

Seth M. Munson · Tyler J. Benton ·  
William K. Lauenroth · Ingrid C. Burke

## Soil carbon flux following pulse precipitation events in the shortgrass steppe

Received: 16 February 2009 / Accepted: 22 August 2009 / Published online: 16 October 2009  
© The Ecological Society of Japan 2009

**Abstract** Pulses of water availability characterize semi-arid and arid ecosystems. Most precipitation events in these ecosystems are small ( $\leq 10$  mm), but can stimulate carbon flux. The large proportion of carbon stored belowground and small carbon inputs create the potential for these small precipitation events to have large effects on carbon cycling. Land-use change can modify these effects through alteration of the biota and soil resources. The goal of our research was to determine how small precipitation events (2, 5, and 10 mm) affected the dynamics of soil carbon flux and water loss in previously cultivated Conservation Reserve Program (CRP) fields and undisturbed shortgrass steppe. Total

carbon loss and duration of elevated carbon flux increased as event size increased in all field types. Time since cultivation increased in importance for carbon flux as event size increased. A comparison of water loss rates to carbon flux suggests that water is limiting to carbon flux for the smallest events, but is less limiting for events above 5 mm. We also describe how water availability interacts with temperature in controlling carbon flux rate. We conclude that small precipitation events have the potential for large short-term losses of carbon in the shortgrass steppe.

**Keywords** Semiarid and arid ecosystems · Water pulses · Soil respiration · Land-use change · Cultivation · Conservation Reserve Program (CRP) · Soil moisture · Soil temperature

---

S. M. Munson  
Department of Forest, Rangeland,  
and Watershed Stewardship, Colorado State University,  
Fort Collins, CO 80523, USA

S. M. Munson  
Graduate Degree Program in Ecology,  
Colorado State University, Fort Collins, CO 80523, USA

T. J. Benton  
Department of Geology and Geological Engineering,  
Colorado School of Mines, Golden, CO 80401, USA

T. J. Benton  
SGS-LTER Research Experience for Undergraduates,  
Colorado State University, Fort Collins, CO 80523, USA

W. K. Lauenroth  
Department of Botany, University of Wyoming,  
Laramie, WY 82071, USA

I. C. Burke  
Haub School and Ruckelshaus Institute of Environment  
and Natural Resources, University of Wyoming,  
Laramie, WY 82071, USA

*Present address:* S. M. Munson (✉)  
USGS-Southwest Biological Science Center,  
Canyonlands Research Station,  
2290 S. West Resource Blvd. Moab, Utah 84532, USA  
E-mail: smunson@usgs.gov  
Tel.: +1-435-7192335  
Fax: +1-435-7192350

---

### Introduction

Semiarid and arid ecosystems are pulse-driven systems (Noy-Meir 1973), in which nearly continuous dry soils are irregularly interrupted by brief wet periods that follow precipitation events (Lauenroth and Bradford 2006). The precipitation regimes in semiarid and arid environments, and therefore the pulsing regimes, are characterized by a high frequency of small precipitation events  $< 10$  mm (Sala and Lauenroth 1982; Lauenroth and Bradford 2009). These small events wet the surface soil (0–5 cm), where microbes and labile soil organic carbon (SOC) are abundant (Parton et al. 1987), and therefore have the potential to promote large carbon effluxes (Birch 1958; Sponseller 2007). This can result from rapid microbial growth (Bottner 1985) and mineralization of accessible SOC, including dead microbial biomass (Bottner 1985), intracellular solutes (Halverson et al. 2000), and the release of nonbiomass organic carbon from soil aggregates (Adu and Oades 1978). Abiotic processes, including carbonate dissolution (Schlesinger 1985) and physical displacement from soil pore space (Huxman et al. 2004) may also contribute

to carbon efflux. Plant response to brief wet periods depends on root depth and prior physiological status (Sala and Lauenroth 1982; Lauenroth et al. 1987) and is generally more delayed than microbial response (Ogle and Reynolds 2004).

Low and episodic precipitation has consequences for the carbon stored belowground, where most of the carbon in semiarid and arid ecosystems resides. Approximately 99% of the carbon stored in the semiarid shortgrass steppe ecosystem is belowground (Burke et al. 2008); of that, 10% of the carbon is in plant roots and the remainder is soil organic carbon. Although the total pool of soil organic carbon is large, annual belowground net primary production is small—on the order of  $200 \text{ g m}^{-2}$  (Milchunas and Lauenroth 2001). Soil carbon efflux counters these inputs and its magnitude is essential to our understanding of carbon balance in this belowground dominated ecosystem.

Land-use change has resulted in a patchwork of large-scale disturbances in the semiarid shortgrass steppe (Lauenroth and Milchunas 1992), which can substantially change soil carbon flux through direct alteration of the plant and microbial community and indirect effects on soil resources and physical characteristics. Dryland (non-irrigated) wheat-fallow cropping has been an extensive land use in the region, with an average of 850,000 ha annually harvested in the shortgrass steppe of Colorado since 1985 (USDA National Agricultural Statistics Service 2008). Wheat-fallow cropping removes perennial vegetation and reduces SOC, including microbial biomass (Burke et al. 1995). The USDA Conservation Reserve Program (CRP) has converted cultivated land to perennial vegetation and currently includes 1 million ha of former shortgrass steppe in Colorado (USDA Farm Service Agency 2008). Although patterns of soil recovery of CRP grasslands are not well documented, there is evidence that microbial biomass and labile SOC pools can increase in as little as 6 years, and completely recover by 50 years (Burke et al. 1995; Robles and Burke 1997). Therefore, time since cultivation disturbance represents a potential gradient in microbial activity and substrate availability.

Our objective was to determine how pulse precipitation events affect the dynamics of soil carbon flux in

previously cultivated CRP fields and undisturbed shortgrass steppe. Specifically, we addressed the following questions:

- 1) How does soil carbon flux respond to pulse events of 2, 5, and 10 mm?
- 2) Does the pulse response of soil carbon flux depend on time since cultivation disturbance?
- 3) What is the relationship between the duration of pulse-driven soil carbon flux and elevated soil water content?

We expect that as the size of the pulse event and time since disturbance increases, water and SOC limitation to microbial activity will also decrease, which creates the potential for high C flux. We also expect there to be interactive effects of water and SOC, such that SOC limitation to C flux will decrease as event size increases.

## Materials and methods

### Study sites

Our study was conducted in undisturbed shortgrass steppe and CRP grasslands near the Central Plains Experimental Range (CPER, Shortgrass Steppe Long-Term Ecological Research site), located 60 km northeast of Fort Collins, CO, USA ( $40^{\circ}49'N$ ,  $107^{\circ}47'W$ ). The climate is semiarid with cold dry winters and warm wet summers. Long-term (68 years) mean annual precipitation and mean annual temperature at the CPER are 341 mm ( $\sigma = 99 \text{ mm}$ ) and  $9.6^{\circ}\text{C}$  ( $\sigma = 1.1^{\circ}\text{C}$ ).

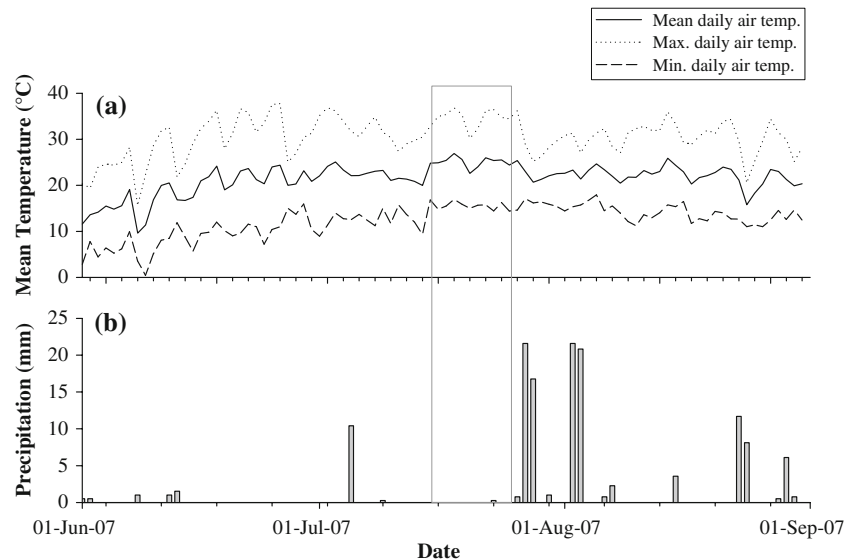
The shortgrass steppe plant community is dominated by the  $C_4$  grasses *Bouteloua gracilis* (plant nomenclature follows Great Plains Flora Association 1986) and *Buchloë dactyloides* (Table 1). Other important plant groups include  $C_3$  graminoids, forbs, dwarf shrubs, and prickly pear cactus. We compared undisturbed shortgrass steppe to two types of grasslands enrolled in the CRP, which varied in the time since cultivation disturbance. Both CRP grassland types had been seeded with a native perennial grass mix composed of *Bouteloua*

**Table 1** Dominant plant species, aboveground net primary production, belowground biomass, total soil organic carbon, and soil texture (% clay, % sand, % silt) in 4-year and 20-year CRP fields, and undisturbed shortgrass steppe (SGS)

Field type	Dominant species (% canopy cover)	ANPP ( $\text{g m}^{-2} \text{ year}^{-1}$ )	Belowground biomass <sup>a</sup> ( $\text{g m}^{-2}$ )	Total soil organic carbon <sup>a</sup> ( $\text{g C m}^{-2}$ )	% Clay <sup>a</sup>	% Sand <sup>a</sup>	% Silt <sup>a</sup>
4-year	<i>Bromus tectorum</i> 22% <i>Salsola iberica</i> 20% <i>Helianthus petiolaris</i> 9%	119	75	375	12	76	12
20-year	<i>Bouteloua curtipendula</i> 23% <i>Bouteloua gracilis</i> 17% <i>Sporobolus cryptandrus</i> 16% <i>Agropyron smithii</i> 12%	118	133	404	19	62	19
SGS	<i>Bouteloua gracilis</i> 49% <i>Buchloë dactyloides</i> 24%	99	270	678	20	62	18

<sup>a</sup>0–5 cm depth

**Fig. 1** **a** Mean, maximum, and minimum daily air temperatures (°C), and **b** precipitation (mm) at the study site from June to August 2007. The gray box indicates the study time period of 15–25 July 2007



*gracilis*, *Bouteloua curtipendula*, and *Agropyron smithii*. The first field type was last cultivated 4 years ago and has a plant community dominated by annual grass and forb species (Table 1). Aboveground net primary production in 2007 was higher than undisturbed shortgrass steppe, but belowground biomass and total soil organic carbon were 28 and 55% of undisturbed shortgrass steppe, respectively. The second field type was last cultivated 20 years ago and has a plant community dominated by perennial grasses from the CRP seed mix. Aboveground net primary production in 2007 was also higher than undisturbed shortgrass steppe, but belowground biomass and soil organic carbon were 49 and 60% of undisturbed shortgrass steppe, respectively. Soils at the sites were classified as Altvan and Ascalon fine sandy loams (mixed mesic Aridic Argiustoll), with a minor component of Renohill Shingle Complex (smectitic mesic Ustic Haplargid). These soils are deep and well drained (Natural Resource Conservation Service 2008). We identified three replicates of each field type. All fields occurred within 15 km of each other and had similar topographic relief (< 3% slope). All CRP fields had a history of continuous dryland wheat-fallow rotation prior to abandonment.

### Experimental design

We sampled a 9-m<sup>2</sup> plot within each field. Each plot was located at least 100 m from the edge of the field and had vegetation that represented the entire field. In the shortgrass steppe, we used exclosures to prevent grazing. We applied water to three 1.5-m<sup>2</sup> subplots, arranged in a checkerboard pattern within the 9-m<sup>2</sup> plot to minimize water movement from neighboring subplots. We added water as a single uniform event to each subplot using a backpack sprayer in 2, 5, and 10-mm events between 15 July and 25 July 2007. Application of 10-mm events resulted in standing water in micro-depressions,

but we did not take measurements until this water had infiltrated. The pulse-event size we applied was randomized with respect to time of day to minimize the effects of diurnal variation in soil temperature. The mean daily air temperature during the study period was 25.0°C (Min: 15.6°C, Max: 34.5°C; Fig. 1a). Variation in mean, maximum, and minimum daily air temperatures were minimal during the 10-day study period ( $\sigma = 1.1, 2.0,$  and  $0.9$ , respectively). There was low precipitation prior to (one 10-mm event occurred on 5 July 2007) and no precipitation during the study period (Fig. 1b).

### Sampling and calculations

We measured soil carbon flux using the LI-6400 soil CO<sub>2</sub> flux chamber (chamber volume: 991 cm<sup>3</sup>; LI-COR, Inc., Lincoln, NE, USA) between 08:00 and 13:00. To avoid repeated disruption of the soil, we used 10-cm diameter PVC collars as a base for the CO<sub>2</sub> flux chamber to rest. We installed these collars 2.5 cm into the soil at least 12 h before flux measurements were taken, and they remained in the soil throughout the study. To minimize the influence of aboveground plant respiration and soil resource heterogeneity, we took measurements at inter-plant locations (> 10 cm from nearest plant). Within each 1.5-m<sup>2</sup> subplot, we took measurements at four chamber locations. We took background measurements before the pulse event and subsequently at 15-min intervals up to 3 h, and at 30-min intervals up to 5 h. We also took additional 24 and 48-h measurements.

We took a soil temperature reading at 5-cm depth concurrently to each soil carbon flux measurement using a soil thermometer incorporated in the LI-6400. We also measured volumetric water content using time-domain reflectometry (TDR) during each flux measurement. The 15-cm TDR probe was inserted diagonally into the soil to a depth of 5 cm. We calculated water-filled pore space

(WFPS) as an integrative index of soil water availability and gas diffusivity (Linn and Doran 1984):

$$\text{WFPS} = \frac{\theta_V}{\text{TP}} \times 100 \quad (1)$$

where  $\theta_V$  is volumetric water content and TP is total porosity = 1-bulk density/particle density. Particle density is  $2.65 \text{ g cm}^{-3}$  for most soils in this region.

We calculated depth of penetration of a rainfall event using an equation developed by Hanks and Ashcroft (1980):

$$D = \frac{W}{\theta_{Vfc} - \theta_{Vi}} \quad (2)$$

where  $D$  (cm) is the depth a precipitation event penetrates in the soil,  $W$  (cm) is the event size,  $\theta_{Vfc}$  is volumetric water content at field capacity, and  $\theta_{Vi}$  is the initial volumetric water content before the event.

We used total carbon ( $\text{g C m}^{-2}$ ) lost from the time the pulse event was applied to the time at which flux measurements returned to background levels as our response variable. We calculated the difference between the integrated area beneath the flux curve and the background carbon flux during the same time interval. We determined the time to return to background soil carbon flux by modeling the decay of soil carbon flux using a double exponential decay function (Xu et al. 2004):

$$R = ae^{-bt} + ce^{-dt} \quad (3)$$

where  $R$  ( $\text{g C m}^{-2} \text{ h}^{-1}$ ) is the soil carbon flux rate after a pulse event,  $a$  indicates the peak flux above background,  $c$  indicates the flux rate before gradual decay of soil carbon flux,  $b$  and  $d$  indicate the decay speed and represent the time required for  $R$  to decline to  $1/e$  ( $e$  is the base for natural log) of its peak value of  $a$  or  $c$ , respectively, and  $t$  is the time since pulse event. The model assumes two phases of soil carbon flux decline: an initial steep decline and delayed gradual decline. The gradual decline phase may be related to the loss of soil moisture or the loss of different pools of carbon accessible to microbes.

We calculated water losses by the difference between the maximum WFPS and 24-h WFPS reading. We determined time to return to background WFPS by modeling the decay of WFPS using a double exponential decay model similar to Eq. (3).

### Statistical analysis

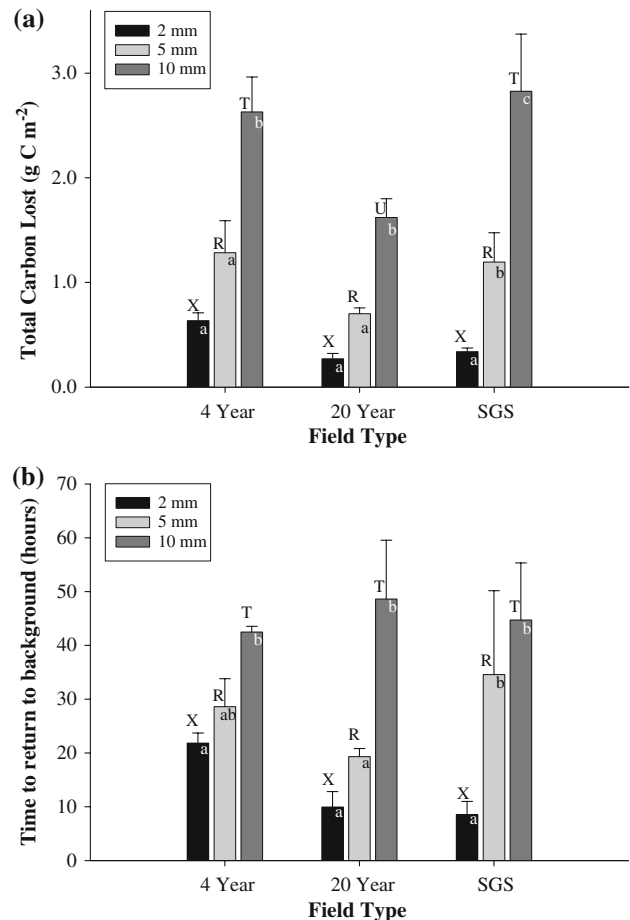
We analyzed carbon flux and water responses using a mixed model ANOVA (Proc Mixed, SAS 9.2; SAS Institute Inc. 2002–2007, Cary, NC, USA). Pulse event size and time since disturbance were treated as main effects. We combined all flux measurements for each field type and used nonlinear regression analysis (SigmaPlot 8.02; SPSS Inc. 2002, Chicago, IL, USA) to

determine the relationship between carbon flux rate and soil moisture and soil temperature.

## Results

Total carbon lost increased as event size increased in all field types and ranged from  $0.3 \text{ g C m}^{-2}$  after a 2-mm pulse in a 20-year CRP field to  $2.8 \text{ g C m}^{-2}$  after a 10-mm pulse in the shortgrass steppe (Fig. 2a). Time since disturbance did not significantly affect total carbon lost for the smallest pulse event. However, 20-year fields had significantly lower total carbon losses than the other two field types for the 10-mm event.

Maximum carbon flux rate was significantly affected by time since disturbance, but not by pulse size. Four-year fields had significantly higher maximum flux rates than the other two field types ( $F = 18.27$ ,  $P = 0.0006$ ). Rates of carbon flux in 4-year fields increased up to 23 times above background after 15 min of the pulse event. For 2 and 5-mm events, flux rates were greatest after the



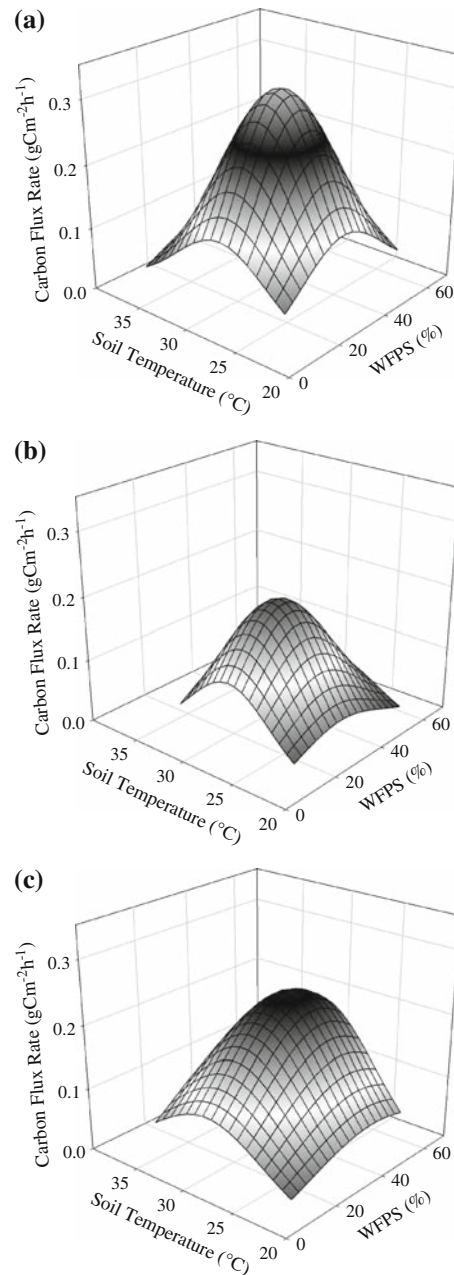
**Fig. 2** **a** Total carbon lost and **b** time to return to background soil carbon flux ( $\pm$  standard error) in three field types for 2, 5, and 10-mm pulse event sizes. Lowercase letters indicate significant differences ( $P < 0.05$ ) between event sizes within field type. Uppercase letters indicate significant differences ( $P < 0.05$ ) for the same event size between field types

first 15 min of soil wetting, which could mean that the maximum rates occurred earlier. It took longer to reach a maximum flux rate after 10-mm events (1–5 h) and there was a gradual return to background rates.

Average times to return to background flux rates increased as event size increased (Fig. 2b). An average time of 22 h was required for 4-year fields after a 2-mm event, which was significantly shorter than 42 h after a 10-mm event. The 20-year fields had a significantly longer average time to return to background for 10-mm events compared to 2 and 5-mm events, whereas 5 and 10-mm events in the shortgrass steppe had a significantly longer average time to return to background than 2-mm events. Field type did not significantly affect time to return to background carbon flux, but there was substantial variability among field types. For example, average time to return to background carbon flux for 2-mm events ranged from over 20 h on 4-year fields to less than 10 h for the 20-year field and the shortgrass steppe; none of these differences were significant.

Soil carbon fluxes were positively, nonlinearly, and interdependently related to WFPS and soil temperature [4-year CRP field:  $f = 0.31e^{-0.5\left(\left(\frac{x-36.3}{17.3}\right)^2 + \left(\frac{y-29.7}{4.6}\right)^2\right)}$ ;  $R^2 = 0.44$ ,  $P < 0.0001$ ; 20-year CRP field:  $f = 0.21e^{-0.5\left(\left(\frac{x-30.1}{17.9}\right)^2 + \left(\frac{y-28.1}{3.9}\right)^2\right)}$ ;  $R^2 = 0.30$ ,  $P < 0.0001$ ]; undisturbed shortgrass steppe:  $f = 0.24e^{-0.5\left(\left(\frac{x-40.1}{26.3}\right)^2 + \left(\frac{y-29.2}{5.4}\right)^2\right)}$ ;  $R^2 = 0.23$ ,  $P < 0.0001$  where  $f$  is carbon flux rate ( $\text{g C m}^{-2} \text{h}^{-1}$ ),  $x$  is WFPS (%) and  $y$  is soil temperature ( $^{\circ}\text{C}$ ) (Fig. 3). Maximum flux rates were observed between 30 and 40% WFPS and soil temperatures between 25 and 35 $^{\circ}\text{C}$  in all field types. There was more variability in WFPS than temperature at which maximum C flux rate occurred in 20-year fields and undisturbed shortgrass steppe, as indicated by a less acute peak in the C flux rate response. Minimum flux rates occurred at low and high soil temperatures and low and high WFPS.

Initial WFPS in the top 5 cm of soil ranged from 7 to 18%. Much of this variability can be explained by variability in clay content; background WFPS significantly increased as the percentage of clay increased ( $r^2 = 0.33$ ,  $P < 0.0001$ ). Maximum WFPS, depth of water penetration, and water loss rates increased significantly with event size (maximum WFPS:  $F = 20.03$ ,  $P < 0.0001$ ; depth:  $F = 51.75$ ,  $P < 0.0001$ , water loss rate:  $F = 25.32$ ,  $P < 0.0001$ ), but were not affected by time since disturbance. Our calculations indicate that 2-mm events reached a depth between 1.6 and 2.1 cm, 5-mm events reached a depth between 4.2 and 4.6 cm, and 10-mm events reached a depth between 8.2 and 9.7 cm. The average time to return to background WFPS after a pulse was 2.2 h for a 2-mm event and 5.9 h for a 5-mm event. These times were significantly shorter than the average time to return to background soil carbon flux for the same size events (Fig. 4). WFPS did not return to background for 10-mm events within our 48 h measurement period. Our best estimate from modeling indicated time to return to background WFPS was at

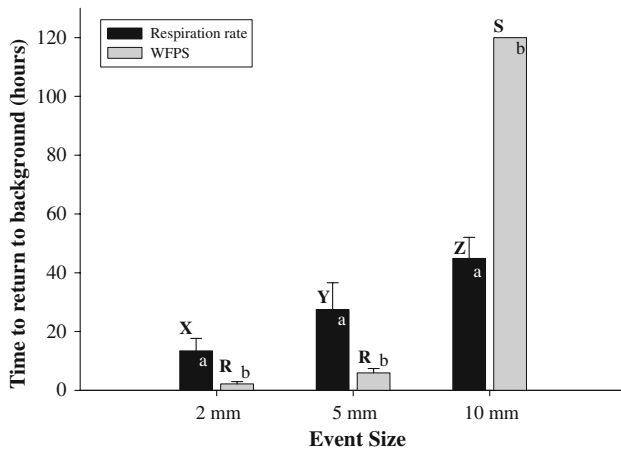


**Fig. 3** Carbon flux rate in relationship to soil moisture (water-filled pore space %) and soil temperature ( $^{\circ}\text{C}$ ) for all pulse-event sizes in **a** 4-year fields, **b** 20-year fields, and **c** undisturbed shortgrass steppe. Non-linear regressions were fit using a five-parameter Gaussian function

least 120 h. There were no significant differences in time to return to background WFPS attributed to field type.

## Discussion

Pulses of water availability trigger pulses of carbon flux in the shortgrass steppe. Increases in pulse size increased the amount of carbon lost and the duration of elevated carbon flux. As the pulse size increased, there was



**Fig. 4** Time to reach background carbon flux rate and water-filled pore space (WFPS) ( $\pm$  standard error) for 2, 5, and 10-mm pulse-event sizes. Lowercase letters indicate significant differences ( $P < 0.05$ ) between time to reach background flux rate and WFPS within an event size. Uppercase letters indicate significant differences ( $P < 0.05$ ) for flux rate or WFPS between event sizes. Time to reach background WFPS for a 10-mm event size represents an estimate beyond the last measurement at 48 h

greater soil water content and increased depth of water penetration (Sala and Lauenroth 1985), which likely extended the duration of microbial activity. In addition, microbial populations may increase over the longer duration of the increased event sizes, leading to higher microbial biomass engaged in carbon flux. Root respiration may have been limited in the first few hours of the precipitation event; especially since there was low green (photosynthetically active) leaf area due to the dry conditions before the study began (June 2007 precipitation was 8% of the mean). Previous research has suggested root activity of *Bouteloua gracilis* is limited when severe drought is followed by a precipitation event (Lauenroth et al. 1987).

We hypothesized that as time since disturbance increased, total carbon flux would increase, resulting from the establishment of long-lived perennial grass species that have high root biomass and higher soil organic carbon (SOC). We found that past disturbance was increasingly important to carbon flux as the event size increased. Time since disturbance did not influence the total carbon flux for 2 and 5-mm events, but 20-year fields had significantly lower total carbon flux than the other fields after 10-mm events. The carbon lost during 2 and 5-mm events may be more contingent on the short-term dynamics of soils in between events, such as an increase in microbial biomass carbon (Fierer and Schimel 2003), labile dissolved organic carbon (Lundquist et al. 1999), and nitrogen availability to microbes (Fisher et al. 1987). Given the relatively short time for SOC to accumulate in 4-year fields, it was surprising that they had carbon losses similar to the undisturbed shortgrass steppe for 10-mm events and the highest maximum carbon flux rates. However, 4-year fields were tilled recently, which breaks down soil aggregates and mixes

aboveground litter into the soil, and have an annual plant community that produces high litter quality (low carbon: nitrogen ratio; Munson 2009).

Our estimates of total carbon lost from interplant spaces of semiarid grasslands ( $0.3\text{--}2.8\text{ g C m}^{-2}$ ) are comparable to fluxes from interplant spaces of a desert shrubland following pulses of the same size ( $\sim 2\text{--}3\text{ g C m}^{-2}$ ; Sponseller 2007). Estimates from interspaces should be lower than from under plants, where there is high organic matter substrate, as well as higher root and microbial biomass (Hook et al. 1991).

Soil temperature interacted with soil moisture to influence carbon flux, which was inhibited at high or low extremes of the environmental controls. Even at optimal soil temperatures, carbon flux was low unless there was sufficient soil moisture, which is characteristic of grasslands and other water limited ecosystems (Noy-Meir 1973). Carbon flux rate reached its maximum at our sites when WFPS was near field capacity for coarse-textured soils, the highest water content at which soil aeration was not limiting (Linn and Doran 1984). High variability in the WFPS at which maximum C flux rate occurred in 20-year fields and undisturbed shortgrass steppe is likely due to a greater proportion of fields with fine-textured soils, which results in higher field capacities. This result highlights the complexity of soil properties in mediating water availability for microorganisms (Liu et al. 2002). The dual and interacting roles of soil temperature and soil water in influencing belowground carbon fluxes are well established in grasslands (Parton et al. 1987; Moorhead et al. 1999) although the details of their effects are controversial (Burke et al. 2003; Giardina and Ryan 2000).

The smallest events (2 and 5 mm) caused a flux response that lasted longer than it took soils to lose water from the pulses, whereas for the largest event (10 mm), carbon flux returned to baseline before the added water had been depleted. This suggests that water is the most limiting factor to soil carbon flux rates for the smallest events, but may be less limiting for events above 5 mm. Other limitations, such as the soil organic carbon supply may limit flux above this event size. This is supported by evidence that time since disturbance only had an effect above 5-mm events. Soil organic carbon stored after disturbance may be necessary for a sustained carbon flux response from large precipitation events. The pulse sizes used in this study may not have been large enough to observe an asymptote in total carbon flux with increasing event size, which has been described in arid and semiarid ecosystems (Huxman et al. 2004). However, since carbon flux returned to background before soil water for 10-mm events, it seems unlikely that events  $> 10$  mm would lead to higher amounts of carbon loss in the short term.

We can use the distribution of rainfall events in the shortgrass steppe to scale up our estimates to approximate annual C efflux. An average shortgrass steppe growing season has forty-five 2-mm events, nine 5-mm events, and three 10-mm events (Sala and Lauenroth

1982). Assuming our results of total carbon lost are applicable to every event of similar size, there is potential to lose  $48 \text{ g C m}^{-2} \text{ year}^{-1}$  from 4-year CRP fields, which represents 39% of carbon in NPP,  $23 \text{ g C m}^{-2} \text{ year}^{-1}$  from 20-year CRP fields (18% of carbon in NPP), and  $34 \text{ g C m}^{-2} \text{ year}^{-1}$  (24% of carbon in NPP) from the shortgrass steppe. These annual estimates do not account for the possibility of progressively lower carbon losses after consecutive events (Sponseller 2007) or differences in flux response due to seasonal changes in temperature. However, they suggest that the cumulative effects of precipitation events  $< 10 \text{ mm}$  could have a large effect on shortgrass steppe carbon balance.

**Acknowledgments** The Shortgrass Steppe LTER project and a Research Experience for Undergraduate (REU) supplement (National Science Foundation Grant No. 0217631) supported this work. We would like to extend our gratitude to all Weld County, Colorado, CRP landowners who generously allowed us to sample in their fields. We also wish to thank Alan Knapp for allowing us to use his LI-COR, Jana Heisler-White and Joe von Fischer for helpful suggestions on sampling approaches, the SGS-LTER staff for their support, and two anonymous reviewers for helpful suggestions in revising this paper.

## References

- Adu J, Oades J (1978) Physical factors influencing decomposition of organic materials in soil aggregates. *Soil Biol Biochem* 10:109–115
- Birch HF (1958) The effect of soil drying on humus decomposition and nitrogen availability. *Plant Soil* 10:9–32
- Bottner P (1985) Response of microbial biomass to alternate moist and dry conditions in a soil incubated with  $^{14}\text{C}$  and  $^{15}\text{N}$ -labelled plant material. *Soil Biol Biochem* 17:329–337
- Burke IC, Lauenroth WK, Coffin DP (1995) Soil organic matter recovery in semiarid grasslands: implications for the Conservation Reserve Program. *Ecol Appl* 5:793–801
- Burke IC, Kaye JP, Bird SP, Hall SA, McCulley RL, Sommerville GL (2003) Evaluating and testing models of terrestrial biogeochemistry: the role of temperature in controlling decomposition. In: Canham CD, Cole JJ, Lauenroth WK (eds) *Models in ecosystem science*. Princeton University Press, Princeton, pp 225–253
- Burke IC, Mosier AR, Hook PB, Milchunas DG, Barrett JE, Vinton MA, McCulley RL, Kaye JP, Gill RA, Epstein HE, Kelly RH, Parton WJ, Yonker CM, Lowe P, Lauenroth WK (2008) Soil organic matter and nutrient dynamics of shortgrass steppe ecosystems. In: Lauenroth WK, Burke IC (eds) *Ecology of the shortgrass steppe*. Oxford University Press, New York, pp 306–341
- Fierer N, Schimel JP (2003) A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. *Soil Sci Soc Am J* 67:798–805
- Fisher FM, Parker LW, Anderson JP, Whitford WP (1987) Nitrogen mineralization in a desert soil: interacting effects of soil moisture and nitrogen fertilizer. *Soil Sci Soc Am J* 51:1033–1041
- Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature* 404:858–861
- Halverson LJ, Jones TM, Firestone MK (2000) Release of solutes by four soil bacteria exposed to dilution stress. *Soil Sci Soc Am J* 64:1630–1637
- Hanks RJ, Ashcroft GL (1980) *Applied soil physics*. Soil water and temperature applications. Springer, Berlin Heidelberg New York
- Hook PB, Burke IC, Lauenroth WK (1991) Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. *Plant Soil* 138:247–256
- Huxman TE, Snyder K, Tissue D, Leffler AJ, Ogle K, Pockman WT, Sandquist DR, Potts DL, Schwinning S (2004) Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141:254–268
- Lauenroth WK, Bradford JB (2006) Ecohydrology and the partitioning of AET between transpiration and evaporation in a semiarid steppe. *Ecosystems* 9:956–967
- Lauenroth WK, Bradford JB (2009) Ecohydrology of dry regions of the United States: precipitation pulses and intraseasonal drought. *Ecohydrology* 2:173–181
- Lauenroth WK, Milchunas DG (1992) Short-grass steppe. In: Coupland RT (ed) *Natural grasslands: introduction and western hemisphere, ecosystems of the world 8A*. Elsevier, New York, pp 183–226
- Lauenroth WK, Sala OE, Milchunas DG, Lathrop RW (1987) Root dynamics of *Bouteloua gracilis* during short-term recovery from drought. *Funct Ecol* 1:117–124
- Linn DM, Doran JW (1984) Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and non-tilled soils. *Soil Sci Soc Am J* 48:1267–1272
- Liu X, Wan S, Su B, Hui D, Luo Y (2002) Response of soil  $\text{CO}_2$  efflux to water manipulation in a tallgrass prairie ecosystem. *Plant Soil* 240:213–223
- Lundquist EJ, Jackson LE, Scow KM (1999) Wet-dry cycles affect dissolved organic carbon in two California agricultural soils. *Soil Biol Biochem* 31:1031–1038
- Milchunas DG, Lauenroth WK (2001) Belowground primary production by carbon isotope decay and long-term root biomass dynamics. *Ecosystems* 4:139–150
- Moorhead DL, Currie WS, Rastette EB, Parton WJ, Harmon ME (1999) Climate and litter quality controls on decomposition: an analysis of modeling approaches. *Global Biogeochem Cycles* 13:575–589
- Munson SM (2009) Plant community and ecosystem change on Conservation Reserve Program lands in Northeastern Colorado. Dissertation, Colorado State University, Colorado
- Natural Resource Conservation Service (2008) Soil survey. <http://soils.usda.gov/survey>. Accessed 2 Aug 2008
- Noy-Meir I (1973) Desert ecosystems: environment and producers. *Annu Rev Ecol Syst* 4:23–51
- Ogle K, Reynolds JF (2004) Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. *Oecologia* 155:123–132
- Parton WJ, Schimel DS, Cole CV, Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Sci Soc Am J* 51:1173–1179
- Robles MD, Burke IC (1997) Legume, grass, and Conservation Reserve Program effects on soil organic matter recovery. *Ecol Appl* 7:345–357
- Sala OE, Lauenroth WK (1982) Small rainfall events: an ecological role in semiarid regions. *Oecologia* 53:301–304
- Sala OE, Lauenroth WK (1985) Root profiles and the ecological effect of light rain showers in arid and semiarid regions. *Am Midl Nat* 114:406–408
- SAS Institute Inc. (2002–2007) SAS/STAT 9.2 user's guide. SAS Institute Inc., Cary, NC
- Schlesinger WH (1985) The formation of caliche in soils of the Mojave Desert, California. *Geochim Cosmochim Acta* 49:57–66
- Sponseller RA (2007) Precipitation pulses and soil  $\text{CO}_2$  flux in a Sonoran Desert ecosystem. *Glob Chang Biol* 13:426–436
- SPSS Inc. (2002) SigmaPlot 8.02 user's guide. SPSS Inc., Chicago
- USDA Farm Service Agency (2008) US Department of Agriculture Conservation Reserve Program acreage report summary of active and expiring CRP acres by state (as of 28 March 2008). <http://content.fsa.usda.gov/crpstorpt/rmepegg/MEPEGGR1.HTM>. Accessed 28 Apr 2008
- USDA National Agricultural Statistics Service (2008) Quick Stats: Agricultural Statistics Data Base. <http://www.nass.usda.gov/QuickStats>. Accessed 28 Apr 2008
- Xu LK, Baldocchi DD, Tang JW (2004) How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. *Global Biogeochem Cycles* 18. doi:10.1029/2004GB002281