2001-2006 Mission
Kearney Foundation of Soil Science: Soil Carbon and California's Terrestrial Ecosystems
Final Report: 2004209, 1/1/2005-12/31/2006

The Effects of Precipitation Change on Soil Carbon Cycling in the California Annual Grassland Matrix

Wendy Chou[1], Whendee L. Silver[1]*, Barbara Allen-Diaz[1]

Summary

Current global climate models predict significant rainfall change for California. The Mediterranean climate, with its pronounced seasonality of rainfall, experienced by California's annual grasslands, makes these grasslands ideal ecosystems for studying changes in the quantity and timing of rainfall. In 2006, we continued our third year of experimental rainfall additions and also explored the effects of natural interannual rainfall variability on net C storage and loss in annual grasslands. Soil respiration and net primary productivity (NPP) were measured in treatment and control plots over three growing seasons (water years, or WYs) that varied in length and intensity. In treatment plots, we increased annual rainfall by 50% and simulated one early- and one late-season storm to increase wet-season length. The early- and late-season rain events significantly increased soil respiration for two to four weeks after wetting, but annual CO_2 fluxes were resilient to 50% augmentation of wet-season rainfall. Interannual variability in precipitation had large and significant effects on C cycling. In the wettest year of the study (WY 05), NPP was 742 ± 111 g biomass m-2, while in the driest year (WY 03), NPP was 483 ± 46 g m-2. Changes in the seasonal timing of rainfall significantly affected soil respiration. Abundant rainfall late in the wet season in WY 04, a year with average total rainfall, led to greater net ecosystem C losses due to a ~50% increase in soil respiration relative to other years. Our results suggest that C cycling in annual grasslands will be more sensitive to altered rainfall distribution, rather than rainfall intensity, and that a longer or later wet season will result in significant C losses from annual grasslands.

Objectives

Our main objective in this study was to investigate the above- and belowground response of annual grassland C cycling to variation in the amount and seasonal distribution of rainfall. We addressed this objective via two separate approaches: a "natural," unmanipulated experiment, in which we exploited the extant interannual variability in rainfall quantity and timing over three seasons; and, coupled with this, a rainfall addition experiment which increased the intensity of wet-season storms (by a 50 % increase over ambient rainfall) and lengthened 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 prior to and immediately following) the natural wet season. The goal of this field-based rainfall manipulation experiment was to identify potential feedbacks to the climate system through changes in ecosystem C storage and loss resulting from altered precipitation regimes.

[1] Division of Ecosystem Sciences, Department of Environmental Science, Policy and Management, University of California – Berkeley

Another research objective we furthered during 2006 was the better understanding of C cycling within the broader annual grassland matrix. Within this matrix are situated perennially moist, spring-fed wetlands featuring a very different environment and microclimate. These wetlands produce N_2O (nitrous oxide) and CH_4 (methane), which are more potent agents of fluxes in these wetlands and constructed a reduced water flow system to simulate a decreased precipitation regime.

Approach and Procedures

The study was conducted at the Sierra Foothill Research and Extension Center (SFREC) located in Browns Valley, Yuba County, California ($39^o15'$ N, $121^o17'$W), which features sloping terrain ranging from 90 to 600 m above sea level, 750 mm y-1 MAP, and 16^o C MAT.

In the annual grassland, the experimental design consisted of three experimental blocks – each with a treatment plot with added rainfall and an unmanipulated control plot, separated by a buffer strip 15-m wide. Plots were 15 × 30 m each and contained only herbaceous vegetation. Control plots received ambient rainfall without alteration. Each year, treatment plots 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 hours via 28 microsprinklers (Model MS VI, Toro, Bloomington, MN). Fall wet-up events took place approximately one to three weeks before the start of the rainy season, and were substantial enough to trigger seedling germination three to four days after wet-up. Late-season wet-ups took place approximately four weeks after the end of the rainy season. Microsprinklers were mounted to 4-foot-tall stakes arrayed in a grid throughout the plot.

During the wet season, sprinklers increased hourly rainfall in treatment plots by 50% by means of an automated delivery system connected to a tipping-bucket rain gauge (Forestry Suppliers, Jackson, MI) and a CR10X datalogger (Campbell Scientific, Logan, UT). The CR10X controlled a 12 VDC-operated valve (Superior Controls, Valencia, CA) upstream of the sprinklers to deliver simulated rain proportional to hourly rainfall. Irrigation water was supplied from a nearby lake and filtered before entering the irrigation system.

Soil moisture and temperature. We sampled soils (0-10 cm depth) bi-weekly by gravimetric methods and by installing automated real-time sensors for volumetric water content (Campbell Scientific CS616, three probes per plot). Soil temperature was obtained hourly in the 0-10 cm depth using automated probes (Campbell Scientific, one probe per plot) or manually via a temperature probe connected to a portable infrared gas analyzer (IRGA, see below). Grassland bulk density was calculated at 1.13 ± 0.05 g cm-3 to 10 cm depth.

Soil respiration. Fluxes of CO_2 across the soil-atmosphere interface were measured biweekly using a Li-6400 IRGA (Li-Cor Biosciences, Lincoln, NE) fitted with a soil efflux chamber (five measurements per plot). We sampled daily or every two to three days following wet-up events until soil respiration was not significantly different between treatment and control plots.

Net primary productivity. Annual NPP was estimated by harvesting peak standing biomass at the end of the growing season. All vegetation was harvested to the ground surface in six 30 ¥ 30-cm quadrants per plot, dried at 65^o C, and weighed. Root biomass was estimated once annually also at peak biomass by harvesting soil cores (8 per plot, 0-15 cm depth) in late spring, washing roots free of soil, drying roots at 65^o C, and weighing. Species composition was estimated annually by a point-intercept method (100 points per plot).

Nitrous oxide and methane. Gas samples were collected from the headspace of static vented chambers temporarily installed in the soil surface (Hutchinson and Livingston 1993). Samples were analyzed by gas chromatography and concentrations over time were fitted to obtain a flux (Matthias et al. 1978).

Results and Discussion

Soil CO_2 fluxes: response to rainfall manipulation. Wet-up events resulted in large pulses of soil CO_2 across the soil-atmosphere interface. The contribution of combined wet-up events to the total C respired per year ranged from about 8 to 18 % (*table 1*). Pulses of CO_2 were related to higher soil moisture content resulting from wet-up treatments. Wet-ups significantly elevated soil moisture in treatment plots relative to controls for 27 and 25 days, respectively, in Fall of WY 03 and Fall of WY 05 (*fig. 1b*). In WY 04, an early fall storm coincided with the timing of the wet-up event (19 September), and soil moisture was elevated for 16 days in treatment plots relative to controls (*fig. 1a-b*). 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 03, 04, and 05, respectively.

Effluxes of CO_2 were generally quite low (0 to 0.2 µmol m-2 s-1) during the period of summer drought, and the largest CO_2 fluxes were observed in response to wetting of dry soil in early fall (*fig. 2a, c, e*). The increased soil CO_2 emissions were observed prior to germination of annual grasses, implying a heterotrophic source (Schimel et al. 1989). Microbes have the capacity to respond rapidly to wetting events in strongly seasonal and dry-land ecosystems (Austin et al. 2004; Huxman et al. 2004a; Huxman et al. 2004b; Liu et al. 2002; Saetre and Stark 2005; Steenwerth et al. 2005; Xu et al. 2004; Xu and Baldocchi 2004). 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 substrate supply. This activity takes place in the span of a few hours to two days and despite elevated respiration rates, does not necessarily alter the microbial biomass (Kieft et al. 1987).

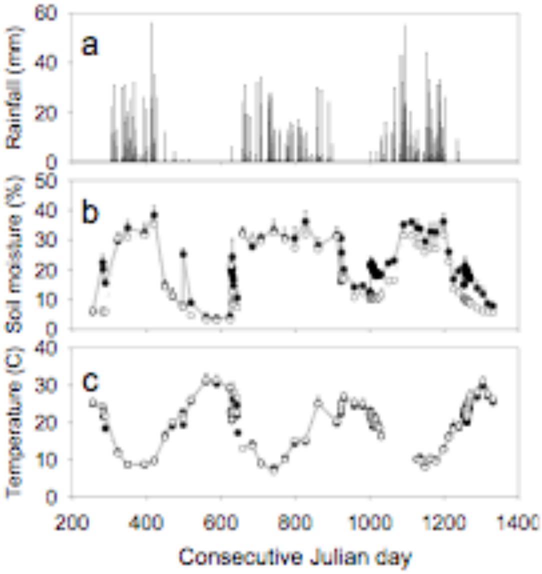
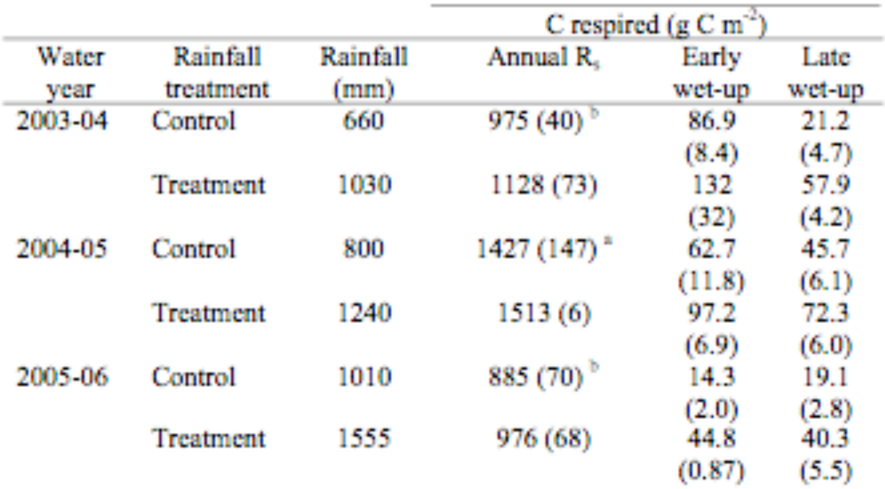


Figure 1. Daily rainfall measured at Browns Valley (Station #84) by the California Irrigation Management Information System, from September 2003 to August 2005. (experimental water additions not shown). (b) Volumetric soil water content from 0-10 cm depth measured in treatment (filled circles) and control (open circles) plots. (c) Soil temperature data measured in treatment and control plots.



			C respired (g C m^{-2})		
Water year	Rainfall treatment	Rainfall (mm)	Annual R_s	Early wet-up	Late wet-up
2003-04	Control	660	975 (40) ^{b}	86.9 (8.4)	21.2 (4.7)
	Treatment	1030	1128 (73)	132 (32)	57.9 (4.2)
2004-05	Control	800	1427 (147) ^{a}	62.7 (11.8)	45.7 (6.1)
	Treatment	1240	1513 (6)	97.2 (6.9)	72.3 (6.0)
2005-06	Control	1010	885 (70) ^{b}	14.3 (2.0)	19.1 (2.8)
	Treatment	1555	976 (68)	44.8 (0.87)	40.3 (5.5)

Table 1. *Soil respiration by rainfall treatment over three water years (means and standard errors). 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. Rs represents the annual C respired and is equal to the sum of instantaneous IRGA measurements from the soil surface, interpolated over time to daily fluxes. Letters next to Rs values indicate significant difference (across water years) when compared with ANOVA. Treatment and control CO_2 effluxes were not significantly different at the timescale of the entire year. The mass of carbon respired differed between treatment and controls at 95% significance level for all wet-up events.*

Soil CO_2 fluxes declined exponentially after the wet-up events and significantly exceeded control plot fluxes for two to four 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 to early-season events (*fig. 2b, d, f*). Individual wet-up events differed slightly in their coefficients of the fitted exponential curves (*fig. 2*). Augmented rainfall treatment resulted in higher soil CO_2 fluxes from treatment plots over controls for all three study years (*fig. 3*), but results were statistically significant only during year three ($p = 0.06$). These differences were due primarily to the early- and late-season wet-up events, documenting the potential sensitivity of these ecosystems to relatively small changes in climate.

We found that CO_2 fluxes were relatively insensitive to our 50% rainfall augmentation. Our treatment increased storm intensity, supplying additional water when soils were already moist from ambient rainfall. Even in control plots, soils reached a maximum field capacity (35 to 40% volumetric water content) each year, beyond which additional irrigation was not likely to be retained (*fig. 1b*). Across years, the augmented rainfall treatment had the largest relative effect on soil moisture in WY 05, when volumetric water content was 23% in treatment plots versus 15% in control plots ($p < 0.001$, *fig. 1b*). Soil moisture was 18% versus 14% in WY 03 ($p = 0.06$), and 23% versus 20% in WY 04 ($p = 0.05$) in treatment and control plots, respectively.

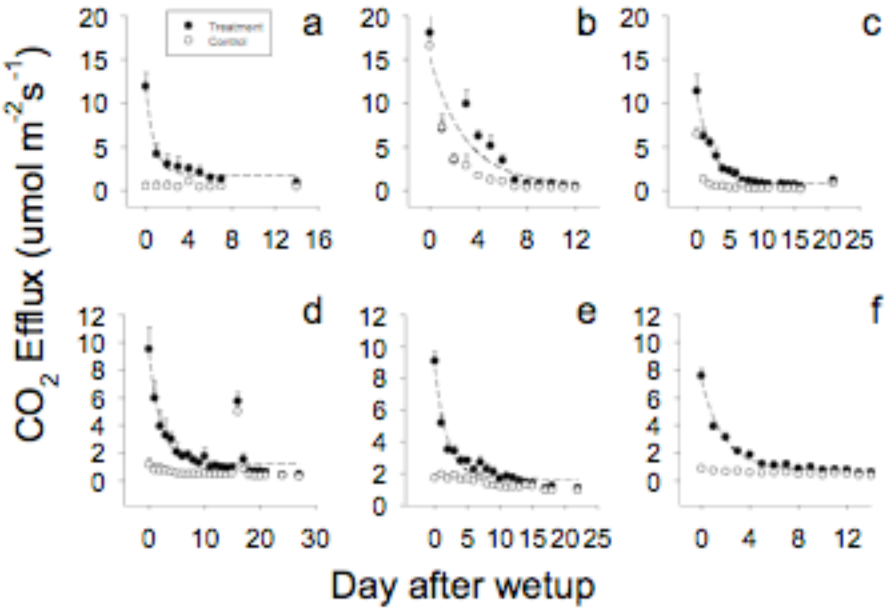


Figure 2. Fluxes of CO_2 following six wet-up events: (a) Fall ’03; (b) Fall ’04; (c) Fall ’05; (d) Spring ’04; (e) Spring ’05; (f) Spring ’06 from treatment and control plots (filled and empty circles, respectively). Data from treatment plots were fitted with exponential decay curves (treatment: filled circles).

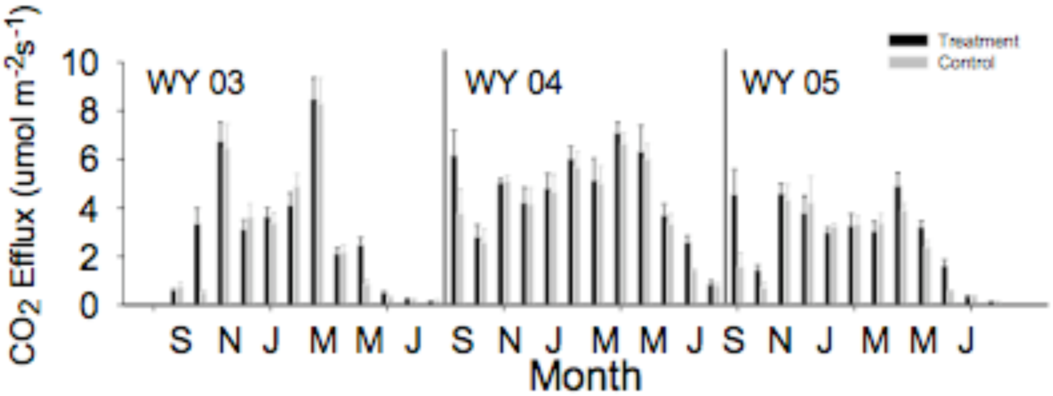


Figure 3. Mean monthly CO_2 fluxes over three water years. Dark bars represent treatment and open bars, control.

Effects of seasonal distribution of rainfall. We observed large and significant differences in the total C respired across years from control plots. Soil respiration was almost 50% greater in WY 04 compared to WY 03 or WY 05 (*table 1, fig. 4*). Increases in respired C were not simply linked to a greater total amount of rainfall. Ambient rainfall during the study increased from 660 mm in WY 03 to 800 mm in WY 04, and to 1010 mm y^{-1} (approximately 30% above 750 mm y^{-1}, the long-term mean) in WY 05. Although WY 04 rainfall was similar to the long-term mean and was less than WY 05 rainfall, rains lasted into June in an unusual two-month extension to the wet season (*fig. 1a*). As a result, the late-season wet-up took place later in the year (July) and soil moisture in treatment plots was higher in the summer of 2005 relative to the previous year's summer (*fig. 1b*). This late-season rainfall in WY 04 occurred in a time typically characterized by warm temperatures and declining soil moisture. Warm, moist conditions elevated soil CO_2 fluxes in May, June, and July of WY 04, when control plots respired 307 ± 23 g C m^{-2}, compared with 54 ± 8 g C m-2 y^{-1} in WY 03, and 118 ± 11 g C m^{-2} y^{-1} in WY 05. Rainfall between May and July was quite low in WY 03 (2 mm) and WY 05 (14 mm), compared to 121 mm in WY 04 (*fig. 4*). Our data show that soil respiration can increase significantly with a shift in the timing of rainfall, even if the total amount of rainfall does not increase.

Soil respiration tends to increase with increasing moisture and temperature (Schlesinger 1977). A combination of moisture and temperature explained approximately 50% of the variability in CO_2 effluxes when data from all months were modeled in a linear regression. Separation of the dataset into growing-season months (November to March, when grasses are active) or drought months (July to August) 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), while soil moisture was the best predictor (with linear fit) during drought months ($r^2 = 0.86$). The significant relationship between CO_2 fluxes and summer soil moisture derives from the fact that drought limits microbial activity in the summer, but temperature limitation plays an important role for plants and microbes during the growing season.

Net primary productivity. Total annual NPP increased significantly with rainfall additions ($p = 0.06$) and decreased significantly ($p < 0.05$) in the driest year, WY03 (*fig.*

5). Root productivity was higher in treatment plots in WY 03 relative to controls (Treatment: 179 ± 23 g m^{-2} y^{-1}, Control: 111 ± 13 g m^{-2} y^{-1}, $p = 0.07$), and root biomass was significantly greater in the drier WY03 than in WY04. The similarity of NPP in WY 04 and WY 05 implies an insensitivity of NPP 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 season's rains. Annual grass senescence is generally inflexible to precipitation variability (Cleland et al. 2006; Jackson and Roy 1989). Thus, annual grassland NPP appears less likely influenced by future changes in the distribution of rainfall than by wet-season rainfall totals, unless altered rainfall regimes under climate change 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, changes in the seasonal distribution or amount of rainfall had no significant effect on plant life form or community structure.

Grassland allocation of C followed expected trends. In years with higher rainfall, proportionally less photosynthate was shunted to belowground biomass production, reflecting lower demand for water capture by plants. An inverse relationship between precipitation and root production was also observed by Dukes et al. (2005) in their multi-year precipitation manipulation in an annual grassland. In our study, shoot productivity was much higher than root productivity over all study years and drove the trends in total NPP. Mean annual root biomass was approximately 100 gm $^{-2}$ over the three-year study. These values are considerably lower than those from other semi-arid ecosystems (Dukes et al. 2005), but are similar to previous estimates at this site (Betts 2003). It is possible that our sampling method underestimated annual belowground NPP (BNPP) by failing to account for intra-annual root turnover (Higgins et al. 2002).

Net ecosystem production (NEP). We calculated NEP using the relationship: NEP = NPP - Rh, in which Rh represents the proportion of soil respiration contributed by bulk soil heterotrophs. We predicted that ecosystem C losses via soil respiration would 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 time step. Values from the current cropland and grassland literature regarding the partitioning of heterotrophic versus root respiration were used to derive Rh given our measurements of Rs, total soil respiration (Hanson et al. 2000; Robertson et al. 1995; Rochette and Flanagan 1997; Swinnen et al. 1994; Wan and Luo 2003). To account for potential underestimates of root production, we also revised our root biomass upward by 50% (1.5 × BNPP; *table 2*).

Of the 18 possible scenarios of NEP (3 water years ¥ 3 root respiration values ¥ 2 levels of rainfall treatment), the ecosystem lost more C than it gained in all but three cases using the measured BNPP, and in all but four cases using the root correction factor (*table 2*). NEP was positive (indicating terrestrial C uptake) only when root respiration was assumed to be 85%, the highest value we tested. We note that this high estimate of the root contribution to soil respiration was obtained from a short-term isotope labeling study and likely reflects a maximum, rather than average, growing-season value. The majority of studies have reported the heterotrophic contribution to soil respiration well above 15% (Hanson et al. 2000). Though high variability may have masked any statistically significant effect of rainfall treatment on NEP, deficits increased in WY 04, when the change in the distribution of ambient rainfall generated a large heterotrophic response (*table 2*).

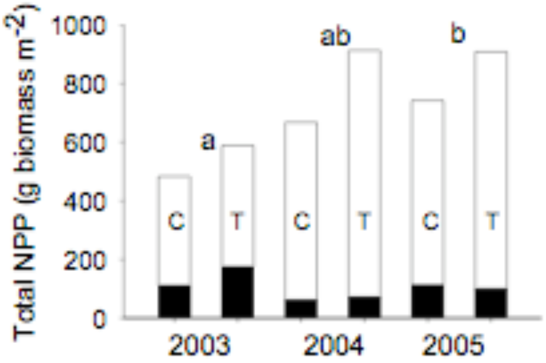
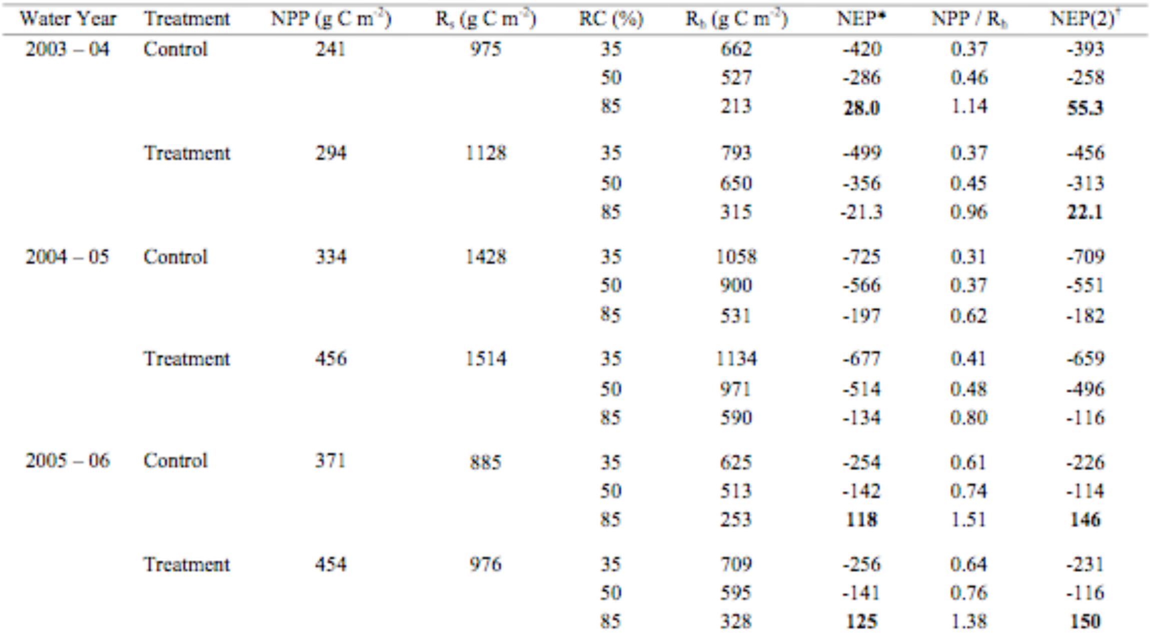


Figure 5. Net primary production data for three water years. The unfilled portion of the bars indicates aboveground biomass and the black portion shows belowground biomass in control (C) and treatment (T) plots. Over three years, a positive relationship was seen between NPP and total annual rainfall, indicated by letters above each water year ($p = 0.02$).

There is growing interest in the source-sink response of grasslands to future climate change, including the potential for grasslands to sequester anthropogenic CO_2 (Frank and Dugas 2001; Jaksic et al. 2006; Jones and Donnelly 2004; Lal 2004). However, previous studies in California grasslands have either shown a muted response to global change factors such as warming, increased CO_2 concentrations, and altered precipitation regime, or positive feedbacks to CO_2 emissions, rather than C sequestration (Dukes et al. 2005; Luo et al. 1996). An exception to this trend is the finding that increased N inputs, representative of escalating anthropogenic N deposition, does increase NPP (Dukes et al. 2005). In our study, we found that increased warm-season rainfall led to lower NEP, as C losses via respiration outweighed C fixation in NPP. Our results are similar to those found in a two-year study of ecosystem C exchange in annual grassland, in which the grassland alternated between a sink in year 1 and a weak source in year 2; the difference in the sign of NEE between years was explained not by total rainfall but by rainfall occurring in the late spring for year 2, which increased respiration by 50 g C m-2 relative to year 1, (Xu and Baldocchi 2004).

Table 2. *Annual soil C balance for different rainfall treatments and three assumed root contribution (RC) values during the growing season. Respiration was assumed to be entirely heterotrophic in origin during the drought season. Values of RC were taken from the literature (see citations in text) and applied to an idealized growing season (October 1 to April 30). Note that Rh = heterotrophic respiration, Rs is the value measured by IRGA from the soil surface, and NPP = net primary production in C mass units. *Net ecosystem production (NEP) was calculated as NPP-Rh. Positive NEP indicates terrestrial C uptake and negative NEP indicates loss of C to the atmosphere. Values in bold indicate scenarios with net positive NEP, which only occurred for the case of RC = 85%. † NEP(2) was calculated as above except belowground NPP was multiplied by 1.5 cf. Higgins et al.(Higgins et al. 2002).*



Water Year	Treatment	NPP (g C m^{-2})	R$_s$ (g C m^{-2})	RC (%)	R$_h$ (g C m^{-2})	NEP*	NPP / R$_h$	NEP(2)†
2003 – 04	Control	241	975	35	662	-420	0.37	-393
				50	527	-286	0.46	-258
				85	213	**28.0**	1.14	**55.3**
	Treatment	294	1128	35	793	-499	0.37	-456
				50	650	-356	0.45	-313
				85	315	-21.3	0.96	**22.1**
2004 – 05	Control	334	1428	35	1058	-725	0.31	-709
				50	900	-566	0.37	-551
				85	531	-197	0.62	-182
	Treatment	456	1514	35	1134	-677	0.41	-659
				50	971	-514	0.48	-496
				85	590	-134	0.80	-116
2005 – 06	Control	371	885	35	625	-254	0.61	-226
				50	513	-142	0.74	-114
				85	253	**118**	1.51	**146**
	Treatment	454	976	35	709	-256	0.64	-231
				50	595	-141	0.76	-116
				85	328	**125**	1.38	**150**

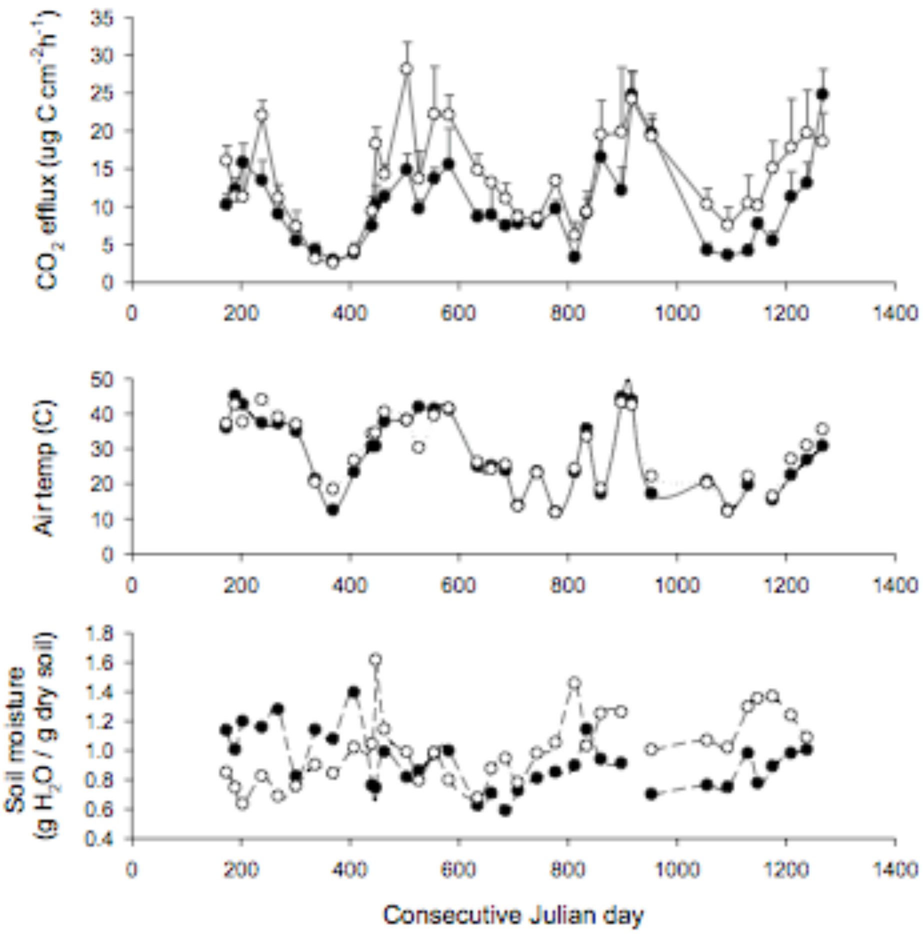


Figure 6. Three years of monthly CO_2 (top), temperature (middle), and soil moisture (bottom panel) data from spring-fed wetlands. Filled circles represent control plots and open circles represent trenched wetlands, which will receive dry-down treatment in 2007.

Trace gas cycling in spring-fed wetlands. Spring-fed wetlands in the grassland matrix were trenched upslope in November 2003 in preparation for drydown treatment. Data collection proceeded on a monthly timestep from June 2003 until May 2006. While we observed dramatic seasonal variation in grassland soil moisture, we saw much less trending in soil moisture in spring-fed wetlands, comparing both among the seasons of an individual year and also among multiple years (*fig. 6*). Reduced moisture variability appears to be a characteristic of these ecosystems. CO_2 fluxes did follow seasonal cycles, and were correlated with cyclical changes in air temperature, with minimum values occurring during winter months (*fig. 6*). We infer that the generally constant presence of available soil water moderates potential fluctuations in soil respiration (limiting such variability to a function of temperature), and by extension, reduces variability in C cycling in spring-fed wetlands. This observation, combined with our grassland data, highlights the role of water availability in controlling ecosystem C cycling in Mediterranean climate systems. Measured effluxes of N_2O and CH_4 were smaller by many orders of magnitude relative to CO_2 effluxes (*fig. 7*). Net effluxes of these gases were highest during the summer months.

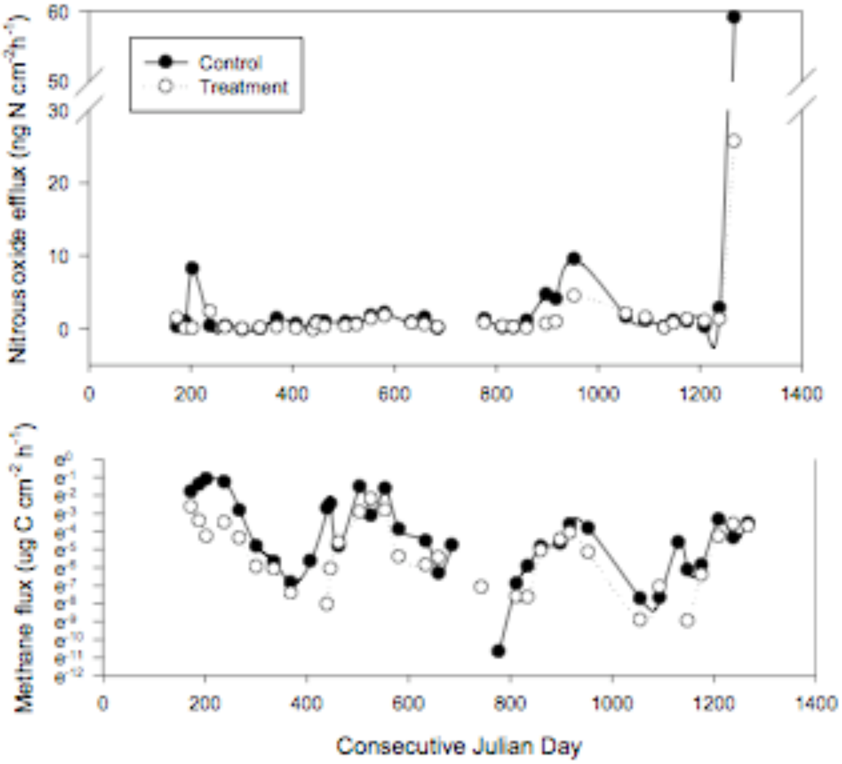


Figure 7. Net effluxes of nitrous oxide (top panel) and methane (bottom panel; note natural log-scale) from spring-fed wetland soils over three years. Treatment refers to trenching upslope in preparation for drydown.

Conclusions

We found that ecosystem-scale C cycling in annual grasslands was more sensitive to the seasonal distribution of rainfall than to the total amount of rainfall in any given year. A higher proportion of annual rain falling late in the water year 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.

Over three years, a 50% increase in water inputs during the wet season had no significant effect on soil respiration, but did increase NPP. This result points to an apparent surplus of soil water for microbes, but not plants, during an average rainy season (Major 1988) and supports existing theory that CO_2 fluxes in annual grasslands are more likely limited by cool temperatures and/or nutrients than by water during the wet season (Chiariello 1989). Although NPP increased with rainfall, this response was outweighed by C losses via heterotrophic respiration, unless only 15% of soil respiration was assumed to be attributable to soil microbes. Even with this assumption, we saw large C sinks in only one of three study years.

Global and regional climate models predict future changes in the temporal distribution of rainfall, coupled with more extreme rain events (NAST 2001). Our data suggest that annual grasslands are likely to become a net source of CO_2 with relatively small changes in the timing of rainfall. At this point, the annual grass community composition does not appear to have shifted significantly in response to the altered precipitation regime; such a community shift (e.g., to perennial plants) would likely affect the storage and turnover of soil C. Further long-term research will help to determine if prolonged change in the seasonal distribution of rainfall would lead these grasslands to a new steady-state condition, or if interannual variability in rainfall leads to dynamic year-to-year shifts in the ecosystem C balance.

References

Austin, A.T., L. Yahdjian, J.M. Stark, J. Belnap, A. Porporato, U. Norton, D.A. Ravetta, and S.M. Schaeffer. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141: 221-235.

Betts, A.D.K. 2003. Ecology and control of goatgrass (Aegilops triuncialis) and medusahead (Taeniatherum caput-medusae) in California annual grasslands. Ph.D. University of California, Berkeley.

Chiariello, N.R. 1989. Phenology of California Grasslands. In Grassland Structure and Function, eds. L.F. Huenneke and H.A. Mooney), pp. 47-58. Kluwer Academic Publishers.

Cleland, E.E., N.R. Chiariello, S.R. Loarie, H.A. Mooney, and C.B. Field. 2006. Diverse responses of phenology to global changes in a grassland ecosystem. Proceedings of the National Academy of Sciences of the United States of America 103: 13740-13744.

Dukes, J.S., N.R. Chiariello, E.E. Cleland, L.A. Moore, M.R. Shaw, S. Thayer, T. Tobeck, H.A. Mooney, and C.B. Field. 2005. Responses of grassland production to single and multiple global environmental changes. *PLOS Biology* 3: e319.

Frank, A.B., and W.A. Dugas. 2001. Carbon dioxide fluxes over a northern, semiarid, mixed-grass prairie. *Agricultural and Forest Meteorology* 108: 317-326.

Hamilton, J.G., C. Holzapfel, and B.E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia* 121: 518-526.

Hanson, P.J., N.T. Edwards, C.T. Garten, and J.A. Andrews. 2000. Separating root and soil microbial contributions to soil respiration: A review of methods and observations. *Biogeochemistry* 48: 115-146.

Higgins, P.A.T., R.B. Jackson, J.M. Des Rosiers, and C.B. Field. 2002. Root production and demography in a California annual grassland under elevated atmospheric carbon dioxide. *Global Change Biology* 8: 841-850.

Hutchinson, G.L., and G.P. Livingston. 1993. Use of chamber systems to measure trace gas fluxes. In: *Agricultural ecosystem effects on trace gases and global climate change,* eds. L.A. Harper, A.R. Mosier, J.M. Duxbury and D.E. Rolston, pp. 63–78.

Huxman, T.E., J.M. Cable, D.D. Ignace, J.A. Eilts, N.B. English, J. Weltzin, and D.G. Williams. 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, T.E., K.A. Snyder, D. Tissue, A.J. Leffler, K. Ogle, W.T. Pockman, D.R. Sandquist, D.L. Potts, and S. Schwinning. 2004b. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141: 254-268.

Jackson, L.E., and J. Roy. 1989. Comparative ecology of annual grasses: Native versus Californian habitats and populations. In: *Grassland structure and function*, eds. L.F. Huenneke and H.A. Mooney, pp. 81-91. Kluwer Academic Publishers.

Jaksic, V., G. Kiely, J. Albertson, R. Oren, G. Katul, P. Leahy, and K.A. Byrne. 2006. Net ecosystem exchange of grassland in contrasting wet and dry years. *Agricultural and Forest Meteorology* 139: 323-334.

Jones, M.B., and A. Donnelly. 2004. Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO_2. *New Phytologist* 164: 423-439.

Kieft, T.L., E. Soroker, and M.K. Firestone. 1987. Microbial biomass response to a rapid increase in water potential when dry soil is wetted. *Soil Biology and Biochemistry* 19: 119-126.

Lal, R. 2004. Soil carbon sequestration to mitigate climate change. *Geoderma*. 123: 1-22.

Liu, X.Z., S.Q. Wan, B. Su, D.F. Hui, and Y.Q. Luo. 2002. Response of soil CO2 efflux to water manipulation in a tallgrass prairie ecosystem. *Plant and Soil* 240: 213-223.

Luo, Y.Q., R.B. Jackson, C.B. Field, and H.A. Mooney. 1996. Elevated CO2 increases belowground respiration in California grasslands. *Oecologia* 108: 130-137.

Major, J. 1988. California climate in relation to vegetation. In: *Terrestrial vegetation of California*, eds. M.G. Barbour and J. Major, pp. 11-74. Wiley Interscience.

Matthias, A.D., D.N. Yarger, and R.S. Weinbeck. 1978. A numerical evaluation of chamber methods for determining gas fluxes. *Geophysical Research Letters* 5: 765-768.

NAST. 2001. Climate change impacts on the United States: Foundation Report U.S. Global Change Research Program.

Robertson, F.A., R.J.K. Myers, and P.G. Saffigna. 1995. Respiration from soil and litter in a sown perennial grass pasture. *Australian Journal of Soil Research* 33: 167-178.

Rochette, P., and L.B. Flanagan. 1997. Quantifying rhizosphere respiration in a corn crop under field conditions. *Soil Science Society of America Journal* 61: 466-474.

Saetre, P., and J.M. Stark. 2005. Microbial dynamics and carbon and nitrogen cycling following re-wetting of soils beneath two semi-arid plant species. *Oecologia* 142: 247-260.

Schimel, J.P., L.E. Jackson, and M.K. Firestone. 1989. Spatial and temporal effects on plant-microbial competition for inorganic nitrogen in a California annual grassland. *Soil Biology and Biochemistry* 21: 1059-1066.

Schlesinger, W.H. 1977. Carbon Balance in Terrestrial Detritus. *Annual Review of Ecology and Systematics* 8: 51-81.

Steenwerth, K.L., L.E. Jackson, F.J. Calderon, K.M. Scow, and D.E. Rolston. 2005. Response of microbial community composition and activity in agricultural and grassland soils after a simulated rainfall. *Soil Biology and Biochemistry* 37: 2249-2262.

Swinnen, J., J.A. Vanveen, and R. Merckx. 1994. Rhizosphere carbon fluxes in field-grown spring wheat – Model-calculations based on C-14 partitioning after pulse-labeling. *Soil Biology and Biochemistry* 26: 171-182.

Wan, S.Q., and Y.Q. Luo. 2003. Substrate regulation of soil respiration in a tallgrass prairie: Results of a clipping and shading experiment. *Global Biogeochemical Cycles* 17.

Xu, L., D.D. Baldocchi, and J. Tang. 2004. How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. *Global Biogeochemical Cycles* 18: doi:10.1029/2004GB002281.

Xu, L.K., and D.D. Baldocchi. 2004. Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. *Agricultural and Forest Meteorology* 123: 79-96.

This research was funded by the Kearney Foundation of Soil Science: Soil Carbon and California's Terrestrial Ecosystems, 2001-2006 Mission (http://kearney.ucdavis.edu). The Kearney Foundation is an endowed research program created to encourage and support research in the fields of soil, plant nutrition, and water science within the Division of Agriculture and Natural Resources of the University of California.