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Interpretation and evaluation of combined measurement techniques for soil CO_2 efflux: Discrete surface chambers and continuous soil CO_2 concentration probes

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Interpretation and evaluation of combined measurement techniques for soil CO_2 efflux: Discrete surface chambers and continuous soil CO_2 concentration probes

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[1] Soil CO_2 efflux is a large respiratory flux from terrestrial ecosystems and a critical component of the global carbon (C) cycle. Lack of process understanding of the spatiotemporal controls on soil CO_2 efflux limits our ability to extrapolate from fluxes measured at point scales to scales useful for corroboration with other ecosystem level measures of C exchange. Additional complications are introduced by the effects of soil water content seasonality and rainfall on the performance of measurement techniques. In this paper we present measurements of soil CO_2 efflux made at two contrasting sites within a characteristic subalpine forest of the northern Rocky Mountains. Comparison of measurements between the soil respiration chamber technique and the soil CO_2 profile technique over daily and seasonal time scales indicated that soil water content plays a major role in the magnitude and seasonality of soil CO_2 efflux, especially after snowmelt or following summer rainfall. Agreement between both techniques was limited during high soil water content conditions and after summer rainfall. Differences in diel hysteresis patterns of soil CO_2 efflux between sites were controlled by the effects of canopy cover and temporal differences in photosynthetic activity of vegetation. Our results indicate that an accurate parameterization of soil water content heterogeneity in space and time must be a critical component of realistic model representations of soil CO_2 efflux from heterogeneous landscapes.

1. Introduction

[2] Soil CO_2 efflux is a natural process by which soil carbon is released into the atmosphere through autotrophic and heterotrophic respiration. Evaluating and predicting soil CO_2 efflux response to differences in hydrologic conditions (e.g., groundwater recharge and discharge areas, soil water content, precipitation, and land cover) are largely constrained by the methods used to measure, interpret, and model soil CO_2 efflux. Rates of soil CO_2 efflux are currently estimated from a wide range of ecosystems with manual soil respiration chambers [*Fang and Moncrieff*, 1996; *Subke and Tenhunen*, 2004; *Welsch and Hornberger*, 2004], automated soil respiration chambers [*Goulden and Crill*, 1997; *Savage and Davidson*, 2001; *Burrows et al.*, 2005], and the soil CO_2 profile technique [*Tang et al.*, 2003; *Jassal et al.*, 2005; *Tang and Baldocchi*, 2005]. Particularly in the last 5 years, the soil CO_2 profile technique has gained popularity because

it can provide continuous and automated measurements at temporal scales useful for comparison with other techniques of ecosystem C exchange such as eddy covariance towers [*Baldocchi et al.*, 2006]. While a wealth of ongoing studies use either technique, a direct comparison of their performance, measurements, strengths, and limitations in space and time is lacking.

[3] It has been suggested that the interactions among precipitation, infiltration, evaporation, transpiration, and soil drainage exert a major control on vegetation activity in water-limited ecosystems [*Ridolfi et al.*, 2000; *Porporato et al.*, 2002]. Large gaps exist in our understanding of the variability of soil CO_2 efflux in response to changing hydrologic conditions across space and time. Traditionally, studies addressing the variability of soil CO_2 efflux focus on its temporal component (e.g., diel, seasonal, and yearly variability) but tend to omit the spatial component inherent to this flux (i.e., landscape-induced variability). This omission limits the capability of temperature-based models [*Lloyd and Taylor*, 1994] to accurately estimate soil CO_2 efflux from areas having different characteristics within similar ecosystems. More importantly, this omission restricts our understanding of how CO_2-producing processes simultaneously develop in space and time to generate the

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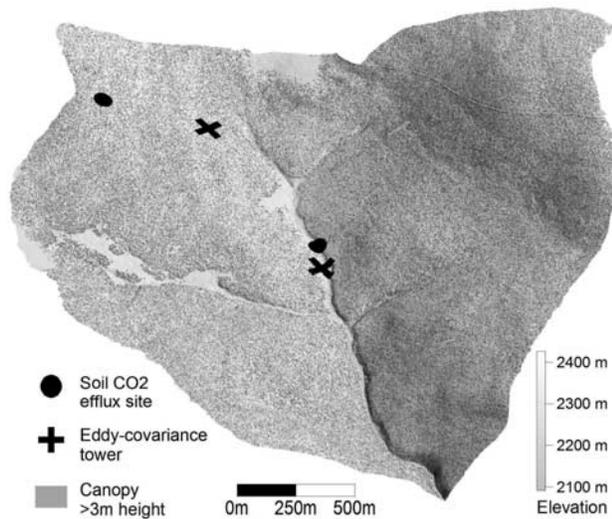[3]Canaan Valley Institute, Davis, West Virginia, USA.

Figure 1. Location of the Tenderfoot Creek Experimental Forest in the Little Belt Mountains of central Montana. The two most common ecosystems of these mountains were selected for this study: a wet riparian meadow and a dry upland forest.

soil CO_2 rates that chambers or soil profile techniques measure.

[4] Recent studies [*Riveros-Iregui et al.*, 2007] demonstrated that soil water content controls the relationship between soil CO_2 efflux and soil temperature, as soil water content (1) enhances soil CO_2 production and (2) inhibits soil CO_2 diffusion. Furthermore, the seasonality of soil water content can control the switch from diffusion- to production-limited soil CO_2 efflux [*Riveros-Iregui et al.*, 2007; *Riveros-Iregui*, 2008; *Pacific et al.*, 2008]. This concept becomes especially important in ecosystems with considerable spatial variability in soil water content induced by landscape morphology (i.e., convex versus concave areas [*Scott-Denton et al.*, 2003; *Pacific et al.*, 2008]). Vegetation cover and soil characteristics further control ecosystem response to changes in environmental conditions [*Huxman et al.*, 2004]. As a result, marked differences in soil water content regimes play a major role in ecosystem response, particularly soil CO_2 efflux, of heterogeneous forests. In this paper, we provide a comparison, over diel and seasonal time scales, of discrete (soil respiration chamber) and continuous (soil CO_2 profile technique) measurements of soil CO_2 efflux made at two sites: a wet riparian meadow and a dry upland forest. Both sites are colocated with eddy covariance towers and are within a characteristic subalpine forest of the northern Rocky Mountains. Through this space-time comparison we seek to (1) determine the mechanisms driving variability in soil CO_2 efflux from riparian meadows and upland forests; (2) compare the performance of soil respiration chambers and solid-state CO_2 probes throughout an entire growing season; and (3) assess, both mechanistically and methodologically, the confidence that these methods offer as providers of soil CO_2 efflux rates from heterogeneous landscapes. This information is essential to improving process understanding of soil CO_2 efflux from large areas, establishing a conceptual framework for soil CO_2 efflux

modeling studies, and adding confidence to current and developing measurement techniques.

2. Methods

2.1. Study Site

[5] This study was located in the Tenderfoot Creek Experimental Forest, in the Little Belt Mountains of central Montana (Figure 1). These mountains are characteristic of the subalpine forests of the northern Rocky Mountains. Two contrasting ecosystems that represent the two dominant systems of these mountains were selected to address the objectives of this study: a wet riparian meadow (hereafter riparian site) and a dry upland forest (hereafter upland site). Vegetation cover at the riparian site is predominantly *Calamagrostis canadensis* (bluejoint reedgrass), whereas the upland site is covered mostly by *Pinus contorta* (lodgepole pine) and *Pseudotsuga menziesii* (Douglas fir) in the overstory and *Vaccinium* spp. in the understory. Elevations are 2169 and 2305 m at the riparian and upland sites, respectively. Mean annual precipitation is 880 mm with ~70% falling as snow [*Farnes et al.*, 1995], and peak snowpack accumulations occur between late March and mid-April [*Woods et al.*, 2006]. Mean annual temperature is 0°C, and the growing season lasts from 45 to 75 days.

2.2. Environmental Variables

[6] Between 9 June 2006 and 7 September 2006 we measured volumetric soil water content (θ) (CSI model 616, Campbell Scientific Inc., Logan, Utah) and soil temperature (T_S) (CSI model 107, Campbell Scientific Inc., Logan, Utah) at 20 cm below the soil surface, at 20-min intervals, and collected the data with a logger (model CR-10x, Campbell Scientific Inc., Logan, Utah). Manual measurements (n = 3) of θ were also taken with a portable meter (Hydrosense, Campbell Scientific Inc., Utah, USA) to obtain an integrated estimate of soil water content over the top 20 cm of the soil profile. Measurements from the CSI Hydrosense meter were experimentally corroborated with regular time domain reflectometry instruments (r^2 = 0.986 and n = 121) to confirm applicability of the CSI Hydrosense instrument under a full range of soil water contents. Precipitation was measured by a tipping bucket rain gauge (TR-525M, accurate to within 1% for up to 50 mm h^{-1}, Texas Electronics, Dallas, Texas, USA), at 20-min intervals and reported on a daily basis.

2.3. Measurements of Soil CO_2 Efflux

[7] Soil CO_2 efflux was measured independently at each site by the soil respiration chamber technique (discrete measurements) and by the soil CO_2 profile technique (continuous measurements). While the performance of soil respiration chambers has been amply evaluated [*Norman et al.*, 1997; *Hutchinson and Livingston*, 2001; *Davidson et al.*, 2002], the performance of the relatively newer soil CO_2 profile technique remains to be critically evaluated in space and time, as well as against soil respiration chambers. Discrete measurements were based on a soil respiration chamber model SRC-1 (footprint of 314.2 cm^2, accuracy within 1% of calibrated range (0–9.99 g CO_2 m^{-2} h^{-1}), PP Systems, Massachusetts, USA) equipped with an infrared gas analyzer (EGM-4, accuracy within 1% of calibrated

range (0–2000 ppm), PP Systems, Massachusetts, USA). Chamber measurements were collected in triplicate every 2–7 days at each site. At each site, a 0.5-m^2 area was roped off to minimize disturbance and vegetation was clipped once a week after measurements were collected. Roots were left intact to minimize disturbance to belowground respiration. Before each measurement, the chamber was flushed with ambient air for 15 s and placed onto the soil, ensuring a good seal between the chamber and the soil surface. Soil CO_2 efflux was calculated by measuring the rate of increase in CO_2 concentration within the chamber and fitting a quadratic equation to the relationship between the increasing CO_2 concentration and elapsed time (as recommended by the manufacturer). In order to minimize introduction of biases during sampling, no chamber measurements were taken before 1000 LT or after 1600 LT.

[8] Continuous soil CO_2 concentration measurements were collected with solid-state CO_2 probes (GMP221 with transmitter, Vaisala, Helsinki, Finland) installed at 5 cm below the soil surface, logging continuously at 20-min intervals with a data logger (model CR10x, Campbell Scientific Inc., Logan, Utah). Soil CO_2 concentrations measured by the probes were corrected for temperature and pressure following compensatory procedures described by *Tang et al.* [2003] and according to the manufacturer's recommendation. When buried in the soil, these probes respond to changes in CO_2 concentrations in less than 5 min [*Tang et al.*, 2003]. Because it is difficult to measure soil CO_2 concentrations near the soil-atmosphere interface (e.g., $z = 0$), we tested the sensitivity of soil CO_2 efflux to variability in atmospheric concentrations by simultaneously using three different CO_2 concentration values (350, 450, and 550 ppm) at the soil-atmosphere interface. We chose these three values on the basis of the range of variability of initial surface CO_2 concentrations measured at each deployment of the soil respiration chamber (ranging between ~390 and ~530 ppm). Our results demonstrate that the assumed values do not compromise calculation of soil CO_2 efflux, as the diel variability of soil CO_2 concentration at 5 cm is much greater than the diel variability of soil CO_2 above the soil surface given the atmospheric buffer. Previous studies [*Tang et al.*, 2005b] have used similar assumptions (~370 ppm at 0.5 m above the soil surface). However, our approach of using all three values provides a confidence error of 200 ppm (at $z = 0$), demonstrating that variations in concentrations at the soil surface introduce little variation in estimated soil CO_2 efflux given the natural diel variability of soil CO_2 at depth (>5000 ppm). Nevertheless, to illustrate this effect, confidence bounds (for 350 and 550 ppm) were estimated and presented with the results. Additional corroboration and confidence is given when comparing continuous and discrete chamber soil CO_2 efflux estimates (see section 3).

[9] Continuous soil CO_2 efflux based on solid-state probes has been estimated in numerous recent studies across multiple ecosystems [*Tang et al.*, 2003; *Jassal et al.*, 2005; *Tang et al.*, 2005a, 2005b; *Baldocchi et al.*, 2006; *Vargas and Allen*, 2008]. To estimate surface efflux, these studies assumed that flux of soil CO_2 was linear with depth, with increasing concentrations with increasing depth. However, these assumptions become invalid when soil CO_2 is greater in shallow soils than in deeper soils, leading to bidirectional concentration gradients and fluxes. This scenario can occur

in response to disturbances such as precipitation and shallow soil wetting [e.g., *Tang et al.*, 2005b]. Because precipitation was sporadic throughout the growing season in our system and we sought to investigate CO_2 flux toward the surface at both diel and seasonal time scales, we calculated soil CO_2 efflux based on concentrations at 0 and 0.05 m using Fick's first law of diffusion,

$$F = -D_P \frac{\partial [CO_2]}{\partial z}, \qquad (1)$$

where F is CO_2 flux between two depths and D_P is the diffusion coefficient for CO_2 in the air-filled pore space. The diffusion coefficient (D_P) was calculated as a function of total porosity (Φ) and air-filled porosity (ε) and using the model proposed by *Moldrup et al.* [1999]:

$$\frac{D_P}{D_O} = \Phi^2 \left(\frac{\varepsilon}{\Phi} \right)^{2+\frac{3}{b}}, \qquad (2)$$

where D_O is the gas diffusion coefficient in free air and b is the *Campbell* [1974] pore size distribution parameter. This parameter has been found to be strongly related ($r^2 = 0.96$) to clay fraction content (CF) through the following relationship [*Clapp and Hornberger*, 1978; *Olesen et al.*, 1996; *Rolston and Moldrup*, 2002]:

$$b = 13.6\text{CF} + 3.5. \qquad (3)$$

[10] Diffusivity of CO_2 in the gas phase is about 4 orders of magnitude higher than in the liquid phase [*Šimůnek and Suarez*, 1993; *Welsch and Hornberger*, 2004]; therefore, we assumed that solubility of the gas phase CO_2 is negligible. The characterization of the distribution of new moisture inputs in the soil, particularly in arid and semiarid environments, remains challenging because of wetting front instability or heterogeneity [*Wang et al.*, 2007]. Soil macropores caused by decaying roots, worm holes, and similar disturbances can cause preferential flow and differences in infiltration patterns [*Geiger and Durnford*, 2000; *Devitt and Smith*, 2002] under ponding [*Hill and Parlange*, 1972; *Glass et al.*, 1989a, 1989b; *Baker and Hillel*, 1990] and nonponding conditions [*Selker et al.*, 1992; *Babel et al.*, 1995; *Hendrickx and Yao*, 1996; *Yao and Hendrickx*, 1996]. Thus, we used the integrated 0–20 cm soil water content based on three replicates as a measure of volumetric water content over the top 20 cm of soil. Previous studies have studied the heterogeneity of new moisture distribution by applying vertical integrations [*Noborio et al.*, 1996; *Timlin and Pachepsky*, 2002] and have found that this estimate is a good representation of soil water content, even in extremely nonuniform conditions [*Topp et al.*, 1982a, 1982b; *Robinson et al.*, 2003]. Similarly, we assumed constant D_P/D_O and temperature (used for density estimation in D_O calculations) over the top 20 cm of the soil. We acknowledge potential inaccuracies introduced by this approach and current probe design constraints for water content profile estimation; however, this is an effective approximation of volumetric soil water content and the D_P/D_O parameter.
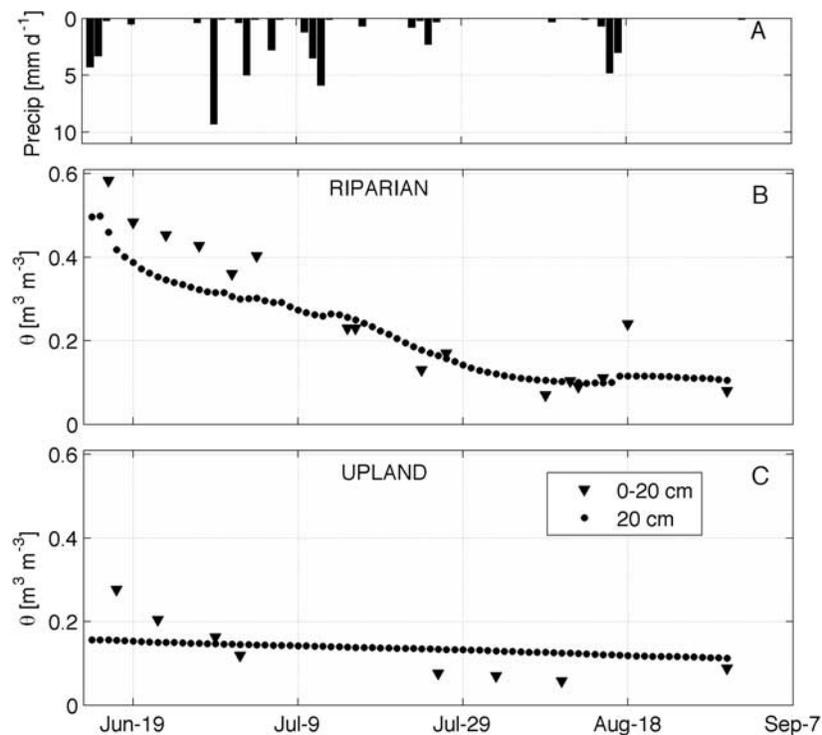
Figure 2. Variability of (a) precipitation and soil water content (θ) for (b) riparian and (c) upland sites for the 2006 growing season. Measurements of θ were made continuously at 20 cm and discretely integrating over 0–20 cm as indicated by the symbols.

[11] Because solid-state soil CO_2 probes are known to release heat after operating for long periods of time [*Hirano et al.*, 2003; *Jassal et al.*, 2005], we installed a double-pole double-throw relay (6 VDC coil voltage, 115 mA, Tyco Electronics, Berwyn, Pennsylvania) in the power line between the battery bank and the solid-state soil CO_2 probes, controlled by the data logger. This setup allowed us to switch the probes on prior to each measurement, including warming time as recommended by the manufacturer, and to switch them off to prevent long-term heating while saving >75% of battery power.

2.4. Ecosystem Respiration

[12] Continuous measurements of land-atmosphere CO_2 and water vapor exchange were made above the canopy of both ecosystems with the eddy covariance method [*Baldocchi*, 2003]. Wind velocity was measured with a triaxial sonic anemometer (CSAT3, Campbell Scientific Inc., Logan, Utah). Carbon dioxide and water vapor fluctuations were measured with an open path, infrared absorption gas analyzer (7500, LI-COR, Lincoln, Nebraska). Measurements were made at 10-Hz frequencies for the duration of the study. Estimates of nighttime ecosystem respiration were selected on the basis of fluxes between 2300 LT and 0400 LT and reported on a daily basis. A $U*$ threshold of 0.2 m s^{-1} was used to ensure periods with enough turbulence and reliable eddy covariance estimates. Because the purpose of the eddy covariance measurements was exclusively to provide a relative comparison, values are presented as nighttime ecosystem respiration fluxes, and no daytime

correction was applied to fluxes to avoid postprocessing and modeling abstraction.

3. Results

3.1. Environmental Variables

[13] The variability of continuous and discrete measurements of volumetric soil water content (θ) is presented in Figure 2. Throughout the growing season, values of θ decreased from over 50 to ~10% at the riparian site and from ~18 to ~12% at the upland site (Figure 2). Given that 70% of precipitation comes as snow and that peak runoff usually occurs between mid-May and early June [*Woods et al.*, 2006], these ecosystems are subject to a rapid spring wet up followed by a prolonged seasonal dry down, typical of subalpine forests. Rainfall was higher in magnitude and occurred more frequently before mid-July, after which rainfall decreased and occurred on only 2 days late in the season (Figure 2). The effects of rainfall on θ differed in magnitude between the wet riparian site and the drier upland site (Figure 2) and depended on antecedent conditions (wet soil versus dry soil). These effects were also reflected, both mechanistically and methodologically, on measured soil CO_2 fluxes (section 3.2).

[14] Soil temperature (T_S) varied both daily and seasonally (Figure 3), with a seasonal maximum toward the end of July at both sites. This time corresponds with the minimum or near-minimum values of θ (Figure 2), maximum soil thermal diffusivity [*Ochsner et al.*, 2001], maximum soil gas diffusivity [*Riveros-Iregui et al.*, 2007], and the initial decrease in potential for biological activity, sporadically
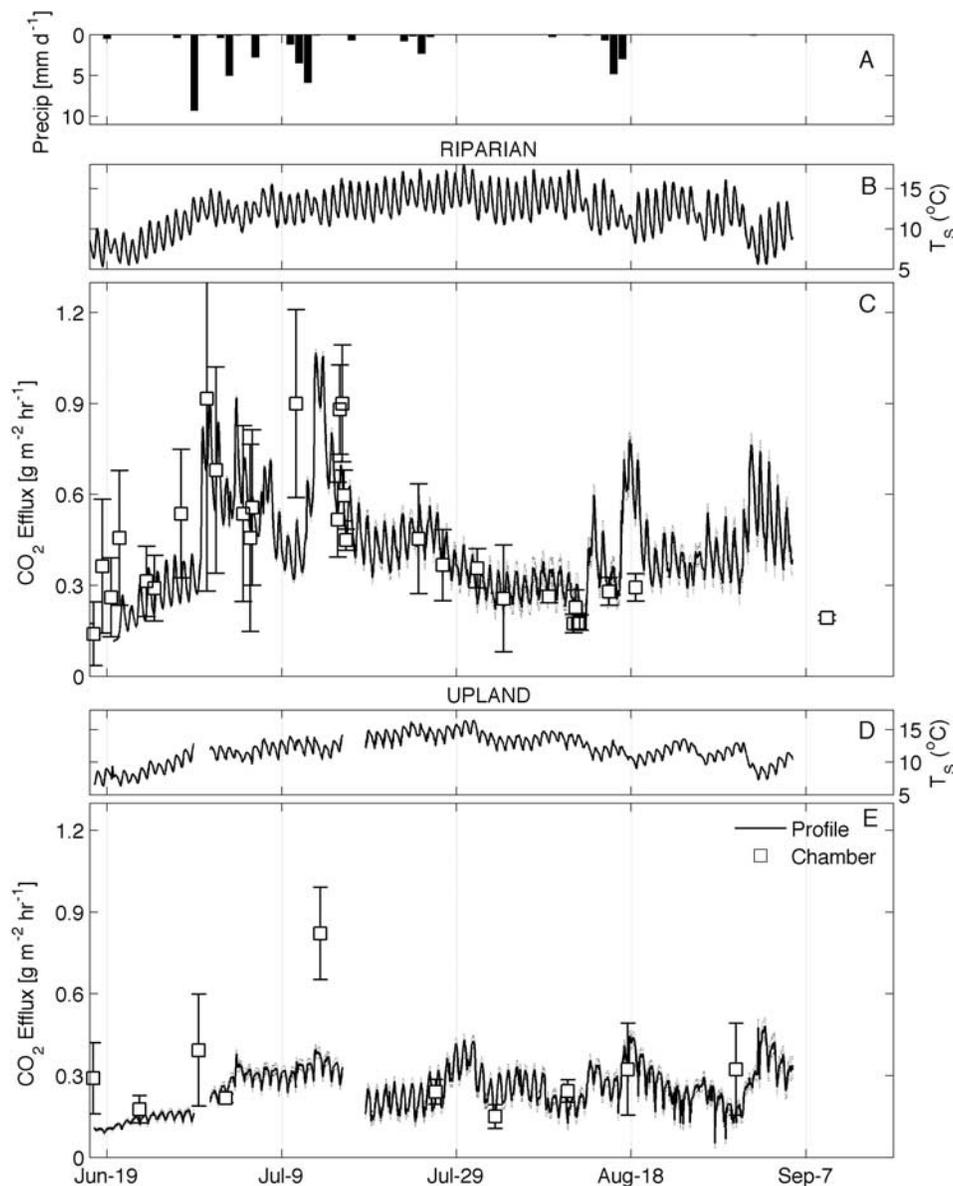
Figure 3. Variability in (a) precipitation, (b, d) soil temperature, and (c, e) soil CO_2 efflux at the riparian and upland sites for the 2006 growing season. CO_2 efflux was measured by the soil CO_2 profile technique (solid-state CO_2 sensors installed at depth) and by the soil respiration chamber technique. Boxes represent the mean, and error bars represent the standard deviation of three chamber measurements.

reset by precipitation events (e.g., 18 August). While the timing of daily T_S maxima was well synchronized between sites, the amplitude of the diel variability of T_S was lower at the upland site (Figure 3) because of the energy buffer imposed by the canopy cover. Overnight freezing temperatures in August drove a decrease in daily T_S maxima at both sites, indicating the decline of the growing season.

3.2. Soil CO_2 Efflux

[15] Both the soil respiration chamber and the soil CO_2 technique measured increasing fluxes early in the growing season at the riparian and upland sites (Figure 3), with the soil CO_2 profile having the advantage of increased sampling frequency, allowing for detailed visualization of the diel dynamics of soil CO_2 efflux. Similar diel dynamics have

been previously studied in detail [*Tang et al.*, 2005a; *Riveros-Iregui et al.*, 2007]; however, high-frequency measurements of soil CO_2 efflux responding to seasonal changes in environmental conditions (e.g., snowmelt and early and late season rainfall) between two sites within the same small-watershed ecosystem is, to our knowledge, unprecedented. Confidence bounds for 350 and 550 ppm at the soil-atmosphere interface ($z = 0$) are shown along with soil CO_2 efflux from the profile technique at both sites. The dotted lines in Figures 3c and 3e, almost identical to the solid lines, demonstrate that the error introduced by our approach is minimal compared to the natural variability of soil CO_2 efflux on a diel and seasonal basis. For the remainder of this paper we will refer to calculations and analyses based on
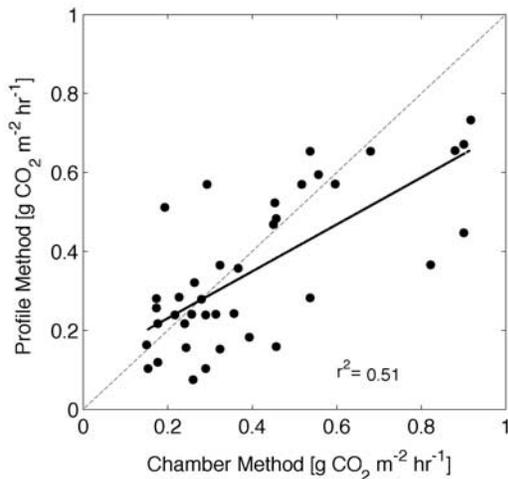
Figure 4. Comparison of instantaneous soil CO_2 efflux measured by both techniques during the 2006 growing season. Data include measurements at the riparian and the upland sites during rainy and dry days.

soil CO_2 concentration of 450 ppm at the soil-atmosphere interface.

[16] Seasonal dynamics recorded by the chamber technique agreed well with estimates by the soil CO_2 profile technique at both sites (Figure 3). However, marked differences throughout the study were imposed by high soil water content and sporadic rainfall. Comparing chamber measurements and instantaneous efflux from the profile technique for the entire season shows moderate agreement for the entire growing season at both sites ($r^2 = 0.51$; Figure 4). This agreement improved considerably when measurements within 2 days of at least 1-mm rainfall were excluded and when chamber measurements made on wet soil ($\theta > 0.25$ m^3 m^{-3}) were further excluded from the comparison at each site (Figure 5). However, by excluding such environmental disturbances from technique comparison, little can be learned about ways to improve technique performance or overcome their limitations; therefore, disagreement due to disturbances must not be omitted from these types of studies.

[17] Chamber measurements fell within the range of diel values of soil CO_2 efflux, except early in the season at the riparian site or following precipitation events at both sites (e.g., 10 and 13 July, Figure 6a). Accumulated on a diel basis (Figure 6b), rates of soil CO_2 efflux indicated that both techniques provide comparable estimates with the exception of those days following precipitation events, when chamber measurements were up to 84% higher than estimates by the soil CO_2 profile technique.

[18] Because the soil CO_2 profile technique is currently applied at different sampling frequencies (e.g., 5 min [*Vargas and Allen*, 2008] and 20 min (this study)), we tested the susceptibility of this technique to sampling frequency and time-of-day biases. Our results demonstrate that high sampling frequencies do not necessarily improve seasonal estimates of soil CO_2 efflux rates (Figure 7). Using the time of day at which the soil respiration chamber was deployed at each site (between 1000 LT and 1600 LT) to

capture instantaneous efflux by the soil CO_2 profile technique, similar seasonal estimates were found using all profile measurements (5973 data points) or interpolating between 34 daytime measurements at the riparian site and 10 daytime measurements at the upland site (Figure 7).

4. Discussion

4.1. What Are the Mechanisms Driving the Main Differences in Soil CO_2 Efflux From Riparian Meadows and Upland Forests?

[19] A major challenge in process understanding of soil CO_2 generation and efflux lies in the spatiotemporal nature of its biophysical controls. The interaction among soil temperature, vegetation, soil substrate, soil physical properties, and the landscape-induced redistribution of soil water can exhibit confounding effects on soil CO_2 efflux processes [*Davidson et al.*, 1998]. However, particularly in subalpine ecosystems, an important element that can be used to our advantage is the redistribution and seasonality in soil water content. There exists a degree of predictability in that snowmelt controls the time of the most dramatic increase in soil water content. Furthermore, landscape morphology redistributes that moisture downslope to lower areas of the landscape. Only through sporadic convective summer storms does the ecosystem receive new moisture inputs that can enhance biological activity. In our study, a seasonal comparison based on landscape position (Figure 3) demonstrates that soil CO_2 efflux at the riparian site was higher for 72% of the growing season, particularly after snowmelt, and when rainfall drove θ higher at the riparian site. Only when similar θ values were found between sites (e.g., after 29 July)
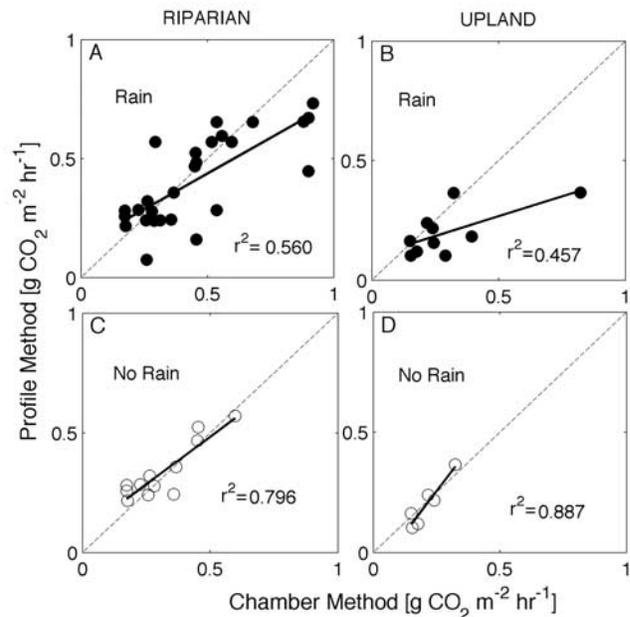

Figure 5. Comparison of techniques between (a, c) riparian and (b, d) upland sites, with all measurements at each site (Figures 5a and 5b), and removing measurements on soil with $\theta > 0.25$ (m^3 m^{-3}) and measurements within 2 days of precipitation over 1 mm (Figures 5c and 5d).
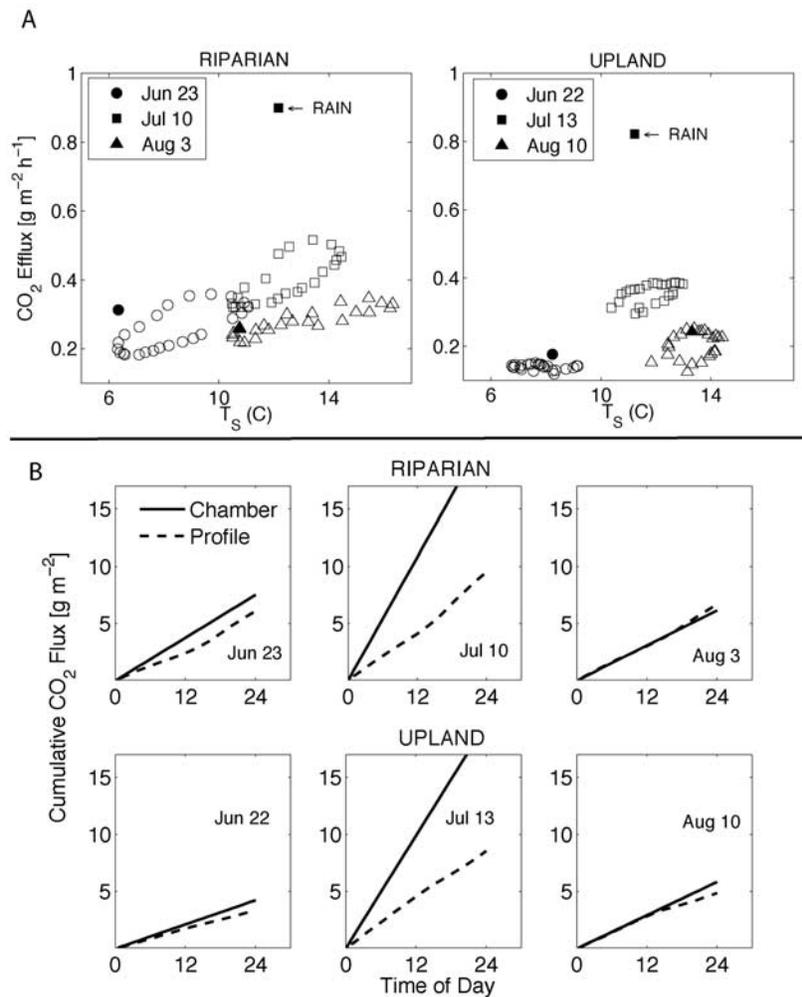
Figure 6. (a) Comparison of soil CO_2 efflux measurements and soil temperature (T_S) made on 3 different days at the (left) riparian and (right) upland sites. Symbols denote day of the year. Open symbols denote measurements by the soil profile technique, and filled symbols denote measurements by the soil respiration chamber. After rain events (i.e., 10–13 July), measurements by the soil respiration chamber are much greater than estimates by the soil profile technique. (b) Comparison of cumulative fluxes over 24-h intervals at different times of the year at the (top) riparian and (bottom) upland sites. Dates of measurements are indicated in each plot and correspond to dates of measurements in Figure 6a. A total of 10.7 mm of rain occurred over 4 days prior to 10–13 July measurements.

were soil CO_2 efflux rates similar or higher at the upland site (Figure 3).

[20] A comparison of soil CO_2 efflux and soil temperature during early, middle, and late season (Figure 6a) between the riparian (wet) and upland (dry) sites demonstrated spatial and temporal differences in diel hysteresis patterns introduced by differences in diel T_S and CO_2 efflux. Recent studies have highlighted the evolution of diel patterns in both soil CO_2 concentrations [*Riveros-Iregui et al.*, 2007] and soil CO_2 effluxes [*Carbone et al.*, 2008]. Diel hysteresis in soil CO_2 concentrations is controlled by water content-limited soil CO_2 diffusion [*Riveros-Iregui et al.*, 2007]. A decline in θ results in enhanced soil CO_2 diffusion, allowing belowground concentrations to remain at steady state ($\partial CO_2/\partial t = 0$ [*Riveros-Iregui et al.*, 2007]). However, while the belowground concentrations can remain at steady state, the observed aboveground efflux (F) is not at steady

state ($\partial F/\partial t \neq 0$), indicating that, particularly in dry soils, diel hysteresis in soil CO_2 efflux is production limited and represents a rapid response of combined heterotrophic and autotrophic activities. Greater hysteresis patterns in efflux at the riparian site (e.g., 23 June at the riparian site versus 22 June at the upland site) are likely due to the effects of faster short vegetation response to photosynthetic activity at this site [*Carbone and Trumbore*, 2007] and the effects of a taller and more complete canopy cover on T_S at the upland site. More circular hysteresis patterns late in the season at the upland site (Figure 6a) indicate enhanced photosynthetic activity of the forest canopy with respect to riparian grasses [*Emanuel*, 2007], and that riparian vegetation (senescing by this time of the year) underwent late season water stress before upland vegetation. This suggests that upland vegetation is better adapted to lower θ, whereas riparian vegetation is adapted to higher θ and is sensitive to θ reduction over the
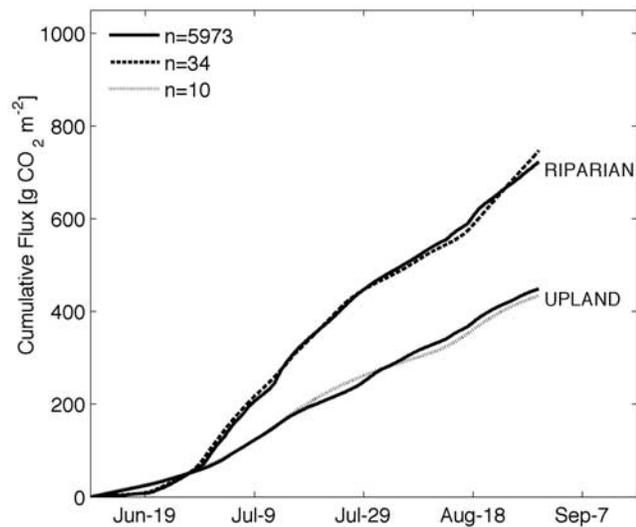
Figure 7. Comparison of cumulative soil CO_2 efflux estimates by the soil CO_2 profile technique, modifying its sampling frequency. Solid lines indicate estimates from 20-min sampling over 83 days (n = 5973). Dashed (n = 34) and dotted (n = 10) lines indicate reduced sampling frequency (every 2–7 days), using the time of the soil respiration chamber deployment as an example. Agreement between high and moderate frequencies suggests little time-of-day and sampling frequency bias. This comparison demonstrates that on a cumulative basis the use of the soil CO_2 profile technique at 20-min intervals yields similar results as when it is used every 2–7 days.

growing season. As a result, the riparian vegetation influence on soil CO_2 efflux diminished over the course of seasonal dry down.

[21] These findings demonstrate how soil water content distribution across the landscape exerts a major control on both spatial and temporal (seasonal) differences of soil CO_2 efflux. We suggest that parameterization of water content heterogeneity in space and time must be a critical component for realistic model representations of soil CO_2 efflux (understood as the balance between production and transport [*Pacific et al.*, 2008]) from heterogeneous landscapes. To date, this fundamental concept remains to be robustly applied and integrated within studies of land-atmosphere exchange at the ecosystem level.

4.2. How Do Two of the Most Commonly Used Methods to Measure Soil CO_2 Efflux Compare Across Sites and Across the Growing Season?

[22] To assess the effects of high soil water content and rainfall on discrepancies between techniques, we compared each site separately, both including and excluding measurements following rainfall and during early season high θ (Figure 5). At both sites technique agreement significantly improved when measurements on wet soil days ($\theta > 0.25$ m^3 m^{-3}) and measurements taken within 2 days of ≥1-mm rainfall were removed from the comparison. The disagreement between techniques following precipitation is to be expected as new water inputs can cause a CO_2 burst in soil air because of a rapid gas displace-

ment in the pore space followed by enhanced biological activity [*Cable and Huxman*, 2004; *Huxman et al.*, 2004]. However, the disagreement caused by the removal of measurements with high θ indicates that parameterization of the soil CO_2 profile method needs to be strongly improved and most likely differentiated between high θ and low θ, especially in ecosystems with large variability of θ. Previous studies attempting this technique corroboration [*Baldocchi et al.*, 2006; *Vargas and Allen*, 2008] do not provide context for when chamber measurements were taken with respect to the seasonality of θ, hence, little can be learned from the agreement (or disagreement) of their techniques. Our results suggest that while good technique comparison can be attained during periods of stable conditions (e.g., constant θ and no rainfall), environmental disturbances will affect method corroboration in space and time. Excluding chamber measurements taken following rainfall would improve technique correlation, but through this or similar exclusions, information on primary controls on soil CO_2 efflux is lost. The strengths and limitations of each method, as well as full system understanding, can only be achieved with the direct comparison of both approaches. A context for environmental conditions under which measurements were taken is necessary to understand technique performance (strengths and limitations) and variability of the fluxes (i.e., distinction between ecophysiological processes and environmental biases).

[23] Analyzing instantaneous fluxes from the soil CO_2 profile technique at different sampling frequencies indicates that on a cumulative basis the soil profile technique is not biased by the time of the day at which sampling occurs or by the sampling frequency itself (Figure 7). This means that on a cumulative basis the use of the soil CO_2 profile technique at 20-min frequency intervals yields similar results as when it is used every 2–7 days. Given that daily minima of soil CO_2 in this system occur before sunrise and daily maxima occur during early to late evening [*Riveros-Iregui et al.*, 2007], sampling soil CO_2 efflux between 1000 LT and 1600 LT (as in the example presented in Figure 7) may correspond to the 24-h mean of soil CO_2 efflux. Our findings suggest that on a seasonal basis, it is more critical to capture spatial variability and seasonal dynamics driven primarily by changes in soil water content than the diel dynamics caused by soil temperature and plant activity. These results demonstrate that while the soil CO_2 probes provide important resolution for short time scales, long-term (seasonal) measurements do not necessarily benefit from this high-frequency sampling. The tradeoff between spatial coverage of chambers and temporal resolution of the soil CO_2 profile technique greatly depends on study goals and whether one is interested in seasonal estimates of soil CO_2 efflux rates or rapid dynamics of this flux.

4.3. What Are the Implications of These Findings for Process Understanding of Soil CO_2 Efflux From Subalpine Ecosystems?

[24] A comparison of measurements by the soil respiration chamber and the soil CO_2 profile technique demonstrates that, accumulated over the growing season, both techniques are within 7% of measurements for the riparian site and within 32% of measurements for the upland site (Figure 8). Similar agreements between techniques have
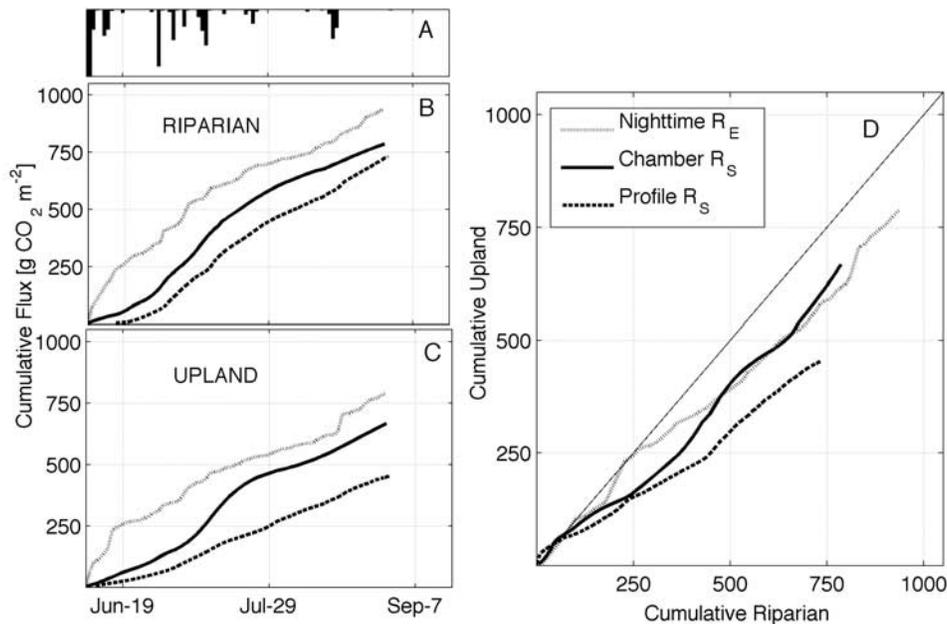
Figure 8. (a) Relative precipitation. (b, c, d) Comparison of cumulative discrete (instantaneous) measurements made by the soil respiration chamber technique (including all data), 20-min measurements by the soil profile technique, and nighttime ecosystem respiration (R_E) by an eddy covariance system at a riparian and an upland site.

been reported [*Tang et al.*, 2003; *Baldocchi et al.*, 2006], but the difference in agreement across sites had not been previously observed. Better agreement at the riparian site is likely due to the higher θ in these areas, which leads to a more homogeneous water content profile in the top 20 cm of the soil, even after precipitation events (Figure 2). New moisture from precipitation can be distributed more homogeneously within the top section of the soil profile. Conversely, because θ is lower at the upland site, the distribution of new moisture from precipitation in the topsoil does not occur as homogeneously, and new moisture does not penetrate as deeply, causing larger differences in diffusivity throughout the soil profile, thus limiting the soil profile technique, especially late in the season.

[25] Compared to nighttime ecosystem respiration, both techniques provide comparable effluxes for each site (Figure 8). While this comparison is not intended for quantitative purposes, it provides the foundations for potential, detailed examinations. For example, the difference in soil CO_2 efflux response between the riparian and upland sites, particularly after snowmelt and precipitation, demonstrates that different landscape positions may not respond uniformly to environmental disturbances, particularly because of differences in θ. On a cumulative basis riparian areas exhibit higher soil CO_2 efflux and ecosystem respiration than upland sites throughout the growing season (Figure 8d). While riparian meadows can occupy a smaller fraction of an entire forest (~2%) [*Riveros-Iregui*, 2008], soil CO_2 efflux from these areas is larger than effluxes from upland forests. Soil CO_2 efflux from chamber measurements was within 16% of nighttime ecosystem respiration at the riparian site and within 15% of nighttime ecosystem respiration at the upland site. However, these relationships, and

the magnitude of differences between sites and throughout the growing season, are nonlinear, which warrants future investigations on how the parameterization of a nonstationary behavior of the landscape can be important to improve current estimates of soil CO_2 efflux from large areas and to improve comparisons with other estimates of C exchange at the ecosystem scale. Direct comparison of multiple techniques (soil respiration chambers, soil CO_2 profile technique, and eddy covariance towers) is necessary to understand the spatiotemporal nature of C fluxes. The findings presented here are essential for enhancing process understanding of soil CO_2 efflux from heterogeneous landscapes, providing a conceptual framework of soil CO_2 efflux useful for modeling studies, and gaining confidence in current and developing soil CO_2 efflux measuring techniques.

5. Conclusions and Implications

[26] 1. Soil water content was a major control on both spatial and temporal (particularly seasonal) differences of soil CO_2 efflux between a riparian meadow and an upland forest, especially after snowmelt and rainfall. Parameterization of water content heterogeneity in space and time must be a critical component of realistic model representations of soil CO_2 efflux rates from heterogeneous landscapes.

[27] 2. Good agreement between the soil respiration chamber technique and the soil CO_2 profile technique can be attained during periods of stable conditions (e.g., constant θ and no rainfall). However, seasonality of soil water content and sporadic rainfall introduce physical effects that limit this agreement and play a major role in method corroboration. Providing a context for environmental conditions under which measurements were taken is necessary

to understanding performance of techniques and the source of the variability in measured efflux.

[28] 3. On a 24-h basis both techniques yield comparable results, except during periods of sporadic precipitation, when the chamber technique yields soil CO_2 efflux rates much larger than those by the soil profile technique. This means that rapid changes in soil physical properties, respiration enhancement, and water-caused displacement of CO_2 within the soil pore space might not be adequately captured by solid-state CO_2 sensors. Nonetheless, these sensors remain a useful tool for capturing changes in soil CO_2 caused by less transient, nonhydrological, ecophysiological processes (i.e., responses of plant and microbial activity to changing environmental conditions).

[29] 4. Differences in diel hysteresis patterns of soil CO_2 efflux between sites were controlled by the effects of canopy cover on soil temperature and temporal differences in photosynthetic activity of vegetation. Particularly in dry soils, diel hysteresis in soil CO_2 efflux is production limited and represents a rapid response of combined heterotrophic and autotrophic activities. More circular hysteresis patterns late in the season at the upland site suggest that upland vegetation is better adapted to low soil water content and that riparian vegetation influence on soil CO_2 efflux diminished over the course of seasonal dry down.

[30] 5. On a seasonal basis soil CO_2 efflux measurements were not biased by the time of the day at which sampling occurred, meaning that long-term (seasonal) measurements do not necessarily benefit from high-frequency sampling by soil CO_2 probes. Furthermore, if the study focuses on seasonality, capturing the spatial variability and seasonal dynamics of efflux driven primarily by changes in soil water content is more important than capturing diel dynamics caused by soil temperature and plant activity.

[31] 6. Both techniques can yield comparable efflux rates with the exception of transient flux events caused by precipitation or diffusion-limited flux caused by wet soils. Direct comparison of multiple techniques (soil respiration chambers, soil CO_2 profile technique, and eddy covariance towers) is necessary to gain insight into the primary controls on soil CO_2 production and transport and the spatiotemporal nature of efflux. Acknowledging technique limitations is important for reporting realistic rates of soil CO_2 efflux.

[32] 7. These results have implications for interpreting and evaluating rates of soil CO_2 efflux measured by soil respiration chambers and the soil CO_2 profile technique, from both mechanistic and methodological perspectives. While the findings presented here were attained in a subalpine forest, they can be applied to current and future studies in a wide range of ecosystems. These implications should be considered when measuring and modeling the dynamics of C cycling at the ecosystem level.

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