

Rain pulse response of soil CO₂ exchange by biological soil crusts and grasslands of the semiarid Colorado Plateau, United States

D. R. Bowling,¹ E. E. Grote,² and J. Belnap²

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[1] Biological activity in arid grasslands is strongly dependent on moisture. We examined gas exchange of biological soil crusts (biocrusts), the underlying soil biotic community, and the belowground respiratory activity of C₃ and C₄ grasses over 2 years in southeast Utah, USA. We used soil surface CO₂ flux and the amount and carbon isotope composition ($\delta^{13}\text{C}$) of soil CO₂ as indicators of belowground and soil surface activity. Soil respiration was always below $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ and highly responsive to soil moisture. When moisture was available, warm spring and summer temperature was associated with higher fluxes. Moisture pulses led to enhanced soil respiration lasting for a week or more. Biological response to rain was not simply dependent on the amount of rain, but also depended on antecedent conditions (prior moisture pulses). The short-term temperature sensitivity of respiration was very dynamic, showing enhancement within 1–2 days of rain, and diminishing each day afterward. Carbon uptake occurred by cyanobacterially dominated biocrusts following moisture pulses in fall and winter, with a maximal net carbon uptake of $0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, although typically the biocrusts were a net carbon source. No difference was detected in the seasonal activity of C₃ and C₄ grasses, contrasting with studies from other arid regions (where warm- versus cool-season activity is important), and highlighting the unique biophysical environment of this cold desert. Contrary to other studies, the $\delta^{13}\text{C}$ of belowground respiration in the rooting zone of each photosynthetic type did not reflect the $\delta^{13}\text{C}$ of C₃ and C₄ physiology.

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1. Introduction

[2] Ecosystem processes in dryland regions are principally dependent on moisture, which is often the most limiting factor for activity of desert organisms [Noy-Meir, 1973, 1974]. There is a growing appreciation that the seasonality of precipitation in these areas can be as important as the amount of precipitation in influencing ecosystem processes, including C dynamics. Much of the southwest United States and northwest Mexico receives summer rain during the North American monsoon [Adams and Comrie, 1997], and the influence is particularly strong in the warm Chihuahuan and Sonoran deserts [Loik et al., 2004]. The cold deserts of the Intermountain region are not strongly influenced by the monsoon; the Great Basin receives little summer rain, and the Colorado Plateau an intermediate amount [Higgins et al., 1997]. Based on these regional differences in seasonality of precipitation, there are likely fundamental differences in the

responses of desert organisms to rain and their influences on C cycling processes. However, knowledge of soil carbon (C) cycling processes in cold deserts of North America lags behind that for the better studied warm deserts.

[3] Precipitation in arid regions is dominated by small events [Huxman et al., 2004; Lauenroth and Bradford, 2009; Reynolds et al., 2004]. In the Canyonlands region of the Colorado Plateau of southeast Utah (location of the present study), 71% of rain pulses are smaller than 5 mm, and 35% are smaller than 1 mm (Figure 1). Contrasting with the fairly regular summer monsoon precipitation of the warm deserts, moisture events in the cold deserts are fairly evenly distributed throughout the year, although there is a little less precipitation in June, and a little more in September and October [Schwinning et al., 2008]. In winter, cold desert soils are near or sometimes below freezing, and precipitation leads to recharge of soils (Figure 2), providing stored water that plants can access during the growing season [Bowling et al., 2010; Obrist et al., 2004; Prater and DeLucia, 2006; Wohlfahrt et al., 2008]. Summer rain falls on hot dry soils with little soil recharge, leading to a functional distinction between winter and summer precipitation that influences ecological processes throughout the cold deserts [Gebauer and Ehleringer, 2000; Kulmatiski et al., 2006; Prev y et al., 2010; Schwinning et al., 2003, 2005b].

¹Department of Biology, University of Utah, Salt Lake City, Utah, USA.

²Southwest Biological Science Center, U.S. Geological Survey, Moab, Utah, USA.

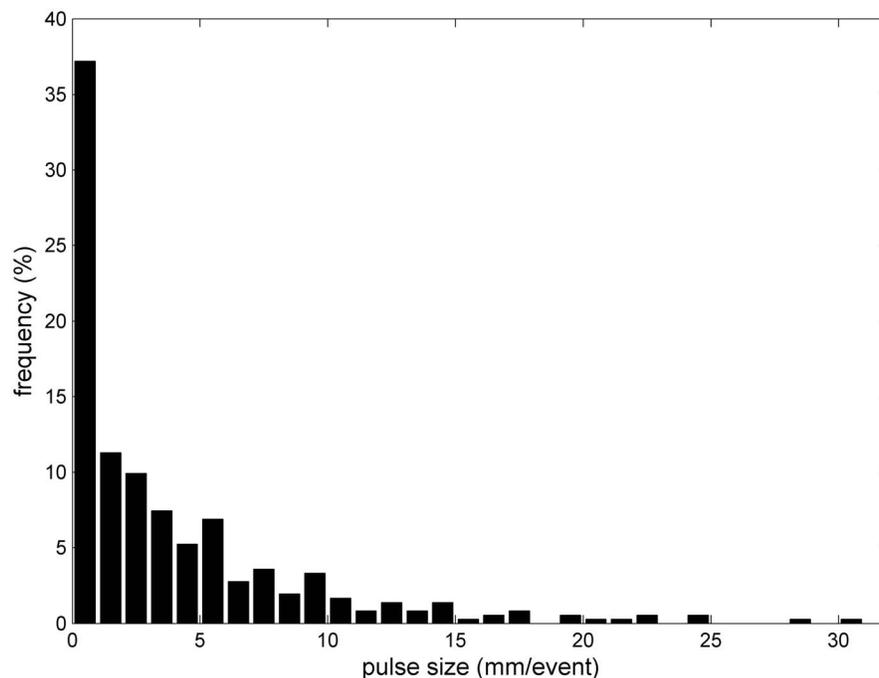


Figure 1. Frequency distribution of precipitation events at Corral Pocket during 1999–2008. Pulses are defined as single or cumulative events separated by 24 or more rain-free hours. A total of 363 pulses occurred during this period, with 1747 h where rain was recorded.

[4] Biological soil crusts (biocrusts) are communities of organisms including cyanobacteria, mosses, lichens, and algae, covering the top few millimeters of the soil surface [Belnap, 2006; Belnap et al., 2003]. Co-occurring with plants, they can cover up to 70% of the surface in drylands around the globe. These drylands compose 40% of the Earth's land surface. Biological soil crusts serve important functional roles, including stabilizing soils against erosion, influencing infiltration of water and germination of plant seeds, and C and nitrogen fixation. Due to their occurrence at the surface of the soil, they dry quickly and are hence very responsive to moisture pulses and temperature. Since soil surface conditions can change frequently, biocrusts are difficult to study in their natural environment; the present study is among very few conducted of biocrust gas exchange in the field.

[5] The pulsed nature of precipitation leads to highly variable soil moisture, particularly near the surface (Figure 2b). This temporally dynamic moisture environment exerts a first-order control on most soil and plant processes. Desert organisms respond differently to rain pulses of varying size. Even the smallest events will influence biocrusts, intermediate pulses might wet the subsurface biotic community to a few cm depth, and typically only larger events are used by plants for carbon gain or growth of roots or shoots [Austin et al., 2004; Belnap et al., 2005]. Hence, desert organisms may respond to moisture pulses in fundamentally different ways.

[6] It is unclear how the seasonality of precipitation of the cold deserts (primarily winter moisture with diminished summer monsoon influence) affects carbon cycle processes in these regions. C₄-dominated grasslands which receive reliable summer rains associated with the North American

monsoon gain most of their carbon in the summer [Emmerich and Verdugo, 2008; Mielnick et al., 2005; Scott et al., 2006, 2009], but the cold desert grasslands of the Great Basin and Colorado Plateau exhibit C uptake primarily in spring [Bowling et al., 2010; Ivans et al., 2006; Obrist et al., 2003]. The warm-season/cool-season distinction does not appear to apply to ecosystem-scale carbon exchange in these colder regions. Seasonal differences in physiological activity of grasses are commonly observed in the warm deserts, with C₃ grasses generally more active in spring, fall and winter and C₄ grasses generally more active in the summer [Cable, 1975; Everett et al., 1980; Fay et al., 2003; Kemp, 1983; Kemp and Williams, 1980].

[7] The lack of understanding of soil carbon exchange processes in the cold deserts motivated this study. The objective was to examine the response of grassland soils of the Colorado Plateau to natural moisture pulses, with a primary focus on soil CO₂ exchange. We investigated the physiological and biogeochemical activity of the soil community (including biocrusts, soil biota, plant roots and rhizosphere communities), using measurements of in situ soil CO₂ and CO₂ isotopes, and soil surface CO₂ exchange. The dynamics of activity of the soil community were assessed in response to moisture pulses over the cold and warm seasons. Soil surface fluxes were examined over a wide range of ambient conditions to elucidate the primary environmental controls on biocrusts and soil community activity. We hypothesized that moisture and temperature, in that order, were the primary factors influencing soil community activity. Following the traditional distinction of cool-season and warm-season grasses, we further hypothesized that the soil communities surrounding both types would be most active in spring, but that C₄ grasses would respond to summer

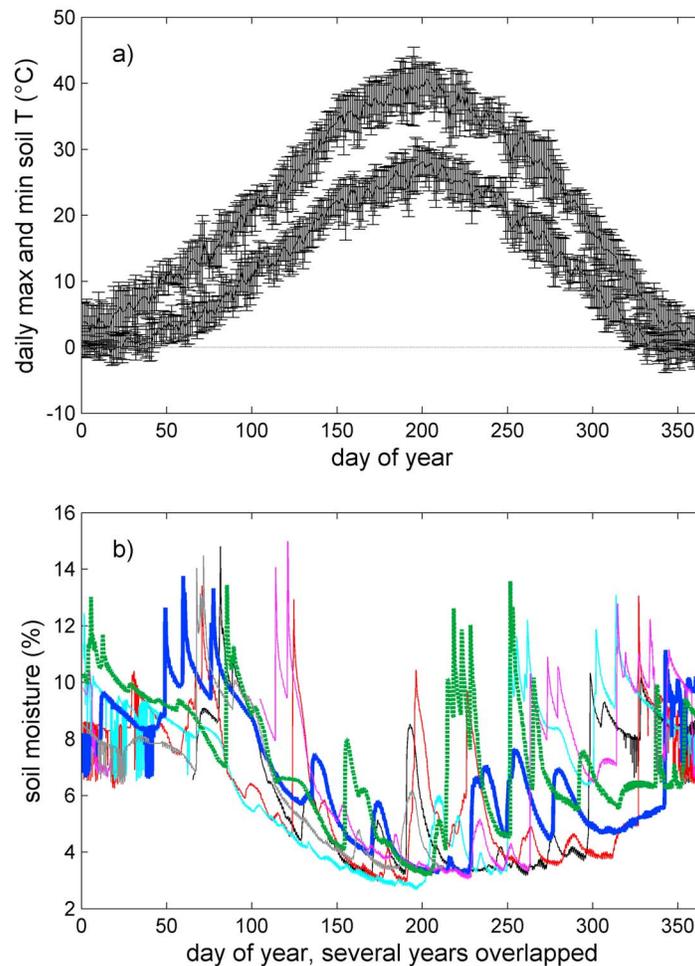


Figure 2. (a) Seasonal pattern of maximum and minimum daily soil temperature (10 cm depth) at Corral Pocket during 2000–2006. Daily means and standard deviations of hourly data are shown. (b) Seasonal pattern of soil moisture (10 cm depth) at Corral Pocket during the same period, with all years overlapped. Each year is a different color; study years were 2003 (thick blue) and 2005 (thick green dashed). Large variation during winter periods indicates ice in the soil.

moisture more than the C₃ grasses, influencing the dynamics of activity of their soil communities.

2. Methods

2.1. Study Location

[8] This research was conducted at two semiarid grassland sites, located ~10 km apart, in southeast Utah, USA. Mean annual temperature is 12.0°C, and mean annual precipitation is 216 mm (1965–2008, Western Regional Climate Center, <http://www.wrcc.dri.edu/>). At these sites, about 33% of precipitation occurs during summer (July–September) and 67% during the rest of the year (Table 1). The first site, Corral Pocket (38.09°N, 109.39°W, 1520 m elevation), is a mixed C₃–C₄ grassland, dominated by the perennial bunchgrasses *Hilaria jamesii* (C₄) and *Stipa hymenoides* (C₃) and the C₃ shrub *Coleogyne ramosissima*, with other C₃ and C₄ grasses and annuals making up a small percentage of total plant cover. Annual vegetation and biological soil crust cover at Corral Pocket vary widely [Belnap *et al.*, 2009] in

response to moisture and the 6–8 weeks of livestock grazing that occurs in late fall and winter. Biological soil crusts at this site were cyanobacterially dominated, with very low biomass (LOD class 1 [Belnap *et al.*, 2008]). During the year of this study (2003), vegetation cover was very low, with only 14% of the ground surface covered by plants [Bowling *et al.*, 2010]. Soils were sandy loams.

[9] The second site, Squaw Flat (SF, 38.14°N, 109.79°W, 1540 m), was located in Canyonlands National Park, and research was conducted there in 2005. This grassland site is dominated by *H. jamesii* (C₄), which was invaded by the annual grass *Bromus tectorum* (C₃) sometime before 1940 (the “historically invaded” site of Belnap and Phillips [2001]). However, the current work was conducted in an area within the grassland that was strongly dominated by *Hilaria* with very little *Bromus* cover. Squaw Flat, located within the national park, has not been grazed since 1974, and crusts are still recovering from this disturbance (LOD class 2–4 [Belnap *et al.*, 2008]), with higher cyanobacterial biomass than Corral Pocket and some moss. During 2005,

Table 1. Precipitation in Canyonlands National Park During the Study Years Compared to the Long-Term (1965–2008) Mean^a

Year	Unit	October–December Preceding Year	January– March	April– June	July– September	Total
2003	mm	52.6	67.3	16.8	47.2	183.9
2005	mm	65.3	57.7	39.9	109.2	271.8
2003	percent of long-term	(91)	167	(41)	(67)	(87)
2005	percent of long-term	113	144	(98)	156	129
Long-term	mm	58.0	40.2	40.9	70.1	211.3

^aFall precipitation (October–December) is shown for the preceding year. Deficits relative to the long-term mean are indicated in parentheses when expressed as percent of long-term mean. Data are from Western Regional Climate Center, <http://www.wrcc.dri.edu/>, for the site “Canyonlands, The Needle” which is ~2 km from Squaw Flat and ~10 km from Corral Pocket.

vegetation cover was 15% perennials and 8% annuals, and the remainder of the sandy loam soil was covered with biocrusts. Further details for these sites, including extensive information about the soils, can be found elsewhere [Bowling *et al.*, 2010; Goldstein *et al.*, 2005]. During 2003, the Canyonlands region was in the fourth consecutive year of severe drought [Bowling *et al.*, 2010]. Precipitation was substantially below normal in 2003, particularly during April–September (Table 1). In contrast, precipitation in 2005 was above normal for most of the year.

2.2. Meteorological Measurements

[10] A variety of environmental parameters were monitored at the sites, including precipitation, soil temperature and moisture at several depths, and photosynthetic photon flux density (PPFD). These were measured using standard methods and sensors as described elsewhere [Bowling *et al.*, 2010]. Environmental data were collected hourly. Additional data were obtained for Corral Pocket from the CLIM-MET monitoring network (<http://esp.cr.usgs.gov/info/sw/clim-met/index.html>).

[11] The time period for a precipitation “pulse” was defined as one or more cumulative hours containing measurable precipitation, with intervals of 24 h minimum between events. Thus, a rainstorm of several hours, followed by a few dry hours, followed by more rain, would be considered a single event. Total precipitation falling within the time period of a single event is referred to as “pulse size.”

2.3. CO₂ Within the Soil: Continuous Measurements—Corral Pocket and Squaw Flat

[12] In this paper we distinguish soil CO₂ (CO₂ mole fraction in the soil air space, $\mu\text{mol CO}_2 \text{ mol air}^{-1}$) from soil CO₂ flux (either soil respiration or net CO₂ uptake, the flux density through the plane at the soil surface, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Soil CO₂ was measured in situ at 5 and 15 cm depth using solid-state optical sensors (GMT222, Vaisala, Inc., Woburn, MA). Sensors were enclosed in capped polyvinyl chloride tubes, and inserted vertically in the soil into a hole drilled with an auger bit. The temperature of the sensor tip was monitored with a thermocouple, and corrections for sensor temperature were made following Tang *et al.*

[2003]. Laboratory tests over a wide temperature range (data not shown) showed that these corrections led to an accuracy of about 10% of reading (e.g., $1000 \pm 100 \mu\text{mol mol}^{-1}$).

[13] Due to calibration drift during warm-up, sensors were left on continuously, with the unavoidable artifact that they physically heated the soil as much as 5°C above ambient soil temperature at the same depth. It was not possible to calibrate the sensors frequently; as a result, they drifted over the season, and at some times the readings were lower than ambient CO₂ in the air. For these reasons, soil CO₂ data from the Vaisala sensors were interpreted in a relative sense (for example, relative changes following a moisture pulse).

[14] To evaluate relative differences among C₃ and C₄ belowground plant activity and the interspace between plants, CO₂ sensors were installed within the rooting zones of individual (1) *Stipa hymenoides*, (2) *Hilaria jamesii* plants, and (3) in the interspace between plants (2 depths per location type, 6 total sensors) at Corral Pocket. At Squaw Flat, failure and drift of 4 sensors led to the use of a single reliable sensor each at 5 and 15 cm, located in the interspace within 10 cm from *Hilaria* plants.

2.4. CO₂ Within the Soil: Flasks—Corral Pocket

[15] At Corral Pocket, permanent 100 m transects were established within the rooting zones of individual *Stipa* or *Hilaria* plants or interspace locations ($n = 10$ samples collected per location type, located roughly in a straight line every 10 m). While the roots of individual bunchgrasses probably overlapped somewhat with their neighbors, only 14% of the ground surface was covered with vegetation, with significant interspace between the bunchgrasses. At each location, 6.4 mm OD stainless steel tubing was inserted into the soil to a depth of 15 cm, and a preevacuated (<4 Pa) 100 mL glass flask (34–5671, Kontes Glass, Vineland, NJ) was attached via a filter (15 μm , Nupro SS-4FW-15, Swagelok, Solon, OH) to the tubing. The stopcock was opened, and the flask was slowly filled to ambient pressure through the filter over several minutes, to minimize influence of sampling on the diffusive profile of soil gases. A worst-case calculation, assuming totally dry soils and using measured soil porosity, indicates that a spherical volume of 3.7 cm radius would be disturbed to achieve a 100 mL sample, centered at the 15 cm depth.

[16] Tubing was left in place for the entire 2003 season and soil gas samples collected several times during June–October to evaluate seasonal differences in interspace and C₃ and C₄ belowground plant activity. The CO₂ and the carbon isotope ratio ($\delta^{13}\text{C}$) of CO₂ in the flasks was measured on an isotope ratio mass spectrometer (IRMS, Delta Plus XL, Thermo-Finnigan, Bremen, Germany) as described by Schauer *et al.* [2005]. Spatial variability of soil CO₂ along each transect was considerably greater than the analytical accuracy of $\sim 1 \mu\text{mol mol}^{-1}$. The CO₂ data are presented relative to the World Meteorological Organization scale, and $\delta^{13}\text{C}$ relative to the Vienna PDB scale ($\pm 0.1\%$).

2.5. Calculation of $\delta^{13}\text{C}$ of Belowground Respiration: Corral Pocket

[17] The $\delta^{13}\text{C}$ of belowground respiration was compared roughly every 3 weeks for *Stipa*, *Hilaria*, and interspace locations at Corral Pocket. The $\delta^{13}\text{C}$ of belowground respiration was calculated from mixing relationships with CO₂ and $\delta^{13}\text{C}$ of CO₂ in the soil gas (measured) and in the air (assumed) as described below. The CO₂ and $\delta^{13}\text{C}$ of CO₂ in the air was estimated from mean values for summer 2003 at Niwot Ridge, Colorado [Bowling *et al.*, 2005]. The exact values for the air are not needed, as we compared the *Stipa*, *Hilaria*, and interspace locations, and these are derived from mixing lines (thus, arbitrary values could be used).

[18] Two separate methods were used to calculate the $\delta^{13}\text{C}$ of belowground respiration. The first is based on linear combination of two gases (the Keeling method), and the other is based on the physical principles of soil gas transport (the Davidson method). Diffusional isotopic fractionation is treated differently by the two models, but both assume steady state conditions in the soil (an important limitation discussed later). The Keeling method utilized a 2-ended mixing model [Keeling, 1958]. Ordinary least squares regressions were performed of $\delta^{13}\text{C}$ versus $1/\text{CO}_2$ from all the soil gas samples in a treatment on a particular sampling date, and the intercept of the regression line (minus 4.4‰) was taken to represent the $\delta^{13}\text{C}$ of belowground respiration, with the standard error of that intercept used as a measure of uncertainty. The soil gas is subjected to a diffusive fractionation of 4.4‰ [Cerling *et al.*, 1991]; the diffusive isotopic effect on soil gas mixing relationships has been described elsewhere [Bowling *et al.*, 2009]. Subtraction of 4.4‰ facilitates comparison of the soil-respired gas with $\delta^{13}\text{C}$ of C₃ and C₄ biomass, and with the second method.

[19] For the Davidson method, equation (1) was used to estimate $\delta^{13}\text{C}$ of belowground respiration, which Davidson [1995] referred to as δ_J

$$\delta_J = \frac{C_s(\delta_s - 4.4) - C_a(\delta_a - 4.4)}{1.0044(C_s - C_a)} \text{‰} \quad (1)$$

This equation was derived from Fick's first law for ¹²CO₂ and ¹³CO₂ separately. Here C and δ refer to CO₂ and $\delta^{13}\text{C}$ of CO₂, respectively, and the subscripts s and a refer to soil and air, respectively. In our case, equation (1) was applied for each soil sampling location individually, for each treatment and each sampling date, and the mean and standard deviation of the resulting δ_J population are presented.

[20] In the text that follows, we use $\delta^{13}\text{C}_{\text{BR}}$ to refer to the $\delta^{13}\text{C}$ of belowground respiration calculated via either

method, and indicate in the figures which method was used. On some of the sampling dates, part of the soil flask collection occurred late in the afternoon or early evening, and the remainder was finished the following morning. On these dates the early and late samples were analyzed separately to calculate $\delta^{13}\text{C}_{\text{BR}}$.

2.6. The $\delta^{13}\text{C}$ of Plant Biomass: Corral Pocket

[21] Grass samples were collected at Corral Pocket in May 2003, as described by Bowling *et al.* [2010]. Fully expanded green leaves and stems were dried to constant mass, finely ground, and the $\delta^{13}\text{C}$ of their bulk tissue was measured via IRMS (DeltaS, Thermo-Finnigan, Bremen, Germany).

2.7. Soil Surface CO₂ Flux: Handheld Chambers—Corral Pocket

[22] At Corral Pocket in 2003, permanent collars to measure soil respiration were established at each of 36 interspace locations, in a 6 × 6 collar configuration, with the corners of each plot located at 20 m spacing along a 100 × 100 m grid. Soil collars were made of polyvinyl chloride, 10.2 cm OD × 8 cm tall, inserted to 4 cm in the soil, and left in place for the season. Soil respiration was measured roughly every 3 weeks during 2003, usually over a 2–3 h period in the afternoon. Respiration measurements were made using a portable photosynthesis system with a soil chamber (LI-6400 and LI-6400-09, LI-COR, Lincoln, NE). A minimum of 20 randomly selected collars were measured on each sampling date. Collars in which annual plants were infrequently found growing were not measured on that date, and the aboveground vegetation was removed in those collars.

2.8. Soil Surface CO₂ Flux: Automated Chambers—Squaw Flat

[23] Two transparent automated flux chambers were used to measure net soil gas exchange (which included respiration and/or carbon uptake by biocrusts) at Squaw Flat in 2005. The design of Riggs *et al.* [2009] was used, which included a polyvinyl chloride collar and a pneumatically operated lid with a frame in the soil. The original design was modified to include hourly calibration with zero and span of known CO₂ mole fraction, measurement of in-line water vapor using a modified relative humidity sensor (HMP-35C, Campbell Scientific, Inc., Logan UT) and measurement of gas temperature using a thermocouple. Flux calculations included corrections for dilution and band broadening due to water vapor. The collars were 38 cm tall × 38 cm inner diameter and contained a soil surface area of 0.11 m². Each collar was inserted into the soil in the interspace between plants by driving to a depth of 35 cm, leaving 3 cm of the chamber protruding above the soil surface, resulting in an intact soil column within the collar. The frame and lid were then installed by excavating around the soil collar, placing the lid on the intact soil column/collar, and the frame buried. This caused disturbance to the soil within 10 cm horizontally outside of the chamber, but the column within the chamber was subjected to minimal disturbance. Biological soil crusts were present in the chambers but not vascular plants.

[24] Measurements for each of the chambers were made once per hour with a closed-chamber period of 4 min. Clear polycarbonate lids allowed sunlight to enter the chambers.

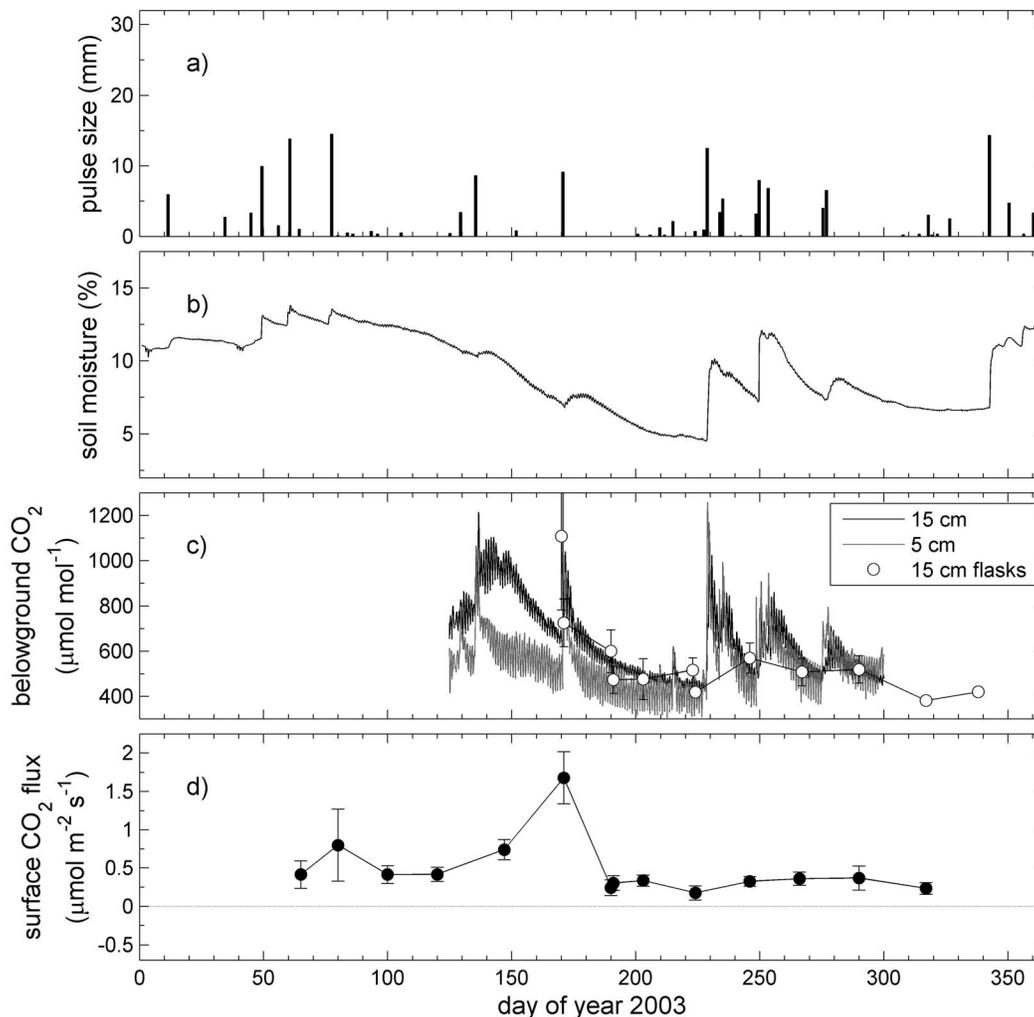


Figure 3. Precipitation, soil moisture, belowground CO₂, and soil surface CO₂ flux at Corral Pocket in 2003. (a) Total precipitation pulse size, (b) soil moisture (10 cm depth), (c) soil CO₂ at 5 and 15 cm depth (mean of 3 sensors per depth), and the mean (± 1 SD) soil CO₂ in 20–30 flasks (15 cm depth), and (d) mean (± 1 SD) surface CO₂ flux measured in 20 or more collars located in the interspace between plants. Positive fluxes indicate carbon loss.

Laboratory tests showed a reduction in PPFD through the lid of 10–20%. The transparent chambers had a small effect on temperature in the chamber in the field (usually an increase). Of 12,894 hourly measurements available in the 2 chambers, 83.8% exhibited 0–1°C change in chamber air temperature during the measurement, and 92.9% showed 0–2°C change. Soil crust temperature was less affected, with 93.7% of hours 0–1°C, and 98.5% 0–2°C. Data gaps were caused by pump failures, power failures, calibration gas loss due to animal damage to tubing, tumbleweeds obstructing the lid, and other problems.

[25] Near-surface soil moisture was monitored within one of the chambers just below the soil surface (~1 cm depth) using a horizontally oriented water content reflectometry probe (CS615, Campbell Scientific, Inc., Logan, UT). Crust temperature was measured in each chamber using thermocouples buried a few mm below the surface (the

junction just deep enough to avoid exposure to direct solar radiation).

3. Results

3.1. Belowground Soil CO₂ and Surface CO₂ Flux: Corral Pocket and Squaw Flat

[26] Most precipitation events at Corral Pocket in 2003 were small, but several events exceeded 5 mm (Figure 3). While these larger events had varying influences on soil moisture (Figure 3b), fairly substantial changes in belowground CO₂ occurred followed each event. Continuously measured CO₂ agreed favorably with flask measurements, with both showing high spatial variability in soil CO₂. Belowground CO₂ initially peaked around day 135 (15 May) and gradually decreased as the soil dried, with four independent periods of sustained increase afterward (Figure 3c).

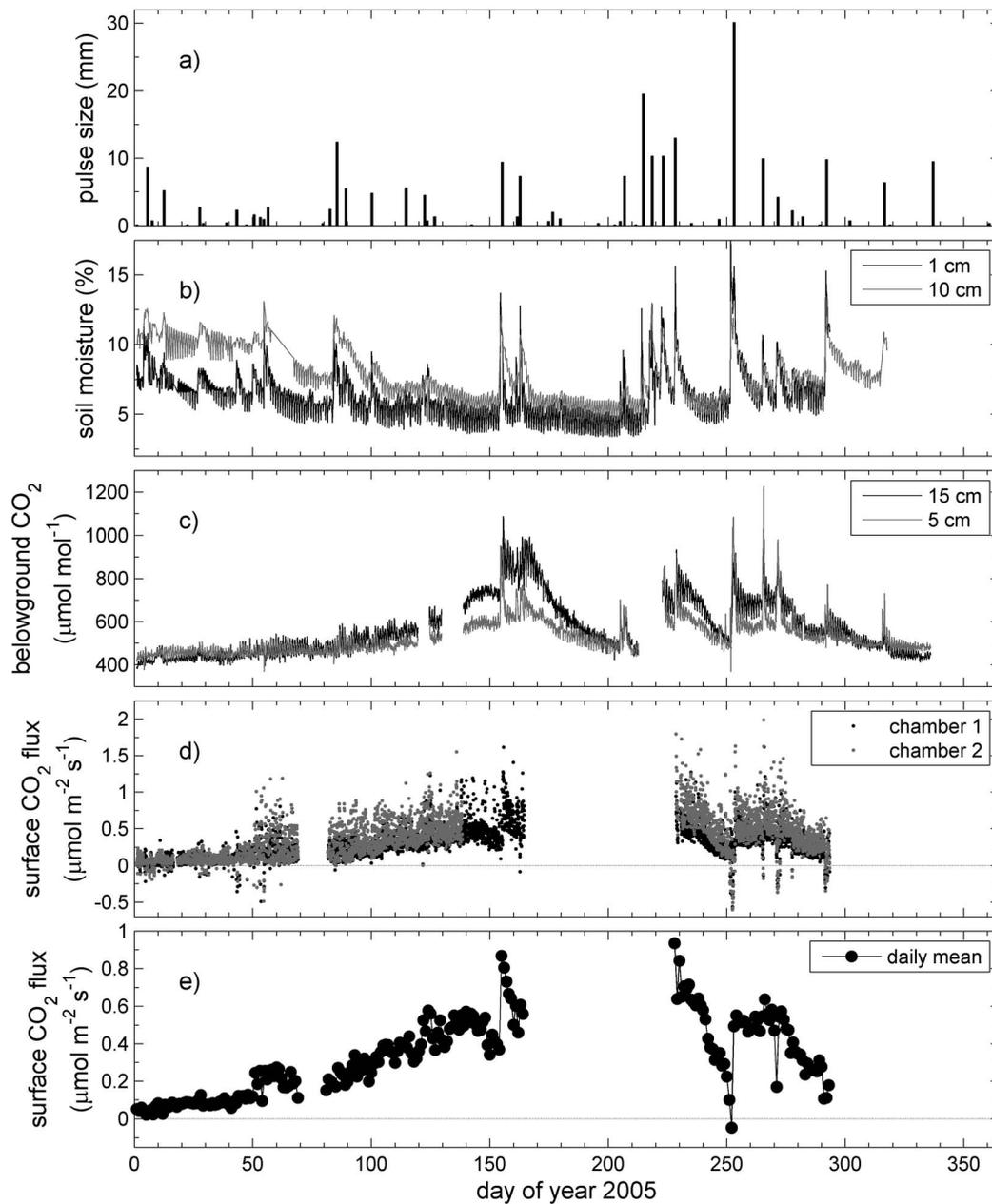


Figure 4. Precipitation (measured at Corral Pocket), and soil moisture, belowground CO₂, and soil surface CO₂ flux at Squaw Flat in 2005. (a–c) Conceptually the same as in Figure 3, with depths indicated (no flasks were collected). (d) Surface CO₂ flux measured hourly in two transparent automated chambers, and (e) daily (24 h) means of the data in Figure 4d (both chambers). Positive fluxes indicate carbon loss, and negative fluxes indicate carbon uptake by biological soil crusts.

Diel oscillation in CO₂ was observed at both depths, and was correlated with soil temperature at each depth (data not shown). The diel peaks of CO₂ were out of phase with each other by a few hours at the two depths. An 8.6 mm rain event on day 135 led to a sustained increase in CO₂ that lasted for ~20 days at 15 cm depth (Figure 3c). In contrast, the CO₂ increase following a similar pulse on day 170 (19 June) lasted only a few days. A 2 mm pulse on day 215 (3 August) led to a very brief increase in CO₂, which occurred when soils were at their hottest (Figure 2) and very dry. Soil respiration fluxes were typically less than 0.5 μmol

m⁻² s⁻¹ except on a few sampling dates (Figure 3d). A notable exception was on day 171 (20 June) after 9.1 mm rain, when fluxes were higher than on other sampling days (1.7 μmol m⁻² s⁻¹). The temporal dynamics of belowground CO₂ following rain (Figure 3c) indicate that periods of higher soil respiration were probably missed by the infrequent manual flux measurement schedule (Figure 3d).

[27] Precipitation during 2005 was fairly evenly distributed throughout the year in this area (Figure 4a; note that precipitation data are from Corral Pocket, ~10 km from Squaw Flat, and some events may not have occurred at both

locations). There were six rain pulses greater than 10 mm, which are large considering the distribution in Figure 1. Soil moisture did not show a pronounced seasonal trend at either depth (compare Figures 2b and 4b), but this was likely due to variability in individual sensor response or placement, since other moisture sensors at Squaw Flat did show seasonal patterns similar to those in Figure 2 (data not shown). The soil surrounding the moisture sensor at 1 cm depth dried quickly and a seasonal pattern was not observed at this depth.

[28] Belowground CO₂ at Squaw Flat was near 400 μmol mol⁻¹ in winter and again in late fall (Figure 4c). There was a general increase in belowground CO₂ as the soil warmed during the first third of the year (up to day 150, 30 May). Moisture pulses during this time did not result in increased belowground CO₂, although the surface flux did increase following moisture near day 50 (19 February, Figure 4d). Soil respiration during this time gradually increased from near zero in midwinter to a daily mean of ~0.5 μmol m⁻² s⁻¹ (Figure 4e). Rain on day 154 (3 June) wet the soil and led to substantial increases in belowground CO₂ and soil respiration (Figure 4). Increased belowground CO₂ persisted for ~20 days, similar to what occurred at Corral Pocket during the same time of year (Figure 3c). Monsoon rains after day 200 (19 July) led to increases in belowground CO₂ and surface CO₂ flux but increases were less sustained than those earlier in the year. Soil respiration decreased systematically during soil drying on days 140–154 (late May to early June), 230–250 (late August to early September), and 273–290 (October); a similar pattern likely occurred in midsummer, given the decrease in belowground soil CO₂ (Figure 4c).

[29] Short periods of net photosynthesis by biocrusts (Figure 4d, negative values) were observed after moisture pulses in January–February (prior to day 60) and in early June (day 162). More sustained periods of C uptake occurred beginning in mid-September following a very large storm (30.1 mm, days 250–253). Several smaller storms occurred in the following weeks with short periods (1–3 days) of net C uptake. Crust photosynthesis was observed in both chambers during most periods when it occurred (Figure 4d). However, despite photosynthetic activity, the daily mean C exchange was almost always respiratory (Figure 4e). It is possible that some uptake following rain occurred undetected when the automated chamber system malfunctioned in the summer, although biocrusts have low photosynthetic rates when soil temperature is high [Grote *et al.*, 2010].

[30] The June moisture pulse at Squaw Flat caused a substantial increase in the temperature sensitivity of soil respiration (Figure 5). Soil moisture increased following rain and influenced belowground CO₂ immediately, but soil respiration did not increase until the following day (Figures 5b and 5c), presumably due to moisture-induced decrease in gas diffusion rate. Prior to rain in early June (day 153), there was little diel change in soil respiration even though daytime soil crust temperature varied by 25°C (Figure 5d). Following rain, the temperature sensitivity increased dramatically within a day, and progressively decreased during the following week.

[31] A similar increase in temperature sensitivity occurred with the moisture pulse of the large September storm

(Figure 6). This pulse, however, resulted in 2–3 consecutive days with net photosynthesis by biocrusts. The first day involved net C uptake, with net C release during a midday rainstorm (Figure 6c, midday on day 251). The second day (252), net C exchange was strongly and nonlinearly related to sunlight (Figure 6e) and strictly negative (uptake). The third day had near zero C exchange, probably involving a combination of decreasing photosynthesis as the biocrusts dried, and increasing respiration at greater depth. By day 254, net exchange was again respiratory, strongly related to crust temperature, but with enhanced temperature sensitivity compared to before the pulse.

3.2. Belowground CO₂ Among Plants and Plant Interspaces: Corral Pocket

[32] There were no obvious differences in the seasonality of belowground CO₂ at Corral Pocket in *Stipa*, *Hilaria*, and interspace locations (Figure 7). Both photosynthetic types, and likely the organisms within their rooting zones, were active in spring (before mid-June, day 165). Belowground CO₂ declined in all treatments as the soil dried, with similar magnitude of increase and length of response following monsoon and fall rains.

[33] The δ¹³C of belowground respiration (δ¹³C_{BR}) was similar on most sampling dates when flasks were collected late in the day (Figure 8), with the two methods of calculation providing fairly similar results. In contrast, there were large differences in δ¹³C_{BR} calculated late in the day and the following morning, sometimes >15‰. Morning flask samples generally had lower CO₂ (data not shown), and this led to larger uncertainty in the morning estimates of δ¹³C_{BR}, but they were much more negative than the evening sampling estimates on 3 of 4 sampling dates. This evening/morning difference also occurred in the interspace sampling locations. The δ¹³C of *Stipa* (C₃) and *Hilaria* (C₄) grass leaves was in the range expected for each photosynthetic type (shaded regions in Figure 8). Regardless of the method used, δ¹³C_{BR} did not fall in the expected range for either C₃ or C₄ locations. Differences associated with morning versus evening sampling were as large as, or larger than, the C₃/C₄ difference on some occasions. There was no obvious shift in δ¹³C_{BR} during dry versus wet periods of the year, and no seasonal trend.

4. Discussion

4.1. Seasonal Patterns in Belowground CO₂ and Soil Surface CO₂ Flux

[34] Belowground CO₂ and soil surface CO₂ flux varied seasonally in these cold desert grasslands, ranging from near-atmospheric soil CO₂ levels with near-zero fluxes in the winter to maximal, but still low, values in spring and summer when moisture was available. These patterns result from the well-established importance of moisture and temperature as first order controls on biological activity in deserts. The seasonal pattern of soil CO₂ contrasts strongly with mesic forests [Jassal *et al.*, 2005, 2008], which maintain much higher CO₂ in the soil during the cold season. Our Utah sites share similarities but important differences with Mediterranean grasslands [Tang and Baldocchi, 2005; Xu *et al.*, 2004]. Soil CO₂ responded quickly to moisture pulses and decreased continually during dry periods in all

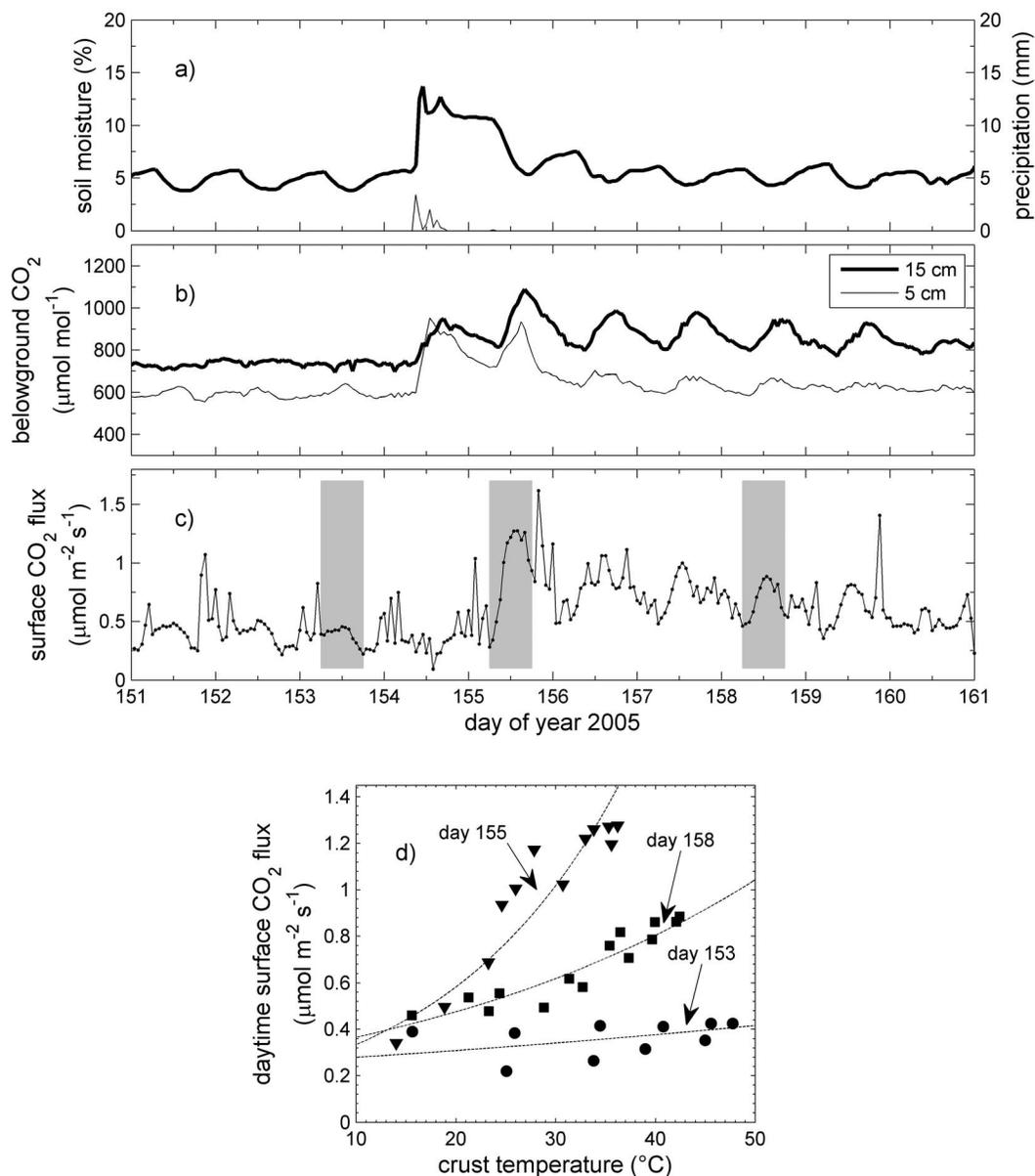


Figure 5. A 10 day period showing response to a late-spring rain pulse (total 9.4 mm) at Squaw Flat, 2005. (a) Soil moisture (1 cm depth, thick line) and precipitation (thin line, right axis), (b) belowground CO₂, (c) surface CO₂ flux, and (d) relationship between surface CO₂ flux and biocrust temperature during the daytime on the days highlighted by the gray boxes in Figure 5c. Lines shown in Figure 5d are fits of the form $y = ae^{bx}$ for each day, and correspond to Q10s of 1.11, 1.57, and 1.32 for days 153, 155, and 158, respectively, following Lloyd and Taylor [1994].

these grasslands, but steady rains and milder temperature in the Mediterranean grasslands [Baldocchi *et al.*, 2006] promoted much higher winter activity than in the cold deserts.

[35] The low soil respiration rates we observed are comparable in magnitude to those from other studies on the Colorado Plateau [Fernandez *et al.*, 2006; Schaeffer and Evans, 2005], and to eddy covariance measurements of net ecosystem C exchange at Corral Pocket [Bowling *et al.*, 2010]. However, they were much lower than soil respiration from Sonoran desert soils [Potts *et al.*, 2006; Sponseller, 2007] and semiarid steppes of Mongolia [Chen *et al.*, 2009] following experimental moisture pulse application. This was

likely due to the low organic carbon content of the inter-space soils (0.8–1.3%) and the relatively low productivity of these cold desert grasslands compared to other grassland sites [Bowling *et al.*, 2010].

[36] When moisture was ample, respiration rate increased with seasonal temperature (days 1–150, Figure 4), and generally decreased as soils dried. Peaks in soil respiration in spring were consistent with the timing of maximum net ecosystem C uptake at Corral Pocket [Bowling *et al.*, 2010] and followed the phenology of the grasses. Respiration increased immediately and substantially following moisture pulses in spring and summer, but considerably less so in

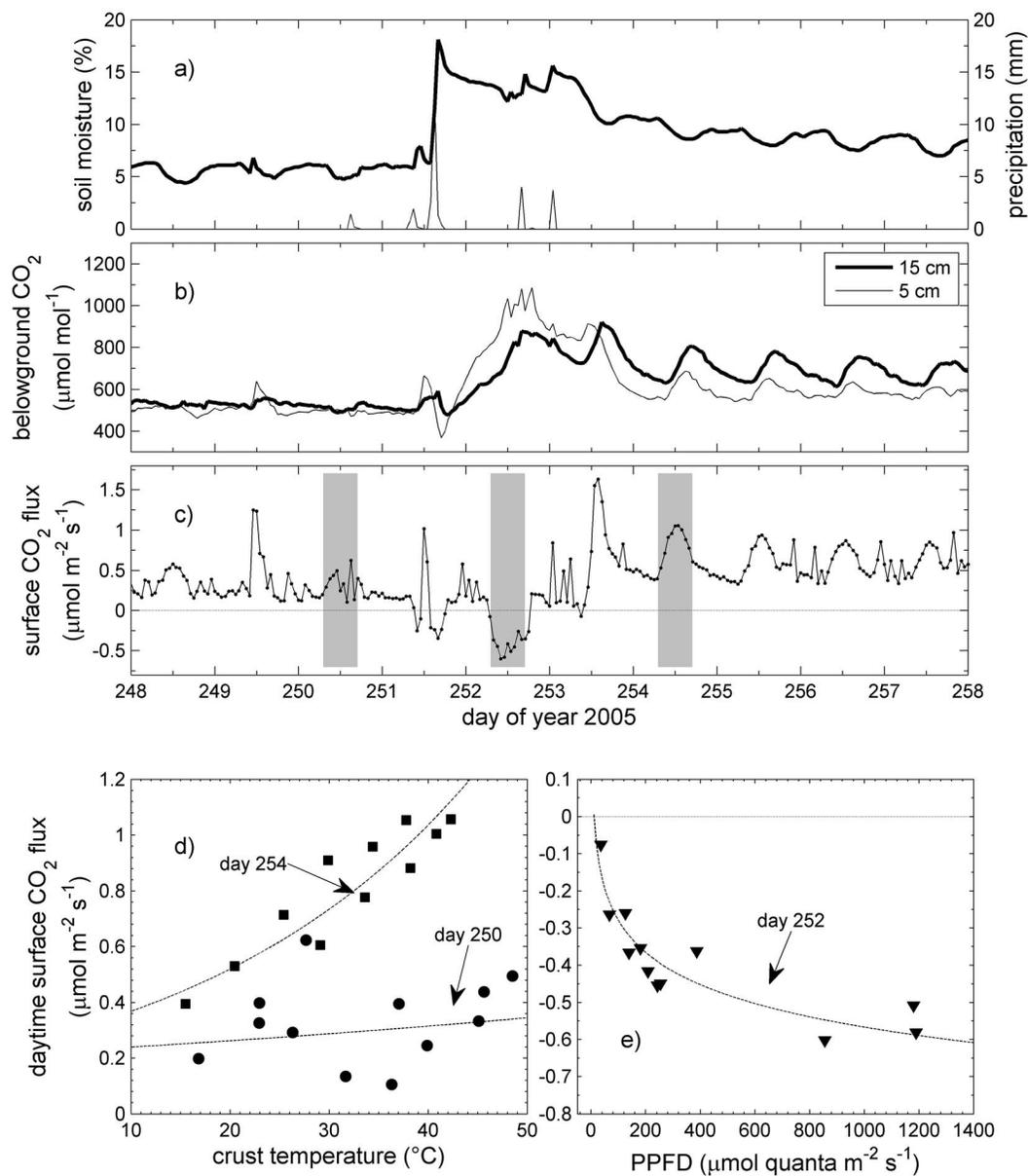


Figure 6. Same as Figure 5, but for a large (30.1 mm) pulse in early September that led to net photosynthesis by biocrusts. A small rain pulse on day 249 was not detected by the rain gauge but influenced belowground CO₂ and the surface flux. The Q10s on days 250 and 254 were 1.10 and 1.36, respectively. Figure 6e shows the relationship between surface CO₂ exchange and photosynthetic photon flux density on day 252; the line is $y = -0.13 \ln(0.09x)$.

winter (Figures 4 and 5). The short-term enhancement of soil respiration following moisture pulses, often called the Birch effect, is a general phenomenon observed in most ecosystems, even mesic forests [Borken et al., 2003; Irvine and Law, 2002; Jarvis et al., 2007; Munson et al., 2010; Savage et al., 2009]. In arid regions the increase can be stronger following addition of rain to soils that have been dry for some time [Austin et al., 2004; Cable et al., 2008].

[37] The respiratory response of dry soils to an initial pulse is often larger than subsequent pulses (see recent review by Borken and Matzner [2009]). Comparing the similar pulses on days 135 (mid-May) and 170 (mid-June)

at Corral Pocket (Figure 3) reveals a dramatic difference in the belowground CO₂ increase. The peak values were similar, but the kinetics of each decrease were very different. The most likely explanation for this is one of substrate limitation. During long dry periods, respiratory substrates accumulate in the soil, and upon wetting additional organic compounds are released through microbial cell lysis. These substrates are consumed by surviving microbes during the first pulse and incorporated into the growing microbial community, and are thus not available as substrates for subsequent wetting events [Borken and Matzner, 2009; Fierer and Schimel, 2003; Kieft et al., 1987; Saetre and

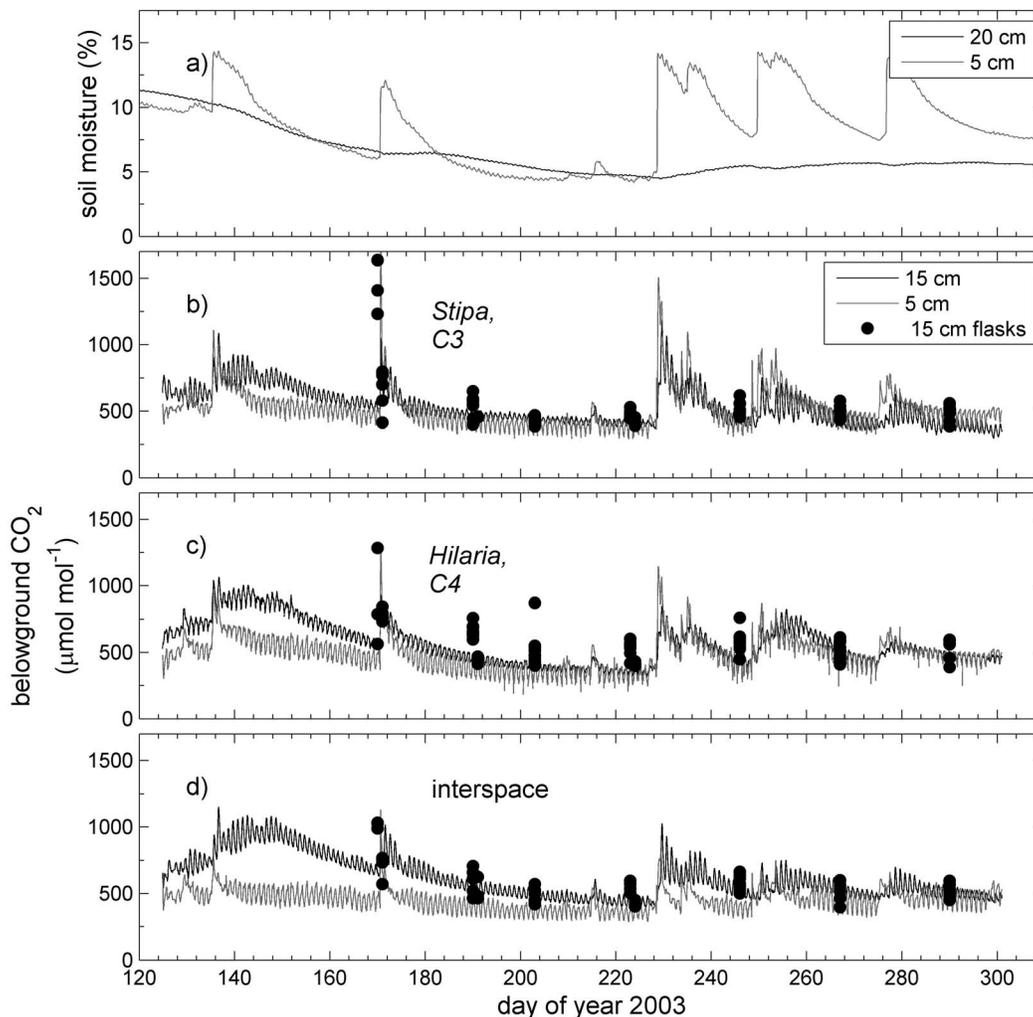


Figure 7. (a) Soil moisture and (b–d) belowground CO₂ at Corral Pocket, May–October 2003. Belowground CO₂ is shown separately for three locations, within the rooting zone of the C₃ grass *Stipa hymenoides* (Figure 7b), the C₄ grass *Hilaria jamesii* (Figure 7c), or the interspace between plants (Figure 7d). Symbols show the CO₂ in soil air collected at 15 cm depth along transects of each location type ($n = 10$ flasks per location type). The data in Figures 7b–7d were averaged at each depth and shown in Figure 3.

Stark, 2005]. Pulse size also seems to be an important controller of total C mineralized [Cable and Huxman, 2004; Misson *et al.*, 2006; Munson *et al.*, 2010; Sponseller, 2007].

[38] Rain enhanced not only the rate of soil respiration, but also its temperature sensitivity (Figures 5 and 6). Prior to late-May rain at Squaw Flat on day 154, there was almost no diel variability in soil CO₂, but afterward a strong daily pattern was apparent. This involved short-term increases in Q₁₀ from 1.1 to 1.6. While other factors influence the relation between temperature and soil respiration [Davidson *et al.*, 2006a, 2006b], this increase is strong evidence for the highly dynamic involvement of the soil microbial community (including biocrusts). In dry soils, the increase following initial wetting involves activation and growth of a dormant microbial community, which requires time for osmotic adjustment, enzyme production, and diffusion of extracellular enzymes and their substrates [Fierer and Schimel, 2003; Stark and Firestone, 1995]. There can be changes

in microbial community composition that occur over a short time frame following wetting, but these do not always occur [Fierer *et al.*, 2003]. The change in temperature sensitivity may reflect changes in the availability of labile C rather than in the intrinsic sensitivity of the pool being consumed [Curiel Yuste *et al.*, 2010].

[39] Many studies have shown that temperature sensitivity of respiration is a function of soil moisture over longer timescales [Borken *et al.*, 1999; Curiel Yuste *et al.*, 2007; Gaumont-Guay *et al.*, 2006; Jassal *et al.*, 2008; Subke *et al.*, 2003; Xu and Qi, 2001]. These have generally involved data collected over several months that are binned for different moisture classes. To our knowledge, only two other studies have reported enhanced temperature sensitivity of respiration in response to individual wetting events. The first was an analysis using eddy covariance data from the Sonoran desert [Jenerette *et al.*, 2008], and showed that this is a frequent phenomenon at the whole-ecosystem scale for sites

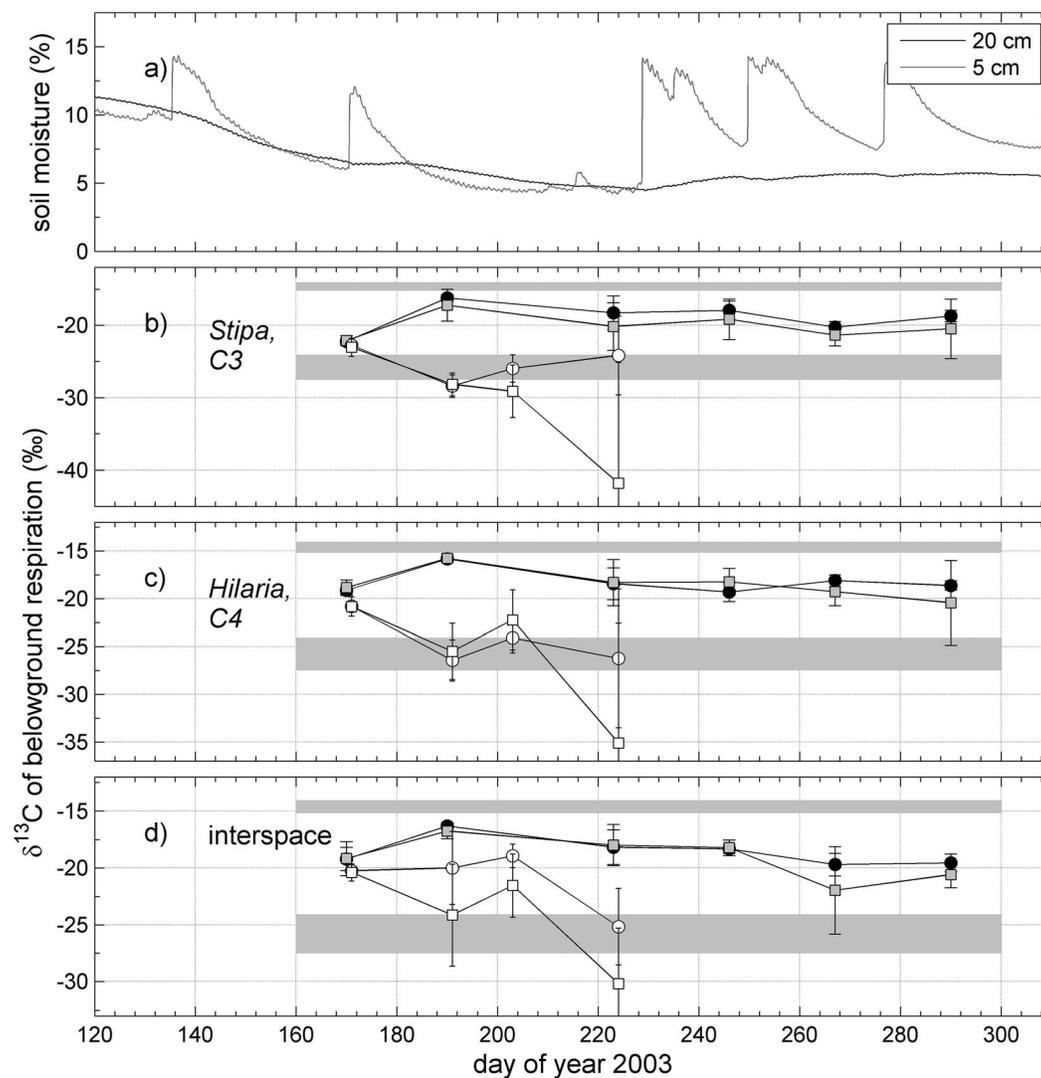


Figure 8. (a) Soil moisture and (b–d) the $\delta^{13}\text{C}$ of belowground respiration at Corral Pocket, May–October 2003, at the locations described in Figure 7. The $\delta^{13}\text{C}$ of respiration was calculated using the Keeling method (circles) and the Davidson method (squares) as described in the text. Solid (black or gray) symbols are for afternoon/early evening sample collection; open symbols are for morning sample collection. In some cases, error bars are smaller than the symbols. The shaded boxes show the range of $\delta^{13}\text{C}$ of bulk leaf tissue measured for *Stipa* (−27.5 to −24.1‰, $n = 10$) and *Hilaria* (−15.2 to −14.1‰, $n = 11$) plants during May, and indicate a general range for the C₃ and C₄ endpoints. Note the ordinate scales differ in the panels.

with consistent summer precipitation provided by the monsoon. The second was an artificial irrigation experiment of biocrusts in the Kalahari desert [Thomas and Hoon, 2010]. Application of a tiny amount of moisture (1.4 mm) to biocrusts led to a short-term increase in temperature sensitivity of respiration, consistent with our observations. Under conditions of heavy wetting (120 mm water applied), the initial increase showed a Q10 which was much larger than reasonable (12.6) for a solely microbial response [Thomas and Hoon, 2010]. Other factors probably contribute to CO₂ exchange following wetting, such as physical displacement of CO₂ from soil pores by water, CO₂ solubility in water, chemical interaction with carbonate minerals,

and possibly adsorption on mineral surfaces [Ball et al., 2009; Parsons et al., 2004; Serrano-Ortiz et al., 2010].

[40] Net C uptake by biocrusts, and its dependence on sunlight, is unequivocal evidence of the dynamic involvement of the biocrust microbial community following wetting. The automated soil chambers captured several episodes of net C uptake following natural wetting events. These events were generally brief, lasting 2–3 days at most, and in most cases the daily average showed net C loss (Figure 4). The transition from photosynthetic dominance by biocrusts to net respiration by the soil biotic community occurred over a few days as soils dried (Figure 6). Enhanced temperature sensitivity of soil respiration was still apparent in the days

following net crust uptake (Figure 6). Overall rates of C gain in biocrusts are determined by their species composition, as moss-lichen-dominated biocrusts from this region fix up to four times more C than cyanobacterially dominated biocrusts [Grote *et al.*, 2010]. Livestock grazing can eliminate lichens and mosses from biocrusts, as they have low resistance to disturbance by compression [Belnap and Eldridge, 2001]. Soils in ungrazed grasslands of the region are covered by moss-lichen crusts [Belnap *et al.*, 2006], and it is likely that the biocrust communities at our sites were of similar composition before the introduction of livestock. Therefore, biocrusts at our sites were possibly more significant C sinks in the past than we have observed because they likely included the late-successional mosses and lichens.

[41] Our results, and previous studies with biocrusts, have shown rates of net photosynthesis and respiration in biocrusts are strongly moisture dependent [Cable and Huxman, 2004; Lange, 2002, 2003a, 2003b; Lange *et al.*, 1998], including some short-term field studies [Thomas and Hoon, 2010; Thomas *et al.*, 2008; Wilske *et al.*, 2008]. Whereas laboratory and field wetting experiments provide important process information, the in situ wetness in the natural environment is the primary determinant of process rates for biogeochemical cycling associated with crusts. Thus our results, as well as those from the 2 year study of rock lichens by Lange [2002, 2003a, 2003b] provide unique insight into controls on the activity periods and rates in biocrusts in the field. These studies underscore the extreme temporal variability of biocrust and soil community activity and highlight the need for continuous measurements in the field to understand soil ecological processes.

4.2. Belowground CO₂ Among Plants and Plant Interspaces

[42] Using CO₂ as an indication of belowground activity, we expected to find phenological differences in the physiology of the C₃ (*Stipa*) and the C₄ (*Hilaria*) grasses across the season. We further expected to find evidence of lower activity in the plant interspaces, as has been found in comparisons of soil respiration and belowground CO₂ under C₃ shrubs, C₄ bunchgrasses, and interspaces between them [Barron-Gafford *et al.*, 2011]. Neither was observed, indicating there is little or no difference in activity periods between these two species in southern Utah, and that the plant/interspace distinction may not be as obvious in our case as we assumed. Irrigation experiments have demonstrated that *Stipa* and *Hilaria* in this area can both utilize summer rain pulses, with enhanced photosynthesis and transpiration [Schwinning *et al.*, 2003]. One might expect that these grasses, particularly the C₄ *Hilaria*, would respond to summer rains with increased belowground activity, through root growth [e.g., Cui and Caldwell, 1997], ion uptake respiration, or microbial activity (free-living or root symbionts) in response to root exudation.

[43] Although there were increases in belowground CO₂ following summer rain pulses, the level of activity in summer was much lower than in spring (Figure 7). Neither the continuous CO₂ measurements nor the flask measurements provided an indication that C₄ grasses were more active than C₃ grasses in summer. Eddy covariance observations over several years at Corral Pocket [Bowling *et al.*, 2010], and experiments with precipitation exclusion shelters [Schwinning *et al.*,

2005a, 2005b], have provided evidence that cold desert grasslands of Utah are predominantly dependent on winter precipitation. However, during years of abundant late-summer precipitation, both the C₃ *Stipa* and the C₄ *Hilaria* can be highly productive in late July through September (J. Belnap *et al.*, unpublished data, 2010).

[44] The δ¹³C of respiration from C₃ and C₄ plants generally reflects that of their bulk tissues [Lin and Ehleringer, 1997; Sun *et al.*, 2010]. There are important isotope effects associated with plant C allocation and metabolism [Bowling *et al.*, 2008], but these are small relative to the difference in δ¹³C of leaf tissue of the C₃ and C₄ photosynthetic types. Changes in C₃ and C₄ composition are reflected in δ¹³C of respiration seasonally in Great Plains grasslands, including the semiarid shortgrass steppe [Lai *et al.*, 2006; Shim *et al.*, 2009; Still *et al.*, 2003], in C₃–C₄ crop rotations [Rochette *et al.*, 1999], and following conversion of tropical forests to C₄ pasture [Neill *et al.*, 1996]. Hence we expected the δ¹³C of respiration in locations dominated by C₃ or C₄ bunchgrasses to reflect their physiology, and that δ¹³C_{BR} would indicate their relative activity at different times of the season. However, the observed δ¹³C_{BR} was mostly intermediate between the C₃ and C₄ range for all treatments and did not reflect plant photosynthetic type in the simple fashion predicted (Figure 8). It is possible that the roots of these bunchgrasses overlapped more than we thought, an expectation which was based on the large amount of bare ground and horizontal distance between plants. We are not aware of studies which have examined the horizontal extent of roots in these species. A study of the congeneric *Hilaria rigida* reported horizontal rooting distributions that were maximally ~1.5 m² [Nobel and Franco, 1986], corresponding a radius of 0.7 m. Considering that 86% of our land surface was bare soil, their study provides some evidence for our assumption that the roots of C₃ and C₄ species were largely separated. We note, however, that vesicular-arbuscular mycorrhizal fungal spores in mixed C₃–C₄ plant systems are intermediate between the C₃ and C₄ leaf endpoints [Allen and Allen, 1990], suggesting that respiration from fungal hyphae in the interspaces may also be intermediate in isotope ratio (as we have observed for soil CO₂). Fungal metabolism can lead to fractionation in δ¹³C of up to 4‰ [Hobbie *et al.*, 2004], further complicating interpretation of δ¹³C of belowground CO₂.

[45] Contrary to our expectations, there was no clear seasonal pattern in δ¹³C_{BR}. On the sampling dates where δ¹³C_{BR} was measured in late afternoon and again the next morning (such as days 191–192), there was a large diel change, with substantially more negative δ¹³C_{BR} in the morning. These patterns were consistent regardless of whether the Keeling or Davidson method was used to calculate δ¹³C_{BR}. It is highly unlikely that diel changes in δ¹³C of respiration of such a large magnitude actually occurred, particularly since the changes were quite similar for both C₃ and C₄ plants, and occurred also in the interspace. The soils at Corral Pocket are high in inorganic carbon [Bowling *et al.*, 2010; Goldstein *et al.*, 2005], and soil carbonates may play a role in short-term CO₂ dynamics in arid soils [Serrano-Ortiz *et al.*, 2010]. However, the δ¹³C of CO₂ evolved from calcite precipitation would be more enriched (less negative) than the C₄ range [Serna-Perez *et al.*, 2006; Stevenson and Verburg, 2006].

[46] The most probable explanation for the observed diel pattern in $\delta^{13}\text{C}_{\text{BR}}$ is a temporal change in the relative gradients of $^{12}\text{CO}_2$ and $^{13}\text{CO}_2$ associated with non-steady-state diffusion [Nickerson and Risk, 2009a]. This could occur if the respiration rate alone, and not $\delta^{13}\text{C}$ of respiration, changed over the diel course, such as driven by soil temperature. The isotope ratio of soil CO₂ represents a mixture of CO₂ in the air and CO₂ from biological respiration, with additional isotope effects due to diffusion [Bowling et al., 2009; Cerling et al., 1991; Davidson, 1995]. Moyes et al. [2010] used a model of soil diffusive transport to demonstrate that when the CO₂ production rate is small, and the diel amplitude of the respiratory production rate is large, the $\delta^{13}\text{C}$ of soil CO₂ and of the soil surface flux can exhibit diel oscillations as large as 10‰. In our case, with low flux rates and large diel variability in flux rate, it appears that the isotopic transient associated with diffusion was large enough to obscure even the expected C₃ and C₄ isotopic patterns in soil CO₂. Diel patterns in $\delta^{13}\text{C}$ of soil respiration have been reported in a variety of ecosystems [Moyes et al., 2010] and are usually attributed to biological processes. A growing body of evidence indicates that the physical details of soil gas transport must be carefully considered to interpret isotopic patterns of soil CO₂ [Moyes et al., 2010; Nickerson and Risk, 2009a, 2009b; Phillips et al., 2011; Risk and Kellman, 2008]. These studies suggest caution in interpreting isotopic data for soil CO₂ in low flux environments.

5. Conclusions

[47] This study demonstrated that belowground biological activity of mixed C₃–C₄ grasslands of the Colorado Plateau, and the biological soil crust community, were quite responsive to moisture pulses. Rain led to increased soil respiration, with enhanced short-term (daily) sensitivity to temperature, which lasted for several days to a few weeks. Lack of significant summer rain was associated with a significant decrease in summer ecological activity when compared to seasonal patterns in the warm deserts. Biological soil crusts were responsive to moisture events, with their activity generally limited to a few days following rain when surface soils were moist. The soils at these sites were a small source of C during most of our study period. However, photosynthesis by the autotrophic components of the biocrusts resulted in a few short time periods when the soils acted as a small C sink. Before these areas were grazed by livestock, these soils were likely covered by lichen-moss soil crusts that have much higher C fixation rates than cyanobacterially dominated crusts. Therefore, these systems may have formerly been C sinks throughout much of the year instead of C sources. The conceptual partitioning of grasses into cool-season and warm-season functional types, while applicable in other semiarid regions, does not appear apply to the cold desert of the Colorado Plateau.

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- J. Belnap and E. E. Grote, Southwest Biological Science Center, U.S. Geological Survey, Moab, UT 84532, USA.
- D. R. Bowling, Department of Biology, University of Utah, Salt Lake City, UT 84112, USA. (david.bowling@utah.edu)