

Differential soil respiration responses to changing hydrologic regimes

Vincent J. Pacific,¹ Brian L. McGlynn,¹ Diego A. Riveros-Iregui,^{1,2} Howard E. Epstein,³ and Daniel L. Welsch⁴

Received 7 January 2009; revised 13 March 2009; accepted 20 May 2009; published 15 July 2009.

[1] Soil respiration is tightly coupled to the hydrologic cycle (i.e., snowmelt and precipitation timing and magnitude). We examined riparian and hillslope soil respiration across a wet (2005) and a dry (2006) growing season in a subalpine catchment. When comparing the riparian zones, cumulative CO₂ efflux was 33% higher, and peak efflux occurred 17 days earlier during the dry growing season. In contrast, cumulative efflux in the hillslopes was 8% lower, and peak efflux occurred 10 days earlier during the drier growing season. Our results demonstrate that soil respiration was more sensitive to drier growing season conditions in wet (riparian) landscape positions.

Citation: Pacific, V. J., B. L. McGlynn, D. A. Riveros-Iregui, H. E. Epstein, and D. L. Welsch (2009), Differential soil respiration responses to changing hydrologic regimes, *Water Resour. Res.*, 45, W07201, doi:10.1029/2009WR007721.

1. Introduction

[2] Soil respiration is a critical component of ecosystem carbon source/sink status [Oechel *et al.*, 1993; Cox *et al.*, 2000; Heimann and Reichstein, 2008; Luyssaert *et al.*, 2008] and is strongly controlled by soil water content (SWC) [Schaphoff *et al.*, 2006; Riveros-Iregui *et al.*, 2007; Pacific *et al.*, 2008], and therefore precipitation [Oechel *et al.*, 1993; Mu *et al.*, 2008]. Over the last 100 years, estimated mean global precipitation over the land surface has increased by 0.3–4% [Yu *et al.*, 2008]. This intensification of the hydrologic cycle is predicted to increase by up to 20% in North America over the next century [Christensen *et al.*, 2007]. Peak snowmelt-dominated streamflow is occurring 1–4 weeks earlier [Stewart *et al.*, 2005], and is predicted to occur an additional 3–5 weeks earlier over the next century [Stewart *et al.*, 2004]. These alterations to the hydrologic cycle (at seasonal to annual time scales) will likely lead to strong changes in SWC, and therefore soil respiration. However, large uncertainty exists in the response of soil respiration to changes in SWC across different landscape positions (e.g., wet and dry areas).

[3] Intermediate SWC is optimal for soil respiration [Davidson *et al.*, 2000; Sjogersten *et al.*, 2006]. Soil respiration is limited at low SWC by root and microbial desiccation stress [Orchard and Cook, 1983; Linn and Doran, 1984] and at high SWC because of bidirectional limitations in diffusion of gas and nutrients to plants and microorganisms [Skopp *et al.*, 1990; Moldrup *et al.*, 2000]. Previous research has indicated that higher soil water inputs can increase soil respiration at dry sites and decrease

respiration at wet sites, and lead to similar soil CO₂ efflux across wet and dry landscape positions [Davidson *et al.*, 1998; Savage and Davidson, 2001]. However, Davidson *et al.* [1998] and Savage and Davidson [2001] were limited by few sampling locations and small spatial coverage. Here we document dynamic and strongly contrasting soil respiration response at wet (riparian) and dry (hillslope) landscape positions to wetter and drier growing season conditions (and therefore different approaches to and departures from optimal intermediate SWC) from 32 locations in a complex subalpine watershed.

2. Methods

[4] The study site was the upper Stringer Creek Watershed (~380 ha), located in the United States (U.S.) Forest Service Tenderfoot Creek Experimental Forest (TCEF, Lewis and Clark National Forest, latitude 46°55'N, longitude 110°52'W) of central Montana. The spatial heterogeneity of this site offers an ideal scenario to address soil respiration variability due to strong, natural biophysical gradients in the drivers of soil respiration. The elevation is 1840 to 2421 m, with a mean of 2205 m. Mean annual temperature is 0°C, and mean annual precipitation is 880 mm, with ~70% falling as snow from November through May. Air temperature, precipitation, snow depth, and snow water equivalent were collected from 1994 to 2006 from the Onion Park SNOTEL (snow survey telemetry) site (2258 m, located approximately 2 km to the south of the upper Stringer Creek Watershed). Streamflow was measured by the U.S. Forest Service Rocky Mountain Research Station from 1996 to 2006 at the upper Stringer Creek Flume (located within 400 m of the field plots along Stringer Creek).

[5] Eight transects (approximately 50 m long) originating at Stringer Creek and extending up the fall line through the riparian and adjacent hillslope zone included two riparian and two hillslope measurement locations along each transect (32 total measurement locations). The overstory vegetation in the hillslopes is mainly lodgepole pine (*Pinus contorta*), the understory vegetation is grouse whortleberry (*Vaccinium scoparium*), and riparian vegetation is predominantly bluejoint reedgrass (*Calamagrostis canadensis*). In

¹Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, Montana, USA.

²Now at Department of Ecology and Evolutionary Biology, University of Colorado at Boulder, Boulder, Colorado, USA.

³Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia, USA.

⁴Canaan Valley Institute, Davis, West Virginia, USA.

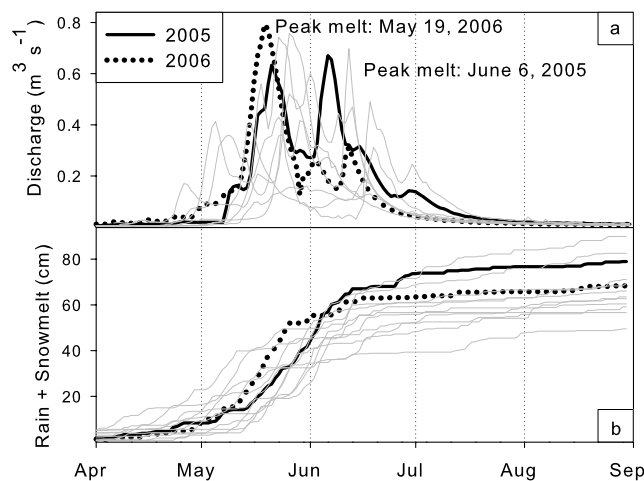


Figure 1. Stream runoff and cumulative water inputs (rain and snowmelt). (a) Streamflow during 2005 (solid line), 2006 (dotted line), and 1997–2006 data record (grey lines). (b) Cumulative water inputs (rain and snowmelt) during 2005 (solid line), 2006 (dotted line), and 1994–2006 data record (grey lines). Peak snowmelt occurred on 6 June in 2005 and 19 May in 2006 (10-year average was 29 May). Cumulative water inputs were slightly higher in 2005 than 2006 (74.4 versus 69.3 cm); however a higher percentage fell as rain during the 2005 growing season (34% versus 20%).

the hillslopes, the major soil group is loamy skeletal, mixed Typic Cryochrepts, while the riparian zones are composed of highly organic clayey, mixed Aquic Cryoboralfs [Holdorf, 1981].

[6] We collected measurements of soil temperature, SWC, and soil surface CO_2 efflux during contrasting wet (2005) and dry (2006) growing seasons. Measurements were taken from 9 June to 31 August during both years, which was the approximate time of the growing season [Schmidt and Friede, 1996] and period of frequent data collection (every 2–7 days) during both 2005 and 2006. Further, the magnitude of soil respiration outside of this range was small because of very low soil temperatures [Pacific et al., 2008]. One measurement of soil temperature (12 cm soil thermometer, Reotemp Instrument Corporation, San Diego, California, United States; measurement range of -20°C to 120°C) and three measurements of volumetric SWC ($\text{cm}^3 \text{H}_2\text{O}/\text{cm}^3$ soil, integrated over the top 20 cm of soil; Hydrosense portable SWC meter, Campbell Scientific Inc., Utah, United States) were collected on each sampling day at each of the 32 locations. Three surface CO_2 efflux measurements were collected at each measurement location with a soil respiration chamber (SRC-1 chamber with a footprint of 314.2 cm^2 , accurate to within 1% of calibrated range (0 to $9.99 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) in conjunction with an IRGA (EGM-4, accurate to within 1% of calibrated range (0 – 2000 ppm); PP Systems, Massachusetts, United States). The chamber was flushed with ambient air for 15 s then inserted 3 cm into the soil before each measurement began, and each measurement took $\sim 120 \text{ s}$. Cumulative efflux (9 June to 31 August) was estimated by linearly interpolating between measurements collected every 2–7 days. This technique has been demonstrated to be a robust approach

for comparison of efflux measurements across multiple locations over extended periods of time [Riveros-Iregui and McGlynn, 2009]. Analysis of variance (ANOVA) statistics ($\alpha = 0.05$) were employed to test for differences between riparian and hillslope cumulative surface CO_2 efflux, soil temperature, and SWC. The three measurements of SWC and surface CO_2 efflux collected at each location on all sampling days (to account for local variability) were averaged for data analysis.

3. Results

[7] Peak snowmelt-driven streamflow occurred on 6 June in 2005. This was 8 days later than the 10-year average of 29 May (extent of streamflow record, Figure 1), and 18 days later than in 2006. Growing season precipitation was 91% higher in 2005 than in 2006 (Figure 2), and 30% higher than the 13-year average of 20.6 cm (extent of precipitation record) (Figure 1). Cumulative soil water inputs (rain and snowmelt) were slightly greater in 2005 than 2006 (Figure 1), but a higher percentage fell as rain during the 2005 growing season (34% versus 20%). This combination of earlier peak streamflow and less growing season precipitation in 2006 relative to 2005 led to strong differences in SWC and therefore soil respiration across wetter (riparian) and drier (hillslope) landscape positions.

[8] SWC was significantly higher in the riparian zones than the hillslopes during both growing seasons ($p \ll 0.01$) (Figure 2). Maximum volumetric SWC in the riparian zones was similar between years ($\sim 65\%$, limited by porosity), while minimum riparian SWC was much lower during the dry growing season (13% compared to 37%). Maximum and minimum SWC in the hillslopes were similar across both growing seasons ($\sim 30\%$ and 5% , respectively). Soil temperature was significantly higher during the wet growing season ($p \ll 0.01$) (Figure 2). When comparing the riparian zones, cumulative surface CO_2 efflux was 33% larger during the dry year (2006) than the wet year (2005) (1344 versus $1012 \text{ g CO}_2 \text{ m}^{-2}$) ($p \ll 0.01$). Peak efflux in the riparian zones occurred 17 days earlier in the dry growing season (1 July versus 18 July) (Figure 3). In contrast to the riparian zones, comparison of cumulative efflux from the hillslopes showed that efflux was 8% lower (749 versus $809 \text{ g CO}_2 \text{ m}^{-2}$) (insignificant, $p = 0.92$), and peak hillslope efflux occurred 10 days earlier during the dry growing season (1 July versus 11 July). CO_2 efflux from the riparian zones was 25% greater than from the hillslope zones in the wet growing season (2005). In the dry growing season (2006), cumulative CO_2 flux from the riparian zones was 79% greater than from the hillslope zones.

4. Discussion

[9] Our results demonstrate that soil respiration varied considerably in response to changing hydrologic regimes, and that these changes were not monotonic across the landscape. Total soil water inputs (rain and snowmelt) were similar in 2005 and 2006, however peak snowmelt occurred 3 weeks later in 2005 (Figure 1), and precipitation was 91% higher during the wet 2005 growing season (Figure 2). While these differences in precipitation and snowmelt appear extreme, they were well within the range of the 10–13 year data record (Figure 1), in which precipitation

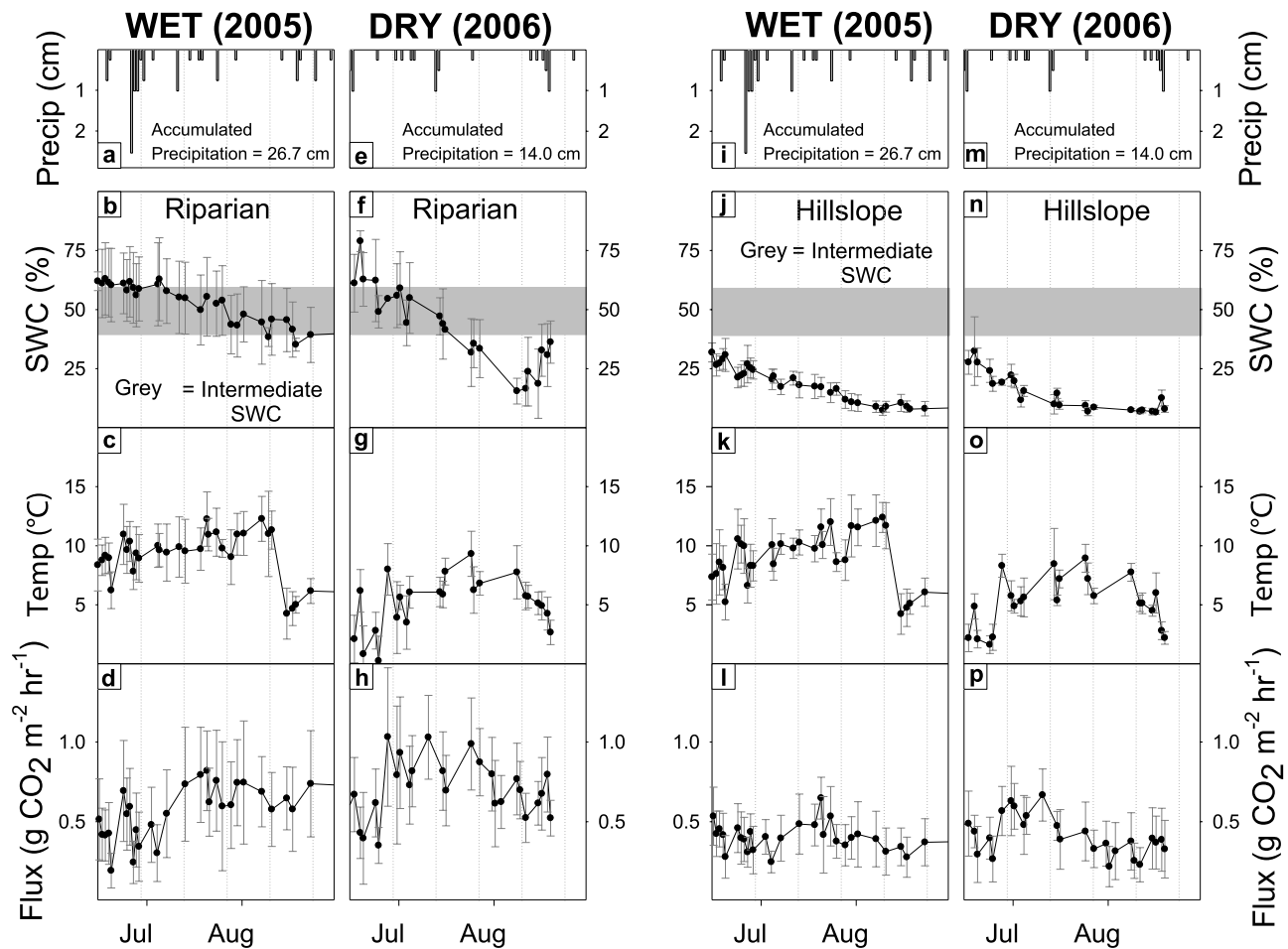


Figure 2. Riparian and hillslope precipitation, soil water content (SWC), and soil temperature during the 2005 (wet) and 2006 (dry) growing seasons. Wet growing season riparian zone (a) precipitation, (b) SWC, (c) soil temperature, and (d) efflux. Dry growing season riparian zone (e) precipitation, (f) SWC, (g) soil temperature, and (h) efflux. Wet growing season hillslope zone (i) precipitation, (j) SWC, (k) soil temperature, and (l) efflux. Dry growing season hillslope zone (m) precipitation, (n) SWC, (o) soil temperature, and (p) efflux. Measurements were collected between 9 June and 31 August during both 2005 and 2006 from 14 riparian and 18 hillslope measurement locations across eight transects. Symbols indicate average values, and error bars indicate one standard deviation; n ranged from 8 to 32 on each sampling day. Across the 2005 and 2006 growing seasons, $n = 366$ and 252 in the riparian zones, respectively, and 450 and 292 in the hillslopes. Grey boxes denote intermediate SWC (optimal for soil respiration), defined as 40–60% in the TCEF [Pacific *et al.*, 2008]. Precipitation was 91% higher in 2005 than 2006.

varied by 169% and the timing of peak snowmelt varied by 30 days. We show that changes in hydrologic regimes, even within the range observed over the last decade, can lead to large but differential soil respiration responses across landscape.

[10] The combination of later snowmelt and higher precipitation during 2005 increased the duration of SWC in the riparian zones above the intermediate level optimal for soil respiration [Davidson *et al.*, 2000; Sjogersten *et al.*, 2006] (defined as 40–60% in the TCEF [Pacific *et al.*, 2008], indicated by grey boxes in Figure 2). High SWC can simultaneously decrease both soil CO_2 production and transport [Pacific *et al.*, 2008] because of bidirectional limitations in diffusion of CO_2 , oxygen, and nutrients [Skopp *et al.*, 1990; Moldrup *et al.*, 2000]. SWC in the riparian zones was greater than 60% at the beginning of

both growing seasons (Figure 2). However, SWC remained above intermediate (optimal) levels for ~ 2 weeks longer during the wet 2005 growing season, leading to a longer period of inhibited soil respiration in the riparian zones. When comparing riparian zones, cumulative efflux was 33% higher in the dry (2006) growing season than the wet (2005) growing season, and peak efflux occurred 17 days earlier during the dry growing season (Figure 3). Increased efflux in the riparian zones during the dry growing season was likely due to a shorter period of above intermediate SWC, and therefore a longer duration of relatively high soil CO_2 production and diffusion [Pacific *et al.*, 2008]. In contrast, comparison of efflux in the hillslopes between the wet and the dry growing season showed that cumulative efflux was 8% lower, and peak efflux in the hillslopes occurred 10 days earlier during the dry growing season,

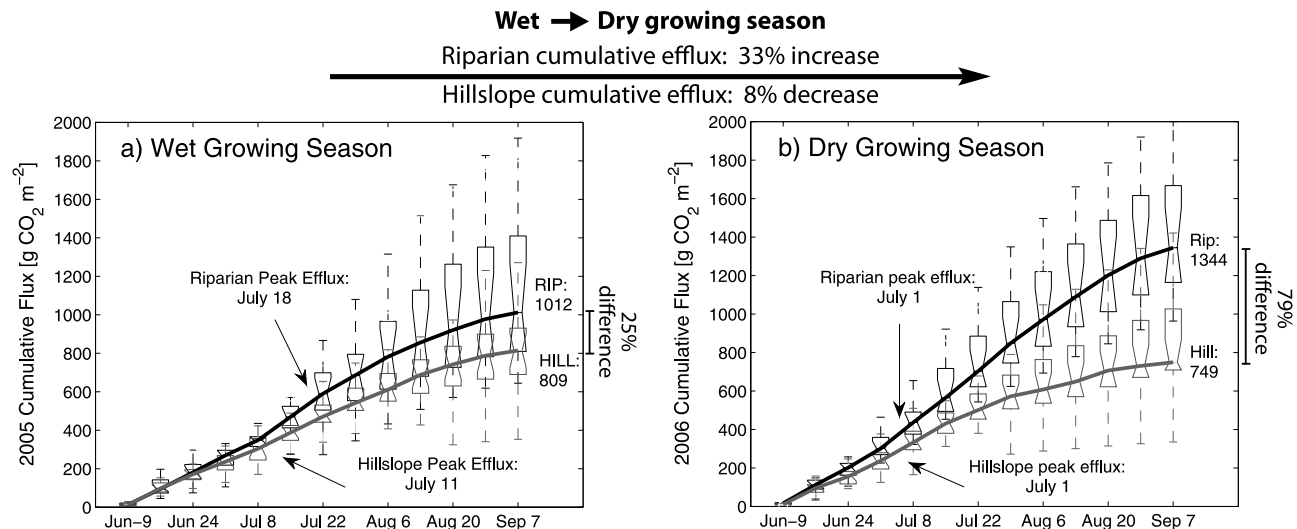


Figure 3. Cumulative riparian and hillslope growing season soil CO_2 efflux during the wet and dry growing seasons. Cumulative growing season efflux (measurements collected from 9 June to 31 August) at riparian (black) and hillslope (grey) zones during (a) the wet growing season (2005) and (b) the dry growing season (2006). Boxes represent interquartile range, lines denote the cumulative median, and whiskers represent 1.5 times the interquartile range. Measurements are from 14 riparian and 18 hillslope locations across eight transects. Total number of measurements (n) were 366 and 450 in the riparian and hillslope zones, respectively, in 2005, and 252 and 292 in 2006.

(Figure 3). These differences in the timing and magnitude of efflux in the hillslopes between the wet and the dry growing season was likely the result of the quicker decline from near intermediate hillslope SWC during the drier growing season, as soil CO_2 production was inhibited at low SWC by desiccation stress [Orchard and Cook, 1983; Linn and Doran, 1984]. It is likely that changes in soil temperature had a small effect on the variability in soil respiration between 2005 and 2006. Soil temperatures were significantly higher during 2005 ($p \ll 0.01$) (Figure 2), which would promote higher efflux [Hamada and Tanaka, 2001; Raich *et al.*, 2002; Pendall *et al.*, 2004]. However, significantly lower efflux in the riparian zones during 2005 ($p \ll 0.01$) suggest soil temperature did not control soil respiration heterogeneity at this site. Our results indicate that changes in the timing and magnitude of precipitation and snowmelt can cause spatial and temporal variability in the movement of SWC into or out of the intermediate range that is optimal for respiration, the degree of which can vary strongly by landscape position.

[11] We suggest that differences in soil respiration across the landscape between 2005 and 2006 were the result of decreased SWC in 2006 from earlier snowmelt and lower precipitation, however other interpretations are possible. For example, the frequency and timing of precipitation pulses may be more important than the total amount of precipitation [Schwinning and Sala, 2004]. Large increases in soil respiration [Austin *et al.*, 2004; Lee *et al.*, 2004; Daly *et al.*, 2008] often follow precipitation events, the degree of which can vary with both storm frequency and type of vegetation [Fierer and Schimel, 2002], as well as antecedent SWC [Riveros-Iregui *et al.*, 2008]. In 2005, there was a period of intense rainfall at the end of June (Figure 2), which may have stimulated soil respiration and led to the peak in efflux in the hillslopes on 1 July (Figure 3). The later peak in efflux in the riparian zones during 2005 (18 July) may be

due to reduced gas diffusivity following the increase in SWC [Pacific *et al.*, 2008]. These results suggest that the large precipitation events at the end of June controlled the timing of peak efflux. However, these peaks in riparian and hillslope efflux may be due to the rise in soil temperature at the same time periods (Figure 2), which can increase evaporation (and therefore decrease SWC) as well as plant and microbial metabolism. This suggests that predicted rises in temperature may constrain the effects of increased precipitation on soil respiration. Further research is necessary to determine the control of precipitation pulses and interactions between soil temperature and SWC on soil respiration variability following changes in hydrologic regimes.

[12] The results of this study can have large implications for ecosystem carbon balances. We observed large and disproportionate changes in efflux between wet (riparian) and dry (hillslope) landscape positions from a wet to a dry growing season in a subalpine forest in the northern Rocky Mountains of Montana. Mean annual precipitation is projected to increase by up to 20% over the next century in North America [Christensen *et al.*, 2007], and peak snowmelt-dominated streamflow is predicted to occur 20–40 days earlier [Stewart *et al.*, 2004]. Therefore, it is likely that changes in hydrologic regimes may strongly impact carbon source/sink magnitude and status of wet and dry landscape positions. As an example, low Arctic and boreal soils are historically large carbon sinks because of a cold climate and wet soils [Chapin *et al.*, 1980; Ping *et al.*, 2008]. These soils account for 20–60% of the global soil carbon pool and contain 1–2 orders of magnitude more carbon than emitted from anthropogenic activities [Ping *et al.*, 2008; Schuur *et al.*, 2008]. Arctic and boreal soils are predicted to switch to carbon sources as global temperatures increase [Oechel *et al.*, 1993]. When comparing wet landscape positions (riparian zones) between a wet and a dry growing season, we found

significantly lower efflux during the wet growing season, despite higher soil temperatures. These results suggest that possible warming-induced increases in arctic and boreal soil respiration could be constrained by wet soils and increasing precipitation. In contrast, the predicted rise in precipitation in arid and semiarid ecosystems [Christensen et al., 2007] could increase soil respiration in these water-limited areas. This rationale is supported by our comparisons of soil respiration at dry landscape positions (hillslope zones) between a wet and a dry growing season, in which we found higher efflux during the wet growing season. Higher soil respiration across dry landscapes could have a large impact on the global carbon cycle, as arid and semiarid lands cover 41% of the Earth's surface [Reynolds et al., 2007]. The results of our study demonstrate that soil respiration responses to changes in SWC are not monotonic across the landscape. Rather, changes in soil respiration at wet and dry landscape positions can occur in opposing directions and with different magnitudes. The greatest changes may occur with drying of wet landscape positions.

5. Conclusions

[13] On the basis of measurements and analysis of riparian and hillslope soil surface CO₂ efflux, SWC, and soil temperature across contrasting wet and dry growing seasons with large differences in snowmelt and precipitation timing and magnitude, we conclude the following.

[14] 1. Wetter landscape positions were more sensitive to drier growing season conditions. When comparing the riparian zones, cumulative soil CO₂ efflux was 33% higher during the dry (2006) growing season. In contrast, comparison of hillslope zones showed that cumulative efflux was 8% lower during the dry growing season.

[15] 2. Drier growing season conditions led to earlier peaks in both riparian and hillslope cumulative soil CO₂ efflux, with the greatest changes in wet (riparian) landscape positions. Peak riparian and hillslope efflux occurred 17 and 10 days earlier during the drier growing season.

[16] This research provides insight into the coupling of soil respiration to alterations in the hydrologic cycle (e.g., snowmelt and precipitation timing and magnitude). We suggest wetter landscape positions could show the greatest changes in soil CO₂ efflux and therefore the greatest shifts in carbon source/sink status.

[17] **Acknowledgments.** We gratefully acknowledge field assistance from K. Jencso, B. McNamara, K. Conde, and A. Allen. We would like to thank W. McCaughey of the Rocky Mountain Research Station, Forest Service, USDA, and the Tenderfoot Creek Experimental Forest for extensive logistical support and research site access. This work was funded by the NSF Integrated Carbon Cycle Research Program (ICCR, NSF grants EAR0404130, EAR0403924, and EAR0403906) and fellowships awarded to V. J. Pacific from the Big Sky Institute NSF GK-12 program and the Inland Northwest Research Alliance (INRA). D. A. Riveros-Iregui acknowledges support from the 2007 American Geophysical Union Horton Research Grant, a NSF Doctoral Dissertation Improvement grant (DEB-0807272), and the USGS 104b Grant Program, administered by the Montana Water Center. We are also grateful for very informative comments from three anonymous reviewers, whose suggestions significantly improved an earlier version of this manuscript.

References

- Austin, T. A., M. L. Yahdjian, J. M. Stark, J. Belnap, A. Porporato, I. C. Burke, U. Chormanska, D. Ravetta, and S. M. Schaeffer (2004), Water pulses and biogeochemical cycles in arid and semiarid ecosystems, *Oecologia*, **141**, 221–235, doi:10.1007/s00442-004-1519-1.
- Chapin, F. S., P. C. Miller, W. D. Billings, and P. I. Coyne (1980), Carbon and nutrient budgets and their control in coastal tundra, in *An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska*, edited by J. Brown et al., pp. 458–483, Dowden, Hutchinson, and Ross, Stroudsburg, Pa.
- Christensen, J. H., et al. (2007), Regional climate projections, in *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by S. Solomon et al., pp. 847–940, Cambridge Univ. Press, Cambridge, U. K.
- Cox, P. M., R. A. Betts, C. D. Jones, S. A. Spall, and I. J. Totterdell (2000), Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model, *Nature*, **408**, 184–187, doi:10.1038/35041539.
- Daly, E., A. C. Oishi, A. Porporato, and G. Katul (2008), A stochastic model for daily subsurface CO₂ concentration and related soil respiration, *Adv. Water Resour.*, **31**, 987–994, doi:10.1016/j.advwatres.2008.04.001.
- Davidson, E. A., E. Belk, and R. D. Boone (1998), Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest, *Global Change Biol.*, **4**, 217–227, doi:10.1046/j.1365-2486.1998.00128.x.
- Davidson, E. A., L. V. Verchot, J. H. Cattaneo, I. L. Ackerman, and J. E. M. Carvalho (2000), Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia, *Biogeochemistry*, **48**, 53–69, doi:10.1023/A:1006204113917.
- Fierer, N., and J. P. Schimel (2002), Effects of drying-wetting frequency on soil carbon and nitrogen transformations, *Soil Biol. Biochem.*, **34**, 777–787, doi:10.1016/S0038-0717(02)00007-X.
- Hamada, Y., and T. Tanaka (2001), Dynamics of carbon dioxide in soil profiles based on long-term field observation, *Hydrol. Processes*, **15**, 1829–1845, doi:10.1002/hyp.242.
- Heimann, M., and M. Reichstein (2008), Terrestrial ecosystem carbon dynamics and climate feedbacks, *Nature*, **451**, 289–292, doi:10.1038/nature06591.
- Holdorf, H. D. (1981), Soil resource inventory, Lewis and Clark National Forest, interim service report, For. Supervisor's Off., Lewis and Clark Natl. For., Great Falls, Mont.
- Lee, X., H. J. Wu, J. Singler, C. Oishi, and T. Siccama (2004), Rapid and transient response of soil respiration to rain, *Global Change Biol.*, **10**, 1017–1026.
- Linn, D. M., and J. W. Doran (1984), Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils, *Soil Sci. Soc. Am. J.*, **48**, 1267–1272.
- Luyssaert, S., E. D. Schulze, A. Börner, A. Knohl, D. Hessenmoller, B. E. Law, P. Ciais, and J. Grace (2008), Old-growth forests as global carbon sinks, *Nature*, **455**, 213–215, doi:10.1038/nature07276.
- Moldrup, P., T. Olsen, P. Schjønning, T. Yamaguchi, and D. E. Rolston (2000), Predicting the gas diffusion coefficient in undisturbed soil from soil water characteristics, *Soil Sci. Soc. Am. J.*, **64**, 94–100.
- Mu, Q., M. Zhao, S. W. Running, M. Liu, and H. Tian (2008), Contribution of increasing CO₂ and climate change to the carbon cycle in China's ecosystems, *J. Geophys. Res.*, **113**, G01018, doi:10.1029/2006JG000316.
- Oechel, W. C., S. J. Hastings, G. Vourlitis, M. Jenkins, G. Riechers, and N. Grulke (1993), Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source, *Nature*, **361**, 520–523, doi:10.1038/361520a0.
- Orchard, V. A., and F. Cook (1983), Relationship between soil respiration and soil moisture, *Soil Biol. Biochem.*, **15**, 447–453, doi:10.1016/0038-0717(83)90010-X.
- Pacific, V. J., B. L. McGlynn, D. A. Riveros-Iregui, D. L. Welsch, and H. E. Epstein (2008), Variability in soil respiration across riparian-hillslope transitions, *Biogeochemistry*, **91**, 51–70, doi:10.1007/s10533-008-9258-8.
- Pendall, E., et al. (2004), Below-ground process response to elevated CO₂ and temperature: A discussion of observations, measurement methods, and models, *New Phytol.*, **162**, 311–322, doi:10.1111/j.1469-8137.2004.01053.x.
- Ping, C., G. J. Michaelson, M. T. Jorgenson, J. M. Kimble, H. E. Epstein, V. E. Romanovsky, and D. A. Walker (2008), High stocks of soil organic carbon in the North American Arctic region, *Nat. Geosci.*, **1**, 615–619, doi:10.1038/ngeo284.
- Raich, J. W., C. S. Potter, and D. Bhagawati (2002), Interannual variability in global soil respiration, 1980–94, *Global Change Biol.*, **8**, 800–812, doi:10.1046/j.1365-2486.2002.00511.x.
- Reynolds, J. F., et al. (2007), Global desertification: Building a science for dryland development, *Science*, **316**, 847–851, doi:10.1126/science.1131634.

- Riveros-Iregui, D. A., R. E. Emanuel, D. J. Muth, B. L. McGlynn, H. E. Epstein, D. L. Welsch, V. J. Pacific, and J. M. Wraith (2007), Diurnal hysteresis between soil CO₂ and soil temperature is controlled by soil water content, *Geophys. Res. Lett.*, **34**, L17404, doi:10.1029/2007GL030938.
- Riveros-Iregui, D. A., and B. L. McGlynn (2009), Landscape structure control on soil CO₂ efflux variability in complex terrain: Scaling from point observations to watershed scale fluxes, *J. Geophys. Res.*, **114**, G02010, doi:10.1029/2008JG000885.
- Riveros-Iregui, D. A., B. L. McGlynn, H. E. Epstein, and D. L. Welsch (2008), Interpretation and evaluation of combined measurement techniques for soil CO₂ efflux: Discrete surface chambers and continuous soil CO₂ concentration probes, *J. Geophys. Res.*, **113**, G04027, doi:10.1029/2008JG000811.
- Savage, K. E., and E. A. Davidson (2001), Interannual variation of soil respiration in two New England forests, *Global Biogeochem. Cycles*, **15**, 337–350, doi:10.1029/1999GB001248.
- Schaphoff, S., W. Lucht, D. Gerten, S. Sitch, W. Cramer, and I. C. Prentice (2006), Terrestrial biosphere carbon storage under alternative climate projections, *Clim. Change*, **74**, 97–122, doi:10.1007/s10584-005-9002-5.
- Schmidt, W. C., and J. L. Friede (1996), Experimental forests, ranges and watersheds in the northern Rocky Mountains: A compendium of outdoor laboratories in Utah, Idaho and Montana, *Gen. Tech. Rep. INT-GTR 334*, Intermt. Res. Stn., For. Serv., U.S. Dep. of Agric., Ogden, Utah.
- Schuur, E. A. G., et al. (2008), Vulnerability of permafrost carbon to climate change: Implications for the global carbon cycle, *BioScience*, **58**, 701–714, doi:10.1641/B580807.
- Schwinning, S., and O. E. Sala (2004), Hierarchy of responses to resource pulses in arid and semi-arid ecosystems, *Oecologia*, **141**, 211–220.
- Sjogersten, S., R. van der Wal, and S. J. Woodin (2006), Small-scale hydrological variation determines landscape CO₂ fluxes in the high Arctic, *Biogeochemistry*, **80**, 205–216, doi:10.1007/s10533-006-9018-6.
- Skopp, J., M. D. Jawson, and J. W. Doran (1990), Steady-state aerobic microbial activity as a function of soil water content, *Soil Sci. Soc. Am. J.*, **54**, 1619–1625.
- Stewart, I. T., D. R. Cayan, and M. D. Dettinger (2004), Changes in snow-melt runoff timing in western North America under a “business as usual” climate change scenario, *Clim. Change*, **62**, 217–232, doi:10.1023/B:CLIM.0000013702.22656.e8.
- Stewart, I. T., D. R. Cayan, and M. D. Dettinger (2005), Changes towards earlier streamflow timing across western North America, *J. Clim.*, **18**, 1136–1155, doi:10.1175/JCLI3321.1.
- Yu, Y. Q., H. Zhi, B. Wang, H. Wan, C. Li, H. L. Mu, W. Li, W. P. Zheng, and T. J. Zhou (2008), Coupled model simulations of climate changes in the 20th century and beyond, *Adv. Atmos. Sci.*, **25**, 641–654, doi:10.1007/s00376-008-0641-0.

H. E. Epstein, Department of Environmental Sciences, University of Virginia, 211 Clark Hall, Charlottesville, VA 22904, USA. (hee2b@viginia.edu)

B. L. McGlynn and V. J. Pacific, Department of Land Resources and Environmental Sciences, Montana State University, 334 Leon Johnson Hall, Bozeman, MT 59717, USA. (bmcglynn@montana.edu)

D. A. Riveros-Iregui, Department of Ecology and Evolutionary Biology, University of Colorado at Boulder, Boulder, CO 80309, USA. (riveros@colorado.edu)

D. L. Welsch, Canaan Valley Institute, P.O. Box 673, Davis, WV 26260, USA. (danny.welsch@canaanvi.org)