

HYDROLOGIC-CARBON CYCLE LINKAGES IN A SUBALPINE CATCHMENT

by

Diego Andrés Riveros-Iregui

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Dr. Brian L. McGlynn

Approved for the Department of Land Resources and Environmental Sciences

Dr. Bruce D. Maxwell

Approved for the Division of Graduate Education

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VITA

Diego Andrés Riveros-Iregui was born in Fusagasugá, Colombia, on September 26th 1976. He is the fifth child of Néstor S. Riveros and Lilly Iregui de Riveros. Diego received a High School diploma (1991) from the Colegio Diocesano Ricaurte in Fusagasugá and a B.S. in geology (1999) from the Universidad Nacional de Colombia at Bogotá. Between 1998 and 2000, he worked for the Instituto Colombiano de Minería y Geología, INGEOMINAS, as a research assistant, in Bogotá. In 2002 Diego received an A.S. in computer science from Inver Hills Community College, and in 2004 he received a M.S. in geology from the University of Minnesota.

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ABSTRACT

The feedbacks between the water and the carbon cycles are of critical importance to global carbon balances. Forests and forest soils in northern latitudes are important carbon pools because of their potential as sinks for atmospheric carbon. However there are significant unknowns related to the effects of hydrologic variability, mountainous terrain, and landscape heterogeneity in controlling soil carbon dioxide (CO₂) efflux. Mountainous terrain imposes large spatial heterogeneity in the biophysical controls of soil CO₂ production and efflux, including soil temperature, soil water content, vegetation, substrate, and soil physical properties. Strong spatial and temporal variability in biophysical controls can lead to large heterogeneity in the magnitude of soil CO₂ efflux. This dissertation research investigates the relationships between these biophysical controls and the resultant CO₂ efflux across the soil-atmosphere interface in a 393-ha subalpine catchment of the Northern Rocky Mountains. This study incorporates knowledge gained through field observations (2 growing seasons) at multiple locations distributed across the watershed, and a range of empirical analytical techniques including a modeling approach to estimate point to catchment scale soil CO₂ efflux. Variability in soil CO₂ efflux was strongly related to topography and landscape structure. Riparian meadows were found to have the highest rates of cumulative soil CO₂ efflux across the entire watershed, likely due to more accumulation of soil water than upland sites, leading to enhanced plant and microbial respiration in riparian meadows. Landscape context and appreciation of organized heterogeneity are critical to estimation and interpretation of watershed-scale rates of soil CO₂ efflux and for up-scaling plot or point measurements of soil CO₂ efflux to larger spatial scales. This dissertation provides examples and suggestions for corroboration and integration of soil and canopy level CO₂ fluxes and for process understanding of spatiotemporal variability of biogeochemical processes driven by the hydrologic cycle.

CHAPTER 1

INTRODUCTION

For decades, much scientific research has focused on the water and carbon (C) cycles for their crucial role on both biotic and abiotic processes. The interplay between these two cycles on the template dictated by the Earth's surface, results on what is known to us as ecosystems. Of great interest to the environmental sciences is the role of ecosystems as transient storage for C and in particular, the exchange of mass and energy along the soil-plant-atmosphere continuum. More than two-thirds of total terrestrial C is stored below ground and exchanged to the atmosphere through plant and microbial activity [Hibbard *et al.*, 2005]. The interactions between hydrology and biogeochemical processes are of critical importance to this exchange, yet the interactions among these concurrent processes are poorly understood. Traditionally, studies seeking to quantify this exchange of C are performed at regional scales [e.g., Ciais *et al.*, 1995; Fan *et al.*, 1998] or at single plot scales [e.g., Howard and Howard, 1993; Robinson and Scrimgeour, 1995; Tang and Baldocchi, 2005], but little information exists on how these processes and their effects integrate from small to larger scales. Large gaps exist in our understanding of the variability of C fluxes from the local point, to the plot, to the watershed scale, and the controls on this variability across scales.

Carbon dioxide (CO₂) in soil air is derived primarily from microbial and root respiration. These processes are dependent on soil temperature, soil water content, soil nutrient status, and vegetation cover. These parameters also vary spatially in response to

different environmental gradients imposed by the landscape and temporally as a result of the temporal scale at which each driver occur. For example, radiation differences occur at diel scales and have been found to influence spatial and temporal variation of temperature [*Korkalainen and Lauren, 2006*], and spatial variation of vegetation and litter accumulation [*Stage, 1976; Webster et al., in press*], which can in turn result in differences in soil carbon content. Concurrently, landscape structure and gravity exert a major control in the lateral redistribution and spatial variability of water in the soil, defining wet and dry areas of the landscape [*Western et al., 1998; Western et al., 1999*], which can in turn result in spatial differences among many processes mediated by water. The spatial variability of soil CO₂ as a response to environmental gradients processes is well accepted [*Hanson et al., 1993; Fang et al., 1998; Scott-Denton et al., 2003*], however, poor understanding of the variables controlling this variability limits our ability to up-scale point scale measurement to larger scales.

Models based on point measurements of CO₂ production and flux used to make predictions over larger areas are increasing in number [e.g., *Richardson et al., 2006; Webster et al., 2008*], but poor understanding of soil CO₂-producing processes and poor data coverage introduces uncertainty into such models. Predictions of soil respiration response to changes in hydrologic conditions are commonly made (and modeled) based on single or few location measurements and extended to complete watersheds. This large discrepancy in spatial coverage limits our understanding of concurrent processes affected by the variability of first order controls. Current efforts to measure net ecosystem production (NEP) at scales greater than a point are often based on the eddy-covariance

method, which is based on CO₂ flux calculations made above the canopy. NEP is currently being estimated at over 400 sites worldwide as part of regional CO₂ flux networks [Baldocchi *et al.*, 2001]. However, approaches to interpret eddy-covariance data are commonly limited by assumptions such as homogeneous soil CO₂ efflux across the landscape and uniform hydrologic effects across the landscape.

I hypothesize that soil water content and water availability is a major, long-term (seasonal) source of temporal and spatial variability in CO₂ efflux during the growing season. I seek to identify the relationship between the biophysical controls of soil air CO₂ and the resultant efflux across the soil-atmosphere interface. Currently, there is a large disconnect between studies that estimate soil CO₂ efflux through models and studies that do it empirically. Most models do not represent field observations, simply because they omit basic concepts including the lateral distribution of soil water, and as a result assume only vertical heterogeneity of soil CO₂ production and efflux. This dissertation represents a novel approach because it incorporates knowledge gained through field observations (2 growing seasons, >5000 measurements taken, not counting automated measurements) into an empirical model to up-scale point-to-catchment rates of soil CO₂ efflux. Today, many flux tower sites around the world are reaching their first decade of continuous measurements of NEP. Yet few of those sites are able to quantify the contribution of soil CO₂ efflux to estimates of NEP, or predict of how hydrologic variability may affect whole-ecosystem processes. Cross verification of measures is critical to gaining confidence in current data collection. Currently, there is a large gap between point scale measurements of soil CO₂ efflux and flux tower measurements of

NEP. The research provided here fills this gap by up-scaling plot-scale measurements of soil CO₂ efflux to watershed scale, and by evaluating the role of a dynamic hydrologic cycle across scales.

Study Site

The Tenderfoot Creek Experimental Forest (TCEF) is located in the Little Belt Mountains of the Lewis and Clark National Forest in central Montana. Tenderfoot Creek drains into the Smith River, which is a tributary of the Missouri River. TCEF elevation ranges from 1,840 to 2,421 meters and has an area of 3,591 hectares. The sub-catchment of study is 393 hectares and contains a second order perennial stream, Stringer Creek (Figure 1.1), with a wide range of slope, aspect, and topographic convergence/divergence. Stringer Creek watershed also provides a wide range of soil temperature and soil water content conditions. Two snow survey telemetry (SNOTEL) stations located in TCEF (Onion Park – 2259 m, and Stringer Creek – 1996 m), providing real-time data on snow depth, snow water equivalent, and climatic variables such as precipitation, radiation, and wind speed. Two stream flumes located in middle and lower Stringer Creek provide continuous discharge data.

Typically, selection of field sampling locations in CO₂ studies does not take into account landscape heterogeneity. Heterogeneity exists at a range of scales. Here, I focus on watershed scale heterogeneity of soil water content, soil temperature, vegetation, and substrate. Each of these variables is partially controlled by landscape position and topography. For this dissertation I undertook a sampling approach where sampling points

were characteristic of the full range of environmental conditions across the Stringer Creek watershed. It has been suggested that high-elevation mountains play an important role in C cycle research, as 70% of the Western U.S. carbon sink occurs at elevations greater than 750 m [*Schimel et al.*, 2002]. I applied a bottom-up approach addressing the heterogeneity of CO₂ forcing variables rather than on the typical top-down focus on vegetation, as in most hydro-ecological models. This unique approach is ideally suited to assessing C exchange in complex, poorly understood, mountainous terrain. Furthermore, the TCEF is an ideal location for this study because of its wide range of topographic settings and aspects, strong elevation gradients, strong seasonality, and the existing infrastructure and data history.

Dissertation Organization

The chapters integrated herein provide a synthesis of some of the interacting process between the hydrologic and the carbon cycle in subalpine ecosystems. In particular, this dissertation focuses on soil CO₂ efflux dynamics from the plot, to the landscape element, to the catchment level and its response to hydrologic and environmental gradients. The work proposed here progresses from the point to the watershed/ecosystem-scale measurement and modeling of soil CO₂ efflux. Each chapter represents the foundation of the next, following nested stages of inquiry. I address two outstanding eco-hydrological, C cycle research questions: the role of hydrology as a spatial and temporal control of soil CO₂ efflux, and the effects of landscape structure in regulating ecosystem C balance.

The general objectives of this dissertation are:

- 1) To evaluate the response of soil CO₂ efflux to environmental effects of soil water content, soil temperature, precipitation, snowmelt, and vegetation cover across temporal scales and across a moderately complex, subalpine watershed;
- 2) To assess the direct effects of dynamic hydrologic conditions on CO₂-producing processes in the soil;
- 3) To provide a conceptual understanding of the variability of soil CO₂ production and efflux at the watershed scale.
- 4) To aid in parameterization and modeling of soil CO₂ efflux from spatial scales useful for comparison with other ecosystem-level measures.

The information presented in this dissertation is essential to linking plot-scale observations to large-scale measurement and modeling of soil CO₂ efflux. It provides fundamental linkages between the fields of hydrology and ecology and is useful to help bridge traditional scientific disciplines and further our holistic understanding of how hydrologic controls propagate into eco(hydro)systems.

Chapter 2 (On the need for reconciling multi-scale approaches in carbon cycle science) evaluates current confidence in estimates of ecosystem CO₂ fluxes obtained from four of the most commonly applied techniques: soil CO₂ chamber and probes, eddy covariance, biometry, remote sensing. Each technique is valuable within its own spatial and temporal resolution. However, reconciling independently measured C flux from each technique to the ecosystem level is important to gain confidence in each technique, as well as in NEP estimates from large spatial and temporal scales. These are current issues

in ecosystem ecology and much work is needed in trying to synthesize different techniques. While current networks (e.g., Fluxnet) are leading synthesis efforts among research sites throughout the world, the mechanisms to bring different measures to comparable temporal and spatial scales greatly differ from one research site to the next.

Chapter 3 (Diurnal hysteresis between soil CO₂ and soil temperature is controlled by soil water content) presents a quantification of the degree to which soil water content controls the relationship between soil CO₂ and soil temperature. This information is important for process understanding introduced in Chapter 4 (Interpretation and evaluation of combined measurement techniques for soil CO₂ efflux: surface chambers and soil CO₂ concentration profiles). This chapter presents measurements of soil CO₂ efflux made at two contrasting sites within the TCEF. Soil water content distribution across the landscape exerts a major control on both spatial and temporal (seasonal) differences of soil CO₂ efflux. This chapter looks at the direct effects of differences in soil water content on soil CO₂ production and efflux between two contrasting sites of the TCEF.

Given the contrasting variability found among continuous measurements at two sites in Chapter 4, Chapter 5 (Landscape structure controls soil CO₂ efflux variability in complex terrain: scaling from point observations to watershed scale fluxes) investigates the spatial and temporal variability of discrete measurements of soil CO₂ efflux across 62 sites of the Stringer Creek watershed. Landscape analysis revealed that the 62 sites are representative of the heterogeneity across Stringer Creek (e.g., slope, aspect, upslope accumulated areas [UAA]). Soil CO₂ efflux measurements also characterized the

temporal variability of effluxes throughout the 83 days of the study. I developed an empirical model based on the UAA-soil CO₂ efflux relationship to up-scale measured soil CO₂ efflux to the entire watershed.

In Chapter 6 (A critical assessment of a process soil CO₂ production and transport model) I apply an existing process soil CO₂ production and transport model to the entire Stringer Creek watershed. I critically corroborate model performance based the independent dataset of CO₂ efflux measurements presented in Chapter 5. The large dataset available for this study allowed for wide spatial comparison of modeled estimates against multiple data sources, providing great benefit to interpretation of model performance and enhancing process understanding.

Finally, Chapter 7 presents a brief summary of the main findings of this dissertation and offers some implications and recommendations for future studies of linkages between hydrology and carbon cycle research.

The chapters presented in this dissertation address many of the current issues in current C cycle research. Unlike traditional ecological studies, these chapters have a fundamental hydrologic association to give this dissertation a physically oriented perspective. I utilized multiple techniques from manual soil respiration chambers, to automated solid-state CO₂ sensors, to eddy covariance towers, to landscape analysis in a comprehensive approach that addressed most fluxes of mass and energy through a typical subalpine forest. The tools and concepts presented here represent a novel approach in eco-hydrology to address some of the emergent patterns in linkages between hydrology

and biogeochemistry and in studies dealing with the complications of using multiple measuring techniques and working across spatial and temporal scales.

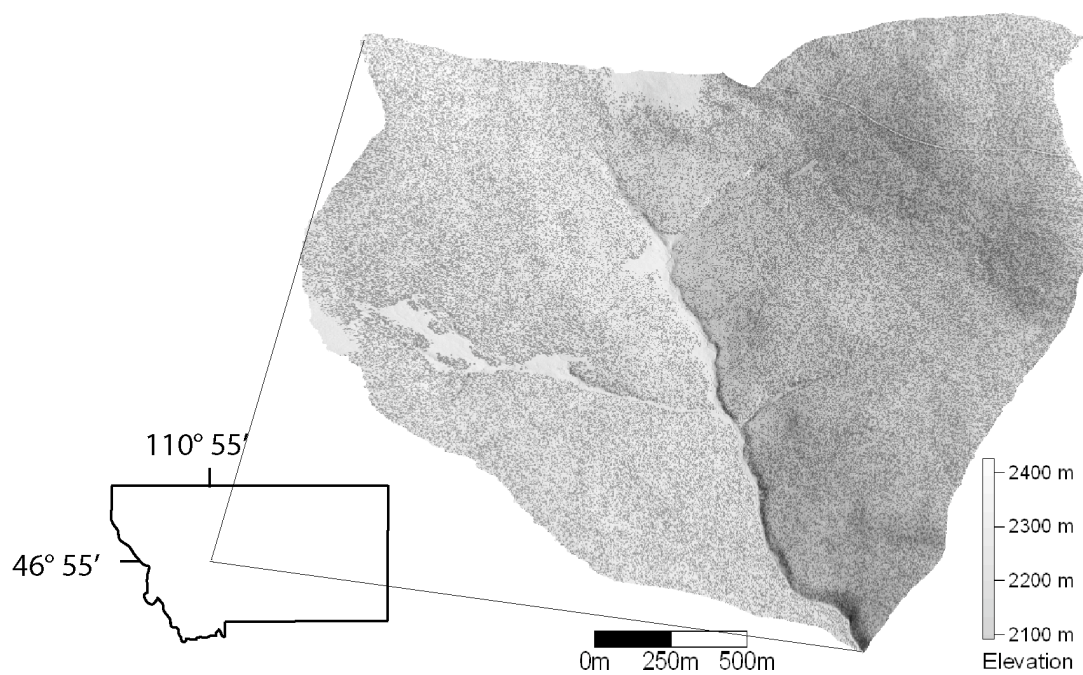


Figure 1.1 Location of the Stringer Creek watershed, in the Tenderfoot Creek Experimental Forest, Little Belt Mountains of Montana.

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CHAPTER 2

ON THE NEED FOR RECONCILING MULTI-SCALE APPROACHES IN CARBON CYCLE SCIENCE

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Abstract

Many flux tower sites worldwide are completing their first decade of continuous measurements of land-atmosphere CO₂ exchange. Estimates of net ecosystem production (NEP), as well as the partitioning of its component fluxes (soil CO₂ efflux, ecosystem respiration, net primary production), are currently being made at a wide range of ecosystems. Current studies provide the basis for cross-site comparison, assessment of biophysical controls on flux dynamics (e.g., precipitation, temperature), and insight into short-long term ecosystem behavior and dynamics. While reconciling estimates from multiple techniques can considerably reduce uncertainty in current NEP estimates and improve our understanding of whole ecosystem processes, this reconciliation exercise remains to be robustly implemented. Here we evaluate current confidence in estimates of ecosystem CO₂ fluxes obtained from four of the most commonly applied techniques. We present a case study that integrates catchment-scale soil CO₂ efflux and nighttime tower-based ecosystem respiration. Area-weighted soil CO₂ efflux from different landscape elements of a 393-ha catchment comprised ~94% of the measured nighttime catchment

ecosystem respiration. We suggest that the characterization of different landscape elements across spatial scales comparable to eddy covariance measurements can help reconcile independent measures of soil CO₂ efflux and tower-based ecosystem respiration, as well as facilitate corroboration with C fluxes measured by other techniques across a range of spatial scales.

Introduction

In the last few years, studies estimating net ecosystem production (NEP) have gained popularity across a wide range of ecosystems [Baldocchi, 2008]. NEP is defined as the balance between carbon uptake and carbon loss from the ecosystem [Lovett *et al.*, 2006] and is commonly expressed by the relationship:

$$NEP = GPP - R_E \quad (2.1)$$

where GPP is gross primary production, and R_E is ecosystem respiration. R_E can be further disaggregated into [Campbell *et al.*, 2004; Law *et al.*, 2003]:

$$R_E = R_A + R_H \quad (2.2)$$

where R_A is autotrophic respiration and R_H is heterotrophic respiration. Multiple techniques can be used to measure/estimate these productivity and respiratory rates, starting from the point scale in the soil, to the canopy scale, to the ecosystem level, and to regional and continental scales. Rates of NEP can be estimated directly with the eddy covariance (EC) technique [Baldocchi *et al.*, 1988], or indirectly by balancing the individual NEP flux components through a bottom-up approach (Figure 2.1). However, given the well-accepted uncertainties and limitations of the EC technique [e.g., Loescher

et al., 2006; *Van Gorsel et al.*, 2007], and due to the spatiotemporal variability of NEP flux components, reconciling these fluxes at the ecosystem level is not trivial.

While accurate corroboration of techniques remains a challenge, additional complications are introduced by poor understanding of the processes. Recent studies [*Piao et al.*, 2007] demonstrate that the response of NEP to higher temperatures can be difficult to predict due to opposing responses of, and feedback between, GPP and R_E . Debate exists on the potential response of soil C [*Davidson and Janssens*, 2006; *Fang et al.*, 2005; *Knorr et al.*, 2005] and ecosystem C [*Cao and Woodward*, 1998] to higher temperatures. The effects of increasing drought frequency and duration [*Jackson et al.*, 2005], more mild winters in temperate zones [*Monson et al.*, 2006], and potential feedbacks to ecosystem warming [*Melillo et al.*, 2002; *Powlson*, 2005; *Schwendenmann and Veldkamp*, 2006] are also critical for determining potential ecosystem C dynamics. Of particular interest is the current and future contribution of belowground R_E (known as soil CO₂ efflux [R_S]) to NEP, as many researchers agree that this flux poses the greatest source of uncertainty in current NEP estimates [*Arain et al.*, 2002; *Barford et al.*, 2001; *Curtis et al.*, 2002; *Davidson et al.*, 2006; *Dragoni et al.*, 2007; *Lee et al.*, 1999; *Moorcroft*, 2006; *Morgenstern et al.*, 2004; *Papale et al.*, 2006; *Reichstein et al.*, 2007; *Savage and Davidson*, 2001; *Schwarz et al.*, 2004; *Valentini et al.*, 2000; *Van Gorsel et al.*, 2007]. Given these opposing responses between belowground and aboveground fluxes [*Piao et al.*, 2007], simple conclusions about the way climate variability may affect whole-ecosystem processes are not yet possible.

A common issue when addressing problems of uncertainty in NEP rates lies on the poor availability of adequate (and co-located) datasets. For example, few sites can demonstrate the contribution of soil CO₂ efflux to total R_E (i.e., the R_S/R_E ratio). Law et al. [1999] compared half-hourly EC calculations of below canopy fluxes with R_E estimates up-scaled from chamber measurements located within the tower's footprint. Their results show that soil CO₂ efflux comprised on average 76% of total ecosystem respiration in a ponderosa pine forest (Table 2.1). Norman et al. [1997] compared EC and closed-chamber systems and reported a R_S/R_E of almost 50% in a black spruce dominated boreal forest, referring to landscape heterogeneity as the primary source of uncertainty in the estimation of R_S/R_E . Subke and Tenhunen [2004] found R_S/R_E to average 41% in a spruce forest in Norway (Table 2.1) using soil CO₂ efflux rates based on an empirical exponential model developed for their system. Subke and Tenhunen [2004] further reported that:

...no single parameter, or combination of parameters, could be identified that could account for the divergence of flux measurements, [hence] no correction on the basis of meteorological conditions was possible, and the scaling of EC fluxes on the basis of the nighttime comparison with [empirically-modeled] chamber fluxes was the best workable option to make flux measurements obtained by either systems comparable.

These findings highlight how a robust characterization of soil CO₂ efflux in combination with traditional EC estimates has not yet been implemented, yet it is needed to overcome issues of spatial heterogeneity, which can commonly appear “inexplicable” and be erroneously attributed to randomness.

Similar corroborations have found a seasonal component to the variability of R_S/R_E . In a red spruce-dominated forest in Maine, Davidson et al. [2006] found that

R_S/R_E gradually increased from 45% in the spring to 65% in the summer, to a maximum of 80% in the fall (Table 2.1). Jassal et al. [2007] reported R_S/R_E ratios of 52% in the spring, to 63% in the summer, to 81% in the fall and 86% in the winter, for a Douglas fir stand on the west coast of Canada. These and similar comparisons (Table 2.1) reveal considerable variability in the contribution of soil CO₂ efflux to R_E across ecosystems and seasons. In spite of the current proliferation of EC sites, frequent lack of soil CO₂ efflux measurements at spatial scales comparable to EC impedes reconciling soil and canopy fluxes.

Due to discrepancies among the temporal resolution of the techniques applied, temporal corroboration of measurements can be even more challenging, and studies more limited. For example, Tang et al. [2005] found well-correlated soil CO₂ efflux and photosynthetic rates in an oak-grass savanna ecosystem. Their work demonstrated that daytime peak photosynthesis drove soil CO₂ efflux, suggesting the need to introduce a photosynthesis parameter into process-based modeling of soil CO₂ efflux. Baldocchi et al. [2006] found that this correlation of photosynthesis and soil CO₂ efflux is a function of soil water content availability. Riveros-Iregui et al. [2007] found that diel cycles of soil CO₂ concentrations can be explained by analyzing the diel cycles of photosynthetically active radiation (PAR) and soil temperature. Because soil temperature lags PAR on a diel basis as an effect of thermal diffusivity of the soil, peak timing of soil CO₂ concentrations occurs at the combined optima of PAR and soil temperature [Riveros-Iregui et al., 2007]. While it had been previously suggested that soil CO₂ is controlled by

both factors, their results indicated coexisting autotrophic and heterotrophic activities, occurring asynchronously.

Because estimation of NEP rates can also be achieved by balancing NEP components (Figure 2.1), estimates based on other techniques such as biometry or satellite observations and their corroboration with traditional techniques are crucial and play an important role in NEP studies. For example, Barford et al. [2001] compared 9 years of EC estimates of NEP with 8 years of biometric inventories of net primary production (NPP [Figure 2.1]) in a mid-latitude deciduous forest. The good correlation found between the two approaches is encouraging (~80%); however, their study benefited from an extensive dataset of EC and forest inventory measurements, which are not available at most sites. Curtis et al. [2002] compared EC and biometric inventories across five different forest sites and found good correlation at only one of the five sites (the same site reported by Barford et al., [2001]). They suggested that the lack of temporal overlap of EC and biometric measurements at the other four sites may be the reason for the discrepancy between net flux estimates. Similar studies have extrapolated biometric NPP over multiple years [Miller *et al.*, 2004] to overcome the lack of temporal coincidence of measurements. However, this extrapolation introduced large uncertainty in NPP estimates because it ignored interannual variability of growth rates, which can be high in mature forests [Kostner *et al.*, 2002; Urbanski *et al.*, 2007].

Satellite-based observations such as the Moderate Resolution Imaging Spectroradiometer (MODIS [Running *et al.*, 1999]) have also been used to corroborate NEP estimates. Heinsch et al. [2006] compared four years (2000-2003) of MODIS GPP

and EC estimates of GPP (Figure 2.1) across multiple ecosystems with diverse climate regimes and land cover types. This comparison was performed at the 7x7 km grid resolution centered over each EC tower site. Their results showed that on an annual basis, a fairly strong correlation exists between MODIS GPP and EC-based GPP (~81%). However, on a seasonal basis, poorer correlation was found, especially during the non-summer seasons in the northern hemisphere. The lesser correlation is attributed to the high temporal variability of most environmental and climatic controls during these periods [Heinsch *et al.*, 2006], supporting previous suggestions that common sources of error in MODIS GPP are related to difficulties in estimating climatic variables such as vapor pressure deficit (VPD, [Churkina *et al.*, 1999; Mu *et al.*, 2007; White *et al.*, 2000]).

In this paper we suggest that in spite of an increasing wealth of NEP studies, including the availability of flux partitioning techniques, a reconciliation of multiscale NEP component fluxes has yet to be robustly implemented. We emphasize the importance of characterizing soil CO₂ efflux and its use as a corroborating tool in estimates of NEP, because 1) there is relatively high accuracy and confidence in soil CO₂ efflux measures; 2) poorly quantified, soil CO₂ efflux can be the largest source of uncertainty in NEP rates; and 3) quantification and characterization of soil CO₂ efflux can more strongly constrain NEP estimates than other single component measurement. This paper seeks to provide a brief overview and discussion of direct and indirect methods to estimate NEP, evaluate current confidence in their measurements of land-atmosphere CO₂ exchange, and offer suggestions for reducing uncertainty in estimates of NEP. The remainder of the paper is organized as follows. Section 2 presents a survey of

methods for estimating rates of NEP or its flux components at different spatial and temporal scales. This survey moves from point-scale flux measurements to biome-scale estimates, following nested scales of inquiry. Section 3 presents a synthesis and a case study on how soil CO₂ efflux and process understanding could be scaled-up based on point measurements for comparison to larger spatial scale measurement techniques. This multi-approach, scaling exercise is necessary to improve process understanding of whole-ecosystem processes and gain confidence in NEP estimates from large spatial and temporal scales.

Brief Review of Current Techniques

Measuring Soil CO₂ Efflux

Soil CO₂ efflux is defined as the sum of belowground components of autotrophic and heterotrophic respiration. One of the most common methods for measuring soil CO₂ efflux is soil chambers (Figure 2.1). Chambers are frequently used because of their simplicity and relatively low cost [*Fang and Moncrieff*, 1996; *Pacific et al.*, in review; *Welsch and Hornberger*, 2004]. These techniques are applied spatially from single to multiple points spread over larger areas ($\sim 10^2 \text{ m}^2$), and temporally at intervals that vary from minutes to weeks. Different chamber types exist, including static and automated, or dynamic and manual. Some of the issues related to either chamber type, including the comparison of their measurements, have been previously addressed [e.g., *Burrows et al.*, 2005]. Typically, automated chambers allow for higher temporal resolution of the measurements, whereas dynamic chambers (manually moved) can provide greater detail

on the spatial heterogeneity of soil CO₂ efflux. However, implementation of either chamber type over larger areas (e.g., entire watersheds) is labor-intensive and can become impractical. Additional concerns are introduced by potential physical effects caused by the chambers themselves. Some of the most common effects include elevated headspace air temperatures [Hutchinson and Livingston, 2001], inhibited or excessive turbulence [Fang and Moncrieff, 1996], and disturbance of the air pressure and subsequent alteration of natural CO₂ diffusion in the soil [Davidson *et al.*, 2002; Norman *et al.*, 1997; Pumpanen *et al.*, 2004]. However, in spite of these concerns, and the fact that they are only point-scale measurements, chambers remain one of the most common methods to characterize soil CO₂ efflux heterogeneity through space.

More recently, a technique that provides continuous soil CO₂ efflux measurements has been developed [Baldocchi *et al.*, 2006; Riveros-Iregui *et al.*, 2007; Tang *et al.*, 2003; Vargas, 2007]. With this technique, soil CO₂ concentrations are measured by installing solid-state CO₂ sensors at different depths, overcoming the physical effects introduced by soil chambers. A soil air CO₂ profile is consequently constructed and surface efflux is calculated by using Fick's Law:

$$F = -D \frac{\partial[CO_2]}{\partial z} \quad (2.3)$$

where D is the diffusion coefficient of CO₂ in the air-filled pore space, $\partial[CO_2]/\partial z$ is the difference in soil air CO₂ concentration between two particular depths, and F is the CO₂ flux between the two depths. A source of uncertainty in the use of this technique lies in the accurate estimation of D . Given the difficulty in accurately measuring D without severely disturbing the soil, soil gas transport and respiration studies usually model D

based on soil type and soil water content, as these factors are closely related [Moldrup *et al.*, 1996]. Accurately estimating D is important because it is a determinant factor of the magnitude of flux. Currently, a well-accepted method for the estimation of D [Moldrup *et al.*, 1999] uses a pore-size distribution parameter (b , [Campbell, 1974]), which reflects the water-retention capacity of the soil, to model soil gas diffusivity:

$$D = -\Phi^2 \left(\frac{\varepsilon}{\Phi} \right)^{\left(2 + \frac{3}{b}\right)} \quad (2.4)$$

where Φ is total soil porosity and ε is air-filled porosity. This method is being widely applied and it has been amply tested to model D across a range of soil types and water contents [Baldocchi *et al.*, 2006; Christensen *et al.*, 2006; Kawamoto *et al.*, 2006; Resurreccion *et al.*, 2007]. Its strength lies in the integration of soil water content and soil physical properties as the physical controls on the movement of gas in the soil.

The improvement in the resolution of soil CO₂ efflux methods from discrete soil chamber measurements to continuous measurements by the soil CO₂ profile technique facilitates identification of rapid responses of soil CO₂ efflux to changes in environmental conditions. The benefit of the soil CO₂ profile technique is that soil CO₂ efflux rates are estimated continuously at temporal scales that range from minutes to hours. This facilitates the use of soil CO₂ efflux rates to compare against other continuous measurements such as below-canopy EC CO₂ fluxes, nighttime canopy-atmosphere net CO₂ exchange, and total R_E estimated from empirical models. This comparison of techniques can help constrain current NEP estimates from ecosystems where both below and aboveground fluxes are being measured. While there is a tradeoff between temporal

resolution (soil CO₂ profile technique) and spatial coverage (chambers), the combination of both methods over larger areas can overcome the weakness of each technique. Additional understanding of the spatial variability of biophysical controls such as soil water content and its physical effects on controlling soil CO₂ efflux is critical for estimating soil CO₂ efflux rates as one moves to larger and more heterogeneous landscapes (e.g., entire watersheds). Current lack of studies with good spatial and temporal coincidence of soil CO₂ efflux measurements with other techniques such the EC technique hampers further investigations on the variability of R_g/R_E across different ecosystems.

Eddy Covariance

At the canopy level, estimates of NEP are being made worldwide using the eddy-covariance (EC) technique [Aubinet *et al.*, 2000; Baldocchi *et al.*, 2001; Falge *et al.*, 2002; Law *et al.*, 2002]. This technique uses coupled measurements of vertical wind velocity and atmospheric CO₂ concentrations to calculate net exchange rates of CO₂ across the canopy-atmosphere interface. In the last decade, the EC technique has become essential to the study of ecosystem-scale fluxes of CO₂. EC provides continuous, automated estimates of CO₂ exchange at spatial scales that vary from hundred of square meters to square kilometers and temporal scales that vary from minutes to years [Foken and Wichura, 1996]. This technique also allows for calculations of water vapor flux, and latent and sensible heat fluxes at similar frequencies [Wilson and Baldocchi, 2000]. EC estimates can be averaged over a range of temporal scales (e.g., days, months, seasons,

years), allowing for corroboration with other independent assessments of NEP component fluxes [e.g., *Baldocchi*, 2003; *Goulden et al.*, 1996].

The EC technique is based on the correlation between CO₂ and water vapor concentrations and near surface turbulence [*Baldocchi et al.*, 1987; *Baldocchi et al.*, 1988]. Because atmospheric turbulence is often weak at night over a plant canopy when there is stable thermal stratification of the air column [*Goulden et al.*, 1996; *Hollinger et al.*, 1994; *Loescher et al.*, 2006], nighttime flux data collection has been problematic with the EC technique due to its inability to resolve the full turbulence spectrum, resulting in an underestimation of net CO₂ exchange. While several studies have addressed this particular issue [e.g., *Grunwald and Bernhofer*, 2007; *Gu et al.*, 2005; *Van Gorsel et al.*, 2007], and while most sites use a threshold in atmospheric stability for correcting nighttime fluxes, no particular method has emerged as clearly optimal and nighttime flux corrections are often determined on an site-specific basis [*Falge et al.*, 2001; *Reichstein et al.*, 2005; *Stoy et al.*, 2006].

In addition to measurements at the canopy-atmosphere interface, a few researchers have applied the EC technique in the lowest layers of the canopy [*Baldocchi and Meyers*, 1991; *Falk et al.*, 2005; *Subke and Tenhunen*, 2004]. This allows for the estimation of soil and coarse woody debris respiration, improving quantification of total R_E estimates. Their results suggest that nighttime turbulence in lower parts of some canopies (below the subcanopy wind maximum) can remain intact and as such, EC can be a direct measurement of CO₂ flux below the height of the system (usually 2 or 3 m above the ground surface).

Also at the canopy level, stable isotopes can be used to partition NEP into photosynthesis and R_E (Figure 2.1) in combination with the EC technique [Yakir and Wang, 1996]. The fundamental premise is that during photosynthesis leaves preferentially draw $^{12}\text{CO}_2$ over $^{13}\text{CO}_2$ from the canopy atmosphere. This results in plant organic matter that is ^{13}C -depleted relative to atmospheric air [Bowling *et al.*, 2003a; Ehleringer *et al.*, 2002], releasing relatively more $^{12}\text{CO}_2$ back to the atmosphere during nighttime plant respiration [Farquhar *et al.*, 1989]. As a result there exists a diurnal cycle in the composition of the canopy air where daytime CO_2 is ^{13}C -enriched and nighttime CO_2 is ^{13}C -depleted. This partitioning has been previously achieved at large spatial scales based on discrete sampling [e.g., flask sampling, Bowling *et al.*, 1999; Ogee *et al.*, 2003] and more recently at higher frequency sampling [tunable diode laser absorption spectroscopy (TDLAS); Bowling *et al.*, 2003b; Griffis *et al.*, 2004]. In spite of having lower analytical precision ($\pm 0.25\%$, compared to $\pm 0.02\%$ from flask sampling), TDLAS potentially offers high sampling frequency (~ 2 min) and automation. This tradeoff between precision and sample frequency [Bowling *et al.*, 2003b; Griffis *et al.*, 2004] makes TDLAS more suitable for both high frequency and long term monitoring. While costs of some of the isotopic-based techniques remain high (e.g., $> \$70,000$ for TDLAS) and their collocation with EC instrumentation is difficult at many flux tower sites, great potential exists for implementation of these two techniques as an analytical tool at both the soil and canopy levels. High-frequency measurements of the canopy air isotopic composition can improve process understanding of the seasonal and interannual

photosynthetic activity [*Randerson et al.*, 2002], as well as ecosystem-level responses to physical demands of the environment.

While the EC technique continues to be refined and validated [*Juang et al.*, 2006; *Oren et al.*, 2006], its present role in the estimation of ecosystem-level CO₂ exchange is essential. Most of the complications that arise when using this technique are treated amply in the literature and they warrant separate reviews. Common challenges are introduced by vertical [*Staebler and Fitzjarrald*, 2004; *Vickers and Mahrt*, 2006] and horizontal [*Lee*, 1998; *Park and U*, 2004] advective CO₂ flux. Respired CO₂ can be advected both vertically and horizontally, often leading to an underestimation of nighttime fluxes [*Loescher et al.*, 2006; *Paw et al.*, 2000]. Further difficulties are posed by the matching of EC estimates with the spatial scale of the EC footprint [*Schmid*, 1994; 1997], particularly when dealing with heterogeneous landscapes. The effects of instrumental and systematic errors [*Massman and Lee*, 2002] and the existing uncertainty in the measurements, generally attributed to random errors [*Moncrieff et al.*, 1996; *Richardson et al.*, 2006], remain a topic of investigation in the development and application of this technique.

In spite of their existing limitations, flux tower sites are rapidly increasing in number, with >400 sites currently worldwide [<http://www-eosdis.ornl.gov/FLUXNET/>]. The EC community is becoming increasingly organized, and datasets are widely available. As such, the EC technique provides a critical link between point-scale measurements of soil CO₂ efflux and biometric estimates of NPP for plots, watersheds, or larger areas. The spatial scale at which the EC technique is used can help integrate the

extensive heterogeneity observed by point measurements. The flexibility of averaging EC times over multiple temporal scales that range from hours to years allows for corroboration with other independent measures, either discrete or continuous, performed at a range of temporal scales.

Biometric-based measures of NPP

Field-based net primary production (NPP) estimates are independent measurements usually determined from biomass inventories (Figure 2.1). Biomass inventories can be used to directly measure carbon stocks and assess the net carbon balance for multiple years [*Clark et al.*, 2001; *Miller et al.*, 2004; *Ohtsuka et al.*, 2005]. This technique consists of direct measurements of total biomass growth and litter production at the plot scale. Biometric measurements include measurements of stem, branch, and foliage biomass, stem and leaf area, sapwood volume, coarse and fine root biomass, and detritus production [*Gower et al.*, 1993]. These variables have all been found highly correlated with stem diameter at breast height (DBH) for different species [*Gower et al.*, 1997], and their relationships have been applied to whole ecosystem biomass estimation [*Enquist et al.*, 2000; *West et al.*, 1997]. Biometric NPP rates are often measured periodically (3-5 times/year) and commonly expressed on an annual basis [*Jenkins et al.*, 2001]. Thorough assessments include plots of variable diameters to avoid biases and extend across different landscape elements to capture spatial heterogeneity [*Kashian et al.*, 2005]. Additional measurements can include seasonal and interannual soil C content of soil horizons as an estimate of C accumulation by the ecosystem [*O'Neill et al.*, 2003].

There is an outstanding gap in ecosystem science that hampers correlation of tower-based NEP with other independent measures such as biometric-based NPP. Difficulties include the measurement and separation of above and belowground processes, as each level poses unique challenges due to the different spatial and temporal scales at which measurements are made. For example, aboveground measurements of single-stand growth rates are commonly made in multiple ecosystems. Extrapolating from these single-stand measurements to entire watersheds can introduce uncertainty into NPP estimates, particularly in heterogeneous landscapes [Barford *et al.*, 2001; Houghton *et al.*, 1999; Wang *et al.*, 1999]. The quantification of dead biomass and woody debris is important to characterize the C storage aboveground at each ecosystem [Barford *et al.*, 2001]. Landscape heterogeneity can exert a major control on the accumulation of aboveground C due to steep terrain, localized disturbance, and management practices. Belowground processes introduce additional uncertainty, as processes such as root growth and mortality are difficult to quantify and commonly ignored [Atkin *et al.*, 2007; Gifford, 1995]. Because biometric NPP does not include soil CO₂ efflux, an accurate estimation of belowground C processes is essential to complementing biometry NPP. Analyzing watershed-level rates of soil CO₂ efflux offers one way to advance process understanding derived from biometric NPP. This intercomparison of flux estimates can enhance our ability to characterize and quantify the concomitant variability of above and belowground processes in heterogeneous landscapes.

Satellite-based measures of Gross Primary Production

In recent years, ecosystem CO₂ dynamics have been investigated based on Moderate Resolution Imaging Spectroradiometer (MODIS). Using the spectral reflectance of land cover, this technique is rapidly gaining popularity because it allows estimates of vegetation cover, leaf area index, fraction absorbed photosynthetically active radiation (*FPAR*), GPP, and NPP [Running *et al.*, 1999; Turner *et al.*, 2006] from 1-km² grids for the entire globe in 8-day composites [Running *et al.*, 2004]. Rates of GPP are modeled based on photosynthetic rates and *FPAR*:

$$GPP = \varepsilon \times FPAR \times PAR \quad (2.5)$$

where *PAR* is photosynthetic active radiation at the canopy surface, and ε is the light use efficiency (LUE) term (i.e., the amount of carbon assimilated per unit of absorbed energy) and is calculated as:

$$\varepsilon = \varepsilon_{\max} \times m(T_{\min}) \times m(VPD) \quad (2.6)$$

where $\varepsilon_{\max}$ is a biome-specific maximum LUE, and $m(T_{\min})$ and $m(VPD)$ are thresholds of temperature and vapor pressure deficit (VPD), respectively, that regulate plant functioning [Mu *et al.*, 2007; Running *et al.*, 2004]. Conceptually, ε is a function of both climatic (e.g., temperature, humidity, soil water content) and biologic factors (e.g., vegetation cover) [Justice *et al.*, 1998; Kimball *et al.*, 1997]. Therefore caveats associated with the validation of MODIS GPP rates remain widely discussed [e.g., Plummer, 2006; Xiao, 2006], as the significance and uncertainty of such rates are highly dependent upon some form of land-based corroboration.

While the uncertainty existing in MODIS estimates may be the largest of all the techniques described here, the spatial coverage of MODIS is ideal for comparison among watersheds, ecosystems, and regions across the globe. Further development and validation of MODIS estimates requires comparison of measuring techniques [e.g., *Cohen et al.*, 2003; *Turner et al.*, 2003]. The corroboration of MODIS with sites using land-based techniques can provide bidirectional feedback between ground sites and MODIS because 1) process understanding from ground sites can improve calibration and reduce uncertainty of MODIS estimates in its wider application, and 2) spatial coverage of MODIS can offer a spatial context for ground site intercomparison.

Synthesis: The Role of Soil CO₂ Efflux

It is evident that all methods currently used to measure C fluxes at the ecosystem level have assumptions, limitations, and significant uncertainties, and the usefulness of each method depends upon an understanding of those constraints. While new and emerging techniques might overcome part of the problem, the intercomparison of current techniques can be a solution today. We suggest that soil CO₂ efflux estimates can contribute to the refinement of current NEP budgets across a range of biomes, because despite the spatial scale at which it is measured, there is a relatively high accuracy and confidence in measurements of soil CO₂ efflux. Furthermore, we suggest that a comprehensive corroboration of C fluxes at the watershed level can be divided into two tasks: 1) a spatial corroboration, including issues of scaling, spatial coincidence, and footprint correction of the measures; and 2) a temporal corroboration, including issues of

temporal resolution of each measure, and the feasibility of comparing measurement rates at similar temporal scales among various techniques. Achieving both tasks depends upon data quality, experimental design, and more importantly, the spatial collocation of all techniques.

Spatial Corroboration

How can measurements of soil CO₂ efflux be used to improve confidence of NEP estimates made at the watershed scale, or even larger areas? One obstacle to understanding the spatial patterns of soil CO₂ efflux is the large heterogeneity in soil physical and biogeochemical processes, commonly imposed by the interaction among soil temperature, vegetation, substrate, soil physical properties, and the lateral redistribution of soil water. Further complications are introduced by the superimposed temporal heterogeneity (i.e., the asynchronous response of each variable). As a result, extrapolating from single- or multiple-point measurements to larger areas by only accounting for area size [*Lavigne et al.*, 1997; *Norman et al.*, 1992; *Ryan et al.*, 1997] commonly leads to incorrect estimates of watershed-scale soil CO₂ efflux [*Goulden et al.*, 1996].

One approach to addressing the heterogeneity in soil CO₂ efflux lies in the use of topographic similarity, which can relate to hydrologic similarity [*Beven and Kirkby*, 1979]. Hydrologists and biogeochemists have used this concept to transfer process and response understanding to topographically and thus hydrologically and biogeochemically similar areas [*Band et al.*, 2001; *Boyer et al.*, 1997; *Creed et al.*, 1996; *Creed and Band*, 1998; *McGlynn and McDonnell*, 2003a; b; *Welsch et al.*, 2001]. This idea is conceptually

intuitive because 1) many biogeochemical processes are mediated by both temperature and water content, two variables that often vary predictably with topographic position; and 2) this form of heterogeneity also depends on other abiotic factors (e.g., slope, soil type, upslope accumulated area), which can be considered static over relevant times scales [*Moorcroft*, 2006]. As such, the concept of soil CO₂ response units (CRUs) can help scale soil CO₂ efflux rates from single- or multiple-point measurements to watershed scales or larger areas.

Determining the minimum set of watershed measurements or variables needed to characterize soil CO₂ efflux both spatially and temporally is not trivial. However, new terrain analysis techniques [*McGlynn and McDonnell*, 2003a; *McGlynn and Seibert*, 2003; *McGuire et al.*, 2005; *Seibert and McGlynn*, 2007; *Welsch et al.*, 2001] can help link spatial watershed patterns with biogeochemical processes, aid in transfer and interpolation, and indicate where additional field observations are needed. The new process knowledge gained from such observations [as proposed by *Seibert and McDonnell*, 2002] can help characterize the landscape, discretely or continuously, as an arrangement of response characteristics and thresholds. These predictable, spatially-variable environmental thresholds can be used to extrapolate from point measurements of soil CO₂ efflux to watershed scales to the meso-scale ($>10^6$ m²) by progressively introducing process understanding of the spatial and temporal patterns in the biophysical controls of efflux.

Temporal Corroboration

In a similar way that spatial upscaling can be implemented from single- or multiple-point measurements, the temporal dynamics of each CRU can be investigated and used to extrapolate to larger areas. However, to date, this corroborative exercise remains to be tested in heterogeneous landscapes, as only a few studies have evaluated soil CO₂ efflux dynamics as a result of the variability in its biophysical controls. For example, temporal dynamics of soil CO₂ efflux have been generally investigated along transects (<10² m in length) extending between two trees [e.g., *Scott-Denton et al.*, 2003; *Tang and Baldocchi*, 2005] and at frequency intervals of 2-4 weeks. However, rarely do those transects extend across environmental gradients of soil temperature, soil moisture, and soil type (or comparable to the abovementioned CRUs), and seldom are those measurements applied at frequencies higher than every 2-4 weeks. Pacific et al. [in review] analyzed soil CO₂ efflux measurements across riparian-hillslopes transitions based on soil gas wells and discrete chamber measurements performed 2-3 times per week. Their results show that soil CO₂ efflux rates differ, both in magnitude and timing, across riparian-hillslope transitions. While early in the growing season soil CO₂ efflux is higher in hillslopes than in riparian areas, later in the season soil CO₂ efflux from riparian areas becomes higher than in hillslopes. These findings demonstrate how, at a minimum discretization into riparian and hillslope areas, the concept of CRUs can help extend understanding and measurements of soil CO₂ efflux based on benchmark measurements to larger areas of the landscape. Further benefits of this approach can be gained by measuring soil CO₂ efflux from different CRUs using the soil CO₂ profile technique,

which can improve the temporal resolution of soil CO₂ efflux rates. This technique, already tested in multiple ecosystems [*Suzuki et al.*, 2006; *Tang et al.*, 2003; *Tang et al.*, 2005; *Vargas*, 2007], appears promising but remains to be tested across strong environmental gradients within single ecosystems.

Reconciling Measurements of Soil CO₂ Efflux and NEP: A Case Study

One of the main objectives of the North American Carbon Program (NACP) is the intercomparison of results from interdisciplinary studies as a means to understand the controls of the sink/source status of ecosystems. Traditionally, studies addressing the variability of soil CO₂ efflux have been performed at the point or multiple-point scale [*Fang and Moncrieff*, 1996; *Tang et al.*, 2003; *Welsch and Hornberger*, 2004], but the utilization of these or similar studies to estimate rates of soil CO₂ efflux from larger areas, such as entire watersheds, is not well documented. This is partially because of discrepancies of temporal resolution among techniques (e.g., soil chambers vs. soil CO₂ probes), poor spatial coverage of the measurements (i.e., measurements are made at only few sites), but more commonly, complications of heterogeneous landscapes.

To illustrate the importance of accurate reconciliation of CO₂ flux measurements, we compared discrete soil CO₂ efflux measurements taken at 62 sites throughout a growing season by the soil respiration chamber technique with nighttime R_E estimated by the EC technique at a subalpine forest in Central Montana (Figure 2.2). By simply plotting cumulative seasonal fluxes from all methods, it is evident that R_E by the EC technique represents an integration of the heterogeneity in the landscape observed by soil respiration chambers (Figure 2.3). Furthermore, selecting an R_S value from only one site

without taking into account the natural range of variability of the landscape (Figure 2.3) could cause severe overestimation or underestimation in the R_S/R_E ratio. Further characterization of soil CO₂ efflux heterogeneity and its response to a range of biophysical controls is necessary to reduce equifinality, provide process understanding of within ecosystem dynamics, and increase confidence in measurements of ecosystem responses to environmental changes.

By aggregating soil CO₂ efflux across 62 landscape positions into single toposequences, we found good correlations between upslope accumulated area [UAA; *Seibert and McGlynn, 2007*] and average annual rates of soil CO₂ efflux along moderately sloping SE aspects ($r^2 = 0.82$) and NW aspects ($r^2 = 0.96$) (Figure 2.4). The positive correlation between soil CO₂ efflux and UAA is to be expected in water-limited systems as soils downslope receive soil water drainage from larger areas of the landscape [*Beven and Kirkby, 1979*]. Aspect differences are attributed to soil temperatures 1.96 °C higher in SE aspects than in NW aspects, based on the average of soil temperature measurements over two growing seasons. This suggests that variables including radiation potential and UAA (landscape position) need to be considered to explain landscape-scale soil CO₂ efflux. Moving from these toposequences in the downslope direction toward the riparian meadows, the soil remains saturated more days of the year. In riparian zones, the seasonal soil water content drydown becomes the dominant temporal control on soil CO₂ efflux, as it affects both production of CO₂ and diffusion of CO₂ through the soil column [*Riveros-Iregui et al., 2007*].

Based on the observations presented above, we developed simplifying assumptions about the relationships between landscape position, aspect, and seasonal CO₂ efflux. We applied the concept of CRUs to this catchment using topographic analyses of 3-m and 10-m digital elevation models (DEMs; [Figure 2.2]). Our results revealed that riparian areas comprise ~1.7% of the landscape, whereas NW aspects represent ~49.7% and SE aspects ~48.4% of the landscape. Application of the relationships between UAA and soil CO₂ efflux (Figure 2.4) for each dominant aspect across the range of UAA throughout the catchment (Figure 2.5), allowed estimation of soil CO₂ efflux rates from each CRU (two aspect classes and riparian areas [Table 2.2]).

Our approach allowed for catchment scale (393 ha), soil-based CO₂ efflux estimation and comparison against independent nighttime ecosystem respiration measured by the eddy covariance method at two locations (an upland tower and a riparian tripod). Our results indicated that while nighttime R_E was highest in the riparian meadows, these areas are small and their contribution to total R_E is less than the rest of the forest (Table 2.2). Area-weighted soil CO₂ efflux (R_S) from the entire 393-ha catchment comprised ~94% of the measured nighttime catchment R_E (Table 2.2), demonstrating that nighttime R_E was comprised mostly of soil CO₂ efflux. Further analysis to determine susceptibility of soil CO₂ efflux measurements to time-of-day biases demonstrated that on a seasonal basis, soil CO₂ efflux measurements were not biased by time of the day at which sampling occurs [*Riveros-Iregui et al.*, in review]. While we acknowledge potential underestimation of nighttime R_E compared to total R_E , [*Black et al.*, 2000; *Jarvis et al.*, 1997; *Valentini et al.*, 2000], our approach is intended to

provide a first-order reconciliation example given that causes and theory of daytime correction of EC measurements remain amply debated [e.g., *Massman and Lee*, 2002; *Paw et al.*, 2000, and as discussed in Section 2]. Nonetheless, our results illustrate that the addition of soil CO₂ efflux rates from different CRUs, and from spatial scales comparable to EC, can help reconcile independent measures of R_S and R_E , increase confidence in R_S/R_E ratios from heterogeneous landscapes, and reduce uncertainty in NEP rates based on the EC technique.

The systematic corroboration of empirical estimates of CO₂ flux at both the soil and canopy levels can be a robust technique to investigate interconnected processes of C exchange at the watershed level. Because only so many CRUs can be instrumented and so many soil CO₂ efflux measurements made across large scales before this approach becomes unfeasible, we anticipate that the optimal gain in measurement confidence will be most significant at the canopy to watershed scale (Figure 2.6). However, knowledge gained from nested corroboration at these scales can be extrapolated to other watersheds within similar biomes (e.g., within the northern Rocky Mountains as in the case presented above) to improve our understanding of ecosystem C exchange across larger regions. The proposed approach can subsequently be tested against other techniques at similar spatial scales, such as forest inventories and satellite-based estimates of GPP. We further suggest that this characterization using nested corroboration could be used in association with rates of biometric NPP and MODIS GPP for empirical intercomparison of measurements and technique uncertainty assessment, systematically progressing from the point scale to the watershed scale to larger scales. The synergistic nature of this approach

can be of significant benefit to interdisciplinary studies working at a range of spatial scales because it can 1) provide immediate bidirectional feedback for each site where these techniques are applied, advancing process understanding and model parameterization in that particular system; 2) allow for site comparison and context, that is, evaluation and assessment of how that particular site compares to other sites around the world (e.g., subalpine vs. boreal); and 3) increase confidence in MODIS estimates performed at sites where no land-based data are available for corroboration. The latter rationale poses substantial importance, as the valuable spatial coverage of MODIS is currently compromised by the confidence deficit of its measures.

The accuracy of modeled predictions of C ecosystem dynamics relies on the correctness of empirical measurements [Moorcroft, 2006]. The greatest source of uncertainty in ecosystem models is posed by the large heterogeneity and poor understanding of R_E [Moorcroft *et al.*, 2001]. Improved estimates of R_E based on empirical data can reduce model uncertainty in predictions of long-term EC and biometry. Thus improved process understanding and estimation of soil CO₂ efflux from large areas and its contribution to R_E is crucial for current and future efforts to measure and predict ecosystem C dynamics.

Conclusions

In this manuscript, we suggest that the reconciliation of direct NEP estimates (tower-based) with other independent measurements (soil chambers, biometry, satellites) is critical for determining ecosystem C balance, improving process understanding of

whole-ecosystem processes, promoting ecological modeling, and enhancing our ability to predict ecosystem-level responses to changes in environmental conditions. We focused on four of the most common techniques used to quantify ecosystem C fluxes: soil respiration methods, eddy covariance, biometric-based NPP, and satellite-based measures of GPP. Each technique is valuable within its own spatial and temporal resolution boundaries. However, reconciling C flux rates from each technique to the ecosystem level is important to gain confidence in each technique, as well as in NEP estimates from large spatial and temporal scales. Area-weighted soil CO₂ efflux from different landscape elements of a 393-ha subalpine catchment comprised ~94% of the measured nighttime catchment ecosystem respiration, demonstrating that the characterization of soil CO₂ efflux rates from entire watersheds can increase confidence in tower measurements, as well as facilitate reconciliation of C fluxes measured by other techniques at similar spatial scales. Soil CO₂ response units that account for the characteristic response of different landscape elements can improve estimates of watershed-scale soil CO₂ efflux over estimates that do not account for organized heterogeneity. These estimates can then be transferred to nearby watersheds with comparable characteristics to obtain soil-level estimates at spatial scales that can be useful for comparison with biometric or MODIS-based NPP estimates at regional scales. More long-term comparison studies are needed, particularly addressing the spatiotemporal heterogeneity of soil CO₂ efflux and its biophysical controls, as well as attempting the spatial collocation of multiple techniques.

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Table 2.1 Comparison of soil CO₂ efflux and tower-based ecosystem respiration (R_S/R_E) among different ecosystems. While many flux tower sites have measured land-atmosphere CO₂ exchange for nearly a decade, lack of soil CO₂ efflux rates at spatial scales comparable to towers hampers corroboration of these two fluxes. Even fewer studies have estimated R_S/R_E rates across seasons.

CRU Description	Percent Cover	Chamber-based R_S [g CO ₂ m ⁻²]	Percent Cover	Tower-based nighttime R _E Forest [g CO ₂ m ⁻²]	Tower-based nighttime R _E Ripar. [g CO ₂ m ⁻²]
Riparian Area	1.7%	1408.5	1.7%		935.4
SE Aspects	48.4%	842.4	98.1	786.8	
NW Aspects	49.7%	627.0			
Area-weighted total	99.8%	743.2	99.8%	787.8	

Table 2.2 Modeled CO₂ efflux rates for different CO₂ response units (CRU) in a subalpine forest, and measured nighttime R_E during the 2006 growing season. Area-weighted, seasonal CO₂ efflux from chamber-based comprises 94% of nighttime ecosystem respiration.

Study	Location	Type of Ecosystem	R_S/R_E
<i>Goulden et al.</i> [1996]	Massachusetts, USA	Mid-latitude deciduous forest	0.68
<i>Lavigne et al.</i> [1997]	Central Canada	Black spruce and jack pine boreal forests	0.48-0.71
<i>Norman et al.</i> [1997]	Central Canada	Black spruce and jack pine boreal forests	0.33-0.50
<i>Law et al.</i> [1999]	Central Oregon, USA	Ponderosa pine forest	0.76
<i>Subke and Tenhunen</i> [2004]	Fichtelbebirge mountains, Germany	Norway spruce forest	0.41
<i>Reth et al.</i> [2005]	Lindenberg, Germany	Tilled meadow	0.90
<i>Davidson et al.</i> [2006]	Maine, USA	Red spruce and eastern hemlock mid-latitude forest	0.45 0.65 (summer) 0.80 (fall)
<i>Jassal et al.</i> [2007]	Pacific Coast, Canada	Douglas fir forest	0.52 0.63 (summer) 0.81 (fall) 0.86 (winter)
This study	Central Montana	Lodgepole pine forest	0.94 (Nighttime R_E)

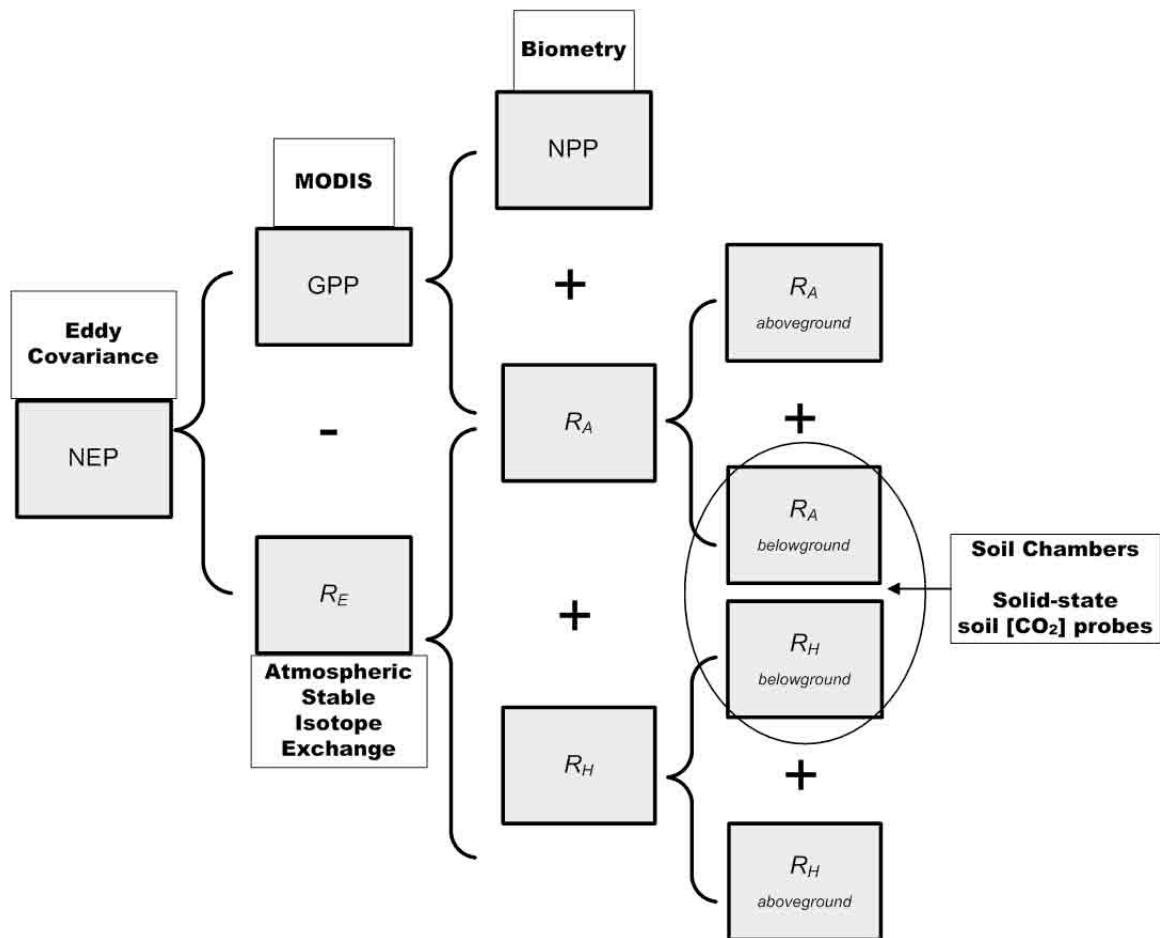


Figure 2.1 Net Ecosystem Production and its photosynthetic and respiratory fluxes. R_A represents autotrophic respiration and R_H represents heterotrophic respiration. Gray boxes represent fluxes and white boxes represent current methods to estimate the associated flux.

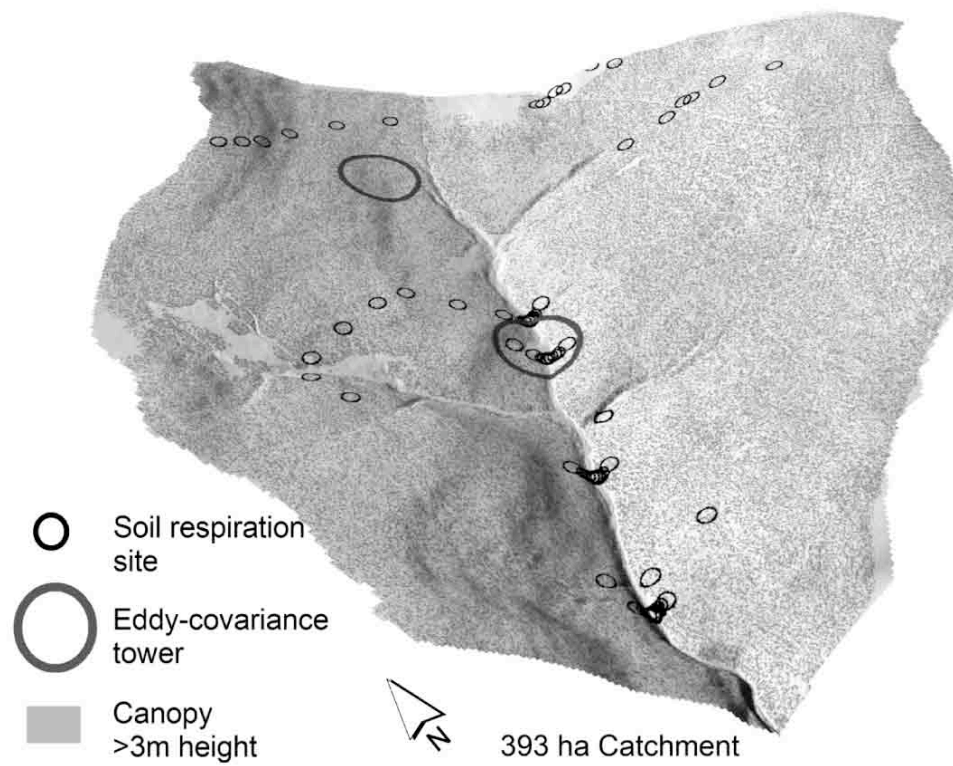


Figure 2.2 Location of the Tenderfoot Creek Experimental Forest (TCEF) in the Little Belt Mountains of Central Montana. The area of study is a 393 ha catchment.

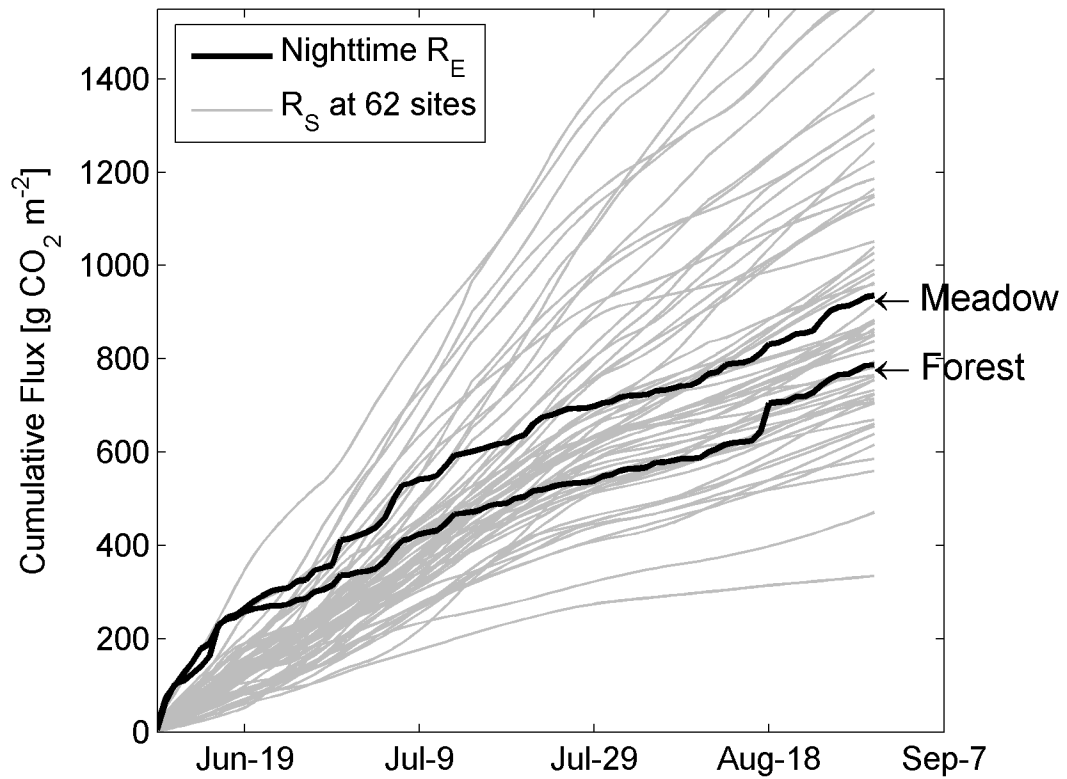


Figure 2.3 Comparison of cumulative CO₂ fluxes for the entire 2006 growing season at a subalpine forest. Bold lines denote nighttime R_E measured with the EC technique. Gray lines denote soil CO₂ efflux (R_S , or the sum of the belowground components of R_A and R_H , as presented in Figure 2.1) at 62 sites distributed throughout the meadow and forest. R_S rates are estimated from discrete measurements by the soil respiration chamber technique. These results demonstrate by selecting an R_S rate from only one site without taking into account the natural range of variability, the R_S/R_E ratio of this ecosystem will be easily overestimated or underestimated.

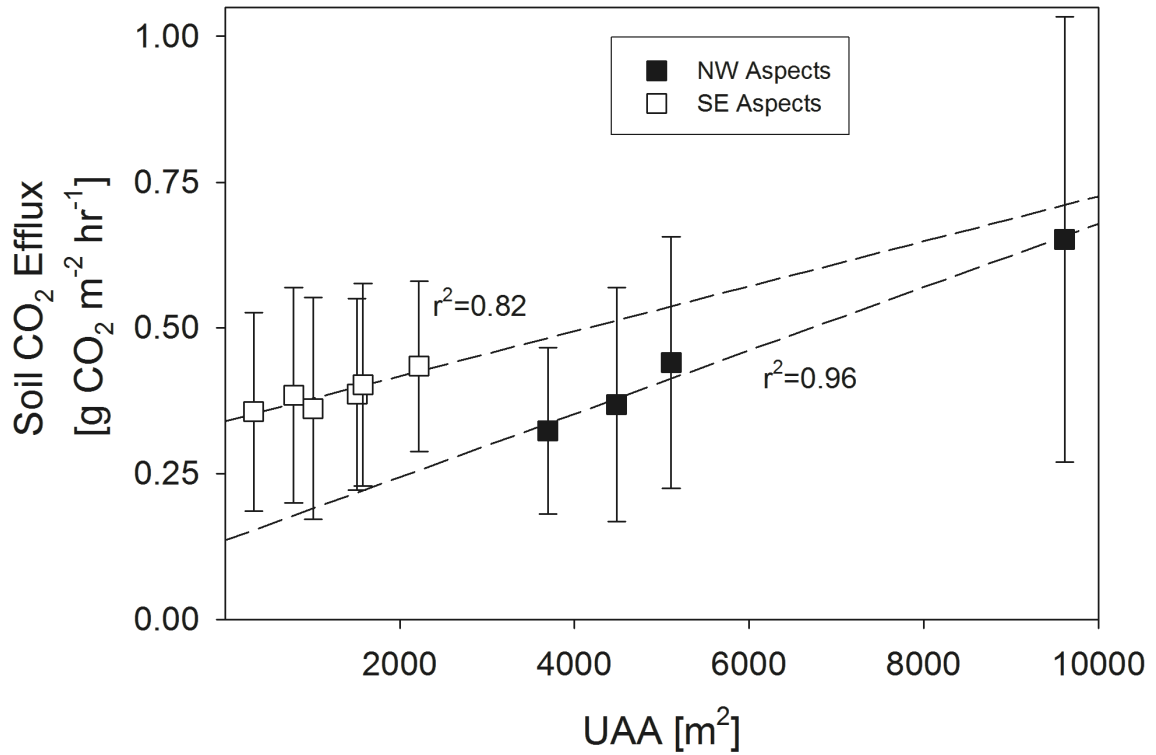


Figure 2.4 Relationship between upslope accumulated area (UAA) and mean soil CO₂ efflux rates along two single toposequences: a SE facing and a NW facing. Bars indicate one standard deviation (n=16 and n=22, for NW and SW aspects, respectively). Soil temperature was on average 1.96 °C lower in NW aspects than in SW aspects. UAA was estimated using a 10-m digital elevation model (DEM) derived from a 1-m Airborne Laser Swath Mapping DEM, according to *Seibert and McGlynn* [2007].

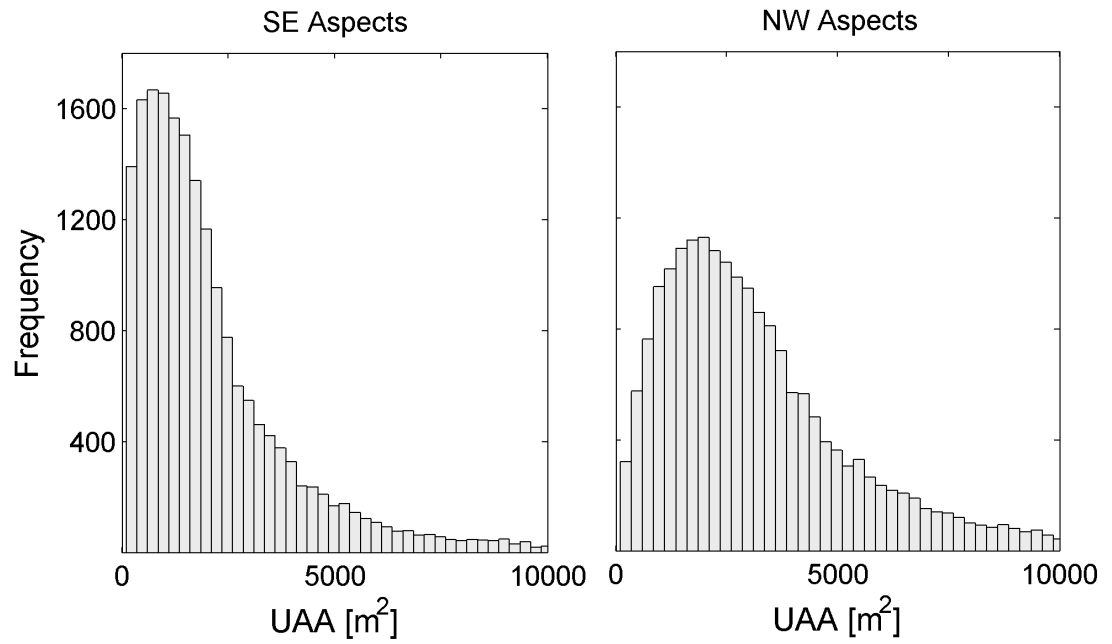


Figure 2.5 Distribution of upslope accumulated area (UAA) and aspect within the area of study. UAA was estimated using a 10-m digital elevation model (DEM) derived from a 1-m Airborne Laser Swath Mapping DEM, according to *Seibert and McGlynn* [2007].

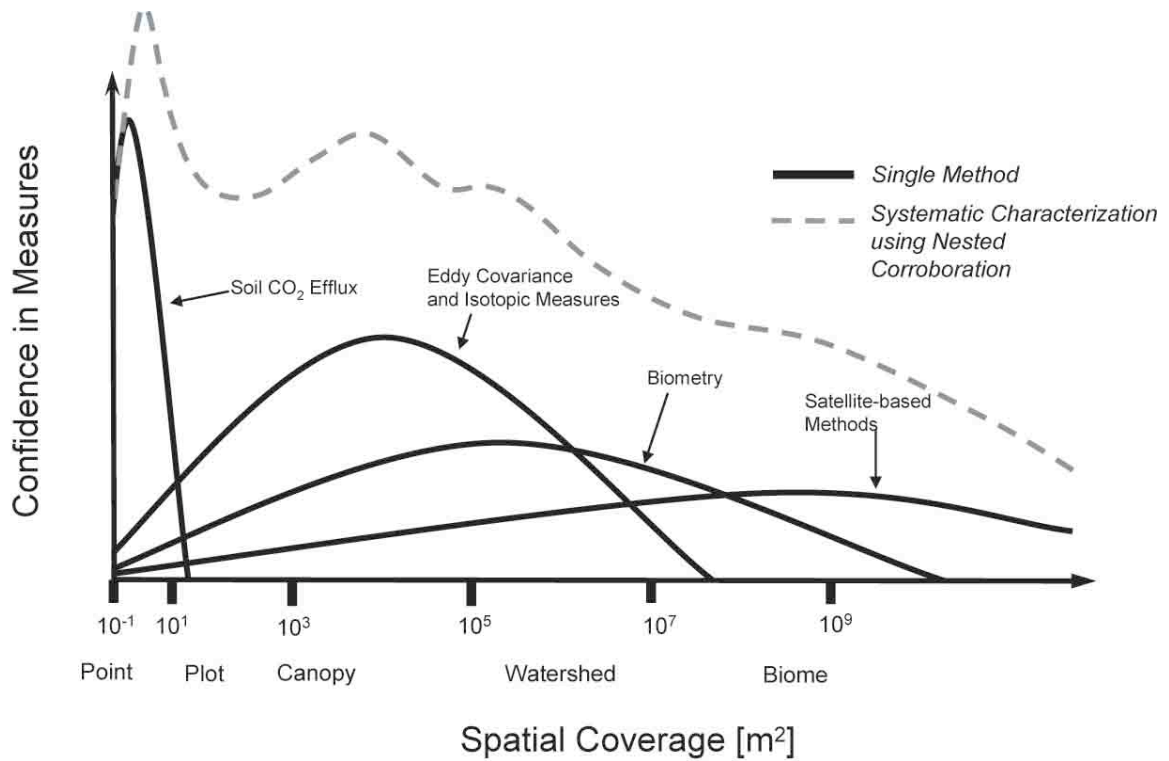


Figure 2.6 Systematic characterization of land-atmosphere CO₂ exchange can be used as an empirical approach to reconcile multiscale approaches in C cycle science and reduce uncertainty in multiple measurements within a particular system. The relative gain in measurement confidence can be particularly significant at the watershed level with the intersection of scale and uncertainty measurement.

CHAPTER 3

DIURNAL HYSTERESIS BETWEEN SOIL CO₂ AND SOIL TEMPERATURE IS
CONTROLLED BY SOIL WATER CONTENT

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Abstract

Recent years have seen a growing interest in measuring and modeling soil CO₂ efflux, as this flux represents a large component of ecosystem respiration and is a key determinant of ecosystem carbon balance. Process-based models of soil CO₂ production and efflux, commonly based on soil temperature, are limited by nonlinearities such as the observed diurnal hysteresis between soil CO₂ concentration ([CO₂]) and temperature. Here we quantify the degree to which hysteresis between soil [CO₂] and soil temperature is controlled by soil water content in a montane conifer forest, and how this nonlinearity impacts estimates of soil CO₂ efflux. A representative model that does not consider hysteresis overestimated soil CO₂ efflux for the entire growing season by 19%. At high levels of soil water content, hysteresis imposes organized, daily variability in the relationship between soil [CO₂] and soil temperature, and at low levels of soil water content, hysteresis is minimized.

Introduction

Soil CO₂ efflux, often referred to as soil respiration, is a substantial component of the carbon budget for terrestrial ecosystems [Valentini *et al.*, 2000; Barford *et al.*, 2001; Schimel *et al.*, 2001], and it is an important part of the global carbon cycle [Raich and Schlesinger, 1992; Schlesinger and Andrews, 2000; Ryan and Law, 2005]. Rates of soil respiration are correlated with soil temperatures across multiple spatial and temporal scales [Raich and Potter, 1995; Risk *et al.*, 2002]. As such, soil temperature plays an important role in many model representations of soil CO₂ production and transport [Lloyd and Taylor, 1994; Winkler *et al.*, 1996; Fang and Moncrieff, 2001; Reichstein *et al.*, 2003]. However, interactions among environmental variables such as temperature and soil moisture may introduce uncertainty into these models. Among the sources of uncertainty in models of soil CO₂ production and transport is daily hysteresis between soil CO₂ flux and soil temperature [Parkin and Kaspar, 2003; Tang *et al.*, 2005; Gaumont-Guay *et al.*, 2006].

Because soil CO₂ flux is controlled by soil [CO₂] [Hirano *et al.*, 2003; Tang *et al.*, 2005; Baldocchi *et al.*, 2006], we investigated hysteresis between soil [CO₂] and soil temperature. Such hysteretic, nonlinear behavior results from diurnal variations in soil [CO₂] and soil temperature that are out of phase with each other, limiting the ability of many power or exponential models (e.g., Q₁₀ [Winkler *et al.*, 1996], Arrhenius [Lloyd and Taylor, 1994]) to adequately predict soil respiration as a function of soil temperature [Davidson *et al.*, 2006]. While hysteresis has been previously observed in natural systems [O’Kane, 2005; O’Kane and Flynn, 2007], a satisfactory explanation of

hysteresis in the context of the soil [CO₂] - soil temperature relationship remains unknown. Our objectives are 1) to demonstrate the decay of hysteresis in diurnal cycles of soil [CO₂] - soil temperature relationships as a function of seasonality (i.e. soil water content) in a typical northern Rocky Mountain forest, 2) to discuss the role of hysteresis as a source of uncertainty in the relationship between soil temperature and soil respiration, and 3) to propose a theoretical explanation for the emergence of hysteretic behavior.

Methods

We collected 89 days of data during the 2006 growing season in a montane conifer forest in the northern Rocky Mountains. This location is subject to a seasonal drydown in soil water content [*Woods et al.*, 2006] and is representative of the high-altitude, semi-arid forests of the western United States. These areas are known to contribute significantly to the North American carbon sink [*Schimel et al.*, 2002; *Monson et al.*, 2006]. We measured soil temperature (T_s ; CSI Model 107, Campbell Scientific Inc., Logan, UT), volumetric soil water content (θ ; CSI Model 616, Campbell Scientific Inc., Logan, UT), and soil [CO₂] (GMP221 with transmitter, Vaisala, Helsinki, Finland) at 20 cm below the soil surface, logging continuously at 20-minute intervals in a datalogger (model CR10x, Campbell Scientific Inc., Logan, UT). Soil [CO₂] was corrected for temperature and pressure following compensatory procedures described by Tang et al. [2003]. The predominant vegetation in the understory is bluejoint reedgrass (*Calamagrostis canadensis*). Additionally, we measured precipitation and

photosynthetically active radiation (PAR) during the same period in a clearing 50 m away. For each day of the growing season, we calculated the magnitude of hysteresis (H_M) as the range of the residuals of a linear least-squares regression between soil $[CO_2]$ and soil temperature, projected on an axis perpendicular to the regression slope. In estimating H_M , we calculated the slope angle after rescaling the entire seasonal range of $[CO_2]$ and temperature from 0 to 1. This metric provides a simple means of quantifying H_M for comparison between days. The absolute scale of H_M is determined a priori by the range of variability in the original data.

Results

During the growing season, soil $[CO_2]$ declined in response to the seasonal drying of the soil, yet fluctuated daily with soil temperature (Figure 3.1). Soil $[CO_2]$ also responded to periodic precipitation. The relationship between soil $[CO_2]$ and T_S is presented in Figure 3.2. When viewed in aggregate, the relationship between 20-minute measurements of soil $[CO_2]$ and T_S appears disorganized (Figure 3.2A). However, it is actually a superposition of highly organized daily hysteresis loops (Figure 3.2B). An important characteristic of these data is a decline in H_M that corresponds to θ , or seasonality, as these two factors are correlated. Early in the growing season, the relationship exhibits considerable hysteresis, but H_M decays until the relationship between soil $[CO_2]$ and T_S is nearly linear (i.e., little or no hysteresis) by the end of the growing season.

To illustrate the decay in hysteresis through the growing season, we present H_M as a function of time (Figure 3.3A) and θ (Figure 3.3B). We observed an apparent change in dynamics of the system at θ levels above approximately $0.25 \text{ m}^3 \text{ m}^{-3}$. Above this water content, H_M is large and exhibits a high degree of variability, ranging from approximately 1000 ppm to 4000 ppm. For drier conditions, H_M is much lower and less variable, ranging from approximately 100 ppm to 1400 ppm. The magnitude of hysteresis increases following late season precipitation events (e.g., on August 18). This supports the argument that H_M is a function of soil moisture; however, large increases in H_M associated with small increases in soil moisture following late season precipitation suggest that the relationship between H_M and θ is both nonlinear and season-dependent.

Discussion

Previous studies [Parkin and Kaspar, 2003; Tang *et al.*, 2005; Gaumont-Guay *et al.*, 2006] have reported the existence of hysteresis between soil $[\text{CO}_2]$ and T_s . However, to date a mechanistic explanation of the processes inducing this hysteresis and determining its seasonal variability is still missing. Lack of a process-based understanding of soil moisture controls on soil respiration limits our ability to assess CO_2 fluxes from terrestrial ecosystems under current and future climate conditions. Having quantified H_M , we now present a framework for explaining the mechanisms underlying the observed hysteresis between soil temperature and soil $[\text{CO}_2]$ and its effects on soil CO_2 production and efflux.

The dynamics of the gas-phase CO₂ can be explained by the following equation [Suwa *et al.*, 2004]:

$$\frac{\partial f_a [\text{CO}_2]}{\partial t} = -\frac{\partial F}{\partial z} + S \quad (3.1)$$

where f_a is the air-filled porosity, S is the net source of the gas-phase CO₂, and F is given by the following relationship:

$$F = -D(f_a) \frac{\partial [\text{CO}_2]}{\partial z} \quad (3.2)$$

where D is the diffusion coefficient of CO₂ in the air-filled pore space. Combining Equations 3.1 and 3.2 and assuming that soil moisture does not vary over the course of a day, the daily dynamics of the gas-phase CO₂ in the soil are explained by:

$$f_a \frac{\partial [\text{CO}_2]}{\partial t} = -\frac{\partial}{\partial z} \left[D(f_a) \frac{\partial [\text{CO}_2]}{\partial z} \right] + k_A(PAR, \theta) + k_H(T_s, \theta) \quad (3.3)$$

where k_A and k_H are the rates of CO₂ production from autotrophic and heterotrophic activities, respectively. Diffusivity of CO₂ in the gas phase is about 10,000 times higher than in the liquid phase [Šimůnek and Suarez, 1993; Welsch and Hornberger, 2004], therefore we assume that solubility of the gas-phase CO₂ is negligible. We note that PAR and T_s vary in time on a daily basis and θ varies in time on a seasonal basis. We also note that changes in θ influence two key physical attributes of the soil: 1) the CO₂ diffusivity, which can be seen directly in Equation 3.3 and 2) the thermal diffusivity [Oke, 1987], which induces lags between air temperature and soil temperature as daily variations in PAR influence the air temperature.

Since PAR reaches a maximum earlier in the day than soil temperature (resulting from delayed heat propagation through the soil, Figure 3.4A), there is a time lag between daily maxima of k_A and k_H , as autotrophic respiration responds to PAR [Liu *et al.*, 2006] and air temperature, whereas heterotrophic respiration responds primarily to soil temperature [Lloyd and Taylor, 1994; Winkler *et al.*, 1996]. This time lag creates hysteresis between soil temperature and the accumulation of CO_2 at a specific depth (Figure 3.4B). However, if D is large enough to facilitate transport of autotrophic and heterotrophic CO_2 from the soil (such as during dry or late-season conditions), the system remains at or near steady state throughout the day, where $\partial[CO_2]/\partial t \approx 0$ (e.g., August 28). Under steady state conditions, production of CO_2 ($k_A + k_H$) and transport

$(-\frac{\partial}{\partial z}[D\frac{\partial[CO_2]}{\partial z}])$ are balanced and there is little or no hysteresis between T_S and soil $[CO_2]$.

During wet conditions, production of CO_2 prevails over transport because 1) D is much smaller than during dry conditions and 2) microbial activity is enhanced by high soil moisture [Or *et al.*, 2007]. Under such conditions, where $\partial[CO_2]/\partial t \neq 0$, hysteresis forms between soil $[CO_2]$ and T_S . Soil $[CO_2]$ increases when production of CO_2 exceeds transport, and decreases when transport exceeds production of CO_2 . The rising limb of the daily hysteresis loop ($\partial[CO_2]/\partial t > 0$) occurs when autotrophic respiration is likely to dominate CO_2 production, whereas the falling limb ($\partial[CO_2]/\partial t < 0$) occurs when heterotrophic respiration is likely to dominate CO_2 production (Figure 3.4B). As a result of the daily lag between k_A and k_H , well-defined daily hysteresis loops may allow visualization of contributions of autotrophic and heterotrophic activities to total soil CO_2 production.

In our study system, the time of daily maximum soil $[\text{CO}_2]$ fell between the times of daily maximum PAR and daily maximum T_s . While it is known that root respiratory fluxes can lag PAR by times that vary from hours to weeks [Stoy *et al.*, 2007], it has been suggested that this time may be very short for understory grasses [<4 h, Carbone and Trumbore, 2007]. Furthermore, Carbone and Trumbore [2007] and similar soil respiration studies [Carbone *et al.*, 2007; Stoy *et al.*, 2007], used soil efflux chambers to measure soil respiration at the soil surface. In our study, we measured soil CO_2 concentrations (soil $[\text{CO}_2]$) in the root zone, thereby excluding the time lag introduced by diffusive transport of CO_2 from the root zone to the soil surface. This greatly shortens the time lag between PAR and the measured respiratory increase caused by plant activity. The sequence of daily maxima (PAR , soil $[\text{CO}_2]$ and T_s , Figure 3.4A) generates a clockwise pattern of hysteresis between soil $[\text{CO}_2]$ and T_s (Figure 3.4B). In the hypothetical absence of a PAR effect on soil $[\text{CO}_2]$ (i.e., no contribution from k_A), clockwise hysteresis may not develop since daily maximum in soil $[\text{CO}_2]$ may not occur before daily maximum in T_s . In fact, counterclockwise hysteresis loops have been reported [Parkin and Kaspar, 2003; Tang *et al.*, 2005; Gaumont-Guay *et al.*, 2006], which suggests that PAR has a smaller effect on soil $[\text{CO}_2]$ in those systems than in ours. By altering thermal diffusivity of the soil, θ affects the time lag between daily maximum PAR and daily maximum T_s contributing, although only to a degree, to hysteresis in this system. As the soil becomes drier, microbial activity declines and the time lag between PAR and T_s decreases due to accelerated soil heat diffusion.

Conclusions

During the early (wet) growing season ($\theta > 0.25 \text{ m}^3\text{m}^{-3}$), hysteresis has a strong effect on the relationship between soil $[\text{CO}_2]$ and soil temperature. Although the relationship is highly organized, soil temperature alone is insufficient to explain changes in soil $[\text{CO}_2]$. The seasonality of soil water content introduces physical effects on soil CO_2 diffusivity and thermal diffusivity that must be considered to explain more fully the response of soil $[\text{CO}_2]$ to soil temperature. Late in the growing season when the soils are drier, hysteresis diminishes and the relationship between these two variables is much more linear. During these periods, traditional relationships between soil $[\text{CO}_2]$ and soil temperature (e.g. Q_{10} , Arrhenius) apply, except after isolated rainfall episodes. Based on chamber measurements at our site, a developed Q_{10} relationship overestimates CO_2 flux by 42 g C m^{-2} (19%) for the entire growing season due to its inability to account for the daily cycle of soil $[\text{CO}_2]$, the variability of soil moisture, and moisture-dependent diffusive transport of CO_2 through the soil column. Only under late-season dry conditions is the Q_{10} relationship able to predict CO_2 flux.

These results have implications for quantitative assessment, process-based understanding, and modeling of production and efflux of CO_2 from soils subjected to strong diurnal and seasonal changes in temperature and moisture. In this study, we demonstrate that diurnal hysteresis between soil $[\text{CO}_2]$ and soil temperature is due mostly to the balance (or imbalance in wet soils) between production and diffusion. The seasonality in soil moisture controls the transition from an imbalanced system (where diurnal hysteresis is observed) to a balanced system (no diurnal hysteresis observed).

The magnitude of hysteresis in the soil [CO₂] – soil temperature relationship is an important indicator of the existence of concomitant, yet independent, autotrophic and heterotrophic soil [CO₂] processes. As such, the role of soil water content in controlling the relationship between soil [CO₂] and soil temperature should be considered when modeling the dynamics of carbon cycling in ecosystems with strong seasonality in soil water content.

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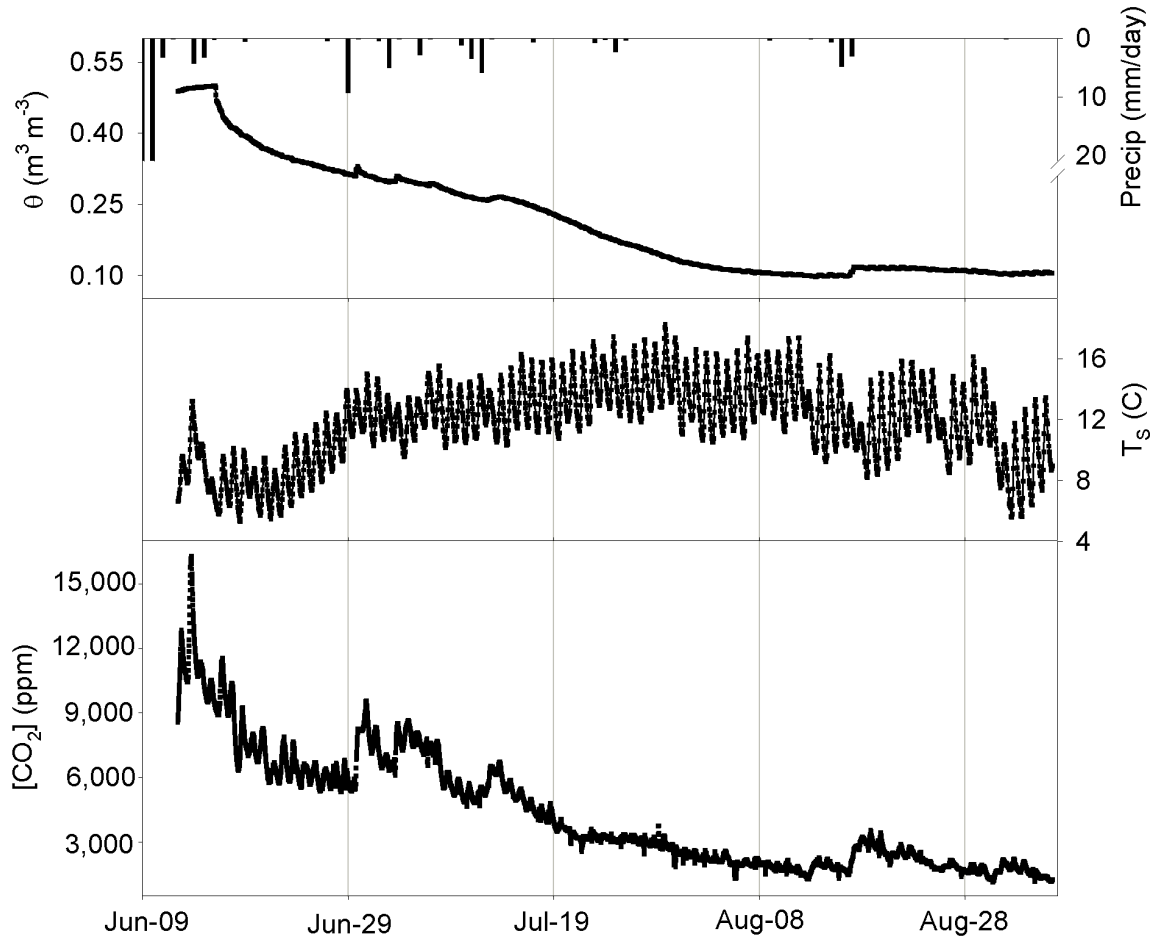


Figure 3.1 Variability of soil water content and precipitation (top), soil temperature (middle) and soil $[\text{CO}_2]$ (bottom) for the duration of the study. Measurements are taken at 20-min intervals for the duration of the study. Precipitation is added on a daily basis.

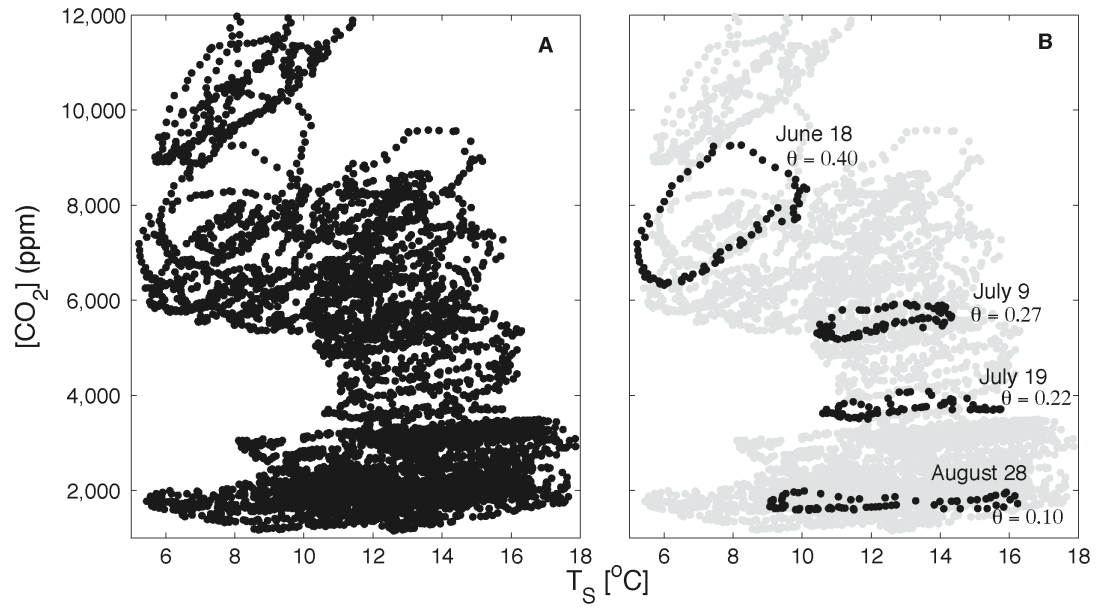


Figure 3.2 (A) Relationship of soil $[\text{CO}_2]$ and soil temperature at 20-min intervals for the duration of the study. (B) Highlighted evolution of hysteresis throughout the growing season. Soil water content values are given in parentheses for each highlighted day.

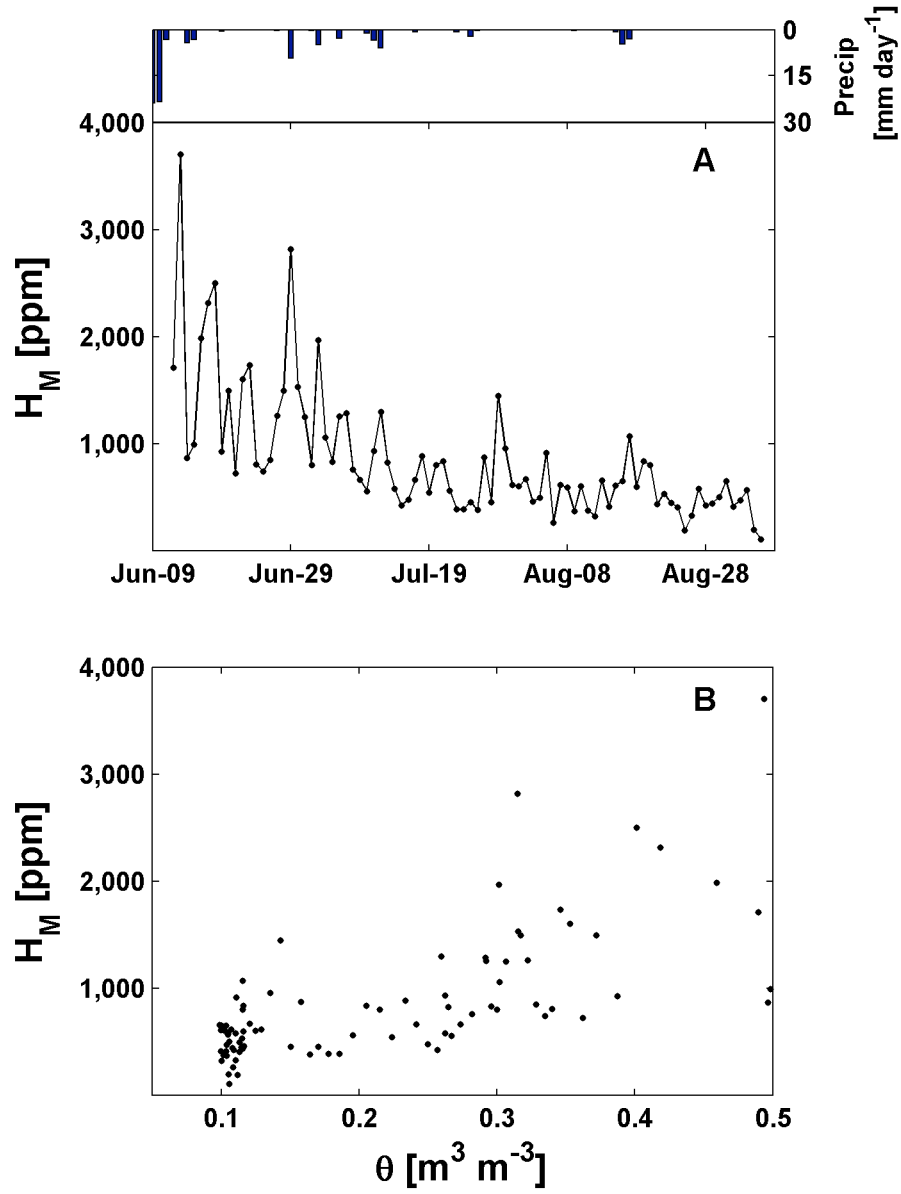


Figure 3.3 (A) Magnitude of hysteresis H_M throughout the growing season. (B) Relationship of H_M and soil water content (θ).

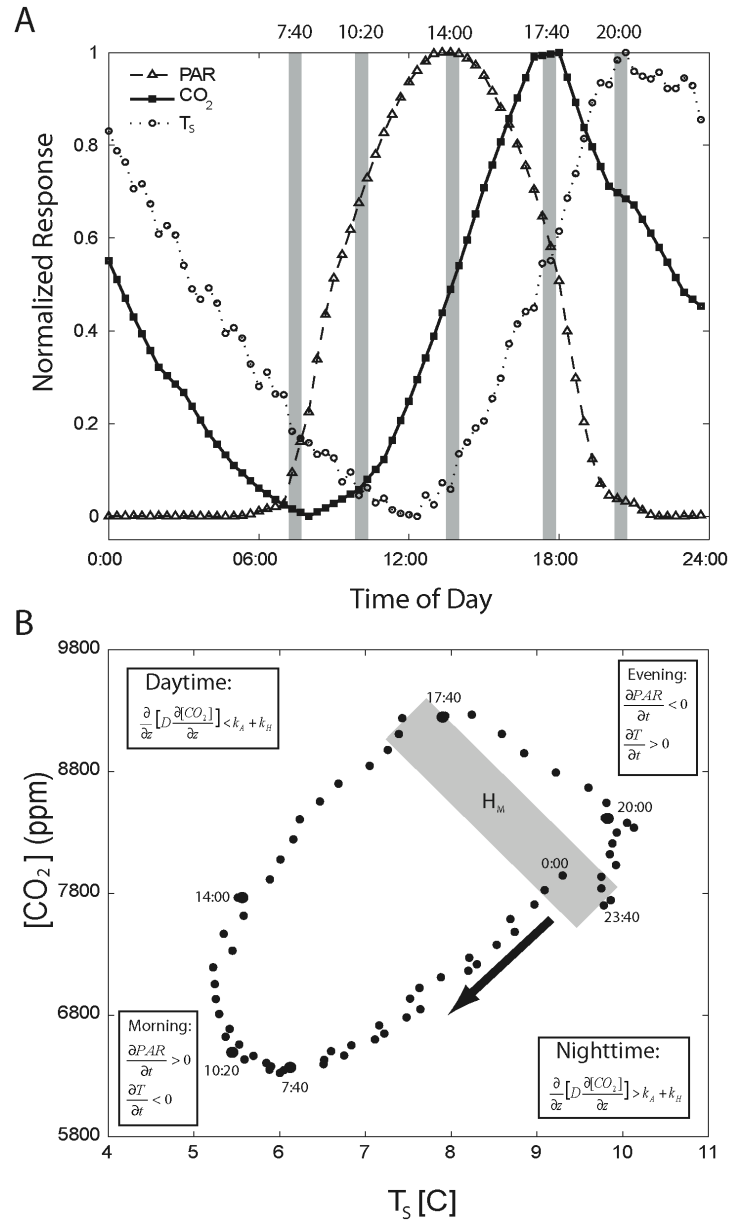


Figure 3.4 (A) Normalized response of PAR, soil $[\text{CO}_2]$, and soil temperature on June 18. Shaded areas are the indicated times of the day in Figure 3.4B (B) Hysteresis between soil $[\text{CO}_2]$ and soil temperature on the same day. The direction of the hysteresis loop is indicated by the arrow. In the morning hours, soil $[\text{CO}_2]$ increases rapidly *independent* of the soil temperature. This coincides with increasing PAR levels. In the evening soil $[\text{CO}_2]$ declines as soil temperature continues to increase. This coincides with decreasing PAR levels. At night, soil $[\text{CO}_2]$ declines with decreasing soil temperature.

CHAPTER 4

INTERPRETATION AND EVALUATION OF COMBINED MEASUREMENT
TECHNIQUES FOR SOIL CO₂ EFFLUX: SURFACE CHAMBERS AND SOIL CO₂
CONCENTRATION PROFILES

Adapted from: Riveros-Iregui D.A., McGlynn, B.L., Epstein, H.E., and Welsch, D.L., (in review). Interpretation and evaluation of combined measurement techniques for soil CO₂ efflux: surface chambers and soil CO₂ concentration profiles. Submitted for publication in Journal of Geophysical Research – Biogeosciences

Abstract

Soil CO₂ 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 CO₂ efflux limits our ability to extrapolate from fluxes measured at the point scale 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 CO₂ 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 CO₂ profile technique over daily and seasonal time scales indicated that soil water content plays a major role in the magnitude and seasonality of soil CO₂ efflux, especially after snowmelt or following summer rainfall. Agreement between the techniques was limited during high soil water content conditions and after summer rainfall. Differences in diel

hysteresis patterns of soil CO₂ 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 CO₂ efflux from heterogeneous landscapes.

Introduction

Soil CO₂ efflux is a natural process by which soil carbon is released into the atmosphere through autotrophic and heterotrophic respiration. Evaluating and predicting soil CO₂ efflux response to differences in hydrologic conditions (e.g., groundwater recharge/discharge areas, soil water content, precipitation, and land cover) are largely constrained by the methods used to measure, interpret, and model soil CO₂ efflux. Rates of soil CO₂ 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 CO₂ profile technique [*Tang et al.*, 2003; *Jassal et al.*, 2005; *Tang and Baldocchi*, 2005]. Particularly in the last five years, the soil CO₂ 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 on-going studies use either technique, a direct comparison

of their performance, measurements, strengths and limitations in space and time is lacking.

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 CO₂ efflux in response to changing hydrologic conditions across space and time. Traditionally, studies addressing the variability of soil CO₂ efflux focus on its temporal component (e.g., diel, seasonal, 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 CO₂ efflux from areas having different characteristics within similar ecosystems. More importantly, this omission restricts our understanding of how CO₂ producing processes simultaneously develop in space and time to generate the soil CO₂ rates that chambers or soil profile techniques measure.

Recent studies [Riveros-Iregui *et al.*, 2007] demonstrated that soil water content controls the relationship between soil CO₂ efflux and soil temperature, as soil water content 1) enhances soil CO₂ production, and 2) inhibits soil CO₂ diffusion. Furthermore, the seasonality of soil water content can control the switch from diffusion- to production-limited soil CO₂ efflux [Riveros-Iregui *et al.*, 2007; Pacific *et al.*, in review]. This concept becomes especially important in ecosystems with considerable spatial variability in soil water content induced by landscape morphology (i.e., convex vs. concave

areas[*Scott-Denton et al.*, 2003; *Pacific et al.*, in review; *Riveros-Iregui et al.*, in review]). 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 CO₂ efflux, of heterogeneous forests. In this paper, we provide a comparison, over daily and seasonal time scales, of discrete (soil respiration chamber) and continuous (soil CO₂ profile technique) measurements of soil CO₂ efflux made at two sites: a wet riparian meadow and a dry upland forest. Both sites are co-located 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 CO₂ efflux from riparian meadows and upland forests; 2) compare the performance of soil respiration chambers and solid-state CO₂ probes throughout an entire growing season; and 3) assess, both mechanistically and methodologically, the confidence that these methods offer as providers of soil CO₂ efflux rates from heterogeneous landscapes. This information is essential to improving process understanding of soil CO₂ efflux from large areas, establishing a conceptual framework for soil CO₂ efflux modeling studies, and adding confidence to current and developing measurement techniques.

Methods

Study Site

This study was located in the Tenderfoot Creek Experimental Forest (TCEF), in the Little Belt Mountains of central Montana (Figure 4.1). 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 2,169 m and 2,305m at the riparian and upland site, 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.

Environmental Variables

Between June 9, 2006 and September 7, 2006 we measured volumetric soil water content (θ ; CSI Model 616, Campbell Scientific Inc., Logan, UT) and soil temperature (T_s ; CSI Model 107, Campbell Scientific Inc., Logan, UT) 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, UT). 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 calibrated to confirm applicability of the CSI Hydrosense instrument with regular TDR instruments ($r^2 = 0.986$). Precipitation was measured by a tipping bucket rain gauge (TR-525M, accurate to within 1% for up to 50mm/hr, Texas Electronics, Dallas, TX, USA), at 20-min intervals and reported on a daily basis.

Measurements of Soil CO₂ Efflux

Soil CO₂ efflux was measured independently at each site by the soil respiration chamber technique (discrete measurements) and by the soil CO₂ 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 CO₂ 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 cm², accuracy within 1% of calibrated range [0 to 9.99 g CO₂ m⁻² hr⁻¹], PP Systems, Massachusetts, USA) equipped with an infrared gas analyzer (IRGA; EGM-4, accuracy within 1% of calibrated range [0 to 2,000 ppm], PP Systems, Massachusetts, USA). Chamber measurements were collected in triplicate every 2-7 days at each site. At each site, a 0.5-m² 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 CO₂ efflux was calculated by measuring the rate of increase in CO₂ concentration within the chamber and fitting a quadratic equation to the relationship between the increasing CO₂ 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 h or after 1600 h.

Continuous measurements were collected with solid-state CO₂ probes (GMP221 with transmitter, Vaisala, Helsinki, Finland) installed at 5 cm below the soil surface, logging continuously at 20-minute intervals with a datalogger (model CR10x, Campbell Scientific Inc., Logan, UT). Soil CO₂ 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 CO₂ concentrations in less than 5 minutes [Tang *et al.*, 2003]. Because it is difficult to measure soil CO₂ concentrations near the soil-atmosphere interface ($z=0$), we tested the effect of three different CO₂ concentration values (350, 450 and 550 ppm) at this depth and evaluated the sensitivity of CO₂ flux estimates to near-surface CO₂ concentrations. We chose these three values based on the range of variability of initial surface CO₂ 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 CO₂ efflux, as the diel variability of soil CO₂ concentration at depth of cm is much greater than the diel

variability of soil CO₂ near 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 200 ppm confidence error (at $z=0$), an effect that remains small compared to natural diel variability of soil CO₂ at depth (>5,000 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 soil CO₂ efflux estimate techniques (see Results). Using these concentrations (0 m, 0.05 m) soil CO₂ efflux was calculated based on Fick's first law of diffusion,

$$F = -D_p \frac{\partial[CO_2]}{\partial z} \quad (4.1)$$

where F is CO₂ flux between two depths, and D_p is the diffusion coefficient for CO₂ 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]:

$$\frac{D_p}{D_o} = \Phi^2 \left(\frac{\epsilon}{\Phi} \right)^{2+\frac{3}{b}} \quad (4.2)$$

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 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]:

$$b = 13.6CF + 3.5 \quad (4.3)$$

Diffusivity of CO₂ in the gas phase is about four orders of magnitude higher than in the liquid phase [Simunek and Suarez, 1993; Welsch and Hornberger, 2004], therefore we assumed that solubility of the gas-phase CO₂ is negligible. The characterization of the distribution of new moisture inputs in the soil, particularly in arid and semi-arid environments, remains challenging due to 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; Glass *et al.*, 1989b; Baker and Hillel, 1990] and non-ponding 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 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 non-uniform conditions [Topp *et al.*, 1982a; b; Robinson *et al.*, 2003]. In doing this, we assumed a constant D_p/D_o parameter over the top 5 cm of soil. While we acknowledge potential inaccuracies introduced by this approach, current constraints of probe design make this approach a good approximation of volumetric soil water content, especially during new moisture additions. Estimation of soil CO₂ efflux by these methods (altogether known as the soil CO₂ profile, or gradient, method) has been repeatedly applied in recent studies

across multiple ecosystems [*Tang et al.*, 2003; *Jassal et al.*, 2005; *Tang et al.*, 2005a; *Tang et al.*, 2005b; *Baldocchi et al.*, 2006; *Vargas and Allen*, in press].

Because solid-state soil CO₂ 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 (DPDT) relay (6 VDC coil voltage, 115 mA, Tyco Electronics, Berwyn, PA), in the power line between the battery bank and the solid-state soil CO₂ probes, controlled by the datalogger. This setup allowed us to switch the probes on prior to each measurement, including warming time as recommended by manufacturer, and switch them off to prevent long-term heating while saving >75% of battery power.

Ecosystem Respiration

Continuous measurements of land-atmosphere CO₂ 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, UT). 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 based on fluxes between 11 p.m. and 4 a.m. 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 post-processing and modeling abstraction.

Results

Environmental Variables

The variability of continuous and discrete measurements of volumetric soil water content (θ) is presented in Figure 4.2. 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 4.2). Given that 70% of precipitation comes as snow and 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 drydown, typical of subalpine forests. Rainfall was higher in magnitude and occurred more frequently before mid-July, after which rainfall decreased and occurred on only two days late in the season (Figure 4.2). The effects of rainfall on θ differed in magnitude between the wet riparian site and the drier upland site (Figure 4.2), and depended on antecedent conditions (wet soil vs. dry soil). These effects were also reflected, both mechanistically and methodologically, on measured soil CO₂ fluxes (see below).

Soil temperature (T_s) varied both daily and seasonally (Figure 4.3), 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 4.2), 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 reset by precipitation

events (e.g., August 18). 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 4.3) due to 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.

Soil CO₂ Efflux

Both the soil respiration chamber and the soil CO₂ technique measured increasing fluxes early in the growing season at the riparian and upland sites (Figure 4.3), with the soil CO₂ profile having the advantage of increased sampling frequency, allowing for detailed visualization of the diel dynamics of soil CO₂ 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 CO₂ efflux in response to seasonal changes in environmental conditions (e.g., 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 CO₂ efflux from the profile technique at both sites. The dashed lines in Figure 4.3 (panels C and E), almost identical to solid lines, demonstrate that the error introduced by our approach is minimal compared to the natural variability of soil CO₂ efflux on a diel and seasonal basis. For the remainder of this paper we will refer to calculations and analyses based on soil CO₂ concentration of 450 ppm at the soil-atmosphere interface.

Seasonal dynamics recorded by the chamber technique agreed well with estimates by the soil CO₂ profile technique at both sites (Figure 4.3). 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 ($r^2 = 0.57$; Figure 4.4). This agreement improved considerably when measurements within two days of 1 mm rainfall were excluded, and when chamber measurements made on wet soil ($\theta > 0.25 \text{ m}^3 \text{ m}^{-3}$) were further excluded from the comparison at each site (Figure 4.5). 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.

Chamber measurements fell within the range of diel values of soil CO₂ efflux, except early in the season at the riparian site or following precipitation events at both sites (e.g., July 10 and 13, Figure 4.6A). Accumulated on a daily basis (Figure 4.6B), rates of soil CO₂ 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 CO₂ profile technique.

Because the soil CO₂ profile technique is currently applied at different sampling frequencies (e.g., 5 min [*Vargas and Allen*, in press]; 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 CO₂ efflux rates (Figure 4.7). Using the time of day at which the soil respiration chamber was deployed at each site (between 10 a.m. and 4 p.m.) to capture

instantaneous efflux by the soil CO₂ 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 4.7).

Discussion

What are the Mechanisms Driving the Main Differences in Soil CO₂ Efflux from Riparian Meadows and Upland Forests?

A major challenge in process understanding of soil CO₂ 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 CO₂ 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 down slope 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 4.3) demonstrates that soil CO₂ 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 July 29) were soil CO₂ efflux rates similar or higher at the upland site (Figure 4.3).

A comparison of soil CO₂ efflux and soil temperature during early, middle, and late season (Figure 4.6A) 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 CO₂ efflux. Recent studies have highlighted the evolution of diel patterns in both soil CO₂ concentrations [Riveros-Iregui *et al.*, 2007] and soil CO₂ effluxes [Carbone *et al.*, 2008]. Diel hysteresis in soil CO₂ concentrations is controlled by water content-limited soil CO₂ diffusion [Riveros-Iregui *et al.*, 2007]. A decline in θ results in enhanced soil CO₂ 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 CO₂ 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., June 23 at the riparian site vs. June 22 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 4.6A) indicate enhanced photosynthetic activity of the forest canopy with respect to riparian grasses [Emanuel *et al.*, in review], 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 growing season. As a result, the riparian vegetation influence on soil CO₂ efflux diminished over the course of seasonal drydown.

These findings demonstrate how soil water content distribution across the landscape exerts a major control on both spatial and temporal (seasonal) differences of soil CO₂ efflux. We suggest that parameterization of water content heterogeneity in space and time must be a critical component for realistic model representations of soil CO₂ efflux (understood as the balance between production and transport [*Pacific et al.*, in review]) 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.

How do two of the Most Commonly Used Methods to Measure Soil CO₂ Efflux Compare across Sites and across the Growing Season?

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 4.5). At both sites technique agreement significantly improved when measurements on wet soil days ($\theta > 0.25 \text{ m}^3 \text{ m}^{-3}$) 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 CO₂ burst in soil air due to a rapid gas displacement 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 CO₂ 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*, in press] 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 , 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 CO₂ 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 eco-physiological processes and environmental biases).

Analyzing instantaneous fluxes from the soil CO₂ 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 4.7). This means that on a cumulative basis the use of the soil CO₂ 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 CO₂ in this system occur before sunrise and daily maxima during early to late evening [Riveros-Iregui *et al.*, 2007], sampling soil CO₂ efflux between 1000 h and 1600 h (as in the example presented in Figure 4.7) may correspond to the 24-hour mean of soil CO₂ 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 CO₂ profile technique provides 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 CO₂ profile technique greatly depends on study goals and whether one is interested in seasonal estimates of soil CO₂ efflux rates or rapid dynamics of this flux.

What are the Implications of These Findings for Process Understanding of Soil CO₂ Efflux from Subalpine Ecosystems?

A comparison of measurements by the soil respiration chamber and the soil CO₂ profile technique demonstrates that, accumulated over the growing season, both techniques are within 17% of measurements for the riparian site and within 21% of measurements for the upland site (Figure 4.8). Similar agreements between techniques have been reported [Tang *et al.*, 2003; Baldocchi *et al.*, 2006], but the difference in agreement across sites had not been previously observed. Higher 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 4.2). 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 top soil 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.

Compared to nighttime ecosystem respiration, both techniques provide comparable effluxes for each site (Figure 4.8). While this comparison is not intended for quantitative purposes, it provides the foundations for potential, detailed examinations. For example, the difference in soil CO₂ efflux response between the riparian and upland site, particularly after snowmelt and precipitation, demonstrates that different landscape positions may not respond uniformly to environmental disturbances, particularly due to differences in θ . On a cumulative basis riparian areas exhibit higher soil CO₂ efflux and ecosystem respiration than upland sites throughout the growing season (Figure 4.8D). While riparian meadows can occupy a smaller fraction of an entire forest (~2%), soil CO₂ efflux from these areas is larger than effluxes from upland forests [*Riveros-Iregui et al.*, in review]. Soil CO₂ efflux from chamber measurements was within 17% 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 non-stationary behavior of the landscape can be important to improve current estimates of soil CO₂ 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 CO₂ profile technique, 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 CO₂ efflux from heterogeneous landscapes, providing a conceptual framework of soil CO₂ efflux useful for modeling studies, and gaining confidence in current and developing soil CO₂ efflux measuring techniques.

Conclusions and Implications

Soil water content was a major control on both spatial and temporal (particularly seasonal) differences of soil CO₂ 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 CO₂ efflux rates from heterogeneous landscapes.

Good agreement between the soil respiration chamber technique and the soil CO₂ profile technique can be attained during periods of stable conditions (e.g., constant θ , 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 understand performance of techniques, and the source of the variability in measured efflux.

On a 24 hr basis both techniques yield comparable results, except during periods of sporadic precipitation, when the chamber technique yields soil CO₂ efflux rates much larger than those by the soil profile technique. This means that rapid changes in soil physical properties, respiration enhancement, as well as water-caused displacement of CO₂ within the soil pore space might not be adequately captured by solid-state CO₂ sensors. Nonetheless, these sensors remain a useful tool for capturing changes in soil CO₂ caused by less-transient, non-hydrological, ecophysiological processes (i.e., responses of plant and microbial activity to changing environmental conditions).

Differences in diel hysteresis patterns of soil CO₂ 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 CO₂ 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 CO₂ efflux diminished over the course of seasonal drydown.

On a seasonal basis soil CO₂ 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 CO₂ probes. Further, 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.

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 CO₂ profile technique, eddy covariance towers) is necessary to gain insight into the primary controls on soil CO₂ production and transport and the spatiotemporal nature of efflux. Acknowledging technique limitations is important for reporting realistic rates of soil CO₂ efflux.

These results have implications for interpreting and evaluating rates of soil CO₂ efflux measured by soil respiration chambers and the soil CO₂ 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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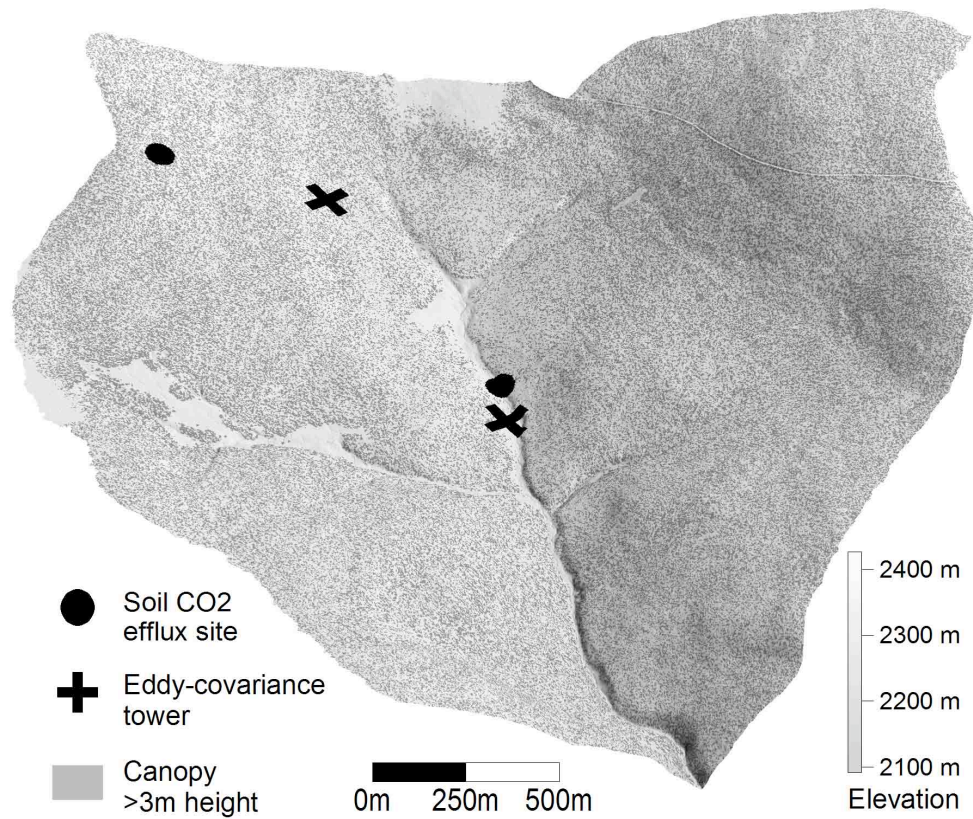


Figure 4.1 Location of the Tenderfoot Creek Experimental Forest (TCEF) in the Little Belt Mountains of Central Montana. The two most common ecosystems of these mountains were selected for this study: a wet riparian meadow and a dry upland forest.

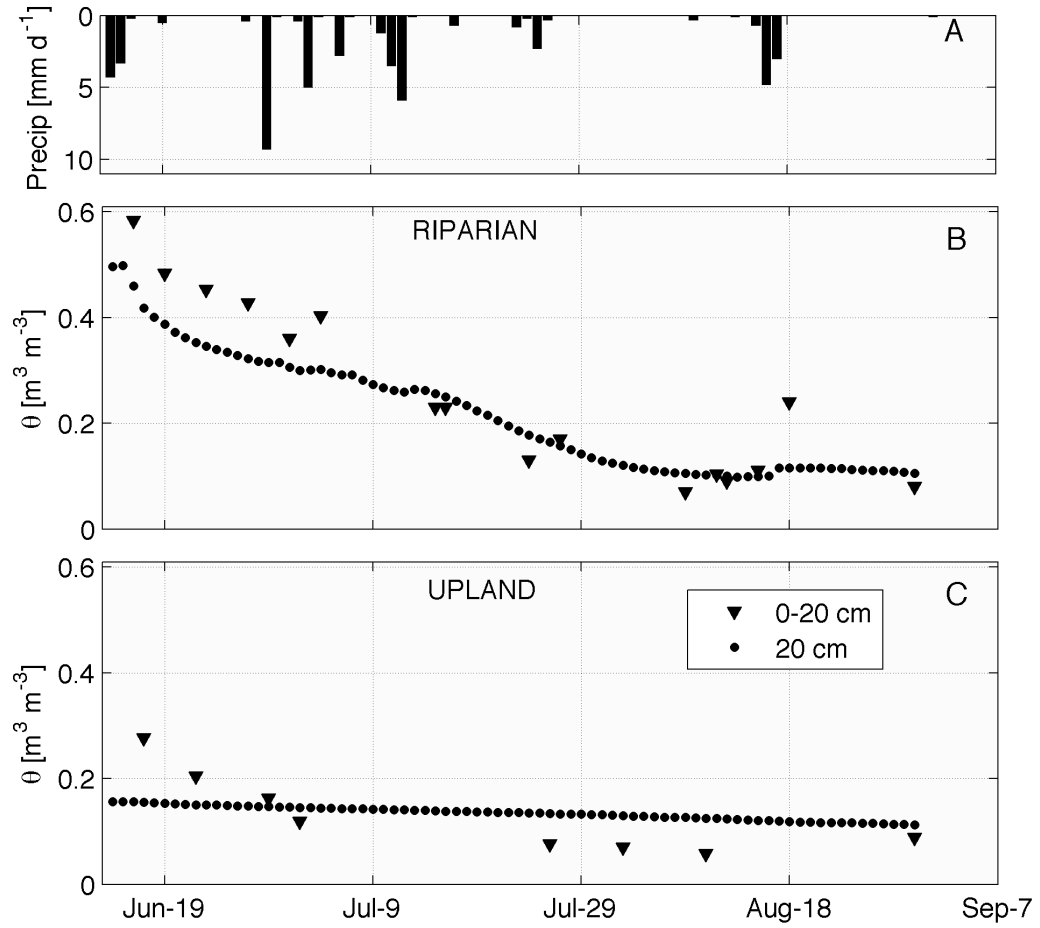


Figure 4.2 Variability of precipitation (A) and soil water content (θ) for riparian (B) and upland (C) sites for the 2006 growing season. Measurements of θ were made continuously at 20 cm, and discretely integrating over 0-20 cm as indicated by the shapes.

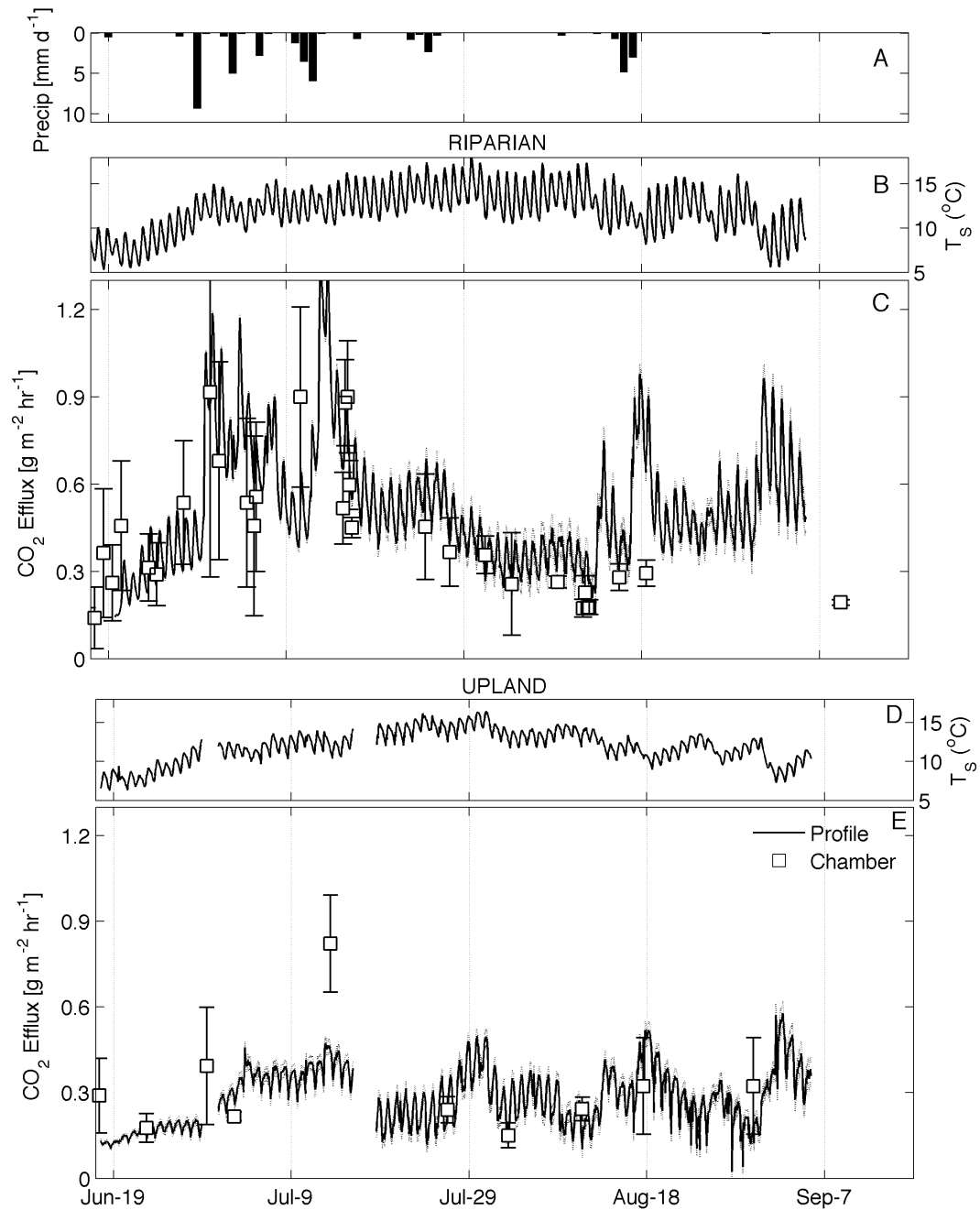


Figure 4.3 Variability in precipitation (A), soil temperature (B, D) and soil CO₂ efflux (C, E) at the riparian and upland site for the 2006 growing season. CO₂ efflux was measured by the soil CO₂ profile technique (solid-state CO₂ sensors installed at depth), and by the soil respiration chamber technique. Boxes represent the mean and error bars represent the standard deviation of 3 chamber measurements.

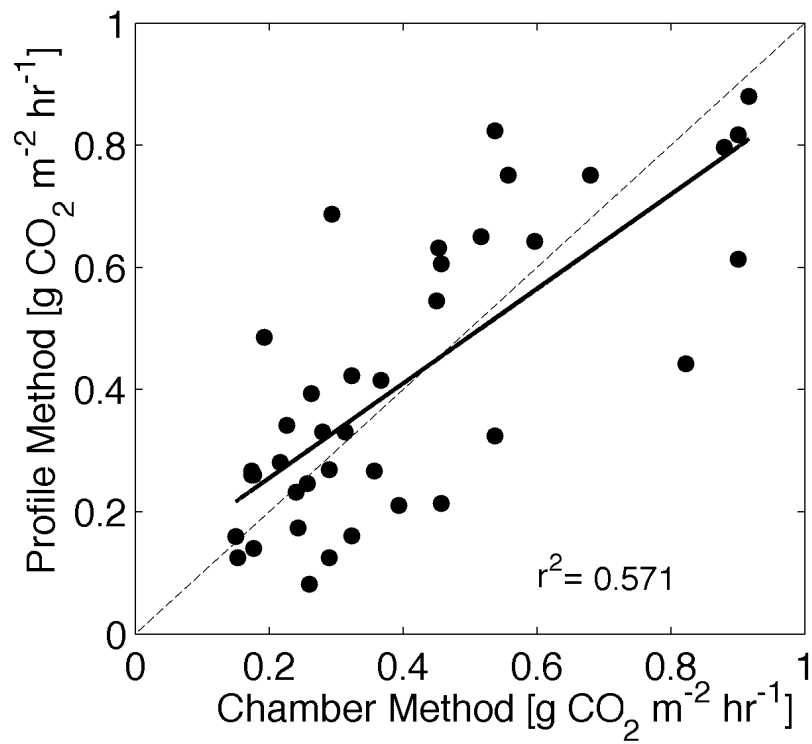


Figure 4.4 Comparison of instantaneous soil CO₂ efflux measured by both techniques during the 2006 growing season. Data in this figure include measurements at the riparian and the upland site during rainy and dry days.

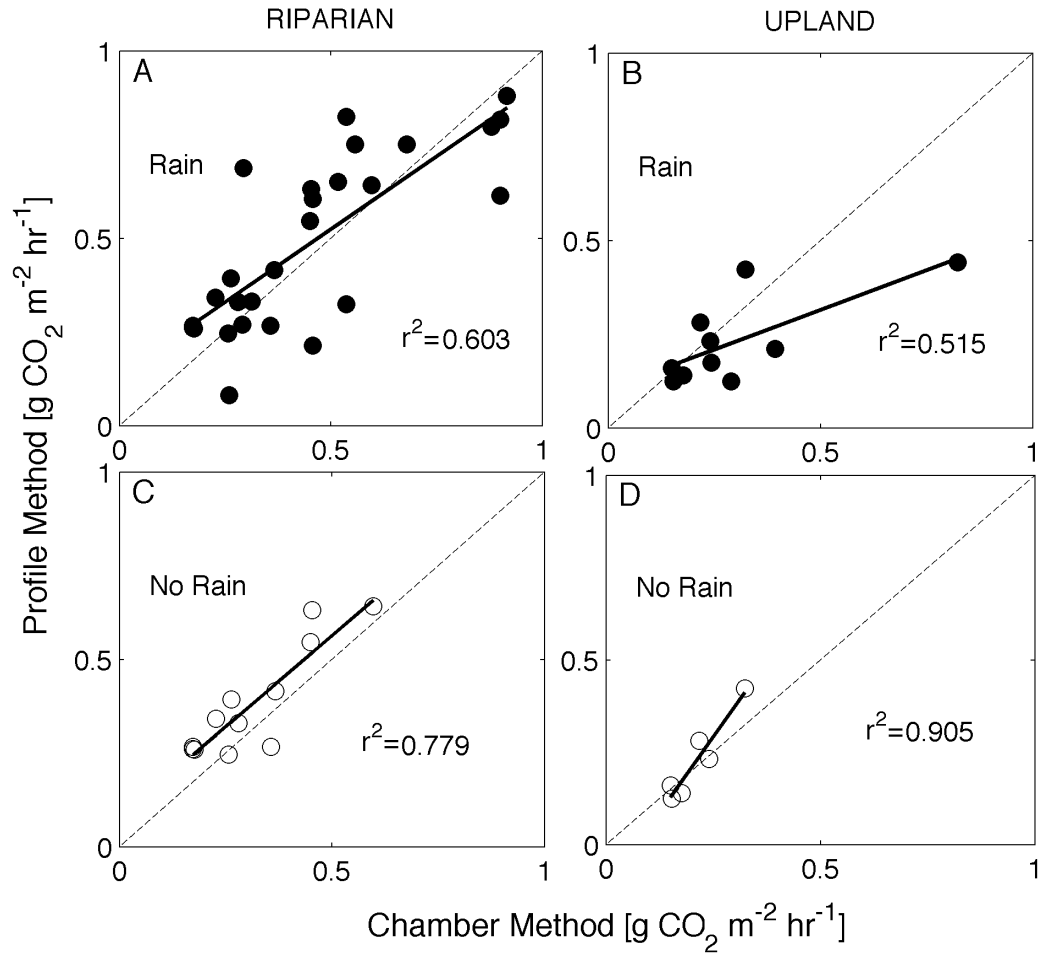


Figure 4.5 Comparison of techniques between riparian (A, C) and upland (B, D) sites, with all measurements at each site (A, B), and removing measurements on soil with $\theta > 0.25 \text{ [m}^3 \text{ m}^{-3}]$ and measurements within 2 days of precipitation over 1 mm (C, D).

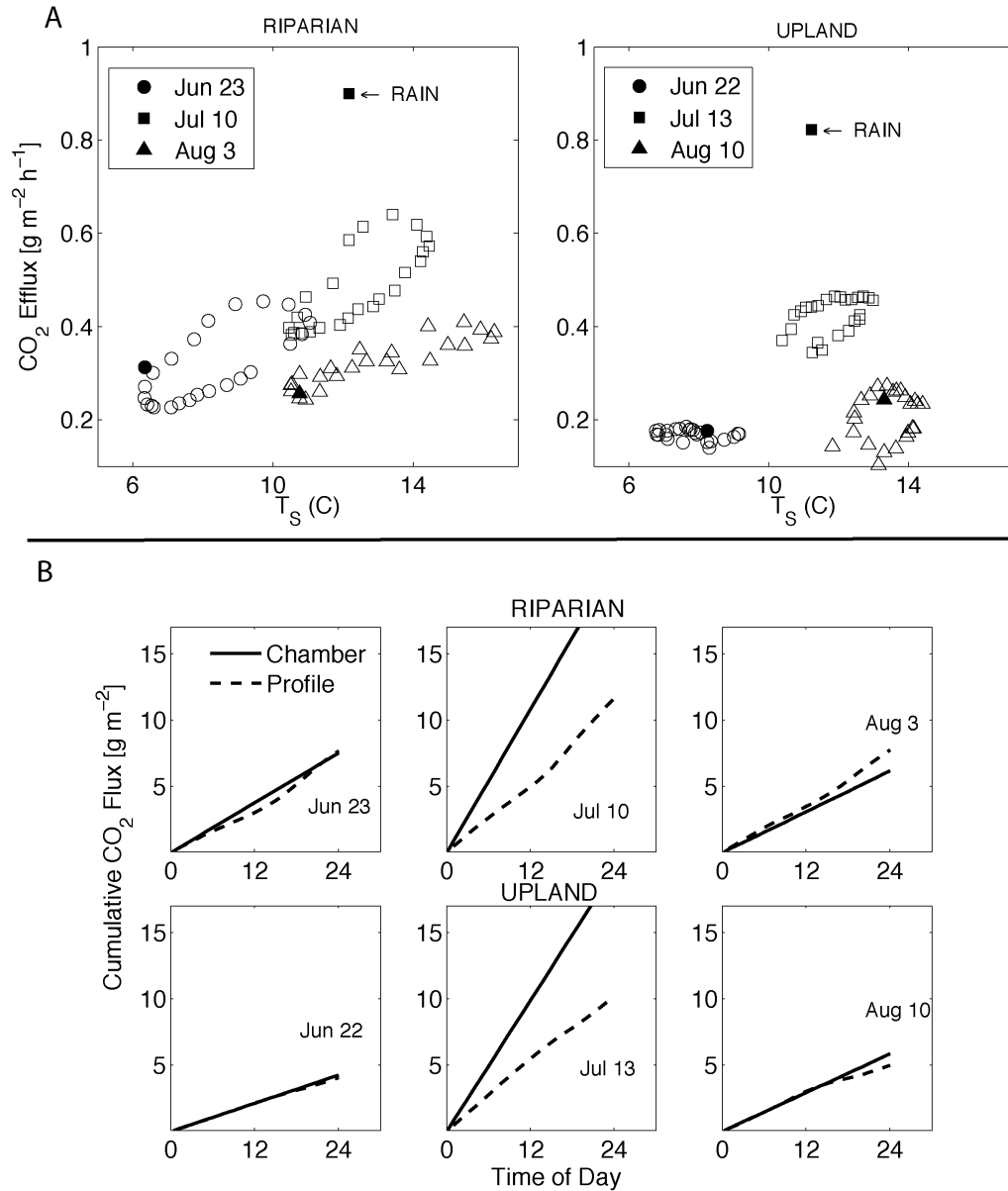


Figure 4.6 A) Comparison of soil CO_2 efflux measurements and soil temperature (T_s) made on three different days at the riparian (left panel) and upland (right panel) sites. Shapes denote day of the year. Open symbols denote measurements by the soil profile technique and filled symbols denote measurements by the soil respiration chamber. After rain events (i.e., July 13-16), measurements by the soil respiration chamber are much greater than estimates by the soil profile technique. B) Comparison of cumulative fluxes over 24-hr intervals at different times of the year at the riparian (top three) and upland (bottom three) site. Dates of measurements are indicated in each box and correspond to dates of measurements in Figure 4.6A. A total of 10.7 mm of rain occurred over 4 days prior to July 13-16 measurements.

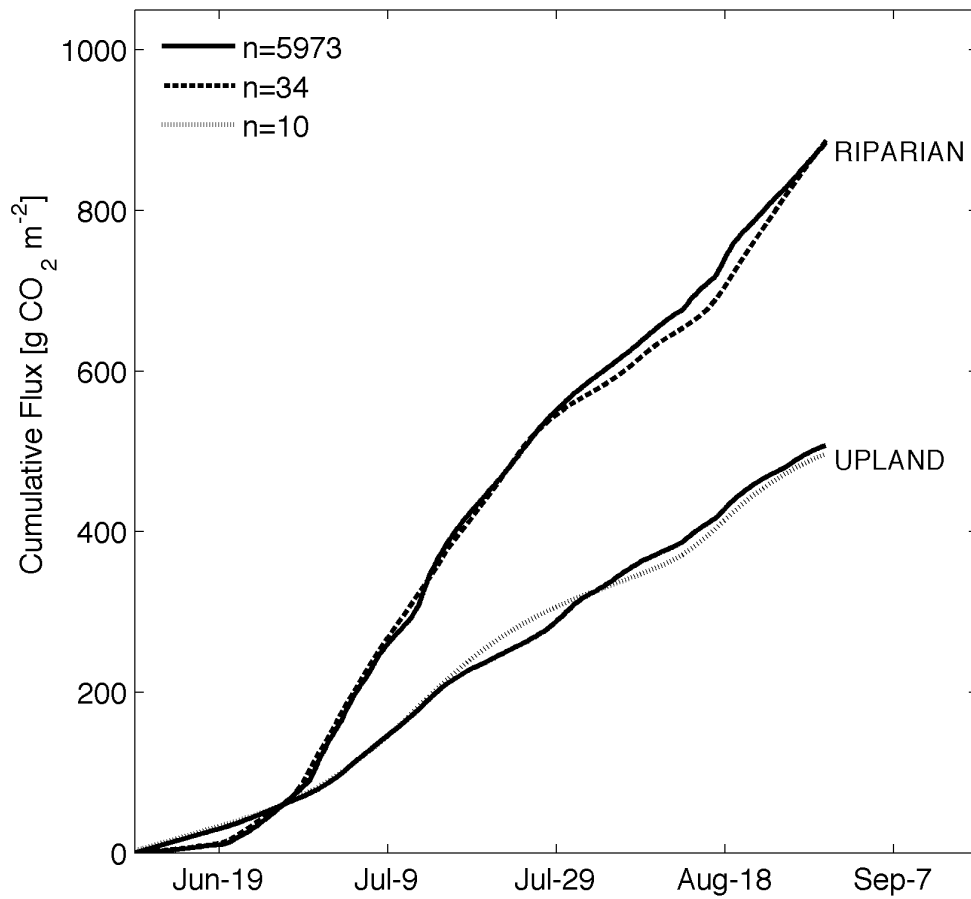


Figure 4.7 Comparison of cumulative soil CO₂ efflux estimates by the soil CO₂ profile technique, modifying its sampling frequency. Straight lines indicate estimates from 20-min sampling over 83 days (n=5973). Dashed (n=34) and dotted (n=10) lines indicate reduced sampling frequency (every 2-7 days), 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 CO₂ profile technique at 20-min intervals yields similar results as when it is used every 2-7 days.

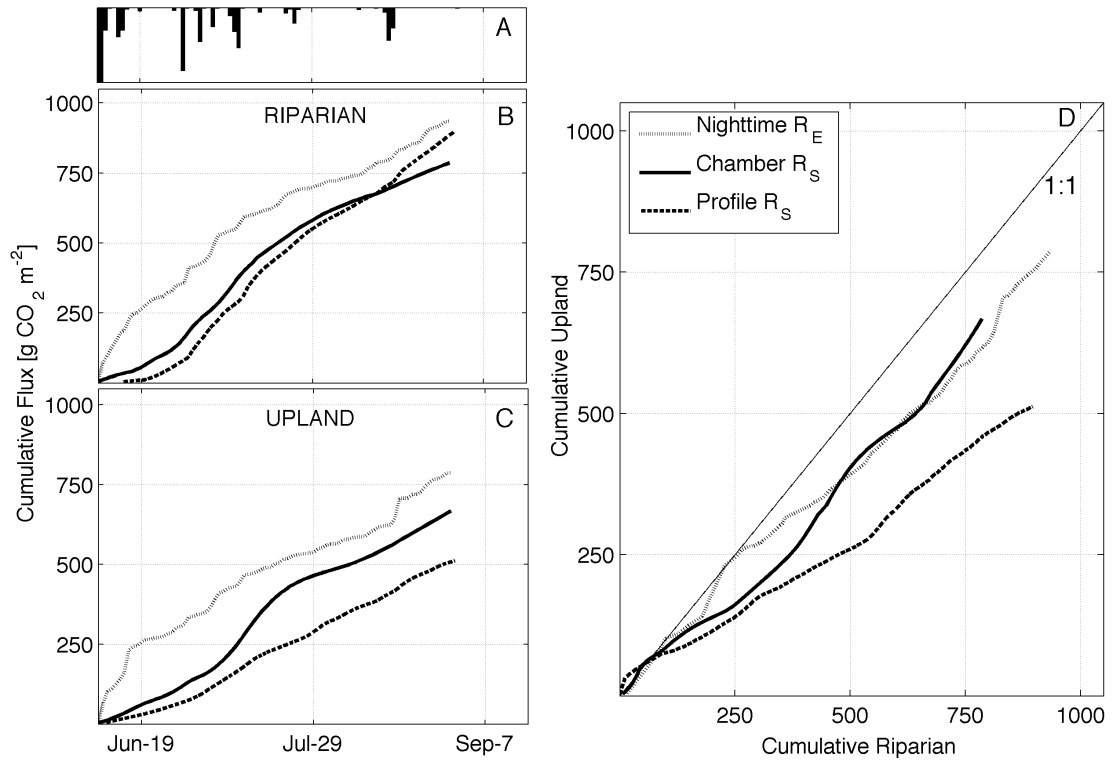


Figure 4.8 Comparison of cumulative discrete (instantaneous) measurements made by the soil respiration chamber technique (including all data), 20-min measurements by the soil profile technique, and nighttime ecosystem respiration (R_E) by an eddy covariance system at a riparian and an upland site (B, C, D). Relative precipitation is indicated in panel A.

CHAPTER 5

LANDSCAPE STRUCTURE CONTROLS SOIL CO₂ EFFLUX
VARIABILITY IN COMPLEX TERRAIN: SCALING FROM POINT
OBSERVATIONS TO WATERSHED SCALE FLUXES

*Adapted from: Riveros-Iregui D.A., and McGlynn, B.L., (in review).
Landscape structure controls soil CO₂ efflux variability in complex
terrain: scaling from point observations to watershed scale fluxes.
Submitted for publication in Water Resources Research*

Abstract

We investigated the spatial and temporal variability of soil CO₂ efflux across 62 sites in the northern Rocky Mountains. The sites were distributed across a 393-ha, moderately complex watershed and were characteristic of the spatial heterogeneity of the landscape (e.g., slope, aspect, upslope accumulated areas [UAA]). Growing season (83-day) cumulative soil CO₂ efflux varied from ~300 g CO₂ m⁻² to ~1900 g CO₂ m⁻², depending upon landscape position, with a median of 879.8 g CO₂ m⁻². Our findings revealed that highest soil CO₂ efflux rates were observed in areas with persistent high soil water content (riparian meadows), whereas lower soil CO₂ efflux rates were observed on forested uplands (98% of the watershed). Furthermore, we found that UAA, a surrogate measure of the lateral redistribution of soil water, was positively correlated with seasonal soil CO₂ efflux at all upland sites ($r^2=0.51$), increasing in explanatory power when sites were separated by the two major aspects of the watershed (SE aspects $r^2=0.65$; NW aspects $r^2=0.61$). We used the UAA-soil CO₂ efflux relationship to up-scale measured soil CO₂ efflux to the entire watershed and found watershed-scale soil CO₂ efflux of

799.45 $\pm$ 151.1 g CO₂ m² over 83 days. These estimates compared well (within 2%) with independent eddy-covariance estimates of nighttime ecosystem respiration measured over the forest canopy for the same period (absolute error of 11.7 g CO₂ m² over 83 days). We applied this empirical model to three synthetic watersheds with progressively reduced complexity and found that seasonal estimates of soil CO₂ efflux increased by 50%, 58% and 98%, demonstrating the importance of landscape structure in controlling soil CO₂ efflux magnitude. Our study represents an empirical quantification of seasonal watershed-scale soil CO₂ efflux and demonstrates that UAA (i.e., landscape position) is an important control on large-scale (~km²) variability of soil CO₂ efflux particularly in semi-arid, subalpine ecosystems.

Introduction

Soil CO₂ efflux, also known as soil respiration, is an important component of the C cycle, and its accurate quantification has significant implications for ecosystem C balances and models [Raich and Schlesinger, 1992; Raich and Potter, 1995; Valentini *et al.*, 2000]. One obstacle to accurately quantifying soil CO₂ efflux is the large spatial heterogeneity in the physical and biogeochemical processes leading to soil CO₂ production and efflux. Particularly in complex terrain, interactions among spatially variable soil temperature, soil water content, vegetation, substrate, and soil physical properties induce large heterogeneity in the magnitude of soil CO₂ efflux [Kang *et al.*, 2003; Scott-Denton *et al.*, 2003; Kang *et al.*, 2006]. Further complications are introduced by the superimposed temporal heterogeneity (i.e., the asynchronous response of soil CO₂

to each variable). As a result, estimating soil CO₂ efflux from large areas has proven problematic [Goulden *et al.*, 1996], commonly leading to highly uncertain estimates.

Despite the number of studies measuring rates of soil CO₂ efflux, studies addressing the heterogeneity of soil CO₂ efflux at large scales (e.g., watershed scale [$\sim\text{km}^2$]) based on ground-based measurements remain limited to non-existent. Many of the known estimates of soil CO₂ efflux rates from entire watersheds come from area-weighted extrapolations of measurements at single or few sites [Norman *et al.*, 1992; Lavigne *et al.*, 1997; Ryan *et al.*, 1997; Webster *et al.*, in press-a]. However, little assessment has tested the representativeness of such sites for the entire area of study. Other studies use temperature-based relationships to model soil CO₂ efflux rates for large areas [Hollinger *et al.*, 1994; Randerson *et al.*, 2002; Richardson *et al.*, 2006; Larsen *et al.*, 2007], providing useful estimates for comparison with other techniques (e.g., eddy covariance). However, while these and similar approaches offer estimates of soil CO₂ efflux rates from large areas, they typically treat the landscape as large homogeneous plots. Such homogeneities rarely exist in natural systems, and little understanding can be gained about processes or heterogeneity occurring within these “black box” areas.

Watershed morphology and heterogeneity can exert important influences on the magnitude of soil CO₂ efflux rates. For example, physical organization of landscapes is manifested in aspect variations and differences in surface energy balance distributions across a watershed. Radiation differences have been found to influence spatial variation of temperature [Korkalainen and Lauren, 2006], and vegetation and litter accumulation [Stage, 1976; Webster *et al.*, in press-a], which in turn can result in differences in soil

carbon content. Concurrently, landscape structure (shape) and gravity exert a major control in the vertical and lateral redistribution of water in the soil, which typically defines wet and dry areas of the landscape [*Western et al.*, 1998; *Western et al.*, 1999]. In fact, wetness differences have been found to control differences in soil CO₂ fluxes [*Riveros-Iregui et al.*, in review-a] partially because plant and microbial activities are dependent on soil water content, and transport (diffusivity) of soil CO₂ is inversely correlated with soil water content [*Riveros-Iregui et al.*, 2007; *Pacific et al.*, in review].

Given the spatiotemporal heterogeneity of soil CO₂ efflux, estimating soil CO₂ efflux rates from entire watersheds requires thorough understanding of the biophysical and landscape controls. Spatially, soil CO₂ efflux can vary across topographic positions [*Webster et al.*, in press-b; *Pacific et al.*, in review; *Riveros-Iregui et al.*, in review-b], aspect [*Webster et al.*, in press-a], vegetation cover [*Scott-Denton et al.*, 2003; *Tang et al.*, 2005; *Scott-Denton et al.*, 2006], and across different land uses [*Jacobs et al.*, 2007; *Nouvellon et al.*, 2008]. Temporally, soil CO₂ efflux can vary with changing hydrologic [*Riveros-Iregui et al.*, 2007; *Pacific et al.*, in review] and climatic conditions [*Vargas and Allen*, 2008]. Given the broad range of landscape elements that can exist within a single watersheds (e.g., riparian meadows, forested hillslopes, contrasting aspects), and due to the different responses that soil CO₂ efflux can exhibit to different environmental conditions (e.g., precipitation, seasonal drying of the soil, temperature), it is important to determine the overarching control on soil CO₂ efflux across large and heterogeneous areas. Investigating and quantifying the fundamental role of landscape-induced heterogeneity on soil CO₂ production and efflux can improve our understanding of the

variability of this flux at the watershed scale, and reduce the uncertainty in estimates of soil CO₂ efflux from heterogeneous areas.

We investigated the spatial and temporal variability of soil CO₂ efflux across 62 sites in the northern Rocky Mountains. The sites were distributed across a 393-ha, moderately complex watershed and were characteristic of the spatial heterogeneity of the landscape (e.g., slope, aspect, upslope accumulated areas). This forest is ideal for soil CO₂ efflux research as it exhibits the full range in soil temperature, soil water content, soil nutrient status, and vegetation cover, and is characteristic of sub-alpine watersheds in the northern Rocky Mountains. The objectives of this study were to 1) evaluate growing-season (June thru August) soil CO₂ efflux across 62 landscape positions and quantify its spatial heterogeneity; 2) assess the role of landscape structure and drainage pattern on controlling the magnitude of soil CO₂ efflux; and 3) present an empirical framework for quantifying large-scale (km²) soil CO₂ efflux rates for complex terrain watersheds. The information presented here is essential to linking plot-scale observations to large-scale estimates of soil CO₂ efflux, to enhancing parameterization and modeling of soil CO₂ efflux from heterogeneous areas, and is useful in combination with other ecosystem-level measures of C exchange (e.g., flux towers).

Methods

Study Site

This study was located in the Tenderfoot Creek Experimental Forest (TCEF), in the Little Belt Mountains of central Montana [46° 55' N; 110° 54' W]. This location is

characteristic of the lodgepole-dominated forests of the northern Rocky Mountains, believed to contribute significantly to the North American carbon sink [*Schimel et al.*, 2002]. The greater TCEF elevation ranges from 1,840 to 2,421 meters and has an area of 3,591 hectares. 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. A 393-ha sub-watershed that contains a second-order perennial stream, Stringer Creek, was selected as the watershed of interest due to its wide range of slope, aspect, and topographic convergence/divergence [*Riveros-Iregui et al.*, in review-b].

Within the Stringer Creek watershed, we selected 62 sites to measure soil CO₂ efflux via a combination of 5 hillslope and 4 hillslope-riparian-hillslope (HRH) transects distributed across the watershed (Figure 5.1). Each hillslope transect contained between 4 and 6 sites, whereas each HRH transect contained 8 sites, for a combined total of 62 sites (11 riparian meadow sites, 51 upland forest sites) across Stringer Creek watershed. Because our goal was to examine the variability of soil CO₂ efflux in response to differences in biophysical controls (e.g., soil temperature, soil water content, vegetation cover), site selection was targeted toward those areas of the landscape that offered natural biophysical gradients, while maintaining the practicality of daily to sub-weekly manual measurements at each site. Terrain analysis confirmed that site selection was characteristic of the distribution of upslope accumulated area (an indicator of landscape variability) across the watershed (see Results). Further details on site characteristics have been described in previous studies [*Riveros-Iregui et al.*, 2007; *Riveros-Iregui et al.*, in

review-a; b].

Terrain Variability

A 1-m digital elevation model (DEM) derived from Airborne Laser Swath Mapping was re-sampled to 3-m and 10-m DEMs for Stringer Creek. The re-sampled DEMs were then used to calculate upslope accumulated area (UAA [m^2]) for each pixel in the watershed, based on the triangular multiple flow direction algorithm (MD_{∞} [Seibert and McGlynn, 2007]). Also known as the local contributing area, UAA represents the amount of area draining to a specific location in the landscape [Beven *et al.*, 1979; McGlynn and Seibert, 2003] and serves as an estimate of relative wetness potential. This and similar topographic indices have proven useful for comparison of soil moisture patterns among sites of the same watershed [Burt and Butcher, 1985; Western and Grayson, 1998; Western *et al.*, 1999; Grayson and Western, 2001] and across larger regions [Rodhe and Seibert, 1999; Zinko *et al.*, 2005; Sorensen *et al.*, 2006]. Riparian zone delineation was accomplished using a 3-m elevation threshold above the stream channel following flow paths to the stream, according to the delineation algorithm proposed by McGlynn and Seibert [2003], and corroborated with field observations and measurements [Jencso *et al.*, in review] .

Environmental Variables

We report on a set of measurements of soil temperature (T_S) and volumetric soil water content (θ) recorded during the 2006 growing season. Continuous measurements of T_S were recorded every 4 hours at 13 of the 62 sites at 5 cm depth with I-Button

temperature loggers (DS1922L, temperature range -40°C to 85°C , Maxim Integrated Products, Sunnyvale, CA), during the period between July 17 and October 16, 2006. Based on these measurements, we calculated the number of days that daily T_S rose above the mean T_S at all sites. This estimate allowed for comparison between landscape elements, providing an assessment of variability of T_S at the watershed scale during the growing season.

Continuous measurements of θ were made using water content reflectometry probes (CSI Model 616, Campbell Scientific Inc., Logan, UT) at three sites (riparian meadow, lower hillslope, and upper hillslope) installed horizontally at 20 cm. Given the large dataset of T_S and θ measurements, our results are summarized to illustrate distinct dynamics of these variables at the watershed scale.

Soil C:N Content Ratio, Biomass C:N Content Ratio, and Fine Root Biomass

Soil carbon and nitrogen content ratios (C:N) were measured in a subset of sites (45), including riparian meadow sites and upland forest sites. Soil samples were collected by sampling the top 25 cm of soil with a hand auger (5 cm in diameter). In the lab, samples were dried, sieved, and ground in preparation for analysis. Total C and N contents were determined in a TruSpec CN Determinator (Leco Corporation, St. Joseph, MI) through combustion under an oxygen atmosphere at 950°C , using helium as a carrier. This instrument has a precision of 0.3 ppm for C and 40 ppm for N. Additionally, above and belowground biomass of the dominant vegetation from riparian meadows and upland forests was collected for similar C:N content ratio analysis (Table

5.1). Results are presented as the mean and one standard deviation of three measurements.

Fine root biomass (≤ 0.5 cm in diameter) was quantified at 19 of the 62 sites by sampling the top 25 cm of soil with a hand auger (5 cm in diameter). Soil cores were collected in triplicate and dried at 60° C, and roots were manually separated and weighed. Estimates of fine root density are presented as the mean and one standard deviation of three measurements [kg m^{-3}].

Soil CO₂ Efflux

Each of the 62 sites consisted of a 0.5-m² area flux plot, roped off to minimize disturbance. Soil CO₂ efflux measurements were collected using a soil respiration chamber model SRC-1 (footprint of 314.2 cm², accuracy within 1% of calibrated range [0 to 9.99 g CO₂ m⁻² hr⁻¹], PP Systems, Massachusetts, USA) equipped with an infrared gas analyzer (IRGA; EGM-4, accuracy within 1% of calibrated range [0 to 2,000 ppm], PP Systems, Massachusetts, USA). Chamber measurements were collected at each of the 62 sites following similar procedures to those described in Pacific et al. [in review] and Riveros-Iregui et al. [in review-a]. Briefly, before each measurement the soil 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 CO₂ efflux was calculated by measuring the rate of increase in CO₂ concentration within the chamber and fitting a quadratic equation to the relationship between the increasing CO₂ concentration and elapsed time (as recommended by the manufacturer). Three chamber measurements were collected at each site between 1000 h and 1600 h every 2-7 days.

Due to the broad spatial distribution of the sites and travel time across the 393-ha study site, soil CO₂ efflux was not measured at every site on the same day or at the same time of the day. Thus, throughout the 2006 growing season, each site was visited between 10 and 37 times. Here we focus on seasonal estimates (cumulative fluxes) across all sites, as important indicators of the heterogeneity (and magnitude) of soil CO₂ efflux across the watershed. We established a common timeframe among sites by linearly interpolating between measurements for the time period 9 June, 2006 and 30 August, 2006 (83 days total). Previous studies comparing high- and low-frequency measurements demonstrated that sampling frequency, linear interpolation between measurements, and time of day do not compromise or bias estimates of soil CO₂ efflux when analyzed cumulatively (seasonally) [*Riveros-Iregui et al.*, in review-a]. Our approach provided a robust framework for inter-site comparison of seasonal fluxes, while optimizing resources, manual labor, and measurements across 62 spatially distributed sites. We then applied a two-way partitioning analysis (k-means Clustering, Matlab 7.4.0, The Mathworks, Inc.) to the entire soil CO₂ efflux dataset. A two-way partition was chosen as a first approach to separate the 62 sites into two preliminary groups: a cluster of sites with high soil CO₂ efflux, and a cluster of sites with low soil CO₂ efflux. The selected algorithm separates all observations into two mutually exclusive clusters, using an iterative minimization of the sum of the distances from each datapoint to its cluster centroid, and relocating datapoints between clusters until the sum cannot be decreased any further [*Spath*, 1985]. Thus the algorithm is suitable for clustering time series of CO₂ efflux from multiple sites, given that it takes into account the distribution

and behavior (dynamics) of all data at each site for the duration of the observations.

Results

Terrain Variability

The 10-m DEM of Stringer Creek provided the most robust representation of landscape structure and morphology (convergent vs. divergent areas) without being biased by the micro-topography, whereas the 3-m DEM provided a more accurate representation of the micro-scale (e.g., fallen trees, stream channel, manmade structures). Thus we used the calculated 10-m upslope accumulated area (UAA) layer based on the algorithm proposed by Seibert and McGlynn [2007] to represent the likely distribution of soil water drainage and accumulation at the watershed scale. Riparian delineation of the Stringer Creek watershed demonstrated that riparian zones comprised 1.8% of the watershed. The rest of the watershed was divided almost symmetrically by the stream, which runs in a NNE-SSW direction, making NW and SE the two dominant aspects of the watershed (50.0% and 48.2%, respectively).

Based on these topographic variables (UAA, aspect), found to control the redistribution of water and radiation received across the watershed, we tested the representativeness of the selected 62 sites to the entire watershed. Our terrain analysis confirmed that the selected 62 sites were characteristic of both UAA distribution and aspect (Figure 5.2), demonstrating that site selection captured the range and frequency of landscape positions, drainage patterns, and overall complexity of the Stringer Creek watershed.

Environmental Variables

The average soil temperature (T_S) of all measured sites was 8.97 °C between July 17 and October 16, 2006; however T_S varied widely across the watershed from near ~30 °C during the summer in well-exposed areas (riparian meadows) to below freezing in October. Average T_S in riparian meadow sites was 10.21 °C, with 21.5 days above the mean T_S for the watershed (Figure 5.3). SE facing sites showed an average T_S of 8.83 °C, with 14.4 days above the mean for the watershed. NW facing sites showed an average T_S of 7.89 °C, with only 2.5 days above the mean for the watershed (Figure 5.3). In general, three major features were observed to control T_S at the watershed scale: 1) a vegetation effect, in which T_S was buffered in areas with tall canopies (e.g., riparian meadow vs. forested uplands); 2) an aspect effect, in which SE facing sites received more solar radiation than NW facing sites causing differences in amplitude of T_S between aspects; and 3) a soil water content effect (specific heat effect), in which T_S had less diel amplitude in wetter areas of the landscape (lower areas) than in upper areas (drier areas). While other physical effects may also control T_S at smaller scales, these effects illustrate the main observed controls on watershed-scale variability of T_S .

Highest values of volumetric soil water content (θ) were observed toward mid-May and early June following snowmelt, after which values of θ decreased at all sites (Figure 5.4). Snowmelt lasted until mid-May, whereas liquid precipitation was high during June and early July and decreased toward late July and August (Figure 5.4). Spatially, values of θ reached ~0.5 m³ m⁻³ (i.e., at or near soil saturation) in low and

convergent areas of the landscape (riparian zones) immediately after snowmelt. Values of θ were lower in less convergent areas and higher landscape positions (reduced drainage area), where maximum values did not exceed $\sim 0.2 \text{ m}^3 \text{ m}^{-3}$ (Figure 5.4).

Soil C:N Content Ratio, Biomass C:N content Ratio and Fine Root Biomass

Soil C:N content ratios varied from ~ 10 to ~ 40 among the 45 sampled sites of the watershed (Figure 5.5A). Spatially, soil C:N content ratio was negatively correlated to UAA and local slope, β ($r^2=0.38$; $p<0.001$), meaning that areas of the landscape that are relatively wetter had a lower soil C:N content ratio than those areas of the landscape that are relatively drier. Also known as the topographic index [Beven and Kirkby, 1979], the slope-normalized UAA represents a widely applied estimate for relative wetness.

Biomass C:N content ratio varied among species and among aboveground and belowground biomass of riparian meadows and upland forests as shown in Table 5.1. In general, lodgepole pine (*Pinus contorta*) from upland forests had a C:N content ratio between 5 and 10 times higher than C:N content ratio of riparian meadow grasses.

Fine root biomass varied from ~ 2 to $\sim 18 \text{ kg m}^{-3}$ across the 19 sampled sites of the watershed (Figure 5.5B). Spatially, fine root biomass was positively correlated with UAA ($r^2=0.40$; $p<0.001$), meaning that wetter areas of the landscape had a higher content of fine roots than dry areas. These relationships (as presented in Figure 5.5) suggest that these biophysical variables, known to influence soil CO_2 production and efflux, are also topographically organized and their spatial variability is partially mediated by landscape structure.

Soil CO₂ Efflux

Seasonal estimates (83-day accumulations) of soil CO₂ efflux during the 2006 growing season were highly variable across the 62 sampled sites of the watershed (Figure 5.6A). Soil CO₂ efflux varied from ~300 g CO₂ m⁻² to ~1900 g CO₂ m⁻², depending upon landscape position. At first glance, there is a 7-fold difference in effluxes across this montane watershed, with a median of 879.8 g CO₂ m⁻². Because a higher density of sites appear to fall between 600 and 1100 g CO₂ m⁻² and fewer sites had values of 1100 g CO₂ m⁻² or higher (Figure 5.6A), we applied a two-way partitioning algorithm (k-means, see Methods) to the entire dataset. This algorithm separated the 62 sites into two clusters (Figure 5.6B) with centroids of 839 and 1555 g CO₂ m⁻², respectively. Our results revealed that 14 sites were clustered with the higher centroid value, whereas 48 sites were clustered with the lower centroid value (Figure 5.6B). Analysis of the landscape position of each site demonstrated that 11 out of the 14 sites of the higher cluster corresponded to riparian meadow sites, and conversely, sites located in the uplands were consistently classified within the lower centroid values (Figure 5.6B). Two of the remaining 3 sites of the high cluster were located on low hillslopes adjacent to riparian meadows (areas prone to high soil water content), and the third one was located in an elevated NW facing site. Given the consistent high effluxes from this elevated NW facing site, we believe that the site selected was located immediately above a large root or series of roots and received respiration very rapidly from the source.

In summary, k-means clustering revealed that the highest soil CO₂ efflux rates

were observed in areas with persistent high soil water content (riparian meadows), whereas lower soil CO₂ efflux rates were observed on upland forests (Figure 5.6B). Given the consistent differences in CO₂ efflux between riparian meadows and upland forests based on landscape position and the overwhelming fraction of uplands relative to total area (~98%), we investigated the effects of landscape position on soil CO₂ efflux within upland sites. Using the UAA layer calculated from the 3-m DEM, as a measure of the lateral redistribution of soil water caused by local topography, we found a positive correlation between UAA and cumulative soil CO₂ efflux at all sites ($r^2=0.51$; $p<0.001$; Figure 5.7). However, the explanatory power of UAA considerably increased when sites were separated by the two major aspects of this watershed: SE aspects ($r^2=0.65$; $p<0.001$) and NW aspects ($r^2=0.61$; $p<0.001$; Figure 5.7), suggesting that the lateral redistribution of soil water and soil temperature as mediated by landscape structure can control soil CO₂ efflux in upland sites.

We used these relationships (Figure 5.6, 5.7) to upscale measured soil CO₂ efflux to the entire watershed via a two-step approach. First, we discretized the landscape into riparian meadows and upland forests. We area weighed mean efflux from riparian meadows (1572.1 g CO₂ m² over 83 days from 1.8% of the watershed). Second, we applied the UAA-soil CO₂ efflux relationships found for upland sites (Figure 5.7) to the entire distribution of UAA for this watershed. We found that soil CO₂ efflux from SE aspects (48.2% of the watershed) was of 730.5 ± 207.1 g CO₂ m² over 83 days, whereas soil CO₂ efflux in NW aspects (50.0% of the watershed) was 838.4 ± 102.5 g CO₂ m² over 83 days. In combination with efflux from riparian meadows, our study found

watershed-scale soil CO₂ efflux of 799.45 ± 151.1 g CO₂ m² over 83 days (Table 5.2).

These estimates represent an important step to quantifying watershed-scale soil CO₂ efflux, based on empirical relationships developed from repeated measurements of soil CO₂ efflux and landscape structure characteristics.

Discussion

In past investigations, when more than a few data collection sites were located in a given area, they were limited in number and distribution with little assessment of how well characterized the sampling sites were to the rest of the study area. With a wealth of literature on soil CO₂ efflux, studies addressing watershed-scale soil CO₂ efflux remain limited to non-existent. Furthermore, poor temporal resolution of measurements at a small number of sites has further restricted understanding of how soil CO₂ production and efflux change over space and time. Thus, serious complications can arise when, based on limited measurements at potentially biased spatial locations, attempts are made to spatially upscale soil CO₂ efflux. The result is often a modeling approach (e.g., soil CO₂ efflux as a function of soil temperature or solar radiation [*Fox et al.*, 2008]) that allows for temporal extrapolation, and another modeling approach applied on the spatial scale (e.g., as a function of landscape cover or vegetation index [*Vourlitis et al.*, 2000; *Kim et al.*, 2006] or an area-weighted sum of fluxes at single or few locations [*Soegaard et al.*, 2000; *Heikkinen et al.*, 2004; *Webster et al.*, in press-a]). Given the uncertainty in each of these modeling exercises due to limited and/or biased data, watershed-scale estimates of soil CO₂ efflux have not yet been rigorously accomplished.

In this study, we have demonstrated that the selected 62 measurement sites well-characterize the topographic heterogeneity of Stringer Creek watershed (Figure 5.2), therefore we suggest that spatially, there was little bias introduced during site selection and sampling design. Temporally, our repeated measurements varied from 10 to 37 chamber measurements across 62 sites. Previously demonstrated for this ecosystem [Riveros-Iregui *et al.*, in review-a], measurements taken between 1000 and 1600 h introduced little time-of-day bias and frequency bias when estimates are analyzed seasonally (cumulatively), primarily because the seasonality soil CO₂ efflux induced by changes of soil water prevails over diel dynamics driven by soil temperature and plant activity [Riveros-Iregui *et al.*, 2007; Riveros-Iregui *et al.*, in review-a]. Thus our soil CO₂ efflux measurements characterized both the spatial heterogeneity and temporal variability of effluxes throughout the 83-day period across this northern Rocky Mountain watershed.

Environmental Variables and Landscape Structure

One of the outstanding issues in C cycle research and specifically for soil CO₂ efflux is understanding the spatial and temporal heterogeneity induced by landscape structure. Landscape morphology imposes organized heterogeneity on soil temperature and on the allocation/redistribution of water and ultimately soil water content, and this is reflected not only on soil CO₂ efflux but also on its other biophysical controls (e.g., belowground biomass, C:N content ratios). While the timing of snowmelt can differ from year to year depending on the snow energy balance and snowpack accumulation, the spatial pattern of soil water content (θ) is imposed by landscape morphology and

structure. Thus convergent areas (e.g., riparian meadows, convergent slopes) are likely to represent the higher values of θ within a watershed, whereas divergent areas (e.g., divergent slopes) tend to be drier. This results in a degree of predictability in patterns of soil water content, based on topographic position and landscape structure, and to a lower degree, patterns of soil temperature based on aspect, land cover, and surface energy balance. Understanding this structured heterogeneity is crucial for understanding soil organic matter accumulation, decomposition rates of C pools, and ultimately, rates of soil CO₂ production and efflux from heterogeneous areas. More broadly and importantly, the shape of the landscape can impose structure on spatial heterogeneity of many biogeochemical processes mediated by soil temperature, soil water content, and the surface energy balance.

In our study, measurements of soil C:N content ratio and fine root biomass (Figure 5.5) were correlated to wetness indices such as topographic index and upslope accumulated area [Beven and Kirkby, 1979; Seibert and McGlynn, 2007]. These wetness indices have been used in many hydrological and ecological investigations [e.g., Famiglietti and Wood, 1991; Rodhe and Seibert, 1999; Urban *et al.*, 2000; Guntner *et al.*, 2004; Lookingbill and Urban, 2004; Pierce *et al.*, 2005; Zinko *et al.*, 2005; Sorensen *et al.*, 2006] as explanatory variables and natural manifestations of hydrological and biogeochemical correlation to topography and topology. Our findings demonstrate that fine root biomass was higher in wetter locations (relative to drier areas of the landscape), whereas soil C:N content ratios were lower relative to other areas of the landscape, likely as the result of difference in vegetation cover and enhanced soil decomposition and

oxidation. Thus our results suggest that fine root distributions and soil C:N content ratios, biophysical variables that have been related to the production and flux of soil CO₂ [Burton *et al.*, 2000; Maier and Kress, 2000; Pregitzer *et al.*, 2000; Brady and Weil, 2002; Shibistova *et al.*, 2002], also exhibit topographically mediated organization.

How Does Soil CO₂ Efflux Vary across Stringer Creek Watershed?

While previous studies had demonstrated that soil CO₂ efflux can be highly variable across a few landscape positions [Kang *et al.*, 2003; Saiz *et al.*, 2006; Webster *et al.*, in press-b], little understanding has been provided about how topography and landscape structure can control soil CO₂ efflux and how this organized heterogeneity can be used for interpolation, extrapolation, and transfer. In our study, two-way k-means analysis revealed that a first-order categorization of the landscape can simply be made as a binary discretization: riparian meadows and forested uplands (Figure 5.6). Differences in efflux magnitude between these two landscape elements have been previously observed across pairs sites of the same study area [Riveros-Iregui *et al.*, in review-a]; however, our results demonstrated that this magnitude difference in efflux can be consistent across multiple (62) riparian meadow locations (11) and upland sites (51) (Figure 5.6B). The magnitude difference between riparian meadows and upland forests is likely due to the large drainage area of riparian meadows, which results in higher and more sustained soil water content (Figure 5.4) and the feedback to vegetation cover and soil characteristics. Thus while riparian meadows in the Stringer Creek watershed comprise only 1.8% of the landscape, soil CO₂ efflux from these meadows is the highest across the entire watershed (Figure 5.6) and results in a disproportionate 3.5% of total

catchment efflux.

Cumulative soil CO₂ efflux was positively correlated with UAA (Figure 5.7) in upland forests, which comprised ~98% of the watershed area. This is a powerful observation, yet is to be expected given that plant and microbial activities are dependent on water availability. UAA characterizes the relative magnitude of water flow across the landscape, (i.e., drainage pattern), as highlighted in multiple studies [*Beven and Wood*, 1983; *McGlynn and Seibert*, 2003; *McGlynn et al.*, 2004; *McGuire et al.*, 2005; *Sorensen et al.*, 2006; *Seibert and McGlynn*, 2007; *Jencso et al.*, in review], and its relationship to soil CO₂ efflux in drier areas of the landscape is an element that can be of great advantage to large-scale (~km²) quantifications of land-atmosphere CO₂ exchange.

Scaling from Point Observations to Watershed Scale Fluxes

Currently, poor process-based understanding, sparse field measurements across space and time, and a lack of organizing principles, limit our ability to assess soil CO₂ fluxes from areas where biophysical controls (i.e., soil water content, soil temperature, vegetation cover) concurrently vary in space and time. It is well-known that soil temperature can explain soil CO₂ efflux at single plots over short (diel) temporal scales [*Riveros-Iregui et al.*, 2007; *Carbone et al.*, 2008]. However, it is also well-known that soil temperature and temperature-based models (e.g., Q₁₀ [*Lloyd and Taylor*, 1994]) are poor predictors of soil CO₂ efflux at larger spatial scales [*Richardson and Hollinger*, 2005]. In fact, the use of temperature-based models continues to be discouraged for large scales [*Janssens and Pilegaard*, 2003; *Davidson et al.*, 2006; *Richardson et al.*, 2006], likely because soil temperature effects on soil CO₂ have been found to vary widely across

ranges of soil water content conditions and drydown [*Riveros-Iregui et al.*, 2007]. Thus, it is only to be expected that systems with wide spatial differences in soil water content regimes (e.g., entire forests) and/or strong temporal differences in soil water content caused by environmental controls (e.g., snowmelt, droughts, summer drydown) will exhibit poor fits of such models. Furthermore, multi-parameter models require free parameters to constrain respiration models [*Falge et al.*, 2001; *Reichstein et al.*, 2005; *Richardson and Hollinger*, 2005], which make it difficult to interpret actual physical processes. Thus no appropriate parameter has emerged to aid in parameterization and modeling of soil CO₂ efflux variability from large areas.

Our empirical approach offers great potential across large spatial scales, comparable and useful to many other land-atmosphere studies of CO₂ exchange [*Riveros-Iregui et al.*, in review-b], and it allows for context and interpretation for plot and point scales. Our results highlight topographic organization of biogeochemical processes leading to soil CO₂ production and efflux. Using the explanatory power of UAA (~61-65%; Figure 5.7) as the overarching control of seasonal soil CO₂ efflux can be comparable to more complicated, multiple-parameter models previously developed ($r^2 = 0.723$; [*Webster et al.*, in press-b]). Yet the strength of the correlation of UAA and seasonal soil CO₂ efflux in combination with DEM terrain analysis tools [*Seibert and McGlynn*, 2007] and spatial integration makes our approach a crucial tool in landscape characterization and discretization and provides an important link between point scale measurements and ecosystem/watershed scale estimates of soil CO₂ efflux.

Accounting for landscape heterogeneity, drainage patterns, and watershed area,

our up-scaled estimates of watershed-scale soil CO₂ efflux ($799.45 \pm 151.1 \text{ g CO}_2 \text{ m}^2$ over 83 days) compared within ~2% of independent eddy-covariance estimates of nighttime ecosystem respiration previously reported [*Riveros-Iregui et al.*, in review-b] over the forest for the same period (Table 5.2). Counteracting errors can be a part of these estimates, however leaf-level measurements of autotrophic respiration made throughout the season demonstrated that nighttime aboveground respiration is very low in this ecosystem (<8%, unpublished data) and suggest that most of the ecosystem respiration was soil respiration. While it is likely modest, the role of other types of aboveground biomass (e.g., twigs, branches, trunks) in contributing to ecosystem respiration remains to be addressed.

Nonetheless, the level of comparison between soil-based measurements capturing and accounting for structured heterogeneity and independent tower measurements is highly encouraging. Our study demonstrates topographic/topologic controls on the magnitude of soil CO₂ efflux. The temporal scales of this organization remain to be tested and examined. For example, is there legacy of these topographic controls? Further investigations are warranted to address whether these dynamics are a reflection of geomorphic evolution and soil/biogeochemical development or they are simply reflections of contemporary water content dynamics.

The effect of inter-annual climate variability on the spatial variability of soil CO₂ efflux remains unknown, and how climate variability (e.g., dry vs. wet year, late snowmelt, reduced snowpack) will affect different landscape elements within a watershed or if particular elements (e.g., wet riparian meadows) are especially prone to climate

variability. Our findings have important implications for how quantitative assessments of soil CO₂ efflux from heterogeneous landscapes can provide a conceptual framework for soil CO₂ efflux variability based on simple landscape discretization, topographic analysis of landscape structure, and empirical relationships developed from repeated measurements of soil CO₂ efflux.

Can the Shape of the Landscape (Structure) Affect the Generation and Flux of Soil CO₂ in Subalpine Ecosystems?

To further our understanding of the effects of landscape structure and controls on watershed-scale soil CO₂ efflux, we created three synthetic watersheds varying in shape and slope, which were intended to represent progressively simpler models of the Stringer Creek watershed (Figure 5.8). Natural watersheds contain elements from these three synthetic DEMs, yet these three DEMs are simplified versions of the natural system. The three synthetic watersheds are characterized as follows: 1) a symmetrical, convergent (bowl-shaped) watershed; 2) a planar and steep watershed with constant slope; and 3) a planar watershed with more gentle slope (Figure 5.8). Catchment area was comparable to the Stringer Creek watershed, and results are area normalized. For each DEM, we calculated UAA in a similar manner as for Stringer Creek DEMs described previously (Section 2). We applied the same empirical model and used the same two-step approach as for Stringer Creek watershed to estimate watershed scale soil CO₂ efflux from each synthetic DEM (Figure 5.9).

Watershed-scale soil CO₂ efflux estimated from these synthetic watersheds was 50%, 58%, and 98% higher than that measured and up-scaled from the Stringer Creek

watershed (Figure 5.9B). The estimated efflux increased as watershed complexity decreased. Decreasing complexity resulted in reduced water re-routing, modifying lateral redistribution of soil water throughout each watershed. In successively simpler watersheds, UAA values progressively increased in uplands (i.e., uplands became progressively “wetter”), increasing the frequency of high UAA values (Figure 5.9A). Natural systems exhibit heterogeneities in shape (e.g., convergence, steepness, divergence) that influence soil water redistribution, concentrating UAA (or watershed area) to lower parts of the watershed. These heterogeneities were limited in the synthetic DEMs (Figure 5.8B-D), therefore the distribution of soil water was more uniform across the landscape. The least complex watershed (gentle slope; Figure 5.8D) exhibited the highest estimated soil CO₂ efflux, because the structure of this watershed allowed for a more homogenous distribution of UAA than the natural and other two synthetic, but more complex, watersheds .

We calculated the kurtosis of the distribution of UAA values of each watershed as a metric of structural complexity. This metric allowed for inter-comparison of the natural and the three synthetic watersheds (Figure 5.10). Although a simple metric, this analysis (Figure 5.10) demonstrated that for these ecosystems, landscape structure (and resulting UAA distribution) plays a major role in controlling watershed-scale rates of soil CO₂ efflux. This compelling relationship and the inherent conceptual framework warrant further investigation. Specifically, how applicable is this concept across other heterogeneous sites? What are the effects of climate variability on these emergent patterns? What are the process time scales and additional covarying variables affecting

these relationships? What are the specifics of point scale biological and physical processes across these landscape positions and how do they vary? The demonstrated correlation between landscape position/ watershed structure and seasonal estimates of soil CO₂ efflux based on repeated measurements, offers promise for up-scaling rates of soil CO₂ efflux rates from large areas, downscaling from coarser spatial measurements, and interpreting point and plot scale measurements and what aspects of the system they represent [*Riveros-Iregui et al.*, in review-b].

Our study demonstrates that while biophysical heterogeneity is inherent in natural systems, this heterogeneity often exhibits a high degree of organization that can be of advantage to watershed and landscape scale studies.

Conclusions and Implications

Riparian meadows were found to have the highest rates of cumulative soil CO₂ efflux across the entire watershed based on soil chamber measurements across 62 sites of a subalpine watershed and during the 2006 growing season. Riparian meadows have a larger UAA and receive more soil water drainage than upland sites, leading to enhanced plant and microbial respiration in riparian meadows as compared to forested uplands.

Empirically up-scaled soil CO₂ efflux for the entire Stringer Creek watershed (799.5 ± 151.1 g CO₂ m⁻² over 83 days) compared within 2% of independent estimates of nighttime ecosystem respiration measured over the forest canopy with the eddy covariance technique for the same period. The up-scaled estimates were based on landscape discretization, topographic analysis of landscape structure, and empirical

relationships developed from repeated measurements of soil CO₂ efflux.

Topography and landscape structure are strong indicators of the variability and magnitude of soil CO₂ efflux from complex watersheds. Landscape context and controls on heterogeneity are critical to estimation and interpretation of watershed-scale rates of soil CO₂ efflux. Landscape analysis is a critical tool for up-scaling plot or point measurements to larger spatial scales, with regards to soil CO₂ efflux and likely many other biogeochemical processes mediated by soil temperature, soil water content, and the surface energy balance.

Modeled soil CO₂ efflux from three synthetic DEMs, varying in shape and slope with progressively less topographic complexity resulted in 50%, 58%, and 98% higher efflux estimates than that measured and up-scaled from the Stringer Creek watershed. Decreasing complexity resulted in a more homogeneous distribution of UAA across the landscape due to reduced flowpath convergence and divergence, resulting in less lateral redistribution of soil water throughout each watershed.

Our results have important implications for interpreting and evaluating rates of soil CO₂ efflux from heterogeneous landscapes, and improved process understanding of watershed-scale (km²) soil CO₂ efflux variability. This information is necessary to reduce uncertainty in ecosystem exchange of C, promote integration with other measures of ecosystem C exchange (e.g., eddy covariance in heterogeneous landscapes), and enhance parameterization and prediction of watershed-scale fluxes. These implications should be considered when measuring and modeling the dynamics of C cycling at progressively larger scales or when attempting to downscale large-scale measures.

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Table 5.1 C:N content ratio of riparian and upland vegetation at Stringer Creek. Values represent the means of three samples and one standard deviation of the means. Vegetation description is after Mincemoyer and Birdsall [2006].

RIPARIAN MEADOWS			UPLAND FORESTS		
Type	C:N Ratio	S.D.	Type	C:N Ratio	S.D.
<i>Calamagrostis</i> -shoots	17.9	1.0	<i>Vaccinium</i> – leaves	19.5	0.7
<i>Calamagrostis</i> -roots	31.6	11.5	<i>Vaccinium</i> – stems	57.6	2.1
<i>Urtica dioica</i> – shoots	11.4	1.0	<i>Vaccinium</i> – roots	87.0	11.2
<i>Urtica dioica</i> – roots	20.5	1.3	<i>Deschampsia cespitosa</i> – shoots	44.3	0.8
			<i>Deschampsia cespitosa</i> – roots	70.8	12.7
			<i>Pinus contorta</i> – twigs	129.7	7.7
			<i>Pinus contorta</i> – roots	172.2	12.9
			<i>Pinus contorta</i> – live needles	54.0	8.2
			<i>Pinus contorta</i> – dead needles	58.5	8.6

Table 5.2 Watershed-scale estimates of seasonal soil CO₂ efflux for Stringer Creek watershed and three synthetic digital elevation models (DEM), and independent estimates of nighttime ecosystem respiration (R_E) measured above the canopy with an eddy covariance system.

	Stringer Creek	Nighttime R_E [<i>Riveros-Iregui et al.</i> , in review-b]	Watershed 1	Watershed 2	Watershed 3
Description	This study		Convergent (bowl- shaped)	Planar - steep slope	Planar (gentle slope)
Calculated Riparian Area	1.8%		2.5%	0.34%	0.54%
Total Soil CO ₂ Efflux [g CO ₂ m ⁻² 83 days ⁻¹]	799.5 ± 151.1	787.8	1199.8 ± 177.6	1261.9 ± 179.1	1584.1 ± 258.4

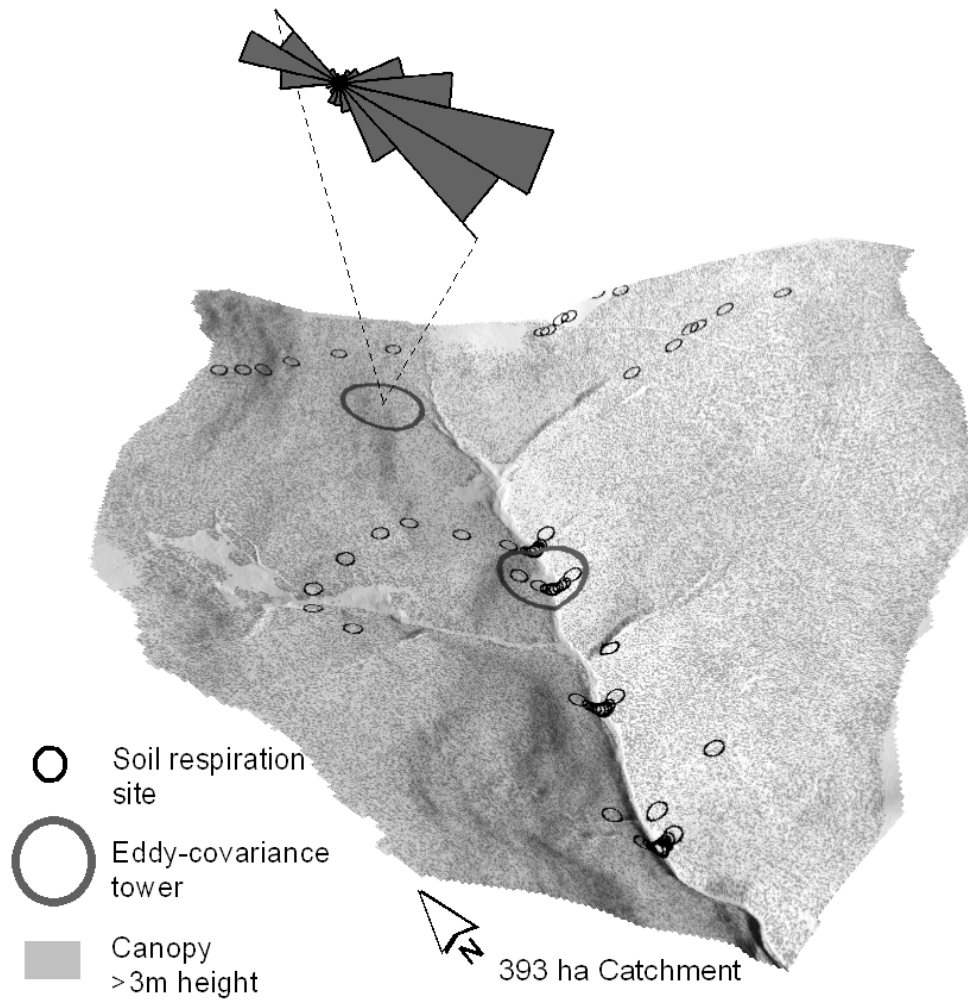


Figure 5.1 Distribution of 62 sites across Stringer Creek Watershed. Stringer Creek is located in the Tenderfoot Creek Experimental Forest, in the Little Belt Mountains of central Montana. Stringer Creek Watershed is ~393 ha in area. Wind rose indicates predominant wind direction for the period between June 9 and August 30, 2006.

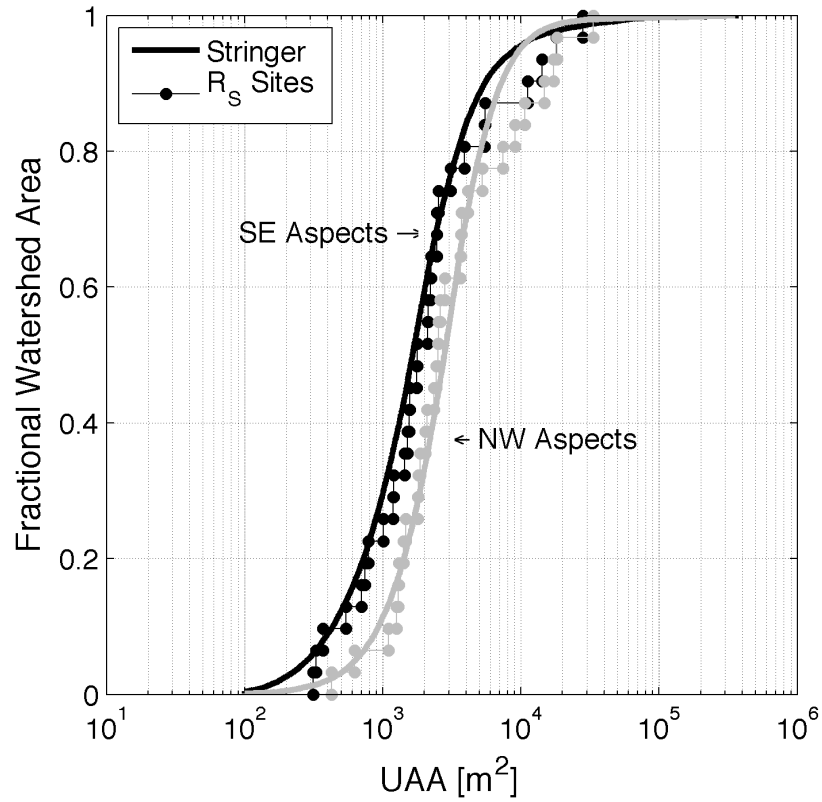


Figure 5.2 Distribution of 10-m upslope accumulated area (UAA) across Stringer Creek Watershed (continuous line), and across sites where soil CO_2 efflux (R_s) was measured. Sites were separated by aspect into the two main categories, SE and NW facing aspects. This analysis demonstrates that the selected sites were characteristic of the distribution of UAA for the Stringer Creek watershed.

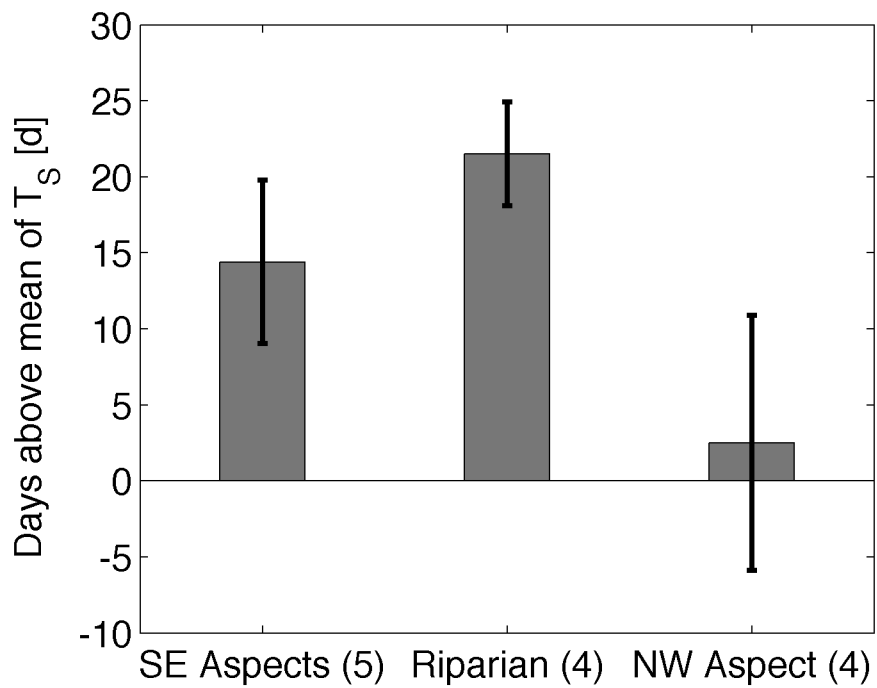


Figure 5.3 Degree-days above the mean for sites in SE aspects (5), riparian meadows (4), and NW aspects (4), based on 4-hr measurements from July 18 to October 17, 2006. Mean is from data at all sites. Bar heights indicate the mean of degree-days at sites within each landscape element and error bars one standard deviation of degree-days of each site.

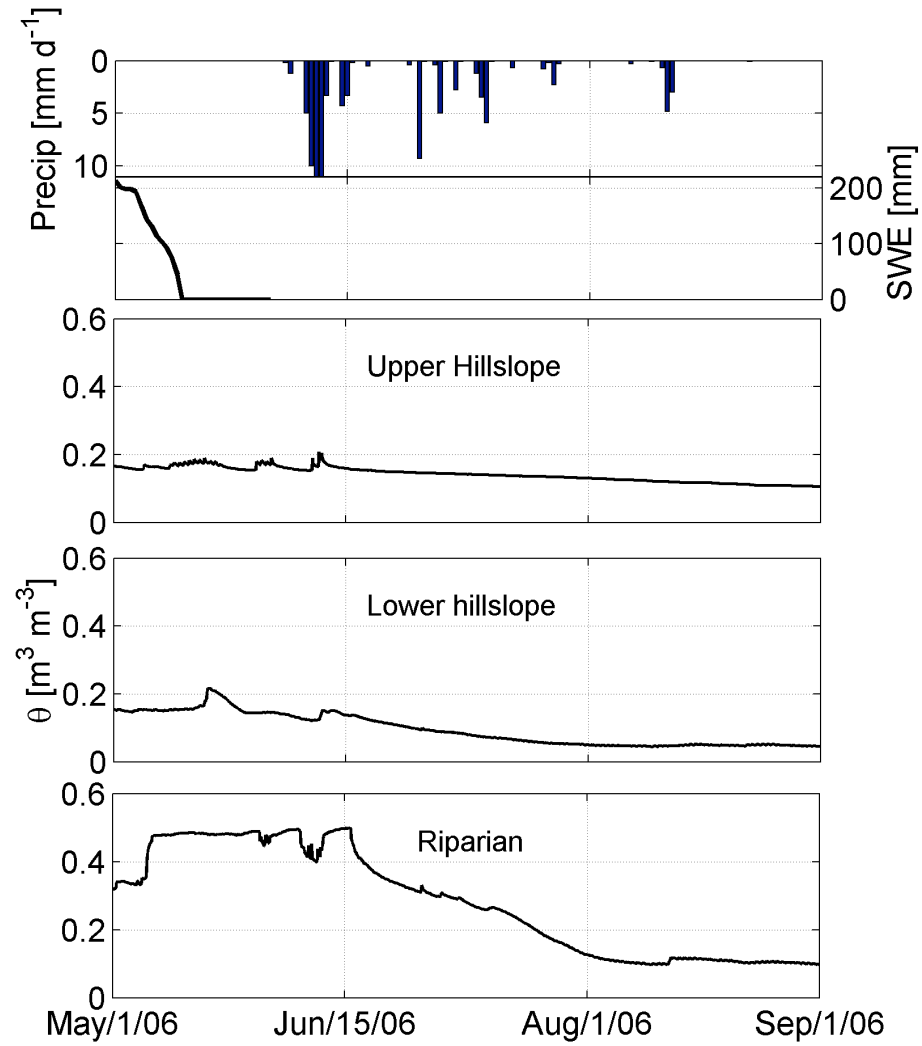


Figure 5.4 Variability of precipitation, snow water equivalent (SWE), and soil water content (θ) at 20 cm across high and low hillslopes, and a riparian meadow of Stringer Creek Watershed for the 2006 growing season.

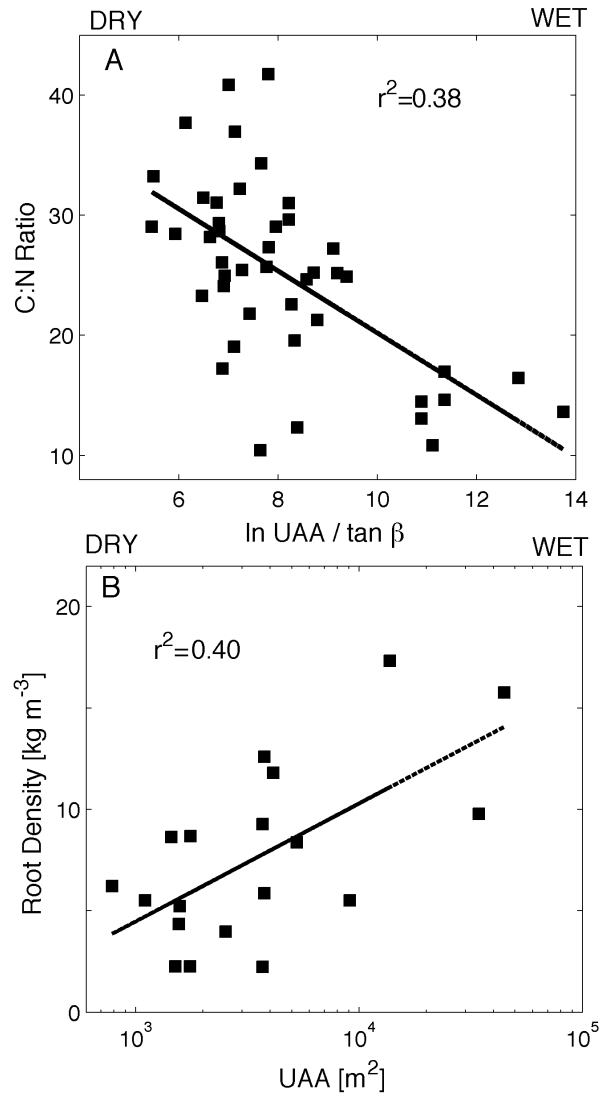


Figure 5.5 A) Relationship between upslope accumulated area (UAA), local slope (β), and carbon and nitrogen content in the soil. B) Relationship between root density [kg m^{-3}] and upslope accumulated area (UAA). Note the log scale for the x axis.

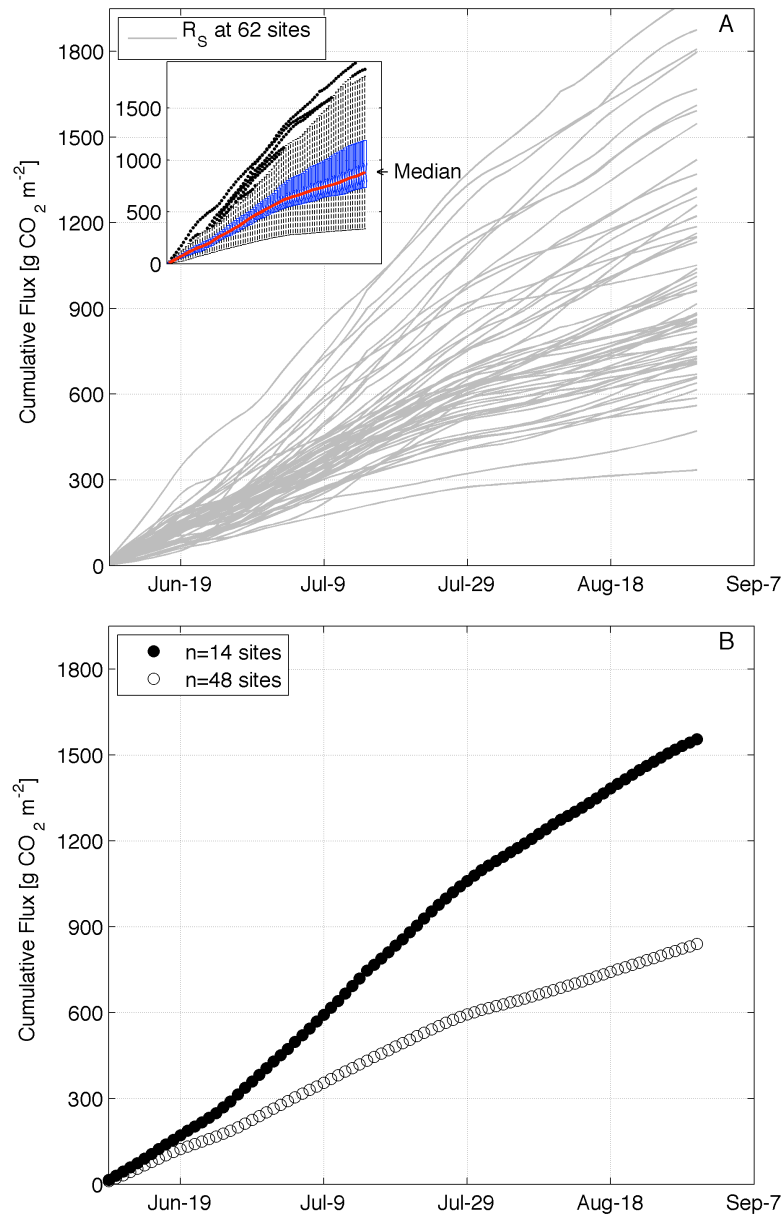


Figure 5.6 A) Variability of cumulative soil CO₂ efflux across Stringer Creek Watershed for 83 days of the 2006 growing season. Note a ~7-fold difference in estimates of soil CO₂ efflux across the watershed. Inset: Cumulative boxplots for the same data. Blue shading (boxes) represents the inter-quartile range, red line indicates the cumulative median, and black dots represent statistical outliers. Note that while riparian meadows comprise only ~1.8% of watershed area, soil CO₂ efflux from these sites is the highest across the watershed and these sites can be portrayed as a statistical outlier. B) Partitioning of sites using cluster analysis demonstrates that 14 sites are classified within the cluster with the higher centroid value (filled circles); 11 of these sites are located in the riparian meadow. Sites located in the hillslopes are consistently classified within the lower centroid values (open circles).

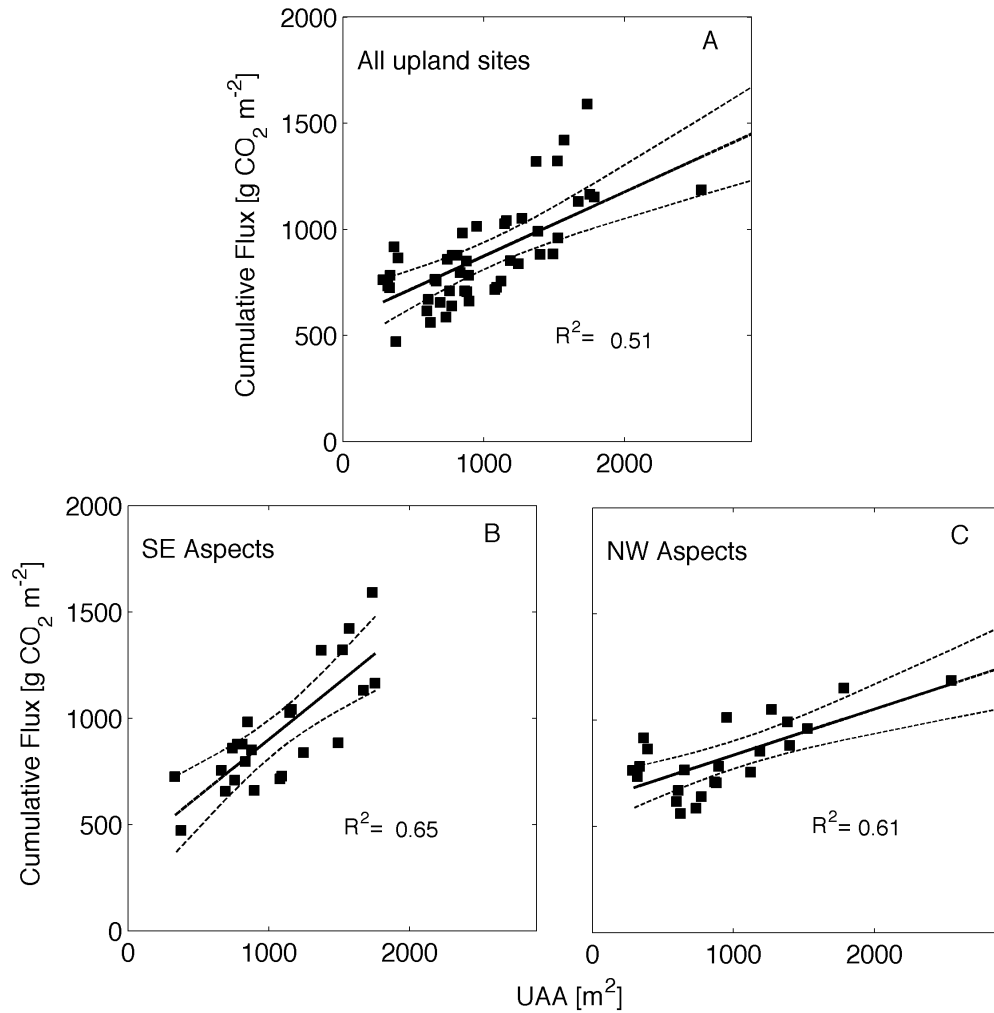


Figure 5.7 A) Relationship between calculated 3-m upslope accumulated area (UAA) and cumulative soil CO₂ flux (R_s) at all upland sites (A), and separated by aspect (B, C). B) The relationship for SE aspects was $R_s = (0.534 \cdot \text{UAA}) + 366.9$. C) The relationship for NW aspects was $R_s = (0.217 \cdot \text{UAA}) + 619.4$. Dashed lines represent the Working-Hotelling 95% confidence band of each regression line.

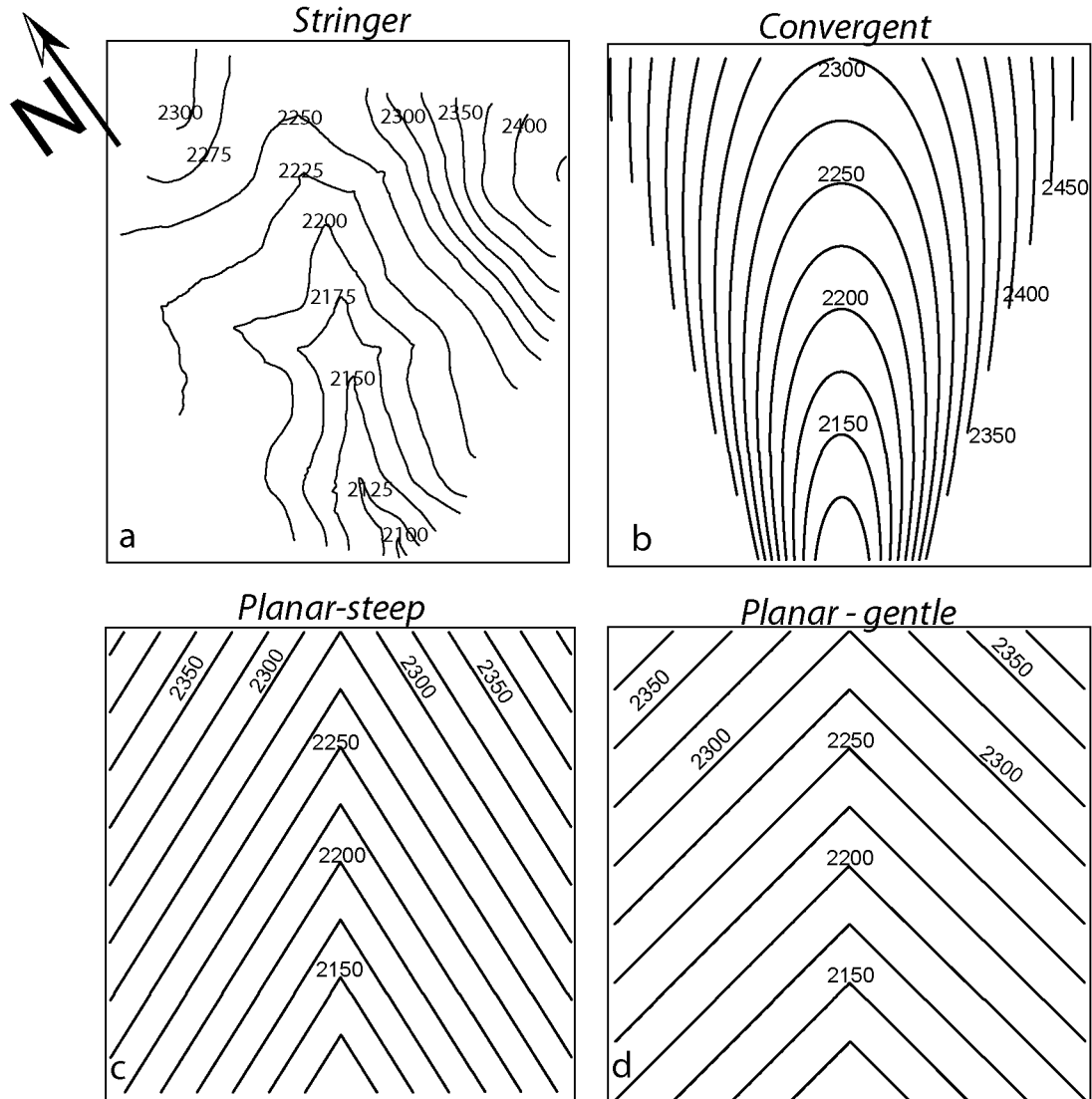


Figure 5.8 A) 25-m contours for Stringer Creek and for three synthetic DEMs characterized as follows: B) a convergent watershed; C) a planar-steep watershed; and d) a planar, gentle slope watershed. Watersheds vary in shape and slope, decreasing in terrain complexity from (a) to (d).

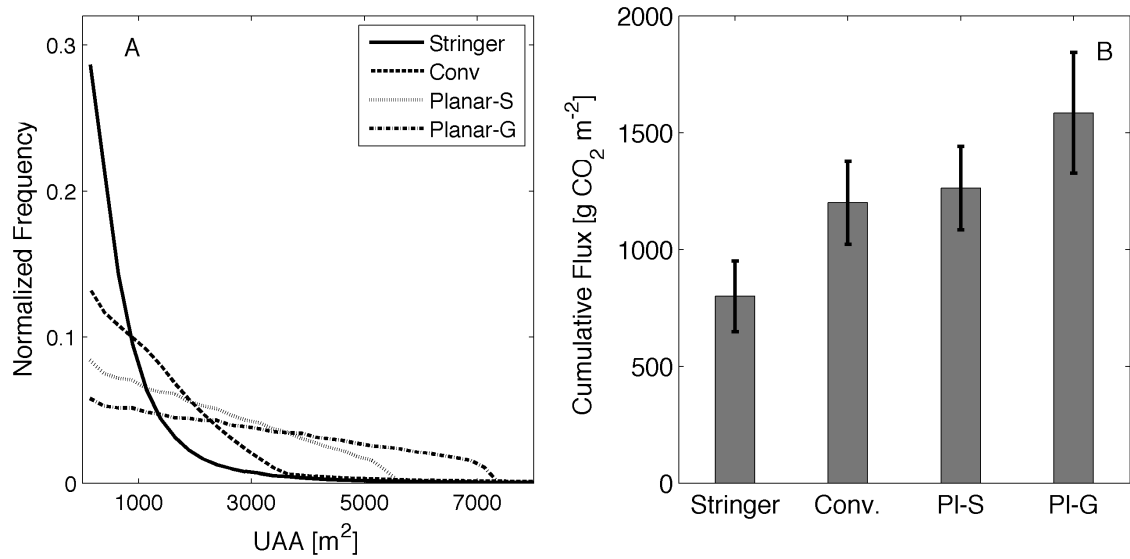


Figure 5.9 A) Distribution of calculated 3-m UAA for Stringer Creek watershed and the three synthetic watersheds presented in Figure 5.8. B) Seasonal soil CO₂ efflux for the same watersheds, based on the relationships found in Figure 5.7.

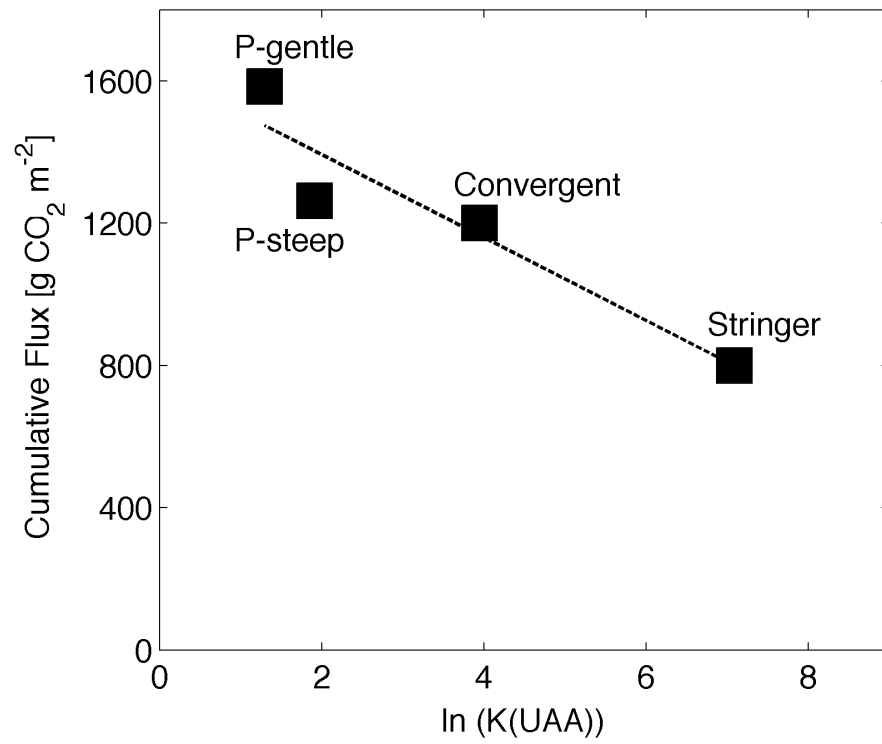


Figure 5.10 Relationship between the kurtosis (K) of UAA and predicted seasonal CO₂ efflux for the Stringer Creek watershed, and the three synthetic cases: a convergent watershed, a planar-steep watershed, and a planar, gentle slope watershed.

CHAPTER 6

A CRITICAL ASSESSMENT OF A PROCESS
SOIL CO₂ PRODUCTION AND TRANSPORT MODELAbstract

We applied a process soil CO₂ production and transport model to a well-studied subalpine watershed of the northern Rocky Mountains. Our approach started at the plot scale and progressively added process understanding to advance to the watershed scale. We corroborated model performance using an independent dataset of soil CO₂ efflux measurements from distributed sites across the same watershed. The model predicted the seasonality of soil CO₂ at a riparian site, simulated short-term (diel) dynamics of soil CO₂ concentrations at the riparian site, and captured seasonal estimates of soil CO₂ efflux at dry sites of the landscape. The model performed poorly when predicting seasonal soil CO₂ efflux at wet sites, likely as a result of poorly modeled soil water content and poorly parameterized microbial activity. Our study demonstrates that thorough corroboration of modeled estimates with adequate independent observations is a key element in process modeling, because it enhances process understanding, reduces chances of equifinality, and determines model validity and utility.

Introduction

Modeling soil CO₂ efflux has been an active research area during the last decade. Many soil CO₂ efflux models have been developed based on empirical relationships

between soil CO₂ efflux and soil temperature [e.g., *Kucera and Kirkham*, 1971; *Ratkowsky et al.*, 1982; *Lloyd and Taylor*, 1994; *Winkler et al.*, 1996], soil water content [e.g., *Orchard and Cook*, 1983; *Davidson et al.*, 2000; *Liu et al.*, 2002; *Yuste et al.*, 2003], substrate and surrogates for substrate supply [e.g., *Raich and Nadelhoffer*, 1989; *Ryan et al.*, 1996; *Janssens et al.*, 2001; *Reichstein et al.*, 2003], and upslope accumulated area [*Riveros-Iregui and McGlynn*, in review]. These relationships are useful because they provide estimates of soil CO₂ efflux based on observations of both soil CO₂ efflux and a major controlling variable and applied to larger areas. However, the performance of these models across temporal and spatial scales remains limited, because interrelationships among controlling variables are likely to be different across scales [*Reichstein et al.*, 2003].

Process-based models have been explored as numerical representations of mechanisms known to govern soil CO₂ efflux [e.g., *Parton et al.*, 1987; *Rastetter et al.*, 1991; *Potter et al.*, 1993; *Suarez and Simunek*, 1993; *Rastetter et al.*, 1997; *Fang and Moncrieff*, 1999; *Welsch and Hornberger*, 2004]. These models are typically developed from system examination and based on physical evidence, and allow for synthesis of process understanding. These models usually involve multiple variables, can provide important explanations for observed variations of soil CO₂ efflux, and their multi-factor structure makes them less site-specific, allowing for further development and transfer. However, the multi-factor structure of process models commonly requires broad assumptions, which make it difficult to parameterize the spatial and temporal interrelationships of variables.

A common problem in soil CO₂ process models is the omission of spatial and temporal variability of soil water content. This omission becomes especially important in moisture-limited systems (e.g., semi-arid areas, snowmelt-driven systems). It has been recently suggested that soil water content can control the spatial [*Pacific et al.*, in review; *Riveros-Iregui and McGlynn*, in review] and temporal [*Riveros-Iregui et al.*, 2007; *Riveros-Iregui et al.*, in review-a] variability of soil CO₂ efflux in these systems. To date, a robust implementation of seasonality and lateral distribution of soil water into models that simulate and predict soil CO₂ efflux is lacking. Yet this information is necessary for accurate estimates of soil CO₂ efflux from large areas. Understanding the effect of soil water content on soil CO₂ efflux from diel to seasonal scales, and from point to ecosystem scales is critical to incorporating the role of soil water as a driver of biogeochemical processes in many ecosystems.

In this paper, we applied an existing process-based soil CO₂ production model [*Fang and Moncrieff*, 1999; *Welsch and Hornberger*, 2004] in combination with a recently developed CO₂ production and transport model [*Riveros-Iregui et al.*, 2007], to a well-studied subalpine watershed of the northern Rocky Mountains. We implemented this model by progressively adding process understanding starting at the plot scale and advancing to the watershed scale. The specific objectives of this study are 1) to critically assess the performance of a soil CO₂ process model to simulate soil CO₂ production and flux in a subalpine watershed; 2) to investigate the role of spatial and temporal variability of soil water content on predicted soil CO₂ efflux; and 3) to corroborate model performance using an independent dataset of CO₂ efflux measurements at distributed

sites across the same watershed. This study progresses from the point to catchment/ecosystem-scale modeling of soil CO₂ efflux. We address two outstanding eco-hydrological, carbon cycle research questions: the role of hydrology as a spatial and temporal control of soil CO₂ efflux, and the role of model-data comparison in the development of realistic soil CO₂ production and efflux models.

Study Site

The study site was the Tenderfoot Creek Experimental Forest (TCEF), a subalpine catchment of the Northern Rocky Mountains. This forest is representative of the lodgepole pine (*Pinus contorta*) dominant subalpine ecosystems of the northern Rocky Mountains and is subject to a steady seasonal drydown in soil water content [Woods *et al.*, 2006; Riveros-Iregui *et al.*, 2007]. The 393-ha catchment of interest contains a 2nd-order perennial stream, Stringer Creek that drains into Tenderfoot Creek, which ultimately drains into the Missouri River. At the TCEF, freezing temperatures and snow can occur every month of the year, and the mean annual temperature is 0 °C [Farnes *et al.*, 1995]. The growing season for the majority of the TCEF is 45 to 75 days, decreasing to 30 to 45 days on the ridges. Mean annual precipitation is 880 mm, of which >70% falls as snow [Farnes *et al.*, 1995]. The Stringer Creek watershed elevation ranges from 1840 to 2421 m and has a full range of slope, aspect, and topographic convergence and divergence. Stringer Creek catchment has been the focus of several soil CO₂ efflux and hydrology studies in the last few years [Riveros-Iregui *et al.*, 2007; Jencso *et al.*, in review; Pacific *et al.*, in review; Riveros-Iregui and McGlynn, in review; Riveros-Iregui

et al., in review-a; b]. Given its relatively simple vegetation cover, Stringer Creek catchment is an ideal site to implement a process-based model focused on the effects of variability in soil water content and soil temperature on controlling soil CO₂ efflux at the catchment scale.

The Model

Soil Water Content Model

Recent studies in subalpine ecosystems have highlighted the importance of soil water content as a control of soil CO₂ production and efflux, both temporally [*Riveros-Iregui et al.*, 2007] and spatially [*Riveros-Iregui and McGlynn*, in review]. To model soil water content at the catchment scale, we used a version of TOPMODEL [*Beven and Kirkby*, 1979] integrated with a soil-vegetation-atmosphere model [*Scanlon et al.*, 2005]. Additionally, this model was combined with a dynamic water stress model [*Emanuel et al.*, 2007], which included calculations of stomatal conductance and transpiration. This three-component model has been applied recently to the Stringer Creek watershed [*Emanuel et al.*, in review] due to its demonstrated ability to represent water-controlling processes at the catchment scale. The model calculates soil water content by solving the water mass balance at each grid cell based on gravity drainage, vegetation cover, and evapo-transpiration, variables known to control water availability and distribution at the catchment scale [*Emanuel et al.*, in review]. The model output was compared to runoff measured by the US Forest Service at the catchment outlet and to total ET measured by an eddy covariance tower [*Emanuel et al.*, in review], validating the use of the model to

accurately predict seasonal hydrologic balance of Stringer Creek catchment. Modeled estimates of soil water content were made at 30-min intervals between June 21 and September 2, 2006. While seasonal trends of simulated soil water content replicated the observations very closely ($r^2=0.97$; [Emanuel *et al.*, in review]) the absolute magnitude of the simulated water content drydown doubled field observations ($28 \text{ m}^3\text{m}^{-3}$ vs. $16 \text{ m}^3\text{m}^{-3}$, respectively [Emanuel *et al.*, in review]).

Soil CO_2 production was calculated as a function of water stress on plant and microbial activities [Simunek and Suarez, 1993; Welsch and Hornberger, 2004]. We calculated soil tension (h) by solving from a widely-applied soil moisture – soil tension relationship [van Genuchten, 1980]:

$$\theta = \theta_r + \frac{(\theta_s - \theta_r)}{\left[1 + (\alpha h)^n\right]^m} \quad (6.1)$$

where θ_r is the residual water content, θ_s is the saturated water content, α is the tension at air entry, m is given by $m = 1 - \frac{1}{n}$, and n is a fitting parameter estimated from observed data. The van Genuchten relationship has been widely applied and proven accurate when predicting diffusivity as a function of air-filled porosity across multiple soil types and porosities [Moldrup *et al.*, 2005a; Moldrup *et al.*, 2005b].

Soil Temperature Model

Soil temperature is known to control soil CO_2 production and efflux at short and long time scales [e.g., Lloyd and Taylor, 1994; Winkler *et al.*, 1996]. To model soil temperature for the entire catchment, we began by using interpolated, distributed air

temperature at 10-m grid resolution derived from the Spatial Observation Gridding System (SOGS) [Jolly *et al.*, 2005; Emanuel *et al.*, in review] for the period between June 21 and September 2, 2006, at 30-min intervals [Emanuel *et al.*, in review]. This scale-independent system has been found to yield a mean absolute error of less than 2 °C [Jolly *et al.*, 2005]. Soil temperature was calculated by applying the heat transfer equation, as described by Horton [2002]:

$$\frac{\partial T}{\partial t} = \frac{\lambda}{C} \frac{\partial^2 T}{\partial z^2} \quad (6.2)$$

where t is time [s], λ is thermal conductivity [$\text{W m}^{-1} \text{ }^\circ\text{C}^{-1}$], C is volumetric heat capacity

[$\text{J m}^{-3} \text{ }^\circ\text{C}^{-1}$], and $\frac{\partial T}{\partial z}$ is the temperature gradient [$^\circ\text{C m}^{-1}$]. In solving Equation 6.2, we

used the approximation of Kang *et al.* [2000], developed to predict spatiotemporal variability of soil temperature in forested soils. This relationship assumes that soil temperature can be estimated at any depth (z) using the following relationships:

When $A_j > T_{j-1}$,

$$T_j(z) = T_{j-1}(z) + [A_j - T_{j-1}(z)] \times \exp\left[-z\left(\frac{\pi}{k_s p}\right)^{\frac{1}{2}}\right] \exp[-k(LAI_j + litter_j)] \quad (6.3)$$

and when $A_j \leq T_{j-1}$,

$$T_j(z) = T_{j-1}(z) + [A_j - T_{j-1}(z)] \times \exp\left[-z\left(\frac{\pi}{k_s p}\right)^{\frac{1}{2}}\right] \exp[-k \times litter_j] \quad (6.4)$$

where A_j is air temperature at the time j , T is soil temperature, k_s is the soil thermal diffusivity ($1.54 \times 10^{-3} \text{ cm}^2/\text{s}$), p is the period of diurnal temperature variation (86,400 s), and k is the extinction coefficient from the Beer-Lambert Law for radiation through canopy as a function of leaf area index (LAI) and ground litter LAI equivalent. We assumed constant LAI for both vegetation ($1.2 \text{ m}^2 \text{ m}^{-2}$) and ground litter ($1.5 \text{ m}^2 \text{ m}^{-2}$) throughout the growing season. Based on calibration with measured soil temperature at two sites, the estimated uncertainty for soil temperature was better than 1.5° C .

Soil CO₂ Production and Transport Model

The dynamics of CO₂ in soil air can be explained by the following mass balance equation [Riveros-Iregui *et al.*, 2007],:

$$f_a \frac{\partial [\text{CO}_2]}{\partial t} = - \frac{\partial}{\partial z} \left[D(f_a) \frac{\partial [\text{CO}_2]}{\partial z} \right] + k_A(PAR, \theta) + k_H(T_s, \theta) \quad (6.5)$$

where f_a is the air-filled porosity, D is the diffusion coefficient of CO₂ in the air-filled pore space, k_A and k_H are the rates of CO₂ production from autotrophic and heterotrophic activities, respectively, PAR is photosynthetically active radiation, T_s is soil temperature and θ is soil water content. It is important to note that PAR and T_s vary in time on a daily basis, whereas θ varies in time on a seasonal basis. As a result, there is asynchronism in the timing and effect of each variable on the resulting soil CO₂. While Equation 6.5 presents the dynamics of CO₂ at any given depth z , the right-hand side (RHS) of Equation 6.5 is divided into two components: a production component ($[k_A + k_H]$) and a transport component ($D \frac{\partial [\text{CO}_2]}{\partial z}$). To implement the production

component, we adapted the soil CO₂ production component of a previously developed model [Fang and Moncrieff, 1999; Welsch and Hornberger, 2004]:

$$\gamma_A f(PAR)B + \gamma_H M \quad (6.6)$$

where γ_A and γ_H are the rates of autotrophic and heterotrophic respirations, respectively, and $f(PAR)$ was a normalized function of PAR, varying from 0 to 1 throughout the season. This model has proven functional across different forested ecosystems [Moncrieff and Fang, 1999; Welsch and Hornberger, 2004; Saiz *et al.*, 2007] because it includes the main effects of environmental factors (i.e., soil temperature, soil water content, soil O₂ concentration) on the generation of soil CO₂ from plant and microbial activities. Rates of autotrophic and heterotrophic activities were calibrated based on optimal rates for θ and T_S found in the literature [Fang and Moncrieff, 1999; Hamman *et al.*, 2008] and corroborated with soil CO₂ efflux rates at the site [Riveros-Iregui *et al.*, in review-a]. B and M are the root fraction (dead and alive) and soil organic carbon content, respectively, which were calibrated across the catchment based on measured fine root biomass and total organic carbon at multiple sites [Riveros-Iregui and McGlynn, in review].

As presented in Equation 6.5, production and transport components have opposite signs, so the transport component provides transport-limited feedback to the model at low values of f_a . Given that diffusivity of CO₂ in the gas phase is about 10,000 times higher than in the liquid phase [Simunek and Suarez, 1993; Welsch and Hornberger, 2004], we assumed that solubility of the gas-phase CO₂ is negligible.

The seasonality of θ controls the transition from a diffusion-limited system to a

production-limited system [see *Riveros-Iregui et al.*, 2007]. This concept, although conceptually intuitive, has yet to be robustly implemented into current modeling efforts of soil CO₂ production and transport. Thus once CO₂ production has been modeled we added the transport component of Equation 6.5 to modeled production. We assumed a homogenous diffusion coefficient (D) across the watershed, based on several calculated values of D as a function of total porosity (Φ) and air-filled porosity (ϵ), and using the model proposed by Moldrup et al. [1999]:

$$\frac{D}{D_o} = \Phi^2 \left(\frac{\epsilon}{\Phi} \right)^{2+\frac{3}{b}} \quad (6.7)$$

where D_o is the gas diffusion coefficient in free air, and b is the [Campbell, 1974] pore size distribution parameter, Φ is total soil porosity, and ϵ is air-filled porosity. This parameter has been found 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]:

$$b = 13.6CF + 3.5 \quad (6.8)$$

This method is currently widely applied and it has been amply tested to model D across a range of soil types and water contents [Baldocchi et al., 2006; Kawamoto et al., 2006; Resurreccion et al., 2007].

We estimated the effects of soil tension in controlling rates of autotrophic and heterotrophic respiration. According to Simunek and Suarez [1993] and Welsch and Hornberger [2004], the CO₂ reduction coefficient, $f_s(h)$, is a function of soil tension as illustrated by the following relationships:

$$f_s(h) = \frac{\log|h| - \log|h_a|}{\log|h_b| - \log|h_a|} \quad h \in (h_b, h_a) \quad (6.9)$$

$$f_s(h) = \frac{\log|h| - \log|h_c|}{\log|h_b| - \log|h_c|} \quad h \in (h_c, h_b) \quad (6.10)$$

$$f_s(h) = 0 \quad h \in (-\infty, h_c) \cup (h_a, -\infty) \quad (6.11)$$

where h_b is the tension when CO₂ production is optimal, and h_a and h_c are soil tension values when respiration ceases because conditions are too wet (h_a) or too dry (h_c).

Field Observations and Landscape Analysis

At one riparian meadow site and one upland forest site (Figure 6.1), we measured volumetric soil water content (θ ; CSI Model 616, Campbell Scientific Inc., Logan, UT) and soil temperature (T_s ; CSI Model 107, Campbell Scientific Inc., Logan, UT) 20 cm below the soil surface. At the same two sites, continuous profile measurements of soil CO₂ were collected with solid-state CO₂ probes (GMP221 with transmitter, Vaisala, Helsinki, Finland) installed 20 cm below the soil surface. All data were logged at 20-minute intervals with a datalogger (model CR10x, Campbell Scientific Inc., Logan, UT). Further details on field measurements have been described in a field-based study [Riveros-Iregui *et al.*, in review-a].

Soil CO₂ efflux was independently measured at 53 sites distributed across the watershed (Figure 6.1) during the 2006 growing season [Riveros-Iregui and McGlynn, in review], following similar procedures to those described in Pacific *et al.* [in review], and Riveros-Iregui *et al.* [in review-a]. Briefly, measurements were collected in triplicate

every 2-7 days, using a soil respiration chamber model SRC-1 (PP Systems, Massachusetts, USA) equipped with an infrared gas analyzer (IRGA; EGM-4, PP Systems, Massachusetts, USA). Further details on field observations are provided in the field studies referenced above.

To estimate relative wetness potential at each site, we calculated upslope accumulated area (UAA [m^2]) for each 3-m pixel of a digital elevation model (DEM) of the watershed, based on the triangular multiple flow direction algorithm [Seibert and McGlynn, 2007]. UAA represents the amount of area draining to a specific location in the landscape [Beven and Kirkby, 1979; McGlynn and Seibert, 2003] and serves as a metric for comparison of soil moisture patterns among sites of the same watershed [Western and Grayson, 1998; Grayson and Western, 2001].

Model Parameterization and Performance

Model parameterization was accomplished using Markov chain Monte Carlo (MCMC) analysis. This approach has been amply used in parameterization of hydrological models [e.g., Kuczera and Parent, 1998; Campbell *et al.*, 1999; Marshall *et al.*, 2004] and more recently in parameterization of ecosystem respiration models [Knohl *et al.*, 2008; Ricciuto *et al.*, 2008]. Six parameters, γ_A , γ_H , h_a , h_b , h_c , and n , were allowed to randomly fluctuate between pre-determined boundaries in an iterative process that was repeated 25,000 times. Parameters were optimized using the Nash-Sutcliffe coefficient of model efficiency (E) during each iteration.

Modeling Strategy

The modeling strategy was divided in three parts. First, we applied the existing soil CO₂ production model (Equation 6.6, or $[k_A + k_H]$ in Equation 6.5) to two contrasting sites of the catchment: a wet riparian meadow site and a dry, upland forest site (Figure 6.1). These two sites have been the focus of previous studies [*Riveros-Iregui et al.*, 2007; *Riveros-Iregui et al.*, in review-a], which include measurements of soil CO₂ efflux, soil water content, and soil temperature at 20-min intervals for 89 days of the 2006 growing season. As an initial modeling approach, we calibrated the soil CO₂ production model to these two sites (given the availability of high resolution data) to ensure the model was able to reproduce field observations at these two contrasting sites.

Second, once E did not improve any further, we applied the diffusion term of Equation 6.5, or $D \frac{\partial[CO_2]}{\partial z}$, to modeled soil CO₂ concentrations. Recent studies [*Riveros-Iregui et al.*, 2007] demonstrated that during high soil water content conditions, production $(k_A + k_H)$ exceeds transport of CO₂ out of the soil $D \frac{\partial[CO_2]}{\partial z}$, resulting in increasing soil CO₂ concentrations over time (i.e., $\frac{\partial[CO_2]}{\partial t} > 0$). Once the soil dries down, production is no longer greater than transport and soil CO₂ concentrations eventually reach near steady state (i.e., $\frac{\partial[CO_2]}{\partial t} \approx 0$). To date, this fundamental concept has not been implemented into process-based models, yet the transport-limited feedback generated by it can be of significant magnitude in wet soils.

Third, once the model was parameterized and calibrated at the riparian meadow and upland forest sites, we applied it to 53, 5-m cells of a digital elevation model (DEM) of the Stringer Creek watershed, from which soil CO₂ efflux was independently measured (see above). We estimated soil temperature and soil water content for the 5-m coverages based on the models for temperature and soil water content described above. We assumed a homogenous soil type (sandy loam) and depth across the entire watershed.

Results

Model Parameterization

Optimized parameters resulting from MCMC analysis are in presented in Figure 6.2. Dotty plots demonstrate that the model was more sensitive to γ_H and h_b than to any other parameter. Based on these plots we selected optimal values of γ_A , γ_H , n , h_a , h_b , and h_c as parameters for the model (Table 6.1). These parameters yielded a combined Nash-Sutcliffe coefficient of model efficiency (E) of 0.0881 at the riparian site and -4.71 at the upland site. In selecting these parameters, we assumed they were constant throughout the watershed.

Long-term (seasonal) Dynamics

The seasonal dynamics of soil CO₂ concentrations are evident in Figure 6.3. In estimating soil CO₂ concentrations, we used the soil CO₂ production and transport model in two steps (as described in the Methods). Observed soil CO₂ concentrations varied from above 12,000 ppm at the beginning of the growing season to about 2,000 by the end

of the summer at the riparian site. Using only the production component of the model, soil CO₂ concentrations varied from around 5,000 ppm at the beginning of the growing season to about 2,000 by the end of the summer. The estimated E was 0.0881 at the riparian site, given that soil CO₂ concentrations were better predicted after July 10 (Figure 6.3A). This coincided with observed soil water content falling below 0.25 m³ m⁻³. However, before this time of the year (or during higher soil water content periods), the model did not predict soil CO₂ concentrations well, likely as a result of soil water content values greater than 0.25 m³ m⁻³.

When the combined production and transport components of the model were used, soil CO₂ concentrations were better predicted, from around 12,000 ppm at the beginning of the summer to below 2,000 toward the end. The estimated E improved from 0.0881 to 0.708 (Figure 6.3B) at the riparian site. However, E did not improve at the upland site (Figure 6.4), suggesting that the transport component of the model does not enhance model performance at the upland site, perhaps because soil water content at the upland site is much lower (mean soil water content was 0.13 m³ m⁻³).

Short-term (diel) Dynamics

The magnitude of short-term (diel) variability in soil CO₂ concentrations was well predicted by the model. Observed diel variation (or $\frac{\partial[CO_2]}{\partial t}$) of soil CO₂ ranged from ~5,000 ppm on June 13, to 2,000 ppm on June 23, to near zero (or $\frac{\partial[CO_2]}{\partial t} \approx 0$) by the end of July (Figure 6.5). This level of prediction is encouraging for applications of the model on diel time scales, yet a further strength of this model was its ability to predict observed

hysteresis in the soil CO₂ – soil temperature relationships at the riparian site throughout the growing season (Figure 6.5). This suggests that the model has the ability to reproduce soil CO₂ generating processes and transport feedbacks on a diel basis, which is significant improvement from traditional power-based models.

Short term CO₂ variability was not predicted as well at the upland site. For example, the diel amplitude of measured soil CO₂ concentrations was ~500 ppm (Figure 6.6), while modeled concentrations varied often by up to 2,000 ppm. This means that the model over-predicted diel variability of soil CO₂ concentrations (i.e., $\frac{\partial[CO_2]}{\partial t}$) at the upland site. Because continuous measurements were made only at one riparian site and one upland site, short-term soil CO₂ variability as predicted by the model could not be tested at other sites.

Spatial Variability of Modeled Soil CO₂ Efflux

Spatially, modeled soil CO₂ efflux varied from 549 to 725 g CO₂ m⁻² over 71 days of the growing season. This corresponds to about 35% variability across 53 sites where soil CO₂ efflux was measured. This result is not consistent with previous measured differences across the watershed, which varied by as much as 700% [*Riveros-Iregui and McGlynn*, in review]. While at first glance the model appears to perform poorly across all sites, there appears to be spatial organization of the errors (Figure 6.7). We used estimated mean absolute error (MAE) as a measure of model performance at the 53 distributed sites where seasonal soil CO₂ efflux was measured and compared MAE to upslope accumulated area (UAA). Our results revealed that the model performed better

at those sites with smaller UAA (i.e., dry sites), such as upland forests [*Riveros-Iregui and McGlynn*, in review], and considerably worse in areas with larger UAA, such as riparian meadows and sites with larger drainage area (Figure 6.7).

Examining modeled soil CO₂ efflux on a seasonal basis (cumulatively), we found that the model performed well at those locations with small UAA (Figure 6.8). While there is some over-prediction at these sites, such over-prediction is generally modest and the model captures the magnitude of seasonal fluxes. However, at sites with larger UAA, its performance progressively declines (Figure 6.8) and modeled CO₂ fluxes are increasingly under-predicted.

Discussion

Traditionally in soil CO₂ research, empirical CO₂ models offer the advantage of assessing the major factors controlling differences in CO₂ fluxes. These models are applied to large areas as a function of a spatial variable (e.g., temperature [*Schlentner and Van Cleve*, 1985], vegetation cover [*Vourlitis et al.*, 2000; *Kim et al.*, 2006], upslope accumulated area and aspect [*Riveros-Iregui and McGlynn*, in review]), and are used to estimate CO₂ efflux. While these models can provide important estimates from large areas, the empirical nature of these models often results in limited process understanding and incomplete physical interpretation. Alternatively, process-based CO₂ models are commonly derived from experimental evidence. They allow for hypothesis testing of physically based mechanisms and are developed upon current understanding of environmental and biological processes [*Luo and Zhou*, 2006]. However, they commonly

suffer from increased complexity [*Parton et al.*, 1987; *Burke et al.*, 2003], which can make model predictions difficult to interpret and relate to observed ecosystem processes, leading to increased parameter and model uncertainty.

While model uncertainty is a limitation of both empirical and process-based models, a coexisting and more critical issue is model validation with existing/observed datasets. In fact, many models that do not appear to suffer from limitations have never been assessed against a wide range of independent observations, representative of the complexity of the system for which the model is intended [*Richardson et al.*, 2006; *Reichstein and Beer*, 2008]. Particularly in soil CO₂ efflux research, process-based models are rarely validated against independent observations made at distributed sites across the ecosystem for which the model was developed. Furthermore, a general misconception is that good model fit means good model parameterization [*Richardson and Hollinger*, 2005], yet this interpretation neglects that model limitations can become important learning opportunities about natural processes. These learning opportunities are enhanced if multiple independent observations are available to validate the model. In our study, the performance of the soil CO₂ production and transport model was validated with spatially and temporally distributed field observations of soil CO₂ efflux throughout the 2006 growing season. These observations were characteristic of the full complexity of the system [*Riveros-Iregui and McGlynn*, in review] and represented the range of existing variability within a typical subalpine forest. Thus the independent dataset available for model validation presents a unique opportunity for assessing the performance of a CO₂ production and transport model at the watershed scale.

Where did the Model Perform Well?

In our study, the soil CO₂ production and transport model performed well in three areas. First, the seasonality of soil CO₂ was well predicted at the riparian site (Figure 6.3), especially after implementation of the transport-limited component. Model efficiency improved from 0.0881 to 0.701, and mean absolute error (MAE) decreased from 1690 ppm to 1130 ppm. This is an important improvement considering concentrations at this site can reach over 15,000 ppm. At the upland site model efficiency did not improve after implementation of the transport-limited component. This may be linked to the considerably lower soil water content at this site compared to the riparian site [*Riveros-Iregui et al.*, in review-a]. In fact, efficiency decreased from -4.7 to -16.5 and MAE increased from 425 ppm to 873, suggesting that diffusion of CO₂ is not a limiting variable of soil CO₂ efflux (i.e., all produced CO₂ leaves the system as efflux), especially at time scales longer than a day. This observation, along with previous findings [*Riveros-Iregui et al.*, 2007; *Pacific et al.*, in review], suggests that soil water content can also be a control on soil CO₂ concentrations by limiting soil CO₂ diffusion.

The model was also successful when simulating short-term (diel) dynamics of soil CO₂ concentrations at the riparian site (Figure 6.5). The inclusion of a photosynthetically active radiation (PAR) variable (Equation 6.6) as an explanatory variable for autotrophic activity improved the generation of hysteresis patterns in the soil CO₂ – soil temperature relationship at the riparian site. As recent studies have demonstrated, there is a temperature-independent component in soil CO₂ production [*Liu et al.*, 2006; *Riveros-Iregui et al.*, 2007] that can be explained by the variability of PAR [*Riveros-Iregui et al.*,

2007; *Vargas and Allen*, 2008]. However to date, poor understanding of PAR effects on soil CO₂ efflux results in poor variable implementation especially at the watershed scale. In fact, we found that short-term CO₂ dynamics were not predicted as well at the upland site, because the model over-predicted the diel variation of soil CO₂ concentrations (Figure 6.6). This is likely because PAR was uniformly calibrated into the model as a normalized variable (varying from 0 to 1) and applied to the entire catchment. It is well-known that time of C allocation and assimilation can differ among vegetation types and size [*Ekblad and Hogberg*, 2001; *Bowling et al.*, 2002; *Tang et al.*, 2005; *Carbone and Trumbore*, 2007] and this can be expected in Stringer Creek given the differences in vegetation cover of this watershed: riparian grasses vs. conifer forests. We suggest that improved parameterization of PAR effects on soil CO₂ efflux is needed, as well as estimation of understory vegetation contribution to total soil CO₂ efflux.

The third aspect where the model performed well was during validation against seasonal estimates of soil CO₂ efflux at those sites of the landscape with low UAA (i.e., mostly upland areas, Figure 6.7). In fact, when considering all sites, MAE was 288.8 g CO₂ m⁻² 71 d⁻¹, whereas if only those sites with UAA below 1400 m² were considered (32 sites total) MAE was 77 g CO₂ m⁻² 71 d⁻¹. Given that the mean flux from these 32 sites is 639.8 g CO₂ m⁻² 71 d⁻¹, and that upland forests represent ~98% of the watershed area [*Riveros-Iregui and McGlynn*, in review], the estimated MAE of this calculation remains modest (~12%) compared to the magnitude of total fluxes. This error is comparable to estimated errors using this model at a small slash pine plantation in Florida [*Moncrieff and Fang*, 1999], a deciduous forest in Virginia [*Welsch and Hornberger*,

2004], and a young spruce forest in Ireland [Saiz *et al.*, 2007]. However, in our case validating the model with independent data from 32 sites provided higher confidence of model performance across most forested areas of the watershed.

Where did the Model Perform Poorly?

The model performed poorly when predicting seasonal soil CO₂ efflux at sites with large UAA (i.e., wet sites). Similar deficiencies had been observed while using the model across temporal changes in soil water content [Moncrieff and Fang, 1999; Welsch and Hornberger, 2004; Saiz *et al.*, 2007]. However, in our study the model performed poorly across spatial changes in soil water content. We suggest that the consistent under-prediction of the model at wet sites is the result of two deficiencies in our adapted model. First, the seasonal drydown of modeled soil water content was over-predicted by almost twice as much [Emanuel *et al.*, in review]. This means that modeled late-season soil water content was very low at all sites, including those sites that are consistently wet. To date, modeling soil water content remains a challenge in hydrological studies, given that it can be controlled by multiple variables (e.g., topography [Beven and Kirkby, 1979], deep drainage to groundwater [Toth, 1963], infiltration, hydraulic conductivity and runoff [Dunne and Black, 1970; Dunne, 1978], lateral redistribution of soil water [Western and Blöschl, 1999], evapotranspiration [Eagleson, 1978; Rodriguez-Iturbe *et al.*, 1999], disturbance [Bosch and Hewlett, 1982], vegetation cover [Burgess *et al.*, 1998]). Thus we expect soil CO₂ efflux models will remain dependent upon uncertainties in existing soil water content models.

A second deficiency in the model lies in our understanding of microbial respiration rates. Microbial communities have been found to be quite heterogeneous in space [*Fierer et al.*, 2003] and time [*Lipson and Schmidt*, 2004]. Both soil temperature [*Zogg et al.*, 1997] and soil water content [*Kieft et al.*, 1993; *Lundquist et al.*, 1999; *Schimel et al.*, 1999] are known to control soil microbial community composition. Given the sensitivity of the model to microbial respiration rates (Figure 6.2), a constant microbial respiration rate across the watershed is not a very realistic assumption. Because quantifying microbial activity and determining microbial community composition was beyond the scope of our study, we suggest further studies integrating spatial observations of soil microbial composition and observations of soil CO₂ efflux are needed.

How did the Process-Based Model Perform at the Watershed Scale?

Process-based models are important tools that allow for implementation of the assumed mechanisms underlying soil CO₂ production and transport while facilitating hypothesis testing and process verification. However adequate observations and thorough model assessment are necessary to determine model validity and utility. In our study, a process-based model predicted seasonal estimates of soil CO₂ efflux in dry sites of a subalpine catchment well. Given that upland forests correspond to 98% of the watershed area [*Riveros-Iregui and McGlynn*, in review], the model is an apparent good predictor of aggregated rates of catchment-scale soil CO₂ efflux. In fact, when compared to aggregated rates of field-based estimates of soil CO₂ efflux ($683.9 \text{ g CO}_2 \text{ m}^{-2} \text{ 71 d}^{-1}$ [*Riveros-Iregui and McGlynn*, in review]), eddy-covariance derived estimates of

nighttime ecosystem respiration ($673.9 \text{ g CO}_2 \text{ m}^{-2} \text{ 71 d}^{-1}$ [*Riveros-Iregui et al.*, in review-b; a]), mean estimates of soil CO_2 efflux at dry sites based on the process-based model ($639.9 \text{ g CO}_2 \text{ m}^{-2} \text{ 71 d}^{-1}$) compared within 6% and 5% of each independent measure. By simulating dry sites near the median of the measured soil CO_2 effluxes (Figure 6.7), the process-based model yielded an apparently good model performance. However, thorough model assessment indicated that the model did not capture soil CO_2 effluxes at the wet sites of the landscape, where measured efflux was up to 98% higher than modeled efflux. This under-prediction presents a clear example of how independent observations can become key in limiting equifinality in process modeling.

Our study demonstrates that the synergistic nature of full model-data integration can provide bidirectional feedback, as process models can benefit from field knowledge, and empirical data and sampling design can be further expanded and augmented according to modeling results. However, the spatiotemporal interdependencies of variables are difficult to measure, synthesize into a conceptual framework, represent mathematically, and parameterize. Even with adequate conceptualization and model structure, process parameterization can be problematic. Thorough corroboration using model-data integration becomes an essential bottom-up approach in process modeling, enhancing process understanding and reducing uncertainty in current approaches to measure and model C fluxes.

Conclusions

We applied an existing process soil CO₂ production and transport model to a well-studied, moderately complex watershed of the northern Rocky Mountains. The model performed well in three areas: 1) it predicted the seasonality of soil CO₂ at a riparian site, especially after implementation of a transport-limited component; 2) it simulated short-term (diel) dynamics of soil CO₂ concentrations at the riparian site, reproducing hysteresis patterns in the soil CO₂ – soil temperature relationship at this site; and 3) it captured seasonal estimates of soil CO₂ efflux at dry sites of the landscape. The model performed poorly when predicting seasonal soil CO₂ efflux at wet sites, likely as a result of poorly modeled soil water content at these sites and poorly parameterized microbial activity.

The large dataset available for this study allowed for wide spatial comparison against multiple data sources, providing great benefit to interpretation of model performance and enhancing process understanding. We demonstrated that if only modeled estimates of seasonal estimates of soil CO₂ efflux at dry sites are taken into account, these estimates compared well with independent estimates of measured soil CO₂ efflux, and independent eddy-covariance estimates of nighttime ecosystem respiration. However, the large dataset available for model validation was useful in determining poor model performance at wet sites of the watershed, suggesting that lack of model assessment can result in significant equifinality.

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Table 6.1 Selected Soil CO₂ Production Model Parameters based on Markov chain Monte Carlo analysis.

Parameter	Value
γ_H	0.8388
γ_A	0.3283
h_a	9.1137
h_b	30.2073
h_c	7677.8
n	1.743

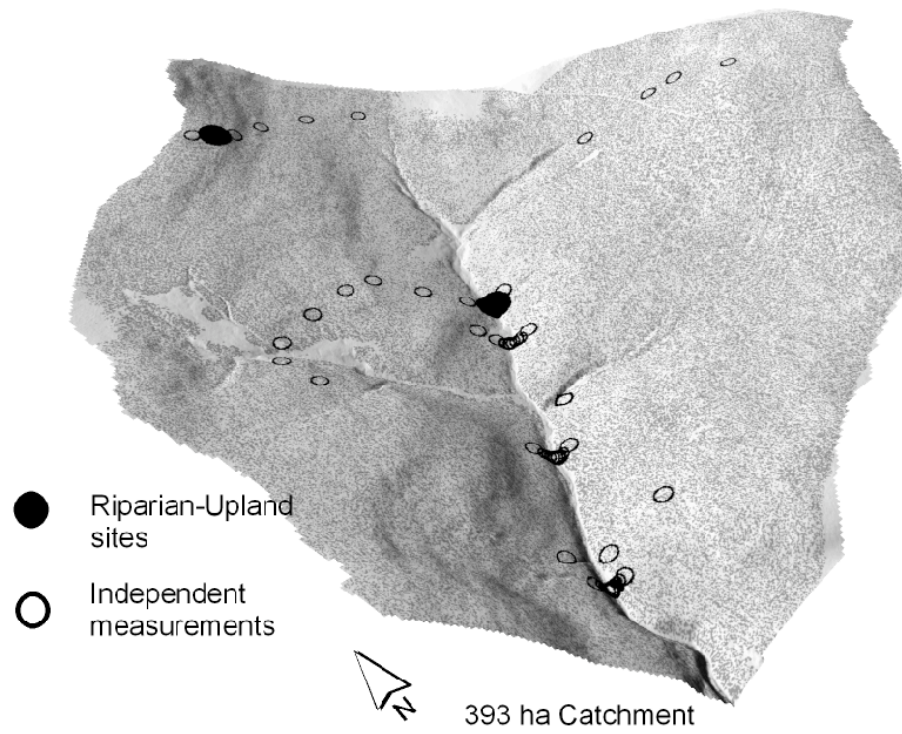


Figure 6.1 Location of riparian and upland (calibration) sites and 53 independent measurement sites.

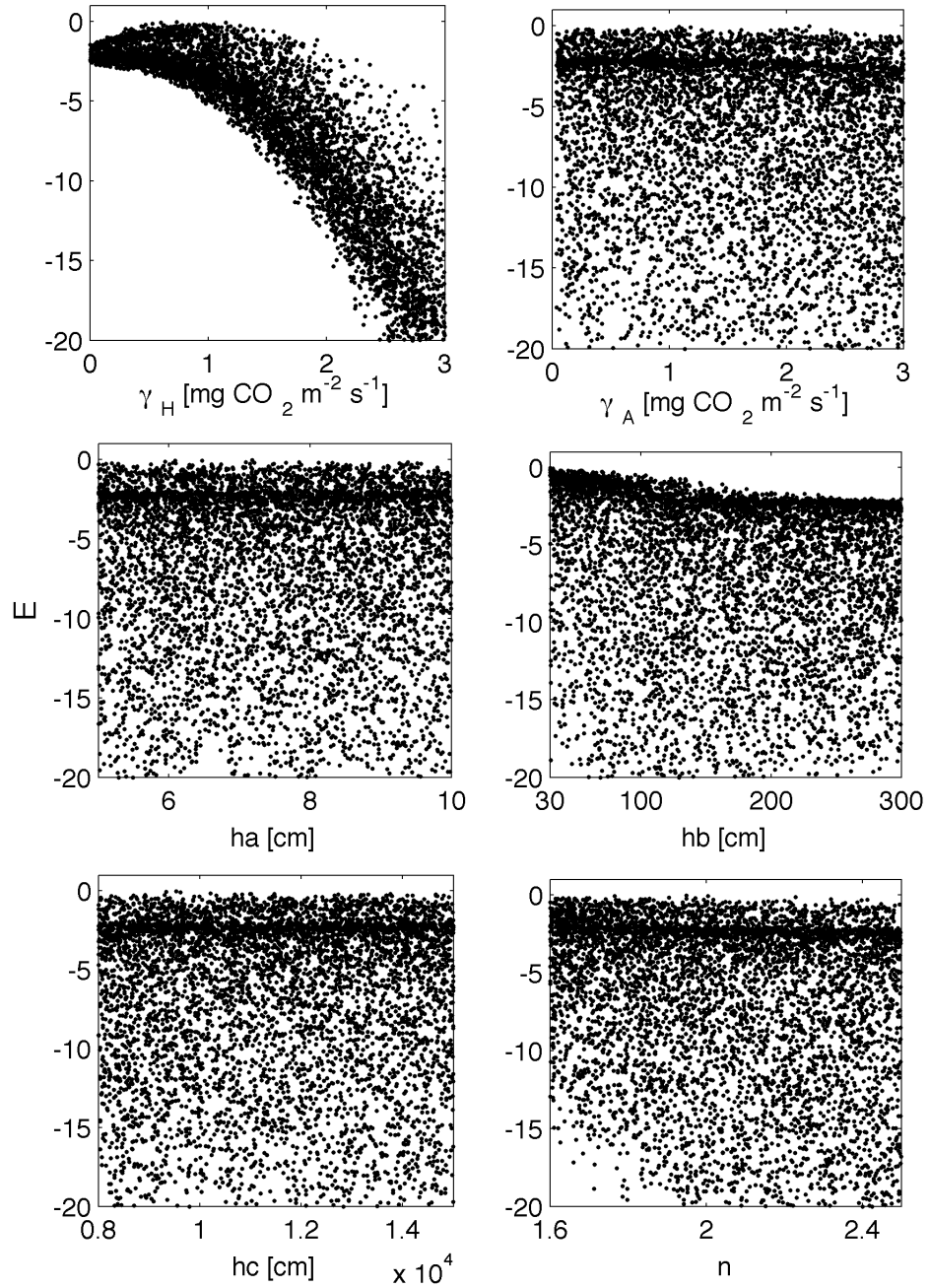


Figure 6.2 Markov chain Monte Carlo (MCMC) analysis for parameter optimization.

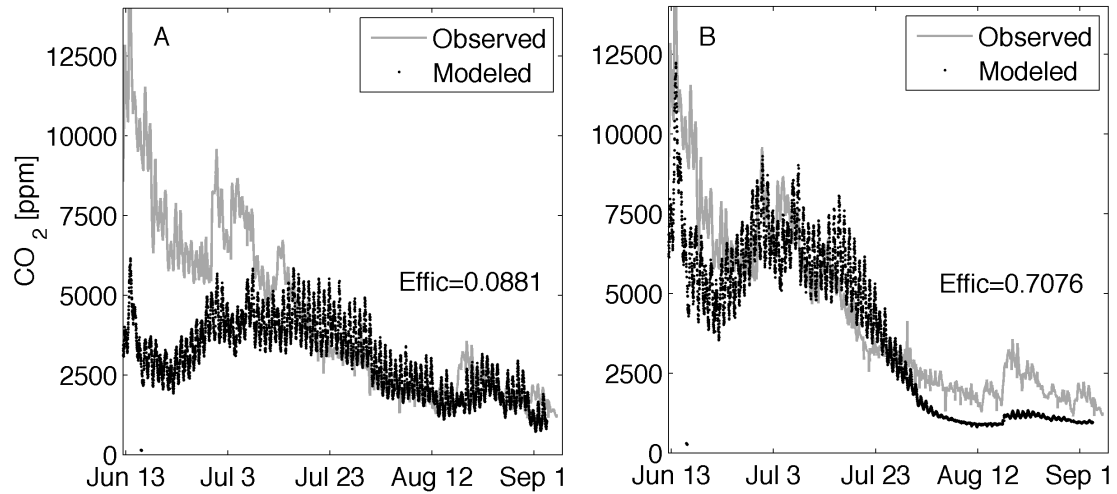


Figure 6.3 Seasonal soil CO₂ concentrations at 20 cm of the riparian site applying (A) only the soil CO₂ production component of the model; and (B) the production and transport components of the model. Model ability to predict soil CO₂ concentrations considerably increased when transport component (transport limitation feedback) was introduced into the model.

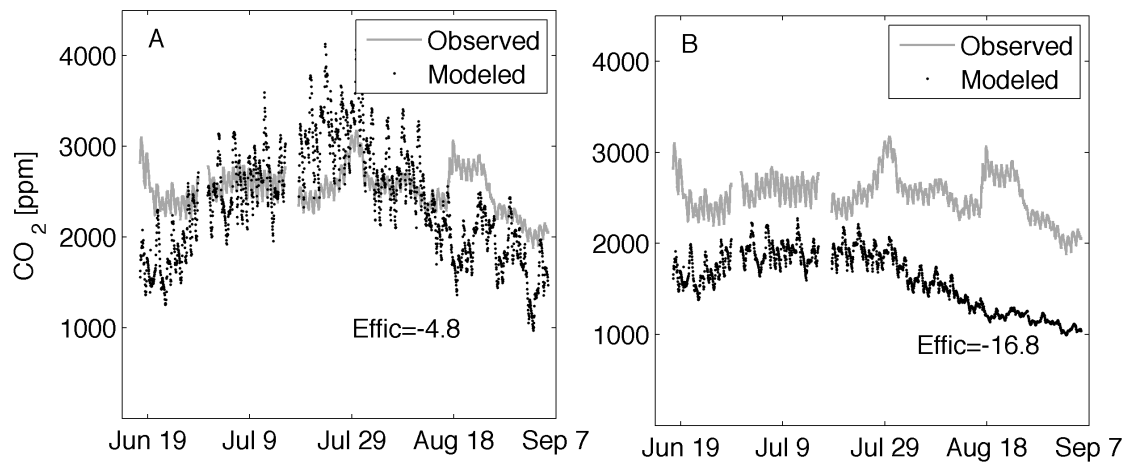


Figure 6.4 Seasonal soil CO₂ concentrations at 20 cm of the upland site applying (A) only the soil CO₂ production component of the model; and (B) the production and transport components of the model.

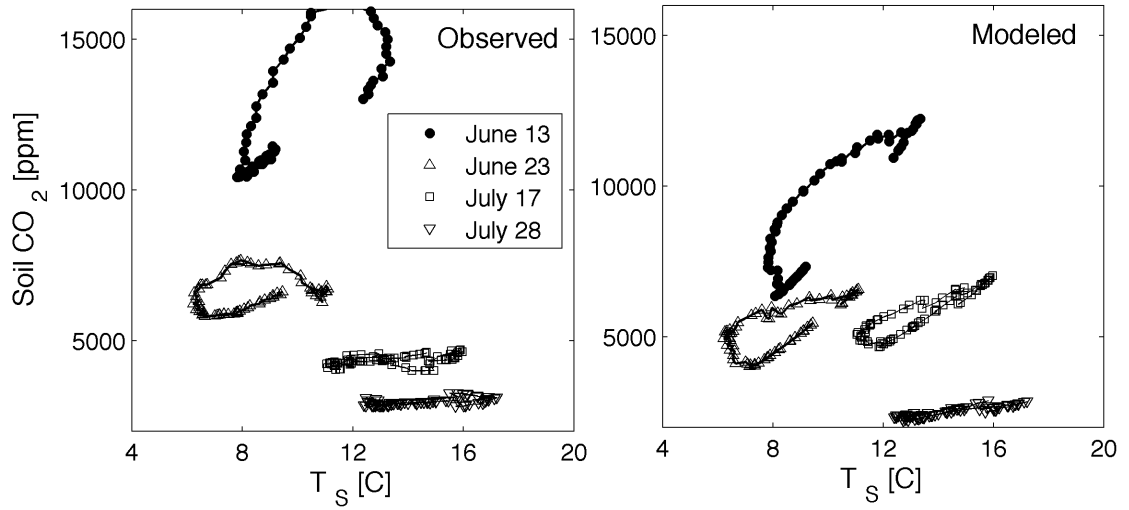


Figure 6.5 Observed and simulated diel variation of soil CO₂ concentrations at 20 cm of the riparian site.

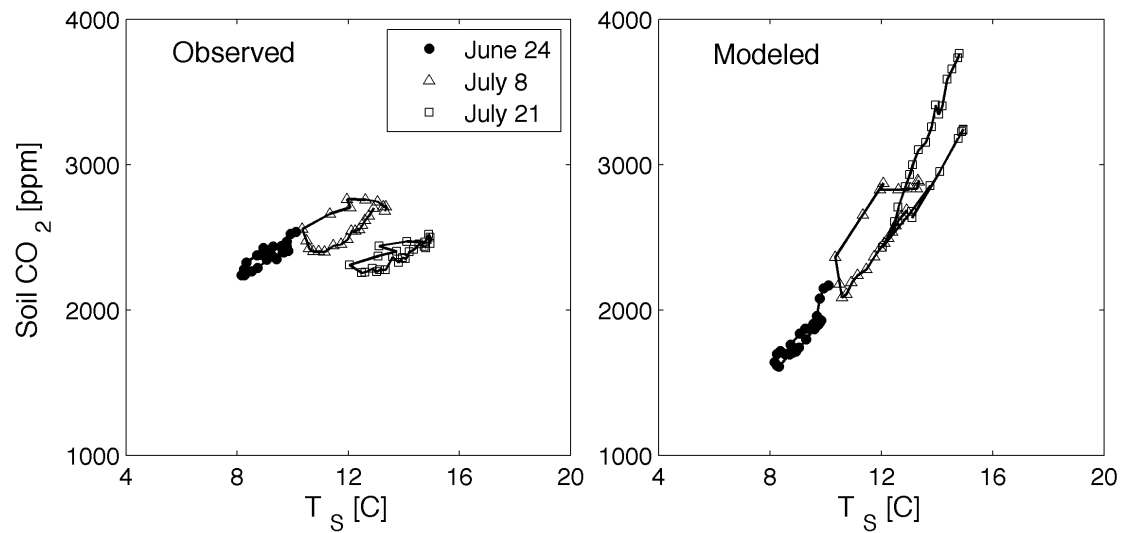


Figure 6.6 Observed and simulated diel variation of soil CO₂ concentrations at 20 cm of the upland site. Soil CO₂ concentration values are much smaller than at the riparian site.

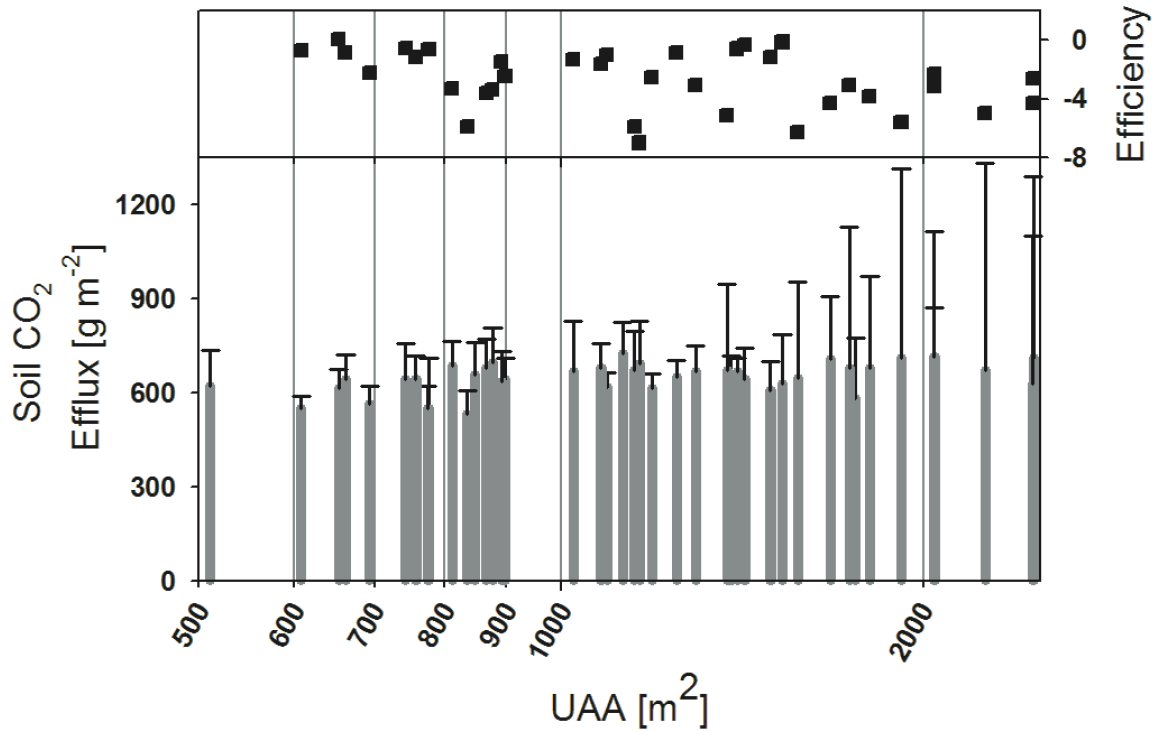


Figure 6.7 (Top) Model performance (efficiency) estimated at multiple sites across a 393-ha watershed and compared with independent measurements reported in Riveros-Iregui and McGlynn [in review]. (Bottom) Estimated cumulative soil CO_2 efflux (bars) at the same sites for the 2006 growing season. Error bars indicate mean absolute error (MAE) compared to measured soil CO_2 efflux for the same period at each site. Upslope accumulated area (UAA) values were calculated from a 3-m DEM. Note log scale in x axis. Model performance was better in areas with low UAA (i.e., dry, upland forests).

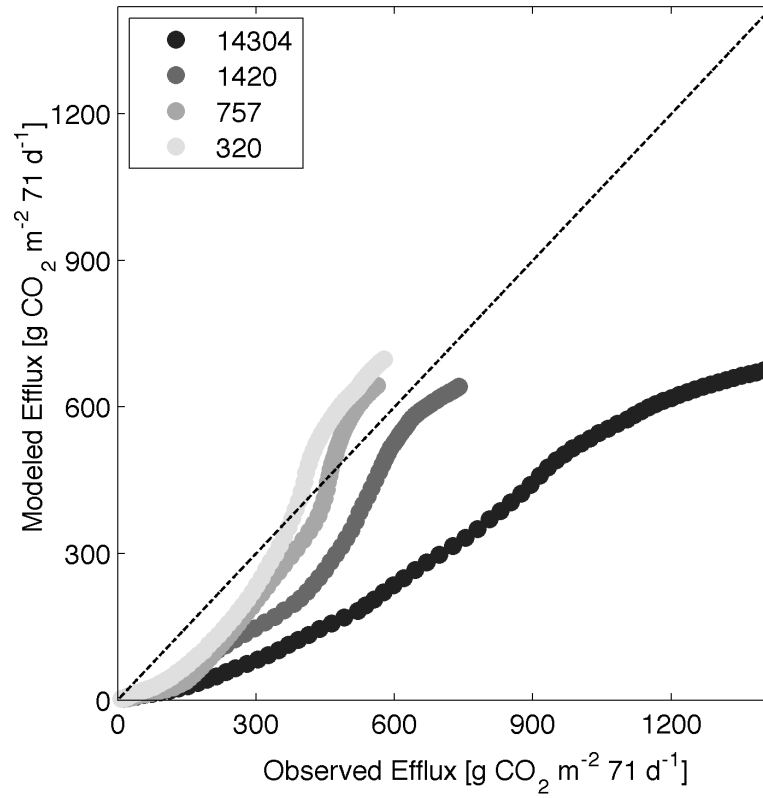


Figure 6.8 Observed vs. modeled seasonal soil CO₂ efflux (g CO₂ m⁻² 71 d⁻¹) at four sites with variable upslope accumulated area (UAA). Values of UAA [m²] for each site are notated by color intensity where darker tones represent larger UAA.

CHAPTER 7

SUMMARY

This dissertation is based on research funded by NSF's Integrated Carbon Research Program (NSF EAR-0404130), which notes that a key research area is the determination of the major processes and mechanisms that control the distribution and redistribution of carbon in soils and its exchange with the atmosphere. I studied the role of a dynamic hydrologic cycle in controlling C exchange from a point in the soil to the ecosystem level. Furthermore, I addressed the large disconnect between point scale measurements of soil CO₂ efflux and tower-based estimates of NEP.

I presented a brief overview (Chapter 2) and discussion of direct and indirect methods to estimate NEP, evaluate current confidence in their measurements of land-atmosphere CO₂ exchange. I suggested that the reconciliation of direct NEP estimates (tower-based) with other independent measurements (soil chambers, biometry, satellites) is critical for determining ecosystem C balance, improving process understanding of whole-ecosystem processes, promoting ecological modeling, and enhancing our ability to predict ecosystem-level responses to changes in environmental conditions.

I presented a specific example (Chapter 3) on how the variability of soil water content can control the balance (or imbalance in wet soils) between production and diffusion, controlling diel hysteresis in the soil CO₂ and soil temperature relationship. I suggested that the role of soil water content in controlling the dynamics of soil CO₂

should be considered when modeling soil CO₂ production and efflux in ecosystems with strong seasonality in soil water content.

In Chapter 4, I demonstrated that soil water content was a major control on both spatial and temporal (particularly seasonal) differences of soil CO₂ efflux between a riparian meadow and an upland forest site of the Stringer Creek watershed. I suggested that the parameterization of soil water content heterogeneity in space and time should be a critical component of realistic model representations of soil CO₂ efflux rates from heterogeneous landscapes.

With investigation of the variability of soil CO₂ efflux at the watershed scale, I found that upslope accumulated area (UAA) was positively correlated with seasonal soil CO₂ efflux (Chapter 5). Based on repeated chamber measurements, I found that riparian meadows had the highest rates of cumulative (seasonal) soil CO₂ efflux across the entire watershed. I found that topography and landscape structure were strong indicators of the variability and magnitude of soil CO₂ efflux from complex watersheds and developed a UAA-soil CO₂ efflux relationship to up-scale measured soil CO₂ efflux to the entire watershed. I suggested that understanding landscape context and controls on heterogeneity are critical to estimation and interpretation of watershed-scale rates of soil CO₂ efflux and are necessary for up-scaling plot or point observations of soil CO₂ efflux to larger spatial scales.

Finally, I applied a process-based model to the entire Stringer Creek watershed (Chapter 6) and found that the model was able to predict the seasonality of soil CO₂ concentrations at a well-studied riparian site (Chapter 3). I used extensive field

observations (Chapter 5) as a corroboration tool and found that the model predicted seasonal estimates of soil CO₂ efflux at dry sites of the watershed and performed poorly at wet sites, as a result of incorrectly estimated soil water content at these sites and poorly parameterized microbial activity. I suggested that model-data integration provides critical feedback as process models can benefit from field knowledge, and empirical data can be further expanded according to modeling results.

Based on the training and understanding gained through this dissertation I recommend for future research:

- 1) “Organized heterogeneity” is an important concept that must be considered in studies addressing spatiotemporal heterogeneity of environmental variables controlled by multiple factors. This concept is critical to the process understanding of these variables and facilitates model conceptualization and parameterization.
- 2) The use of multiple approaches/techniques is critical in studies that bridge traditional scientific disciplines, because it provides relevance to all disciplines and strengthens interdisciplinary studies.
- 3) Process understanding is an important outcome from field observations that facilitates related model development and prediction. Modeling approaches should emphasize hierarchy in model parameterization according to the targeted spatial and temporal scales of the predictions. This will facilitate model performance and agreement, as well as reduce the use of free parameters in the process-based models.

The work presented here progressed from the point scale to watershed/ecosystem-scale measurement and modeling of CO₂ flux. This dissertation elucidated two important gaps in the hydrological and environmental sciences: the role of hydrology as a spatial and temporal control of soil CO₂ efflux, and the effects of terrain variability in regulating ecosystem carbon balance. Each chapter presented in this dissertation builds upon the knowledge gained in the previous chapter, following nested stages of inquiry. I emphasize the use of multi-scale, multi-technique studies as a way to reduce uncertainty in current C flux measurements. I examined short (diel) and seasonal dynamics of soil CO₂ dynamics at the plot scale and investigated similar dynamics at other locations to gain insight into watershed-scale variability of first-order controls on CO₂. The work presented in this dissertation has relevance to ecology, hydrology, biogeochemistry, and atmospheric science studies that address the spatiotemporal flux of elements related to biotic and abiotic processes.