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Variability in soil respiration across riparian-hillslope transitions

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Abstract The spatial and temporal controls on soil CO_2 production and surface CO_2 efflux have been identified as outstanding gaps in our understanding of carbon cycling. We investigated both across two riparian-hillslope transitions in a subalpine catchment, northern Rocky Mountains, Montana. Riparian-hillslope transitions provide ideal locations for investigating the controls on soil CO_2 dynamics due to strong, natural gradients in the factors driving respiration, including soil water content (SWC) and soil temperature. We measured soil air CO_2 concentrations (20 and 50 cm), surface CO_2 efflux, soil temperature, and SWC at eight locations. We investigated (1) how soil CO_2 concentrations differed within and between landscape positions; (2) how the timing of peak soil CO_2 concentrations varied across riparian and hillslope zones; and (3) whether higher soil CO_2 concentrations necessarily resulted in higher efflux (i.e. did surface CO_2 efflux follow patterns of subsurface CO_2)? Soil CO_2 concentrations were significantly higher in the riparian zones, likely due to higher SWC. The timing of peak soil CO_2 concentrations also differed between riparian and hillslope zones, with highest hillslope concentrations near peak snowmelt and highest riparian concentrations during the late summer and early fall. Surface CO_2 efflux was relatively homogeneous at monthly timescales as a result of different combinations of soil CO_2 production and transport, which led to equifinality in efflux across the transects. However, efflux was 57% higher in the riparian zones when integrated to cumulative growing season efflux, and suggests higher riparian soil CO_2 production.

Keywords CO_2 · Carbon dioxide · Efflux · Gas diffusion · Hillslope · Riparian

Introduction

Soil respiration is widely understood as the sum of root respiration (autotrophic) and microbial (heterotrophic) decomposition of soil organic matter (SOM), and is an important part of the global carbon cycle (Raich and Schlesinger 1992; Raich and Potter 1995; Risk et al. 2002a). Variability of soil respiration has been the focus of many studies, yet most were limited to short temporal (Kang et al. 2003, 2006; Sjogersten et al. 2006) or spatial (Fang et al. 1998; Musselman et al. 2005; Baldocchi et al. 2006) scales within

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relatively homogeneous terrain. While these studies have provided essential knowledge on primary controls on soil respiration, little can be inferred about the variability of these controls across natural environmental gradients imposed by topography in complex terrain.

Gas-filled soil pores typically contain 10–100 times the concentration of atmospheric CO_2 (Welles et al. 2001). In the standing paradigm of soil water content (SWC)–temperature–CO_2 relationships, soil temperature is considered to be the primary control and SWC the secondary control on soil CO_2 production (defined as the combination of heterotrophic and autotrophic respiration) (Raich and Schlesinger 1992; Raich and Potter 1995; Risk et al. 2002a). However, SWC can become the dominant control on soil CO_2 production in very wet (Happell and Chanton 1993; Buchmann et al. 1997, 1998; Welsch and Hornberger 2004) or dry (Conant et al. 1998, 2004; McLain and Martens 2006; Riveros-Iregui et al. 2007) environments due to oxygen limitations (Skopp et al. 1990) and moisture stress (Orchard and Cook 1983), respectively. It is generally understood that increases in soil temperature (Hamada and Tanaka 2001; Raich et al. 2002; Pendall et al. 2004) and SWC (Davidson et al. 2000; Kelliher et al. 2004) promote higher rates of soil respiration, however, the switch from temperature to SWC as the primary control of soil CO_2 production remains poorly understood.

The drivers of soil respiration can be spatially variable, partially in response to topographic position. For example, soil temperature is often dependent upon aspect, with southern aspects receiving more solar radiation than northern aspects (in the northern hemisphere) (Kang et al. 2006). SWC can vary across the landscape (Grayson and Western 2001; McGlynn et al. 2002; Kang et al. 2004; Wilson et al. 2005), with convergent areas, especially those in riparian zones, often having higher SWC and more sustained water tables (Beven and Kirkby 1979; Pennock et al. 1987; McGlynn and Seibert 2003). Riparian areas generally have a greater accumulation of SOM than hillslopes because frequent saturation retards microbial decomposition (Schlesinger 1997; Oades 1988; Sjogersten et al. 2006). Given the large variability in the drivers of respiration imposed by topography, thorough process understanding is necessary to determine the relative controls of soil CO_2 concentrations and surface CO_2 efflux across landscape positions.

A common misconception is that soil surface CO_2 efflux can serve as a surrogate for soil CO_2 production (i.e. higher efflux is the result of higher production). At long timescales (seasonal) production and efflux are likely equivalent, however at shorter timescales (hours to days) differences can result from changes in CO_2 stores in the soil. These include changes in concentrations, water-filled pore space, or change of CO_2 from gaseous to liquid phase (Risk et al. 2002b). Efflux is not only a function of production, but also of transport (Hamada and Tanaka 2001; Risk et al. 2002b; Riveros-Iregui et al. 2007), which is controlled by SWC and static soil properties such as porosity, connectivity, and tortuosity of pore spaces (Moldrup et al. 2001; Hillel 2004). SWC impacts gas transport (Millington 1959; McCarthy and Johnson 1995; Moldrup et al. 2000), as increases in the water-filled pore space greatly limit soil gas diffusivity (Washington et al. 1994; Davidson and Trumbore 1995; Moldrup et al. 2004). Thus, studies of soil respiration should examine both soil CO_2 production and transport, because similar efflux, or "efflux equifinality" (comparable efflux with different combinations of the variables) at short timescales could be a result of different combinations of soil CO_2 production and changing CO_2 stores in the soil.

In this study we present measurements of soil CO_2 concentrations and surface efflux along two riparian-hillslope transitions in a subalpine catchment characteristic of the northern Rocky Mountains. We investigated the natural variability of both CO_2 concentrations and efflux in response to topographically controlled gradients of soil temperature and SWC to answer the following questions:

1. How do soil CO_2 concentrations and surface CO_2 efflux differ within and between landscape positions through time?
2. Do higher soil CO_2 concentrations necessarily result in higher efflux (i.e. does surface CO_2 efflux follow patterns of subsurface CO_2)?

Materials and methods

Site description

This study was conducted in the upper-Stringer Creek Watershed, a subcatchment of Tenderfoot Creek, located in the United States Forest Service Tenderfoot Creek Experimental Forest (TCEF). The TCEF (lat. 46°55′ N, long. 110°52′ W) is located in the Little Belt Mountains of central Montana (Fig. 1). TCEF elevation ranges from 1,840 to 2,421 m with a mean of 2,205 m and encompasses 3,591 ha. The upper-Stringer Creek Watershed is 380 ha and has a wide range of slope (5–45%), aspect, and topographic convergence/divergence.

Farnes et al. (1995) characterized environmental variables at the TCEF. Annual precipitation averages 880 mm, with monthly precipitation greatest in December or January at 100–125 mm and declining to 50–60 mm from July to October. Approximately 70 percent of the annual precipitation falls from November through May as snow, with typical winter snow depths of 1–2 m and snow water equivalents of ~600 mm. Mean annual temperature is 0°C, with mean daily temperatures ranging from −8.4°C in December to 12.8°C in July. The growing season is typically 45–75 days, decreasing to 30–45 days on the ridges.

The riparian zones are composed predominantly of bluejoint reedgrass (*Calamagrostis canadensis*) (Mincemoyer and Birdsall 2006), and no trees are present. In the hillslopes, grouse whortleberry (*Vaccinium scoparium*) is the dominant understory species (Mincemoyer and Birdsall 2006), and the overstory vegetation is composed mainly of lodgepole pine (*Pinus contorta*) (Farnes et al. 1995). Other species include subalpine fir (*Abies lasiocarpa*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*). Tree heights average 15 m and leaf area index (LAI) values range from 2.8 to 3.2 (Woods et al. 2006).

The geology is characterized by granite gneiss, Wolsey shales, quartz porphyry, and Flathead quartzite (Farnes et al. 1995), and the most extensive soil types are loamy skeletal, mixed Typic Cryochrepts, and clayey, mixed Aquic Cryoboralfs (Holdorf 1981). Average soil carbon and nitrogen content at 20 cm is 2.3 and 0.17%, respectively, in the riparian zones, and 2.7 and 0.11% in the hillslopes. At 50 cm, average soil carbon and nitrogen content is 1.77 and 0.12%, respectively, in the riparian zones, and 1.3 and 0.06% in the hillslopes. Average soil C:N ratios are 14.1 and 26.1 at 20 cm in the riparian and hillslopes zones, respectively, and 15.4 and 27.7 at 50 cm. Soil bulk density is 0.962 and 0.911 g cm^{-3}, in the riparian and hillslope zones, respectively, and soil root density is 11.5 and 9.6 g root kg^{-1} soil, respectively.

Landscape characterization

Two transects, each crossing one riparian-hillslope transition, were installed within the upper-Stringer Creek Watershed (Fig. 1) in a subalpine watershed characteristic of the northern Rocky Mountains. The transects originate at Stringer Creek, which flows north to south, and extend up the fall line on both the west (Transect 1) and east (Transect 2) side of the creek approximately 50 m through the riparian and adjacent

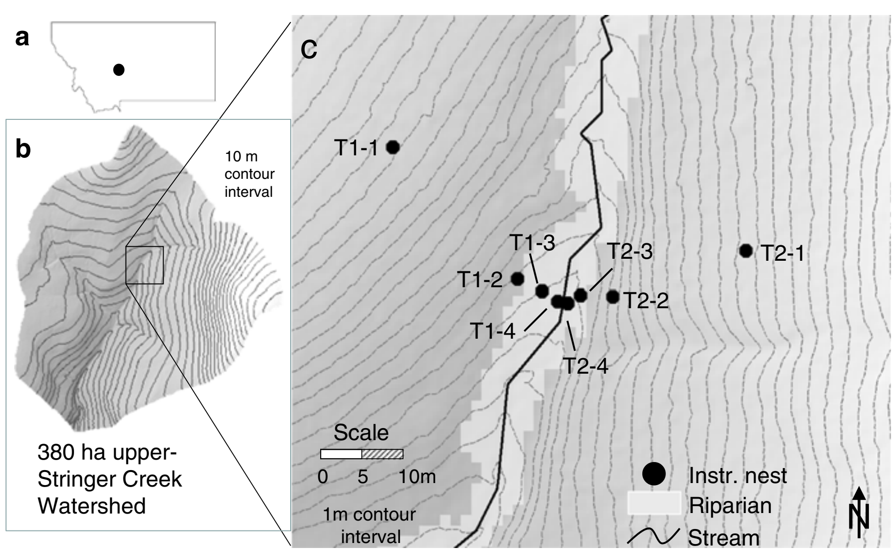


Fig. 1 **a** Location of the Tenderfoot Creek Experimental Forest (within the Lewis and Clark National Forest), MT; **b** LIDAR (ALSM) topographic image (resolution < 1 m for bare earth and vegetation) of the upper-Stringer Creek Watershed; and **c** transect location with measurement nest positions and riparian zone width

hillslope zones (~100 m total across both transects). Transect 1 is characterized by a 12.7 m wide riparian zone of ~5% slope and a convex hillslope (~18% slope). Similarly, the riparian zone on Transect 2 is 11.8 m wide with a ~5% slope, and a convex hillslope (~14% slope). The transect locations were chosen because they are characteristic of riparian-hillslope transitions across the watershed and have median values of riparian zone width and slope.

Four instrumentation nests (two in the riparian zones, and two in the hillslopes) were installed along each transect. The riparian-hillslope transition was defined by a break in slope as well as change in vegetation (bluejoint reedgrass in the riparian zones and grouse whortleberry in the hillslopes). The nests were labeled 1–4, corresponding to their proximity to Stringer Creek, with 1 being the highest hillslope nest (furthest from the creek) (Fig. 1). Gas wells were labeled "20" or "50", corresponding to the 20 or 50 cm completion depth. Thus "T1-1-20" refers to the 20 cm gas well at the first nest location (most upslope) on Transect 1. T2-3 is classified as a hillslope nest due to its soil properties, SWC, and water table dynamics.

Environmental measurements

We report measurements taken from February to October, 2005. To avoid time-of-day biases, data collection along the transect was conducted no earlier than 1000 h and no later than 1600 h, as previous studies demonstrated that sampling between these times represents near-average daily surface CO_2 efflux at this research site (Riveros-Iregui et al. 2007; in press). Sampling of all nests required ~90 min.

Measurements of soil temperature and SWC were collected within a 1 m^2 measurement area at each nest location. Measurements were collected on 1–3 day intervals during the growing season, weekly during the fall and spring, and monthly during the winter. We defined the seasons based upon temperature thresholds and snow depth. Winter was defined as having an average snow depth greater than 0.5 m (November through mid-May), and summer was defined as having average minimum daily temperatures above freezing (mid-June through August). Fall (September and October) and spring (mid-May through mid-June) fell between the summer and winter criteria.

Soil temperature at 12 cm was measured manually at each nest with a soil thermometer (12 cm soil thermometer, measurement range of −20 to 120°C, Reotemp Instrument Corporation, San Diego, California, USA). Volumetric SWC (cm^3 H_2O/cm^3 soil) was measured manually at three locations (due to potential spatial variability of SWC) at each nest with a portable SWC meter that integrated over the upper 20 cm of soil (Hydrosense, Campbell Scientific Inc., Utah, USA). The three SWC measurements at each nest location were averaged for data analysis. Soil temperature and SWC measurements were not collected while snow was on the ground to minimize snowpack disturbance and associated soil CO_2 dynamics.

A time domain reflectometry (TDR) system was developed in the lab following Robinson et al. (2003) to calibrate the Hydrosense portable SWC meter. The performance of the TDR sensor was tested in the laboratory over a wide range of SWC by comparing TDR and gravimetric measurements. To calibrate and test the Hydrosense, TDR-based SWC was measured in the field ($n = \sim 300$) with both sensors over a wide range of SWC. SWC measurements by both instruments were comparable in the upland mineral soil ($r^2 = 0.99$), but the Hydrosense overestimated SWC in the organic riparian soil. Hydrosense measurements in the organic riparian soil were therefore adjusted using the following equation:

$$\begin{aligned} \text{SWC} &= (0.7704 * \text{Hydrosense measurement}) \\ &\quad + 0.8774 \quad (r^2 = 0.986) \end{aligned} \tag{1}$$

Two snow survey telemetry (SNOTEL) stations within 2 km (Onion Park—2,259 m, and Stringer Creek—1,996 m) and a tipping-bucket rain gauge (TR-525 M, accurate to within 1% for up to 50 mm/h, Texas Electronics, Dallas, TX, USA) located on T2 provided real-time data on snow depth, snow water equivalent, and rainfall. Snow depth and snow water equivalent from the Onion Park SNOTEL station were used for data analysis due to its similar elevation. SNOTEL measurements of snow depth were corroborated by monthly manual measurements at each nest location along the transects.

Hydrologic measurements

Groundwater wells screened from the completion depth (0.5–2 m) to within 0.2 m of the ground surface were installed at all riparian zone nests and the hillslope nest adjacent to the riparian-hillslope transition (i.e. T1-2, T1-3, T1-4, T2-2, T2-3, T2-4). Groundwater levels were recorded every 30 min using capacitance rods (±1 mm resolution, Trutrack, New Zealand).

Soil CO_2 concentration measurements

At all nest locations, gas wells that equilibrate with the soil atmosphere were installed at the 20 and 50 cm depth (one gas well per depth per nest to minimize disturbance) following the methods described by Andrews and Schlesinger (2001) and Welsch and Hornberger (2004). The gas wells consisted of a 15-cm section of 5.25 cm (inside diameter) PVC inserted into a hole augered to 20 or 50 cm. The top of the PVC was capped with a rubber stopper (size 11) through which passed two pieces of PVC tubing (4.8 mm inside diameter Nalgene 180 clear PVC, Nalge Nunc International, Rochester, N.Y., USA) that extended above the ground surface. The tubing was joined with connectors (6–8 mm HDPE FisherBrand tubing connectors, Fisher Scientific, USA) to ensure that no gas escaped between measurements.

To measure soil air CO_2 concentrations, the two sections of tubing from the gas well were attached to the IRGA, and the air from the gas well was circulated through the IRGA and returned to the gas well. This technique created a closed loop and minimized pressure changes during sampling (Andrews and Schlesinger 2001; Welsch and Hornberger 2004). When snow was present, soil CO_2 concentrations were measured through 1 m tubing extenders attached to a 2 m post at each nest location prior to snowfall. Soil CO_2 concentrations were not measured between July 18 and August 7, 2005 due to equipment malfunction.

Soil air CO_2 concentrations were measured with portable infrared gas analyzers (IRGA) (model EGM-3, accurate to within 1% of calibrated range [0–50,000 ppm]; PP Systems, Massachusetts, USA;) and (model GM70 with M170 pump and GMP 221 CO_2 probe, accurate to within 1% of calibrated range [0–50,000 ppm]; Vaisala, Finland). The instruments were routinely compared in the field to ensure measurements were within 1%, and both instruments were recalibrated by the manufacturer three times during the duration of the study. Both instruments were allowed a 30 min warm-up time (per the manufacturer's recommendations), then remained on for the duration of measurement. Soil CO_2 concentration measurements from the EGM-3 were internally corrected for air temperature and pressure. Measurements from the GMP 221 were compensated for air temperature and pressure following recommendations by the manufacturer and described in detail by Tang et al. (2003). Each soil CO_2 concentration measurement required 2–5 min (recirculation time) before stabilized values were recorded. Recirculation time did not affect soil CO_2 concentrations in our experimental design or similar designs (Andrews and Schlesinger 2001; Welsch and Hornberger 2004).

Surface CO_2 efflux measurements

A surface CO_2 efflux plot was selected at each nest location, consisting of a 0.5 m^2 area roped off to minimize soil trampling. Vegetation within the efflux plot was clipped to minimize the effect of aboveground autotrophic respiration inside the chamber. Vegetation was clipped approximately once a week after a round of measurements was collected, and roots were left intact to minimize disturbance to belowground root respiration.

Three surface CO_2 efflux measurements were collected from each plot on all sampling days using a soil respiration chamber (SRC-1 chamber with a footprint of 314.2 cm^2, accurate to within 1% of calibrated range [0–9.99 g CO_2 m^{-2} h^{-1}] in conjunction with an IRGA (EGM-4, accurate to within 1% of calibrated range [0–2,000 ppm]; PP Systems, Massachusetts, USA). Before each measurement, the chamber was flushed with ambient air for 15 s and then inserted 3 cm into the soil to ensure a good seal between the chamber and the ground surface. The sampling period lasted for 120 s, or until the CO_2 concentration inside the chamber increased by 60 ppm. To determine the CO_2 efflux during the measurement, a quadratic equation was fitted to the relationship between the increasing CO_2 concentration and elapsed time (per manufacturer's recommendation). We estimated cumulative growing season efflux from June 9 to August 31, 2005 by linearly interpolating between measurements collected every 2–7 days. Previous studies (Riveros-Iregui et al. in press) demonstrated that this was a robust approach for comparison of efflux measurements across multiple locations over extended periods of time.

To collect efflux measurements from the snowpack, a snowshoe was constructed of fine metal screen attached to a 0.5 m^2 PVC frame (2.5 cm inside diameter PVC). A hole was cut into the screen to allow the base of the chamber to be inserted into the snowpack. The chamber was modified to extend its length (by 10 cm) by attaching a metal ring (10 cm diameter) to its base to ensure a good seal with the snowpack. The snowshoe method has been found appropriate as it causes minimal disturbance to the snowpack (McDowell et al. 2000). Surface CO_2 efflux measurements did not begin until the middle of April, 2005 due to equipment malfunction.

Soil gas diffusivity

Given the difficulty in accurately measuring in situ soil gas diffusivity without severely disturbing the soil, we estimated an "effective" diffusivity for the upper 20 cm of the soil profile. Soil gas diffusivity was inversely calculated using Fick's Law and measured values of soil CO_2 concentrations at 20 cm and surface CO_2 efflux (and an assumed atmosphere CO_2 concentration of 400 ppm):

$$F = -D\frac{\partial C}{\partial z} \quad (2)$$

where D is the diffusivity ($m^2\ s^{-1}$), C is the CO_2 concentration (ppm), and z is the depth (m).

This approach provides an estimate of D for each sampling time and allows for relative comparisons between riparian and hillslope zones.

Statistical analyses

Analysis of variance (ANOVA) statistics ($\alpha = 0.05$) were employed to test differences between riparian and hillslope soil CO_2 concentrations, surface CO_2 efflux, soil temperature, SWC, and soil gas diffusivity, with separate analyses for each month due to temporal dynamics at our research site. For these variables, $n = 8$ from Feb through May as measurements were collected from eight nest locations one day each month during the winter (due to limited site access). During the growing season, n ranged from 104 in June to 160 in July due to multiple sampling days each month, with measurements from eight nest locations on each sampling day. Three measurements of SWC and surface CO_2 efflux were collected at each nest location on all sampling days to account for possible measurement error, then averaged for data analysis.

Results

Soil temperature

Spatial variability

Soil temperature (12 cm) was not significantly different between riparian and hillslope landscape positions (Table 1, Figs. 2, 3, 4). Average soil temperature and standard deviation at riparian and hillslope nests were within 0.3 and 0.2°C of each, respectively. Aspect (west versus east) did not affect soil temperature at this study site (Fig. 3).

Temporal variability

Near the middle of June, 2005, when soil temperature measurements began, soil temperatures ranged from 4 to 12°C (Figs. 5, 6), with the lowest soil temperatures under or near patches of snow on the hillslopes. Soil temperatures increased by $\sim$10°C by the beginning of August at most nest locations. A sharp decrease occurred near the middle of August, coincident with cool weather and periodic snow. Soil temperatures then decreased to below freezing by the end of September.

Soil water content

Spatial variability

SWC (integrated over top 20 cm) was significantly different between riparian and hillslope zones ($p \ll 0.01$, Table 1), with higher and more variable SWC in the riparian zones (Fig. 3).

Temporal variability

In the middle of June, 2005, SWC was the highest during the period of measurement (June 12–October 1, 2005), reaching saturation at many riparian nest locations, but remaining below 40% in the hillslopes (Fig. 4). High SWC in June corresponded to recent snowmelt (which peaked in the middle of May). SWC then decreased over the summer, with the

Table 1 Analysis of variance (ANOVA) statistics for riparian versus hillslope soil temperature, soil water content, soil gas diffusivity, surface CO_2 efflux, and soil CO_2 concentrations (20 and 50 cm) from February 6 to September 30, 2005

	n	Temp		SWC		Diffusivity		Efflux	
		F	*p*-value	*F*	*p*-value	*F*	*p*-value	*F*	*p*-value
Feb	8	–	–	–	–	–	–	–	–
Mar	8	–	–	–	–	–	–	–	–
Apr	8	–	–	–	–	–	–	0.07	0.80
May	8	–	–	–	–	–	–	3.76	0.09
June	104	0.80	0.41	280.86	**≪0.01**	47.07	**≪0.01**	0.64	0.43
July	160	0.03	0.86	533.02	**≪0.01**	30.51	**≪0.01**	1.59	0.21
Aug	112	2.09	0.15	912.71	**≪0.01**	47.19	**≪0.01**	35.98	**≪0.01**
Sept	24	0.22	0.64	110.57	**≪0.01**	6.55	**0.03**	1.45	0.26

	n	CO_2-20		CO_2-50		20 vs. 50 (rip)		20 vs. 50 (hill)	
		F	*p*-value	*F*	*p*-value	*F*	*p*-value	*F*	*p*-value
Feb	8	6.93	**0.04**	0.67	0.44	16.42	**0.02**	0.68	0.44
Mar	8	20.39	**≪0.01**	2.93	0.15	18.18	**0.01**	0.01	0.93
Apr	8	0.02	0.89	4.46	0.08	3.56	0.13	0.06	0.81
May	8	0.41	0.85	11.68	**0.02**	86.55	**≪0.01**	0.01	0.94
June	104	55.45	**≪0.01**	159.35	**≪0.01**	64.90	**≪0.01**	43.98	**≪0.01**
July	160	23.53	**≪0.01**	132.87	**≪0.01**	118.96	**≪0.01**	10.75	**≪0.01**
Aug	112	808.24	**≪0.01**	3.39	0.07	188.75	**≪0.01**	90.80	**≪0.01**
Sept	24	69.46	**≪0.01**	6.55	**0.02**	11.82	**≪0.01**	7.31	**0.01**

An α of 0.05 was used for all analyses. If no value is given, data was not collected during that time. Bold numbers indicate significant differences

lowest values (5–10%) in August and September in the hillslopes.

Soil gas diffusivity

Please note that these results give only a general indication of soil gas diffusivity as our calculations used soil CO_2 concentrations at 20 cm and therefore do not account for near-surface soil CO_2 production.

Spatial variability

Soil gas diffusivity was significantly higher in the hillslope zones ($p < 0.05$, Table 1; Figs. 3, 4).

Temporal variability

Soil gas diffusivity generally increased from June through September in the hillslopes, with relatively less change in the riparian zones (Figs. 5, 6).

Snow depth, snow water equivalent, and rainfall

Snow depth and snow water equivalent (SWE) increased over the winter, with April maxima of 126 and 46 cm, respectively, and complete snowmelt by the middle of June (Figs. 5, 6). Manual measurements of snow depth at each nest location corroborated snow data from the Onion Park SNOTEL site. While heterogeneity in snow depth was observed across the transect, there was little variation between snow depth in the riparian and hillslope zones when the data was averaged within each landscape element. Rainfall varied from May to October, with the largest precipitation events during July (Figs. 5, 6).

Groundwater levels

Peak snowmelt occurred on ~June 11, 2005. The groundwater table rose to the near-ground surface at all riparian nests during snowmelt, but rarely rose above the well completion depths (1–2 m) in the

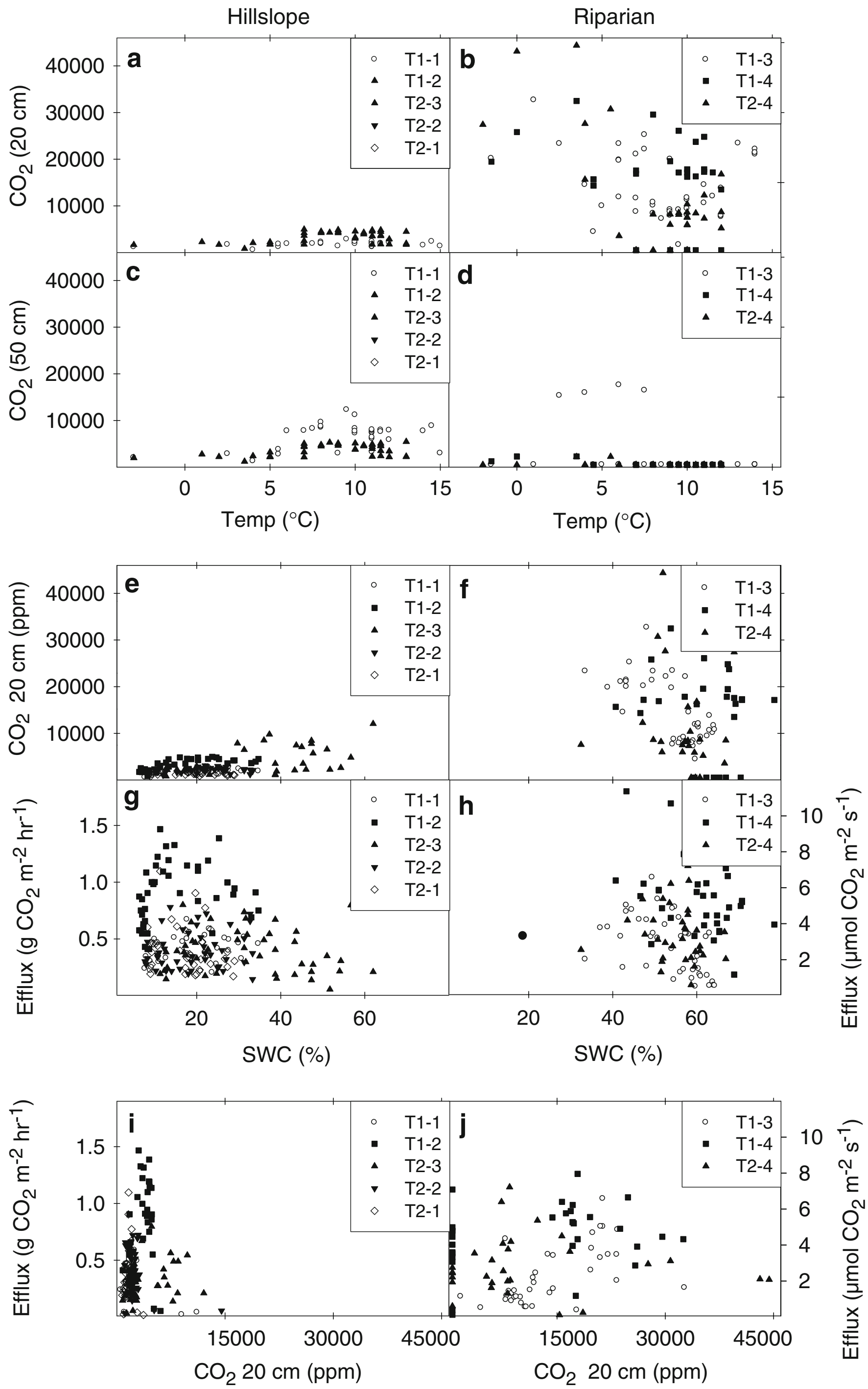
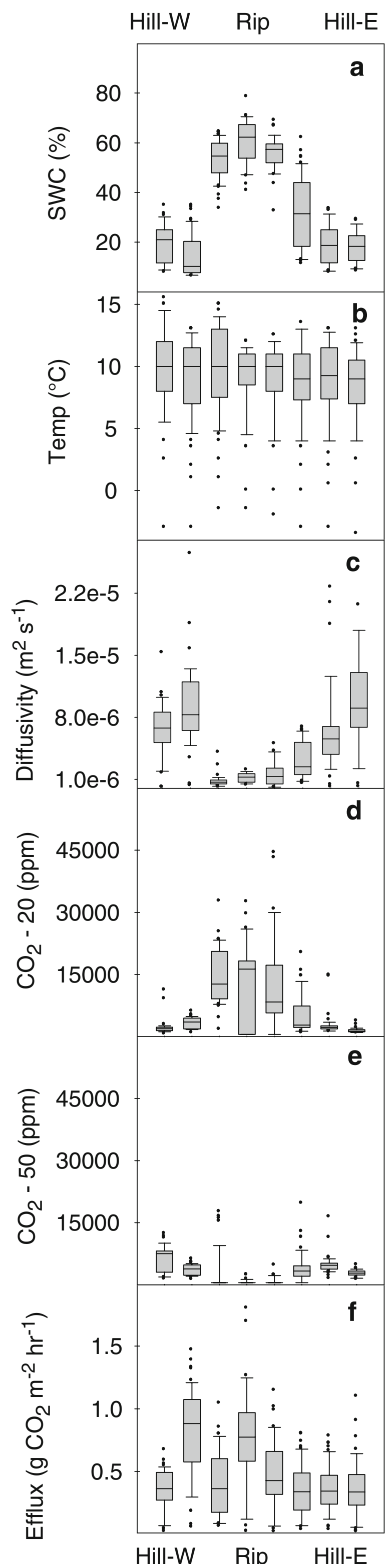


Fig. 2 Bivariate plots of soil temperature and soil CO_2 concentration in **a** hillslope zones, 20 cm, **b** riparian zones, 20 cm, **c** hillslope zones, 50 cm, and **d** riparian zones, 50 cm; soil water content (SWC) and 20 cm soil CO_2 concentration in **e** hillslope zones and **f** riparian zones; SWC and surface CO_2 efflux in **g** hillslope zones and **h** riparian zones; and soil CO_2 concentration and surface CO_2 efflux in **i** hillslope zones, and **j** riparian zones from February 6 to October 1, 2005. Filled symbols denote landscape positions closer to Stringer Creek for both riparian and hillslope zones. Y-axis for surface CO_2 efflux is presented in both g CO_2 m^{-2} h^{-1} and μmol CO_2 m^{-2} s^{-1} to aid in comparison to other studies

hillslopes during the extent of this study (unpublished data). The groundwater table declined over the summer, except during a series of high precipitation events near the end of June, at which point the groundwater table rose ∼5–10 cm at all riparian nests. By late summer or early fall, the groundwater table declined below 50 cm from the ground surface at all riparian nests. Figure 7 presents water table data from T1-4, which was characteristic of other riparian zone groundwater wells.

Fig. 3 Box-plots of riparian and hillslope zone **a** soil water content; **b** soil temperature; **c** soil gas diffusivity; **d** soil CO_2 concentration—20 cm; **e** soil CO_2 concentration—50 cm; and **f** surface CO_2 efflux from February 6 to October 1, 2005. Boxes represent the inter-quartile range, the lines the medians, and the whiskers the 10th and 90th percentiles



Soil CO_2 concentrations

Spatial variability

In general, soil CO_2 concentrations were significantly higher in the riparian zones (Table 1) and often exceeded 20,000 ppm at 20 cm, while hillslope soil CO_2 concentrations generally remained below 5,000 ppm (Figs. 3, 4). There were also significant differences between 20 and 50 cm soil CO_2 concentrations in both the riparian (higher at 20 cm) and hillslope (higher at 50 cm) zones (Table 1, Fig. 8), with the greatest differences in the riparian zones. The magnitude of the difference between 20 and 50 cm riparian soil CO_2 concentrations generally increased from summer to fall (Fig. 5). In contrast to the riparian zones, the magnitude of the difference in hillslope soil CO_2 concentrations by depth decreased from summer to fall (Fig. 6).

Seasonal variability: winter-to-spring

There was a high degree of seasonal variability in soil CO_2 concentrations in both riparian and hillslope zones (Figs. 5, 6), with peaks occurring during both winter and summer. Riparian soil CO_2 concentrations increased over the winter (Fig. 5), with a winter peak of approximately 20,000 ppm between the middle of March and the middle of April, 2005. In contrast, the hillslope zones peaked at approximately 10,000 ppm between the middle of April and middle of May (Fig. 6), which were the highest hillslope concentrations measured during this study.

Seasonal variability: summer-to-fall

There were also temporal differences in summer-to-fall peaks in soil CO_2 concentrations between the riparian and hillslope zones. Peaks in riparian zone soil CO_2 concentrations (average values of ~30,000 ppm) occurred during September, 2005 (Fig. 5), which were

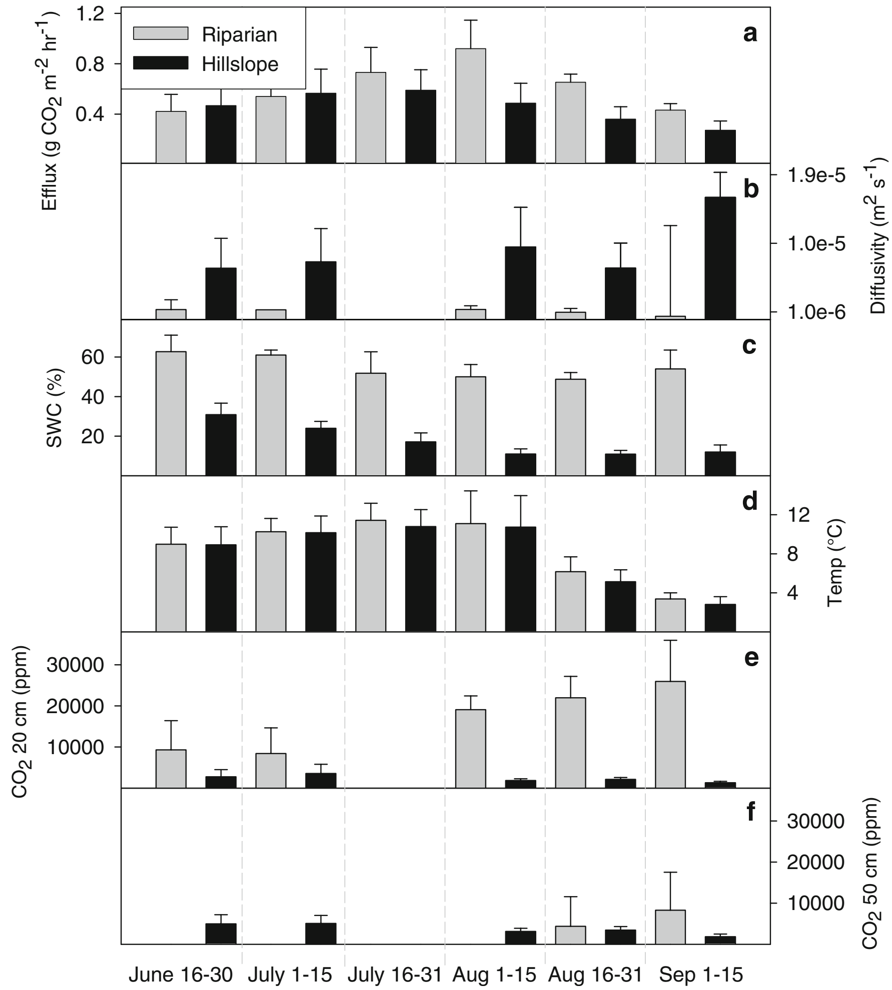


Fig. 4 Two-week average **a** surface CO_2 efflux; **b** soil gas diffusivity; **c** SWC; **d** soil temperature; **e** soil CO_2 concentrations (20 cm); and **f** soil CO_2 concentrations (50 cm) from riparian (*grey*) and hillslope (*black*) landscape positions during the growing season. Whiskers represent one standard deviation (based upon 3 and 5 replications in the riparian and hillslope zones, respectively). Soil CO_2 concentrations were not measured during the end of July due to equipment malfunction (therefore not allowing for calculations of soil gas diffusivity during that time)

the highest riparian concentrations measured during this study. Conversely, the hillslope zones exhibited summer peaks in soil CO_2 concentrations during the beginning of July, with average values of ~5,000 ppm (Fig. 6).

Surface CO_2 efflux

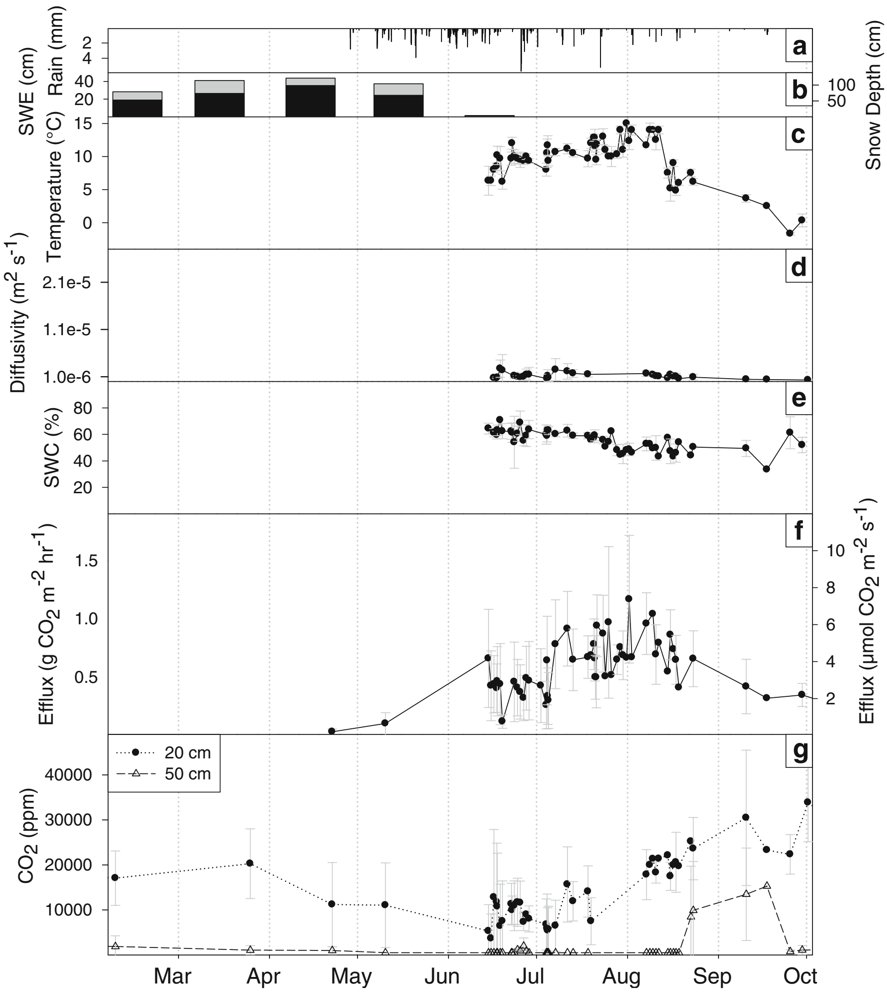
Spatial variability

Soil surface CO_2 efflux was not significantly different between riparian and hillslope zones (Table 1; Figs. 3, 4). However, when making weekly comparisons between each riparian and hillslope nest (rather than monthly comparisons of aggregated riparian and hillslope efflux, Table 1), large differences in riparian and hillslope efflux is evident (Fig. 9).

Seasonal variability

Soil surface CO_2 efflux showed a high degree of seasonal variability in both riparian and hillslope zones (Figs. 5, 6, 8). During late spring, there was snow accumulation of up to 120 cm (Figs. 5, 6), and surface CO_2 efflux was relatively low, $\ll$0.1 g CO_2 m^{-2} h^{-1} in both riparian and hillslope zones. By the middle of June, 2005, the majority of the ground surface was snow-free, and both riparian and hillslope surface CO_2 efflux rose nearly an order of magnitude (Figs. 5, 6). Average hillslope zone surface CO_2 efflux peaked at ~0.5 g CO_2 m^{-2} h^{-1} at most nests between the middle and end of July (Fig. 9). Conversely, riparian zone efflux peaked at ~0.8 g CO_2 m^{-2} h^{-1} (although up to 1.3 g CO_2 m^{-2} hr^{-1} at T1-2) 2–4 weeks later, between the beginning and middle of August (Fig. 9). Both riparian and hillslope zone surface CO_2 efflux remained high

Fig. 5 Riparian data of **a** rain; **b** snow depth (*grey*) and snow water equivalent (SWE—*black*); **c** soil temperature; **d** soil gas diffusivity; **e** soil water content; **f** soil surface CO_2 efflux; and **g** 20 and 50 cm soil CO_2 concentrations from February 6 to October 1, 2005. Plots **c–e** show the average and standard deviation of all riparian nests (based upon 3 and 5 replications in the riparian and hillslope zones, respectively). Soil temperature and SWC were not measured during the winter, and efflux measurements did not begin until the end of April. Y-axis for surface CO_2 efflux is presented in both **g** CO_2 m^{-2} h^{-1} and μmol CO_2 m^{-2} s^{-1} to aid in comparison to other studies



until the middle of August, then gradually decreased throughout September (Figs. 5, 6). Cumulative growing season surface CO_2 efflux (calculated from measurements collected between June 9 and August 30, 2005) was 57% higher ($p = 0.01$) in the riparian zones, averaging 1,346 and 858 g CO_2 m^{-2} in the riparian and hillslope zones, respectively.

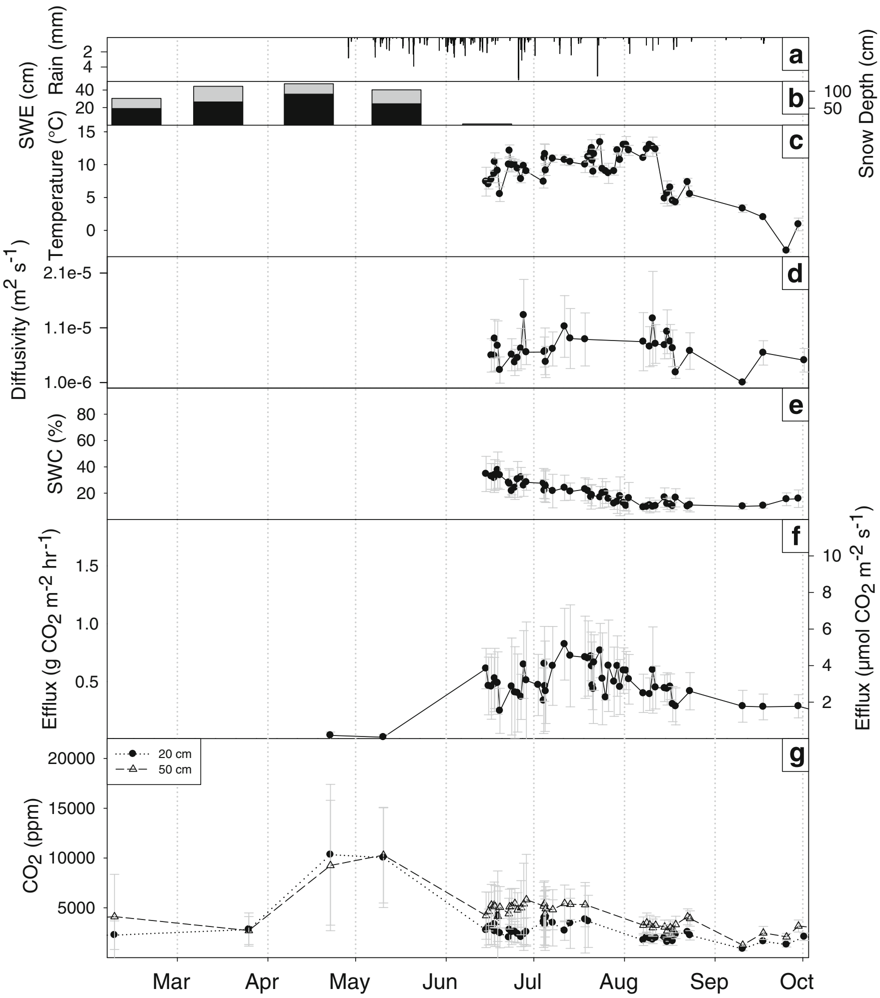
Discussion

How do soil CO_2 concentrations differ within and between landscape positions?

Between landscape positions

Soil CO_2 dynamics varied significantly between riparian and hillslope zones. In general, soil CO_2 concentrations at 20 cm were significantly higher in the riparian zones (Figs. 3, 4). This was likely the result of significantly higher and often intermediate riparian zone SWC (defined as 40–60% at the TCEF) (Figs. 3, 4). Increasing SWC generally promotes higher soil CO_2 concentrations (Davidson et al. 2000; Riveros-Iregui et al. 2007) in response to increased production and decreased transport. Our results are consistent with other investigations (Clark and Gilmour 1983; Davidson et al. 2000; Sjogersten et al. 2006), which concluded that optimal soil respiration occurred at intermediate SWC. In contrast to SWC, soil temperature showed little variability between riparian and hillslope landscape positions (Fig. 3). We infer this was due to differences in canopy cover and SWC. In the riparian zones, despite an open canopy, high SWC (i.e. the high specific heat of water) likely limited the effect of relatively high

Fig. 6 Hillslope data of **a** rain; **b** snow depth (*grey*) and snow water equivalent (SWE—*black*); **c** soil temperature; **d** soil gas diffusivity; **e** soil water content; **f** soil surface CO_2 efflux; and **g** 20 and 50 cm soil CO_2 concentrations from February 6 to October 1, 2005. Plots **c–e** show the average and standard deviation of all hillslope nests (based upon 3 and 5 replications in the riparian and hillslope zones, respectively). Soil temperature and SWC were not measured during the winter, and efflux measurements did not begin until the end of April. Y-axis for surface CO_2 efflux is presented in both g CO_2 m^{-2} h^{-1} and μmol CO_2 m^{-2} s^{-1} to aid in comparison to other studies



incoming solar radiation on soil temperature. In contrast, low hillslope SWC, which can allow the soil to warm faster than areas with high SWC, was offset by dense canopy cover that limited incoming solar radiation in the hillslopes. These differences led to little variability in soil temperature between riparian and hillslope zones. This suggests that soil temperature had little control on the spatial variability of soil CO_2 concentrations, which is consistent with the results of Scott-Denton et al. (2003) in a subalpine forest in Colorado.

Within landscape positions

Soil CO_2 concentrations were more variable in the riparian zones, ranging from "flooded" to 45,000 ppm. In contrast, hillslope soil CO_2 concentrations ranged from only 1,000–10,000 ppm (Fig. 2). These differences were likely in response to greater variability in riparian SWC (Figs. 2, 3). SWC in the riparian zones ranged from ~10 to 80%, while the range of hillslope SWC was generally 5–35%. The exception in the hillslopes was T2-3, which had SWC of up to ~60% just after snowmelt (likely due to its lower elevation and closer proximity to Stinger Creek than other hillslope locations), but low SWC during summer and fall. We partially attribute differences in riparian and hillslope SWC to groundwater table fluctuations. Within the riparian zones, groundwater table elevations ranged from near the ground surface to below groundwater well completion depths (1–2 m). Our results suggest that respiration was inhibited at many riparian gas wells at or near times of saturation, as exemplified in Fig. 7 (which presents data from T1-4). Respiration at 20 cm was impacted by groundwater table fluctuations between the end of

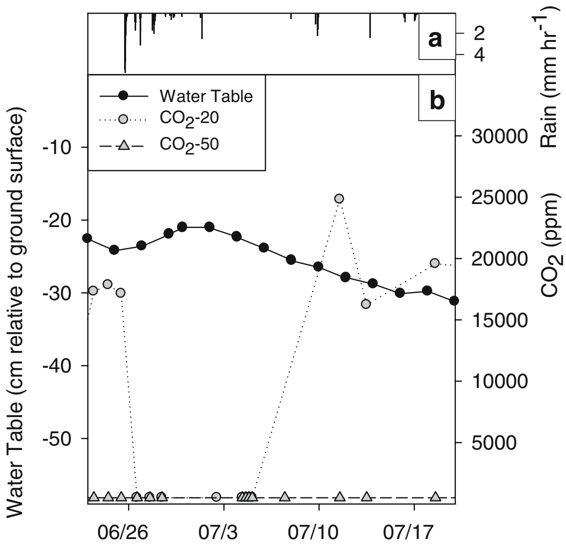


Fig. 7 **a** Precipitation; and **b** water table depth and soil CO_2 concentrations at the T1-4 nest from June 26 to July 20, 2005

June and middle of July in response to a series of precipitation events. As the groundwater table rose to 20 cm, respiration became inhibited. However, as the groundwater table declined below 20 cm, soil CO_2 concentrations quickly increased by over 25,000 ppm. In contrast to the riparian zones, the groundwater table in the hillslopes never rose to within 50 cm of the ground surface during the period of measurement, partially explaining the smaller variability in hillslope SWC and therefore soil CO_2 concentrations.

Soil CO_2 concentration by depth

There were differences in 20 and 50 cm soil CO_2 concentrations, with the largest differences in the riparian zones. Riparian zone soil CO_2 concentrations were significantly higher at 20 cm (Table 1; Fig. 5). This was likely in response to differences in SWC by depth (unpublished data). The magnitude of the difference between 20 and 50 cm soil CO_2 concentrations in the riparian zones increased from early summer to fall (Fig. 5), in conjunction with a decline in groundwater table depth. After snowmelt, many riparian locations at both 20 and 50 cm were saturated, which inhibits soil CO_2 production. 50 cm gas wells remained saturated at many riparian zone nests, while soil CO_2 concentrations at 20 cm quickly increased as the summer progressed and the groundwater table declined below 20 cm (Fig. 7). This led to a spring-fall increase in the difference in soil CO_2 concentrations by depth in the riparian zones.

In contrast to the riparian zones, hillslope soil CO_2 concentrations were relatively homogenous between the 20 and 50 cm depth, with slightly higher concentrations at 50 cm (Fig. 6). The groundwater table in the hillslopes never rose to within 50 cm of the ground surface. This resulted in similar SWC at 20 and 50 cm (relative to the riparian zones), and led to comparable soil CO_2 concentrations by depth. Our results suggest that groundwater table fluctuations and saturated conditions had little to no effect on the small differences in soil CO_2 concentrations observed in the hillslopes. Also in contrast to the riparian zones, the magnitude of the difference in hillslope soil CO_2 concentrations decreased from early summer to fall (Fig. 6). Following peak snowmelt, SWC at 20 cm was higher than at 50 cm in response to greater melt-water infiltration into the upper soil horizons. However, as the summer progressed, SWC at 20 cm decreased more rapidly than at 50 cm, likely in response to high surface evaporation and soil drainage, which led to similar SWC at 20 and 50 cm. We suggest that the decrease in the magnitude of the difference in SWC by depth in the hillslopes led to the spring-fall decrease in the difference of CO_2 concentrations by depth.

How does the timing of peak soil CO_2 concentrations differ between riparian and hillslope zones?

Winter soil CO_2 concentrations

We observed distinct differences in the timing of winter soil CO_2 concentration peaks between the riparian and hillslope zones. Riparian soil CO_2 concentrations peaked at ~20,000 ppm between mid-March and mid-April, 2005, while hillslope nests peaked at ~10,000 ppm 4–8 weeks later, between mid-April and mid-May (Figs. 5, 6). This corresponded to the time of the deepest snowpack and greatest snow water equivalent of the year (120 and 46 cm, respectively, Figs. 5, 6). A deep snowpack can lead to increased soil CO_2 concentrations due to its insulating effects (Sommerfeld et al. 1996; Schadt et al. 2003) (allowing for relatively high production

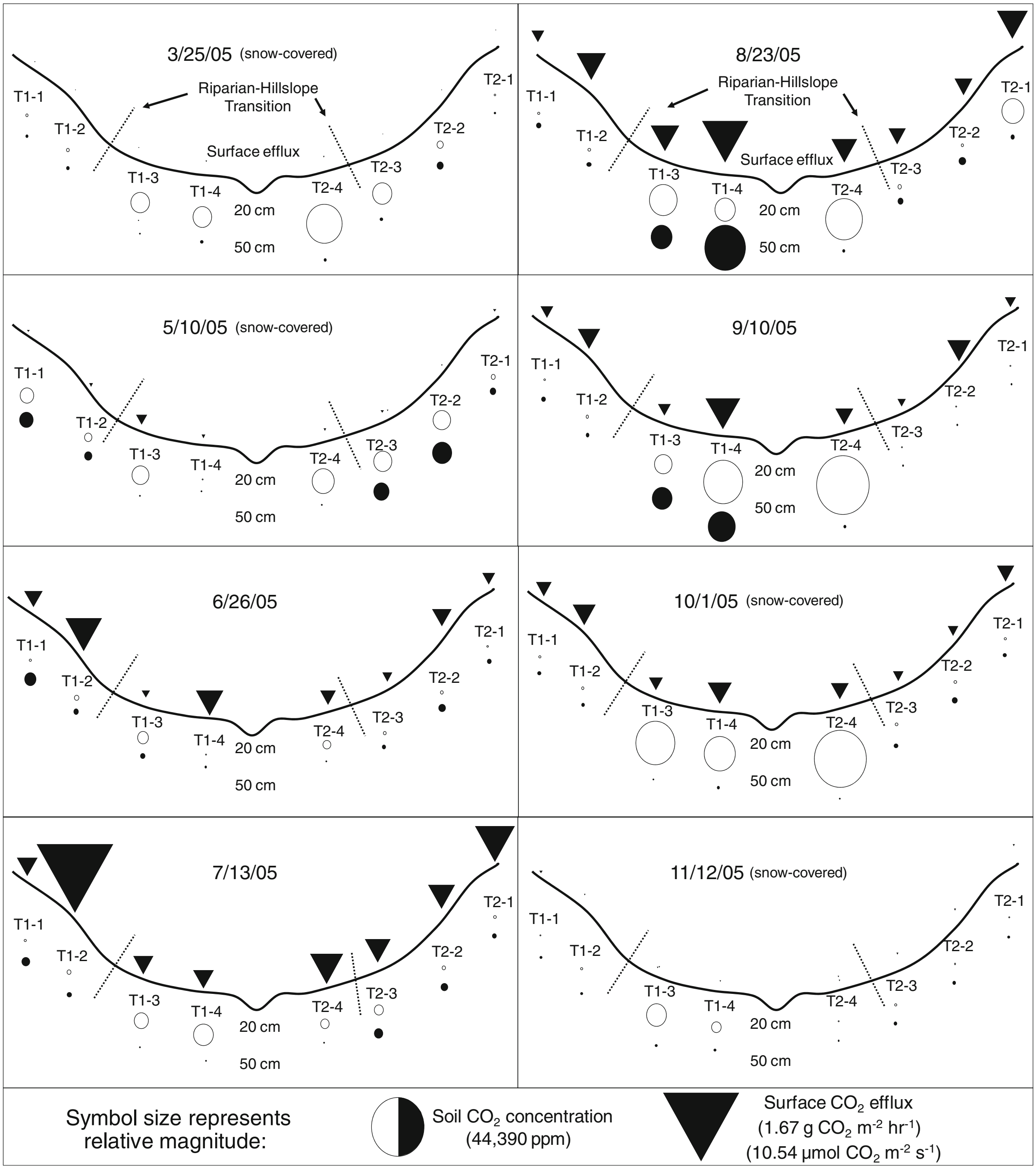


Fig. 8 Cross-section schematics of soil CO_2 concentrations at 20 cm (*white circles*) and 50 cm (*black circles*), and surface CO_2 efflux (*triangles*) at all nest locations at eight points in time. *Note*: symbol size represents relative magnitude

compared to colder soils) and low gas diffusivity (Hamada and Tanaka 2001; Norton et al. 2001). Differences in the timing of peak winter CO_2 concentrations (4–8 weeks later in the hillslopes) were likely the result of differences in the snow energy balance. The snow in the riparian zones became isothermal and ripe sooner than in the hillslopes due to an open canopy (riparian zones melting first were observed in our study watershed). This resulted in earlier melt infiltration, which likely

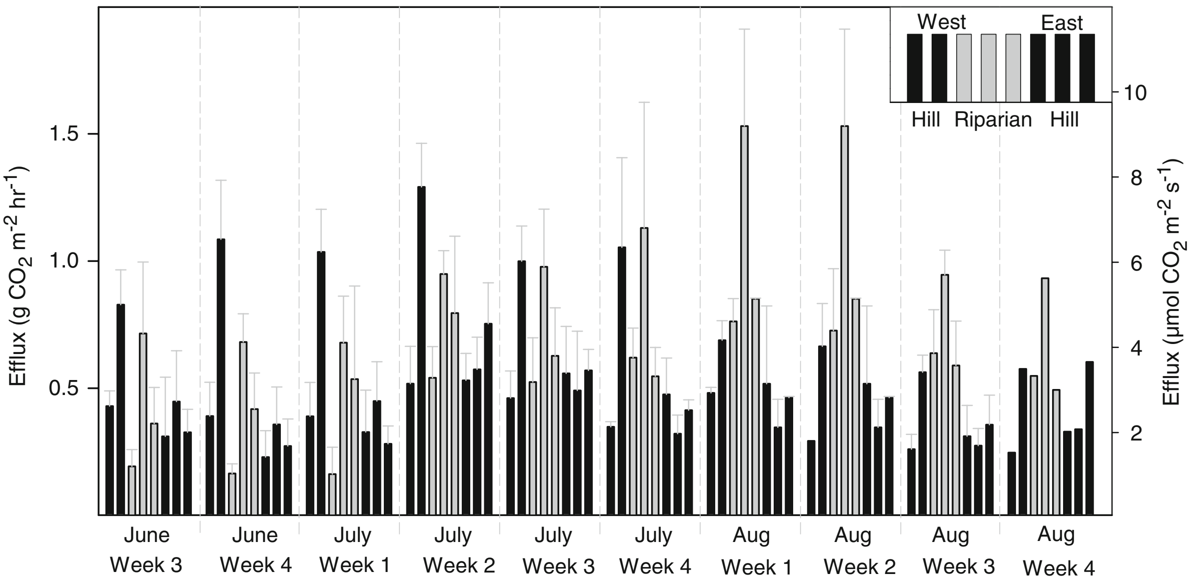


Fig. 9 Weekly surface CO_2 efflux from riparian (*grey*) and hillslope (*black*) nests from June 14 to August 31, 2005. Whiskers represent one standard deviation (based upon 3 and 5 replications in the riparian and hillslope zones, respectively)

stimulated respiration (Brooks et al. 2005; Hirano 2005) and/or increased the diffusive resistance of the snow (Musselman et al. 2005; Monson et al. 2006). Musselman et al. (2005) observed a similar trend, with soil CO_2 concentrations under a deep snowpack increasing sooner in a meadow than in a forest at a subalpine site in Wyoming.

Peaks in winter soil CO_2 concentrations in our study watershed (~20,000 and 10,000 ppm in the riparian and hillslope zones, respectively; Figs. 5, 6) were substantially higher than those measured at other subalpine locations. Musselman et al. (2005) reported a range of 1,000–5,000 ppm at an elevation of 3,100 m in Wyoming; Monson et al. (2006) observed a range from ~500 to 2,700 ppm at an elevation of 3,030 m at Niwot Ridge in Colorado; and Sommerfeld et al. (1996) measured a winter peak of 10,464 ppm at a subalpine meadow at 3,180 m in Wyoming. One possible explanation for higher winter soil CO_2 concentrations at TCEF is its lower elevation (~2,200 m) than those studies cited above. At this elevation in the northern Rocky Mountains, a deep snowpack (~1–2 m) is often present for over 6 months of the year (generally from mid-October to mid-May). Despite similar winter soil temperatures between the TCEF and the above-cited studies, air temperatures were generally higher in the TCEF due to its lower elevation. This increases the likelihood of above-freezing air temperatures to occur intermittently over the winter (which was observed at TCEF). We suggest this increased the frequency of melt-refreeze events, which can impact snowpack structure and metamorphism, gas diffusion, and soil CO_2 concentrations (Musselman et al. 2005, Monson et al. 2006).

Growing season soil CO_2 concentrations

The timing of peak growing season soil CO_2 concentrations depended upon landscape position and was likely the result of differences in soil gas diffusivity, groundwater table fluctuations, and respiration-inhibiting SWC. Peaks in hillslope soil CO_2 concentrations occurred during the middle to end of June, when SWC was high and soil temperature began to rise, which generally increases soil CO_2 production (Hamada and Tanaka 2001; Raich et al. 2002; Pendall et al. 2004). However, hillslope SWC generally remained below 40% (Figs. 3, 4), leading to high soil gas diffusivity (Fig. 4). In contrast, peaks in riparian zone soil CO_2 concentrations did not occur until September (Fig. 5), due to high, respiration-inhibiting SWC. As the groundwater table declined below the depth of many riparian gas wells, resulting in intermediate SWC, it is likely that increases in soil CO_2 production led to sharp rises in soil CO_2

concentrations. This resulted in the highest riparian zone soil CO_2 concentrations of the year. In contrast, maximum hillslope concentrations occurred during snowmelt, which was generally the only time that hillslope SWC approached an intermediate range throughout the study period. Thus, the relative magnitude of riparian and hillslope soil CO_2 concentrations reversed from spring to fall, with higher hillslope values in the spring and larger riparian values during the fall.

How does the timing and magnitude of peak surface CO_2 efflux differ between riparian and hillslope zones?

Similar to soil CO_2 concentrations, the timing of maximum surface CO_2 efflux varied between riparian and hillslope zones, but was more coincident across the transect than the timing of maximum CO_2 concentrations (Fig. 8). Maximum hillslope efflux (0.82 g CO_2 m^{-2} h^{-1}) occurred between the middle and end of July (Fig. 6), while maximum riparian efflux (1.16 g CO_2 m^{-2} h^{-1}) occurred 2–4 weeks later, between the beginning and middle of August (Fig. 5). We suggest that differential timing of riparian and hillslope peak surface CO_2 efflux is partially due to timing of optimal combinations of soil CO_2 production and transport. During the middle and end of July, SWC was the highest measured over the growing season (Fig. 6). This likely led to high hillslope soil CO_2 production (relative to the riparian zones), and resulted in maximum hillslope surface CO_2 efflux between the middle and end of July (Figs. 4, 5). In contrast, riparian zone SWC did not decrease to intermediate values (defined as 40–60% in the TCEF) that are optimal for soil CO_2 production (Clark and Gilmour 1983; Davidson et al. 2000; Sjogersten et al. 2006) until the beginning of August (Fig. 5). This decrease in SWC also led to increased soil gas transport and resulted in maximum surface CO_2 efflux between the beginning and middle of August. Our data indicates that maximum surface CO_2 efflux occurs at optimal combinations of production and transport, the timing of which can vary across riparian and hillslope zones.

In general, differences in riparian and hillslope surface CO_2 efflux were not statistically significant when data was analyzed by month (Table 1). However, when comparing data over shorter timescales, (e.g. biweekly [Fig. 4] or weekly [Fig. 9]), differences in riparian and hillslope soil surface CO_2 efflux become more apparent. Surface CO_2 efflux is controlled by both soil CO_2 production and transport, and it is likely that changes in the drivers of soil respiration become balanced over monthly timescales. For example, a decrease in SWC can simultaneously increase soil gas diffusivity and decrease soil CO_2 production. SWC often decreases more slowly in riparian zones due to riparian zone groundwater storage and upland drainage (lateral redistribution of water), resulting in more sustained groundwater tables (Beven and Kirkby 1979; Pennock et al. 1987; McGlynn and Seibert 2003). It is thus likely that responses in soil CO_2 production and transport to changes in SWC differ between riparian and hillslope zones. This can lead to variability in riparian and hillslope soil surface CO_2 efflux over short timescales (weekly or biweekly), while such differences likely become balanced over intermediate (defined as monthly in this study) timescales. Our results also demonstrate that differences in riparian and hillslope efflux may exist over longer timescales (e.g. across seasons). Cumulative growing season efflux was 57% higher in the riparian zones than the hillslopes ($p = 0.01$) and averaged 1346 and 858 g CO_2 m^{-2}, respectively. We suggest that studies of soil respiration need to collect measurements of soil CO_2 concentrations, soil gas diffusivity, and surface CO_2 efflux over both short (e.g. weekly or biweekly rather than monthly) and long (seasonal) timescales as well as at multiple locations in order to accurately quantify differences in surface CO_2 efflux across the landscape.

Do higher soil CO_2 concentrations necessarily result in higher efflux (i.e. does surface CO_2 efflux follow patterns of subsurface CO_2)?

The efflux of CO_2 from the soil to the atmosphere is strongly controlled by CO_2 concentration gradients (Eq. 2), as efflux increases with increasing concentration gradients (holding other variables in Eq. 2 constant). Soil CO_2 concentrations were significantly higher in the riparian zones (Figs. 3, 4; Table 1). This resulted in concentration gradients from the soil to the atmosphere that were often over an order of magnitude higher than in the hillslopes (e.g. 30,000–400 ppm in the riparian zones versus 3,000–400 ppm in the hillslopes), and suggested that riparian zone soil surface CO_2 efflux would be high. However, high riparian zone SWC limited riparian zone soil gas transport (Washington et al. 1994; Davidson and Trumbore 1995; Moldrup et al. 2004) and led to less than expected surface CO_2 efflux. In contrast, small hillslope CO_2 concentration gradients suggested that soil surface CO_2 efflux would be low in the hillslopes. However, low SWC led to hillslope zone soil gas diffusivity rates that were often over an order of magnitude higher than in the riparian zones (Fig. 4), which resulted in higher than expected hillslope soil surface CO_2 efflux. This variability in transport in response to significant differences in riparian and hillslope SWC ($p \ll 0.01$) led to insignificant differences in monthly-timescale ANOVA analysis (Figs. 2, 4). Despite this, cumulative efflux was 57% higher in the riparian zones over the growing season and suggests 57% greater production in the riparian zones as compared to the adjacent hillslopes.

Conceptual model

Our study suggests that soil surface CO_2 efflux across two riparian-hillslope transitions was controlled by a shift between production- and transport-limiting SWC over seasonal timescales (Fig. 10). Soil CO_2 concentrations often changed concurrent with changes in SWC, with the highest concentrations generally at intermediate SWC. Previous research (Clark and Gilmour 1983; Davidson et al. 2000; Sjogersten et al. 2006) indicates intermediate SWC optimality for soil CO_2 production as sharp decreases in production can occur at very high or low SWC. However, transport generally decreases with increasing SWC. In our study, surface CO_2 efflux was relatively similar between riparian and hillslope zones over short timescales (weekly or monthly) (Fig. 4, Table 1), likely the result of different balances between soil CO_2 production and transport (Fig. 10). Our results indicate that riparian zones had high production and low transport in response to high SWC, while the opposite was true in the hillslopes. This combination of SWC-mediated production and transport led to equifinality in efflux between riparian and hillslope zones at short timescales. However, cumulative growing season efflux was 57% higher in the riparian zones ($p = 0.01$), which suggests higher riparian zone soil CO_2 production. Our conceptual model diagram (Fig. 10) indicates that hillslopes have optimal conditions for efflux in late spring and early summer (following snowmelt, when SWC is near the intermediate zone and soil temperatures begin to increase). In contrast, riparian zones move toward optimal conditions in mid to late summer (after snowmelt drydown, as SWC approaches an intermediate range and soil temperatures are high), partially explaining differences in the timing and magnitude of soil CO_2 concentrations and surface CO_2 efflux.

Implications at the landscape scale

The results of our study illustrate that differences in the spatial and temporal variability of soil respiration may exist in response to topographic gradients and landscape position. High elevation mountain ecosystems play an important role in the global C cycle (Schimel et al. 2002). Therefore, understanding the variability of soil respiration in complex terrain is important, especially for understanding the dynamic

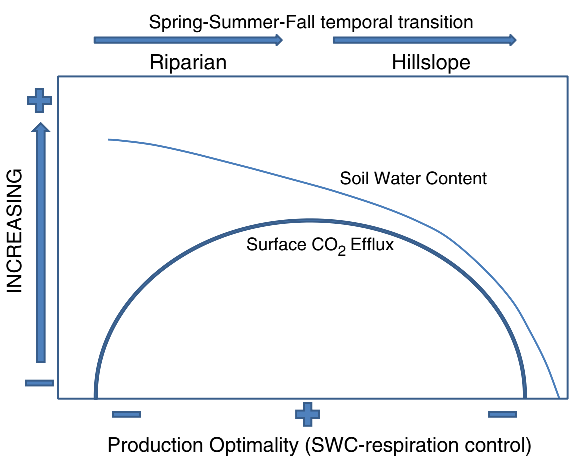


Fig. 10 Conceptual model of soil CO_2 production and optimality of SWC. Surface CO_2 efflux over seasonal timescales is a function of both soil gas production and diffusion. Maximum optimality of surface CO_2 efflux generally occurs at intermediate levels of SWC, which is optimal for soil CO_2 production. Transport generally increases with decreases in SWC. Hillslopes began their spring-to-summer seasonal shift at an intermediate SWC, which led to early season efflux maxima. In contrast, riparian zones began their seasonal shift at high SWC (often saturation), and maxima efflux did not occur until late summer or early fall when SWC approached intermediate values

thresholds and drivers of ecosystem C exchange, attempting to scale point observations to whole watersheds, and simulating and modeling soil respiration. Understanding of the relative controls of environmental variables on the heterogeneity of soil respiration through space and time is also critical for predicting changes in soil CO_2 dynamics in response to climate change (e.g. wet versus dry years, increased/decreased air and soil temperatures, changes in snow depth and timing of peak snowmelt), and ecosystem disturbance.

Conclusions

Based on measurement and analysis of soil CO_2 concentrations (20 and 50 cm), surface CO_2 efflux, soil temperature, SWC, and calculations of soil gas diffusivity across two riparian-hillslope transitions within the upper-Stringer Creek Watershed, we conclude that:

1. Hillslope zone soil CO_2 concentrations peaked during the late spring when snow depth and snow water equivalent were greatest. Conversely, riparian zone soil CO_2 concentrations peaked during the early fall when SWC declined to intermediate (optimal) levels.
2. Surface CO_2 efflux increased over an order of magnitude from spring to summer in both riparian and hillslope zones. Hillslope surface CO_2 efflux peaked between the middle and end of July, while riparian efflux peaked 2–4 weeks later. This differential timing of riparian and hillslope peak surface CO_2 efflux was likely in response to the earlier and more rapid decrease of SWC in the hillslopes.
3. Soil surface CO_2 efflux was relatively homogenous at short timescales across both riparian and hillslope zones as compared to riparian zone soil CO_2 concentrations that were greater and more variable than the adjacent hillslopes. Similar efflux over short timescales was likely the result of equifinality due to differential mechanistic controls on CO_2 production and transport. However, cumulative integration of growing season efflux shows 57% higher riparian zone efflux, which suggests that soil CO_2 production is higher in the riparian zones.

This research provides insight into the biophysical controls of soil respiration: soil temperature, SWC, soil gas diffusivity, snowpack, groundwater table fluctuations, and landscape position. To continue to improve our understanding of the spatial and temporal variability of soil CO_2 dynamics, it is imperative that further studies across a range of spatial and temporal scales be undertaken, especially in complex terrain.

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