassland ecosystems (Hunt *et al.*, 2002). Temperature was not a factor during summer. During the growing season, soil respiration was more strongly dependent on soil temperature, but not rainfall (Fig. 5a). These relationships highlight the importance of seasonality in ecosystem C fluxes when the effects of temperature and moisture are decoupled in time.

Response of NPP to rainfall change

We observed a significant positive linear relationship between aboveground NPP and yearly rainfall (including rainfall manipulations) over the duration of the study (Fig. 6), similar to general patterns observed for in perennial grasslands (Sala *et al.*, 1988; Lauenroth & Sala, 1992; McCulley *et al.*, 2005). However, the similarity of NPP in WY 2004 and WY 2005 (Fig. 7), years when the seasonal timing of rainfall differed substantially (Fig. 1a), highlights the inability of annual plants to respond to changes in late-season rainfall inputs, in stark contrast to observed responses in soil respiration. In all years, annual grasses senesced at similar times, typically before the end of the rainy season. Others have speculated that temperature change, not rainfall variability, dominantly regulates the timing of senescence (Jackson & Roy, 1989; Zavaleta *et al.*, 2003; Cleland *et al.*,

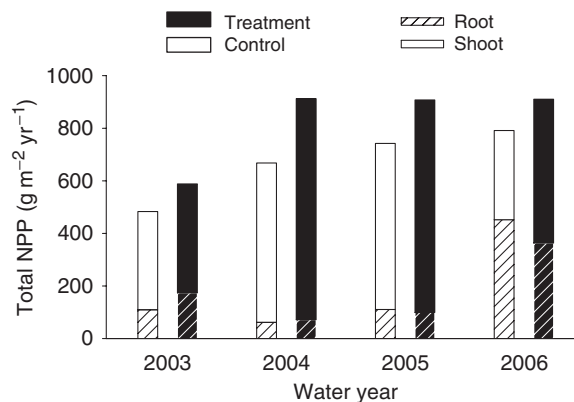


Fig. 7 Total NPP ($\text{g m}^{-2} \text{yr}^{-1}$) for 4 water years. The solid portion of the bars indicates aboveground biomass and the striped portion shows belowground biomass in control (white) and treatment (black) plots. Standard errors of NPP are provided in Table 2.

2006). Thus, annual grassland NPP would appear to be less influenced by future changes in seasonality of rainfall than by changes in rainfall quantity. An exception to this prediction might occur if altered rainfall regimes are accompanied by changes in the life history traits of the dominant vegetation, for example, through increased importance and survivorship of perennial grasses or summer annual species (Hamilton *et al.*, 1999). In this study, we note that changes in the seasonal timing or amount of rainfall had no significant effect on plant life form or community structure.

A high proportion of temperate grassland productivity is often attributable to belowground production, relative to other ecosystem types (Jackson *et al.*, 1997). In this study, shoot productivity was much higher than root productivity over the first 3 years of the study, and drove the trends in total NPP (Fig. 7). Root biomass values were of similar magnitude as those from another California annual grassland site (Dukes *et al.*, 2005), as well as previous estimates at this site (Betts, 2003). In a seasonally dry climate, annual grasslands must respond extremely rapidly to abrupt changes in water availability over their short growing season. Grassland C allocation followed expected trends, with lower belowground biomass allocation in the wettest year (WY 2005) reflecting lower demand for water capture by plants, and conversely, highest root biomass in the driest year (WY 2006). A similar phenomenon was also observed by Dukes *et al.* (2005) in their multi-year precipitation manipulation in an annual grassland.

Response of NEP to rainfall change

We might expect ecosystem C losses via soil respiration to exceed C uptake via NPP with experimental rainfall

additions, due to the greater ability of microbes to respond to increased moisture availability on a daily to monthly timestep. In fact, there were no significant differences in modeled NEP between rainfall treatments for either RC scenario (Table 2). Instead, significantly larger net C losses occurred in WY 2004, when the anomalous rainfall timing in late spring generated a large heterotrophic response. We found that increased warm-season rainfall led to lower NEP, because increased C losses via respiration outweighed increased C fixation in NPP. Our results are similar to those found in a 2-year study of net ecosystem C exchange (NEE) in annual grassland using an eddy covariance approach. In that study, grasslands alternated between a sink in year 1 and weak source in year 2; the difference in the sign of NEE between years was partly explained by rainfall occurring in the late spring for year 2, which increased respiration by 50 g C m^{-2} relative to year 1 (Xu & Baldocchi, 2004). Our results combined with those from Xu & Baldocchi (2004) suggest that heterotrophic respiration in annual grasslands is quite sensitive, relative to NPP, to variability in wet season length.

In WYs 2005 and 2006, the sink or source status of annual NEP was largely determined by the choice of RC, which, as discussed earlier, is a difficult value to measure directly and appears to be highly variable among ecosystems and under differing environmental conditions (Hanson *et al.*, 2000). As one example, values of RC ranging from 54% to 65% were reported for one California annual grassland site undergoing several climate change manipulations (Moore, 2005). These observations have important implications for the C sequestration status of these grasslands and the partitioning of soil respiration between heterotrophic and autotrophic components. There is growing interest in the source-sink response to future climate change of grasslands across the globe, including the potential for grasslands to sequester anthropogenic CO_2 (Frank & Dugas, 2001; Jones & Donnelly, 2004; Lal, 2004; Jaksic *et al.*, 2006). A wide range of results have been published regarding the variable source-sink status of grasslands, with several studies showing grassland sites to be net sinks for CO_2 (Dugas *et al.*, 1999; Lawton *et al.*, 2006; Risch & Frank, 2006; Soussana *et al.*, 2007), net C sources (Novick *et al.*, 2004; Bellamy *et al.*, 2005; Carney *et al.*, 2007; Schipper *et al.*, 2007), or near neutral (Frank & Dugas, 2001; Suyker *et al.*, 2003).

In an ongoing experiment, a California annual grassland did not generally sequester C in response to global change factors such as warming, increased CO_2 concentrations, and altered precipitation regimes (Luo *et al.*, 1996; Dukes *et al.*, 2005; Moore, 2005; Carney *et al.*, 2007). An exception to this trend is the finding that increased N inputs, representative of escalating

anthropogenic N deposition, does increase NPP in annual grasslands (Dukes *et al.*, 2005). In our study, 3 years of direct measurements of the total soil C pool support the idea that these grasslands may be a net C source. Control plots experienced a linear decrease of $150 \text{ g C m}^{-2} \text{ yr}^{-1}$ in total soil C at the 0–10 cm depth (Fig. 4). We did not measure changes to total C in deeper soils. Soil C losses were reported by Bellamy *et al.* (2005) at the rate of 0.6% per year over approximately a 30-year period from European grasslands and Schipper *et al.* (2007) described large losses of soil C from a range of New Zealand soils on the order of $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ over a 30-year period. While the rate of decrease in soil C pools in the current study was striking, it remains to be seen if such C losses would be sustained at a decadal scale. It is possible that these grasslands are continuing to undergo gradual soil C declines following conversion from perennial grasslands centuries ago, as perennial systems have been shown to accumulate soil C relative to annual croplands (McLauchlan *et al.*, 2006).

Studies have also found significant interannual variation in grassland sink-source status depending on environmental conditions (Xu & Baldocchi, 2004), resulting in NEP values closer to neutrality over time. If these grasslands are close to steady-state with regards to soil C, in the absence of large temporal shifts in rainfall (i.e. excluding WY 2004), our findings suggest that the RC to soil respiration in these grasslands would have to be 70% or greater, which is more than the average value generally assumed of perennial vegetation (Hanson *et al.*, 2000).

Conclusions

We found that soil respiration and plant productivity differed in their response to changes in rainfall regimes. NPP increased with increasing wet season rainfall. Soil respiration, however, was more sensitive to rainy season length than to the quantity of rainfall in any given year. A higher proportion of annual rain falling in late spring resulted in greater heterotrophic respiration and a larger ecosystem C deficit than in other years. Experimental rainfall additions influenced soil C fluxes depending on the seasonal timing of the added rainfall. Single-day rain events occurring outside the natural wet season elevated soil respiration on the scale of weeks.

Soil respiration was clearly limited by water in the dry season, but was more likely to be limited by cool temperatures and/or nutrients than by water during the wet season (Evans & Young, 1989). Although NPP increased with rainfall, this response was outweighed by increased C losses via heterotrophic respiration, unless a very small percentage of soil respiration was assumed to be attributable to soil microbes.

Global and regional climate models predict future changes in rainfall timing, coupled with more extreme rain events (NAST, 2001). Several studies investigating shifts in the timing or size of wet-up events have been conducted in a field setting (Hungate *et al.*, 1997; Liu *et al.*, 2002), but these tend to represent short-term manipulations rather than the multi-year study presented here. Our data suggest that heterotrophic respiration in annual grasslands is relatively responsive to changes in the seasonal timing of rainfall. More research is needed to study the long-term effects of altered rainfall timing, especially to determine if these ecosystems will adjust to a new steady-state condition, or if interannual variability in rainfall leads to dynamic year-to-year shifts in the ecosystem C balance.

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Appendix A1 Coefficients and characteristics of exponential decay functions fitting soil respiration data following wet-up

Water year	Season	Y_0	a	b	r^2	Begin date
2003	Fall	1.78	10.0	1.25	0.97	October 8
	Spring	1.26	8.02	0.476	0.78	May 12
2004	Fall	0.701	14.6	0.350	0.77	September 19
	Spring	1.68	6.97	0.521	0.94	July 12
2005	Fall	0.813	10.1	0.428	0.98	September 27
	Spring	0.762	6.54	0.543	0.98	June 7
2006	Fall	0.867	19.7	0.847	0.97	September 21
	Spring	1.23	15.5	0.689	0.77	June 1