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Process-level controls on CO₂ fluxes from a seasonally snow-covered subalpine meadow soil, Niwot Ridge, Colorado

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Abstract Fluxes of CO₂ during the snow-covered season contribute to annual carbon budgets, but our understanding of the mechanisms controlling the seasonal pattern and magnitude of carbon emissions in seasonally snow-covered areas is still developing. In a subalpine meadow on Niwot Ridge, Colorado, soil CO₂ fluxes were quantified with the gradient method through the snowpack in winter 2006 and

2007 and with chamber measurements during summer 2007. The CO₂ fluxes of 0.71 μmol m⁻² s⁻¹ in 2006 and 0.86 μmol m⁻² s⁻¹ in 2007 are among the highest reported for snow-covered ecosystems in the literature. These fluxes resulted in 156 and 189 g C m⁻² emitted over the winter, ~30% of the annual soil CO₂ efflux at this site. In general, the CO₂ flux increased during the winter as soil moisture increased. A conceptual model was developed with distinct snow cover zones to describe this as well as the three other reported temporal patterns in CO₂ flux from seasonally snow-covered soils. As snow depth and duration increase, the factor controlling the CO₂ flux shifts from freeze–thaw cycles (zone I) to soil temperature (zone II) to soil moisture (zone III) to carbon availability (zone IV). The temporal pattern in CO₂ flux in each zone changes from periodic pulses of CO₂ during thaw events (zone I), to CO₂ fluxes reaching a minimum when soil temperatures are lowest in mid-winter (zone II), to CO₂ fluxes increasing gradually as soil moisture increases (zone III), to CO₂ fluxes decreasing as available carbon is consumed. This model predicts that interannual variability in snow cover or directional shifts in climate may result in dramatically different seasonal patterns of CO₂ flux from seasonally snow-covered soils.

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Introduction

There is a growing recognition of the contribution of microbial activity during the snow-covered season to the annual flux of carbon from soils. Microorganisms are thought to be active until temperatures reach as low as -5 to -7°C (Brooks et al. 2005). The microbial community that is active under the seasonal snowpack is phylogenetically and physiologically distinct from the community during the growing season (Schadt et al. 2003; Monson et al. 2006b). This microbial community can reach its maximum biomass over the winter (Brooks et al. 1996; Lipson et al. 2000) suggesting that there are organisms that thrive in the cold but equable environment beneath the snowpack. Isotopic labeling has also demonstrated that CO_2 emissions from winter soils are the result of active microbial oxidation of carbon (Brooks et al. 2005). Although the existence of winter heterotrophic activity has been well documented, our understanding of the environmental controls on the timing and the magnitude of soil CO_2 emissions during the snow-covered seasons is still limited. A process-level understanding is needed to predict how winter carbon losses will change in response to the observed declines in snow cover (Groisman and Davies 2001). Further, because the carbon exchange between the soil and atmosphere is one of the largest fluxes in the global C cycle, it is crucial to quantify the winter contribution to the annual CO_2 flux.

While there has been a recent focus on the emission of CO_2 through seasonal snow covers, there still remain several logistical and methodological challenges to conducting these winter measurements. Many snow-covered sites have poor access in winter, and cold temperatures and often wet conditions provide difficult working conditions for both humans and equipment. Two experimental approaches, surface chambers and snowpack concentration gradient measurements, have been used primarily; their advantages and disadvantages and the differences in the calculated fluxes have been described elsewhere (Suzuki et al. 2006; McDowell et al. 2000; Seok et al. 2009). Briefly, the chamber method directly quantifies the flux to the atmosphere from the snowpack or soil surface and is used for periodic measurements. The gradient approach, pioneered by Sommerfeld et al. (1993), assumes steady state diffusion from the

soil surface to the atmosphere and requires measurements of vertical gas concentration gradients and several snowpack characteristics. In its simplest form, the gradient method requires one gas measurement at the snow–soil interface and a second from the atmosphere above the snow and assumes a linear concentration gradient through the snowpack. Measurements at multiple heights in the snowpack permit an evaluation of nonlinearities in the concentration gradient.

Soil CO_2 fluxes during the snow-covered season have been measured at a rapidly growing number of sites in a variety of natural ecosystems. Reported mean CO_2 fluxes range in magnitude from $0.02 \mu\text{mol m}^{-2} \text{s}^{-1}$ in an arctic tundra site (Jones et al. 1999) to $0.77 \mu\text{mol m}^{-2} \text{s}^{-1}$ in a temperate coniferous forest (McDowell et al. 2000). The frequency of flux measurements using these approaches varies widely among studies, ranging from as often as half-hourly (e.g., Musselman et al. 2005) to as few twice per winter (e.g., Hubbard et al. 2005). While some studies continued for multiple winters (e.g., Mast et al. 1998; Sommerfeld et al. 1993; Zimov et al. 1996), the majority of studies were limited to one snow-covered season. In addition, fluxes were often only measured during the snow-covered season, so it is not possible to quantify the contribution of winter CO_2 fluxes to annual fluxes.

While the importance of winter fluxes from seasonally snow-covered soils to the global C cycle has been clearly demonstrated, our conceptual understanding of the controls over these fluxes within and among years has lagged. During a single snow-covered season at a site, the reported fluxes have been found to increase (Sommerfeld et al. 1996; Monson et al. 2006a), decrease (Jones et al. 1999; Schindlbacher et al. 2007), or reach a minimum in mid-winter (Zimov et al. 1996; Fahnestock et al. 1998; Suzuki et al. 2006). Carbon availability, soil temperature, and soil moisture have all been identified as potential influences (e.g., Mast et al. 1998), but few manipulative experiments have been performed in the field (Williams et al. 1998; Groffman et al. 2006). Further, because of the differences among sites in the timing and depth of snowfall, soil moisture, and productivity, and because of non-linear responses of fluxes to these factors, it may not be possible to create a simple continuous function to predict the magnitude and seasonal patterns of CO_2 fluxes at all snow-covered

sites. However, given the limited set of seasonal patterns across a wide variety of sites, it may be possible to develop a conceptual framework to predict the qualitative seasonal pattern at a given site.

Our goal was to use the gradient approach with CO₂ measurements at multiple heights for calculation of CO₂ fluxes through the snowpack to the atmosphere. Snow flux data were collected at a subalpine meadow site during the snow-covered seasons of 2006 and 2007 and complemented with chamber measurements of CO₂ flux during the growing season of 2007. This approach allowed us to (1) examine the seasonal variability in CO₂ flux (2) estimate the total carbon emissions from the soil during the snow-covered season, and (3) evaluate the importance of the flux during the snow-covered season to annual fluxes. Further, we developed a conceptual framework to describe possible process-level controls on CO₂ fluxes through the seasonal snowpack as a function of snow depth and duration.

Site description

Data presented in this study were collected from November 2005 through October 2007 in a subalpine forest clearing near tree line at the high-elevation Soddie site, within the Niwot Ridge, Colorado, Long-Term Ecological Research area (40°03'N, 105°35'W, 3,340 m asl). This site has an underground laboratory 3 × 9 × 2.4 m in size with line power and a tower equipped with a suite of meteorological instruments sufficient to close the energy balance. Snow cover at the Soddie site generally lasts from late October into June. The continental, high mountain climate of Niwot Ridge has been monitored continuously since the early 1950s at the nearby D-1 meteorological station (3,739 m asl). Mean annual temperature at D-1 is −3.7°C (Williams et al. 1996). Almost 80% of the ~1,000 mm of annual precipitation falls as snow (Caine 1995).

The vegetation in the study area is highly productive. Hand clipping at the end of the growing season produced an estimated 750 g m⁻² year⁻¹ of live aboveground dry biomass, 3–7-fold greater than the estimated 100–240 g m⁻² year⁻¹ for the various plant communities in the nearby alpine ecosystem on Niwot Ridge (Walker et al. 1994). The vegetation near the tower is a mixture of common wet meadow graminoids and forbs such as *Deschampsia*

caespitosa, *Carex* sp., *Dodecatheon pulchellum*, and *Veronica wormskjoldii*. The Soddie meadow is surrounded by old-growth forest of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea Engelmannii*). The soils are classified as a mixed Typic Humicryept (Soil Survey Staff 2006). The Oe horizon (0–7 cm) is followed by a well-developed A horizon (7–34 cm) on top of a B horizon that extends to a depth of 99 cm. Weathered regolith extends below a depth of 3.5 m. Soil carbon in the top 10 cm averages 8.0% (A. Darrouzet-Nardi, unpublished data). Parent material is colluvium, eolian material, and possibly glacial till or a similar coarse-grained deposit. Coarse grains and sands are evident, possibly indicating freeze–thaw mechanisms. Texture is a loamy sand to gravel with little clay content. The area is moderately well-drained.

Methods

Winter sampling

The CO₂ concentrations in and near the snowpack were sampled from paired fixed inlets on a tower and connected by PFA teflon tubing to an infrared gas analyzer (IRGA, LI-COR LI-7000, Lincoln, NE, USA) in the subnivean laboratory. The inlets were located at either end of 60 cm-long cross bars at heights of 0, 30, 60, 90, and 245 cm above the snow/soil interface in 2006, and 0, 10, 30, 60, 90, 120, 150, and 245 cm above the soil/snow interface in 2007. The tower was installed in October of each snow season and snow accumulated naturally around it. There was no disturbance to the snowpack around the tower throughout the entire winter. In both winters, the highest inlet (245 cm) was always located above the snowpack. More details of the sampling array can be found in Seok et al. (2009).

Gas was sampled continuously for 10 min at each height, and analyzed for CO₂ every 10 s. The switching between pairs of inlets down the tower was performed by solenoid valves with PTFE body seals (Cole-Parmer, Vernon Hills, IL, USA). To avoid possible artifacts related to the transition from one inlet to the next, we excluded the first and last 2 min of sampling when calculating a mean concentration for each 10 min interval. A complete cycle

through the tower lasted 80 min. The effective sampling rate per port was $\sim 0.75\text{--}1.5 \text{ l min}^{-1}$. Seok et al. (2009) and Bowling et al. (2009) demonstrate that the pulling air from the snowpack at this rate does not result in any significant artifact from the ventilation induced by the air sampling flow.

CO₂ concentrations in the snowpack reached beyond the factory-calibrated range of 0–3,000 ppm for the LI-7000 instrument. As a result, calibrations above 3,000 ppm were necessary. We performed daily single point calibration (450 ppm) to test the drift of the instrument (0.1% drift over entire sampling period). Multipoint (450, 2,000, 5,000, 6,000, 8,000 ppm) calibrations were conducted biweekly. The calibration gases were created by an automated, mass-flow controlled dilution system, diluting a 1% CO₂ standard (Airgas, Boulder, CO) with breathing air (450 ppm CO₂, Airgas, Boulder, CO).

The winter CO₂ fluxes were calculated using a steady-state diffusion model based on the vertical CO₂ concentration gradients through the snowpack along with records of snow depth, porosity, tortuosity, temperature, and atmospheric pressure following the approach of Sommerfeld et al. (1993) as modified by Seok et al. (2009). The diffusive CO₂ flux (F_{CO_2}) was calculated as proportional to the CO₂ concentration gradient ($\partial C_{\text{CO}_2}/\partial z$) based on Fick's law:

$$F_{\text{CO}_2} = -D_{\text{CO}_2} \left(\frac{\partial C_{\text{CO}_2}}{\partial z} \right)$$

with diffusivity (D_{CO_2}) quantified as

$$D_{\text{CO}_2} = \phi \tau D \frac{P_0}{P} \left(\frac{T}{T_0} \right)^\alpha.$$

For the estimates of porosity (ϕ) and tortuosity (τ), snow density was measured every 1–2 weeks in snow pits using previously published protocols (Williams et al. 1999). We calculated porosity as $\phi = (1 - \rho_{\text{snow}}/\rho_{\text{ice}})$ where ρ_{snow} is the measured density of snow at the height of gas sampling (kg m^{-3}), and ρ_{ice} is the density of ice (917 kg m^{-3}). For the tortuosity constant, we used $\tau = \phi^{1/3}$. The diffusion coefficient of CO₂ (D) was assumed to be $0.1381 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$ at standard temperature (T_0) and pressure (P_0) (Massman 1998). P was the barometric pressure measured using a CS105 Vaisala 212 PTB101B barometer (Campbell Scientific, Logan, UT, USA). Temperatures

(T) at each of the gas sampling heights were measured using type-E thermocouples (Omega Engineering, Inc., Stamford, CT, USA). The 0 cm-inlet level measurement was also used as the estimate of the temperature at the snow–soil interface. Soil moisture was measured as volumetric water content using four CS616-L water content reflectometers with 30 cm-long probes installed vertically into the soil in a 1 m radius from the nearby weather tower (Campbell Scientific, Logan, UT), following the protocol of Bowling et al. (2009). Readings of snow depth were conducted at 1–2 week intervals from calibrated marks on the sampling tower. Gaps in the recorded data were filled by comparison and extrapolating with an ultrasonic distance sensor (SR50-L, Campbell Scientific, Logan, UT), located on the weather tower, or with a daily snow depth record at a nearby SNOTEL site in early 2006 and all of 2007, when the distance sensor was not operational. Because of potential errors of up to 10 cm in the snow depth estimates, the fluxes were only calculated when the upper inlet for a gradient calculation was at least 15 cm below the estimated snow height. The concentration at the snow surface was assumed to be identical to the value at 245 cm regardless of the snow depth. As this diffusion approach has been widely applied in previous snow gas flux studies, results are presented this way in order to be comparable to these other studies. However, the diffusion method underestimates the actual flux because it ignores advection (Massman and Frank 2006). As demonstrated by Seok et al. (2009), advective fluxes can be a significant source of CO₂ efflux at this site. These authors discuss the implications of neglecting this wind pumping effect and present a quantitative estimate for the underestimation of the flux for the environment encountered at the Soddie site.

Summer sampling

Summer fluxes in 2007 were measured using gas measurements from 5 closed, dark, vented, PVC chambers (area 0.110 m^2 , volume 0.022 m^3). The chambers were located $\sim 5 \text{ m}$ away from the winter snow flux tower, and within 30 cm of each other. The chambers were permanently installed to a depth of $\sim 2 \text{ cm}$. At each sampling date the order of measurement was randomly assigned in order to avoid systematic over or under-estimation of fluxes due to

diurnal changes in microclimate in the chambers. After closing the chamber with a PVC lid, air in the headspace of each chamber was sampled over time (every 10 min over 40–70 min of measurement). Gas was withdrawn from the chamber with a polypropylene syringe and CO₂ was analyzed within 8 h on a gas chromatograph equipped with a thermal conductivity detector (Shimadzu GC-8AIE, Shimadzu Scientific Instruments, Columbia, MD, USA). The fluxes were calculated with the equation

$$F_{\text{CO}_2} = \rho V/A(d[\text{CO}_2]/dt),$$

where F_{CO_2} is the gas flux, ρ is the molar concentration (mol m⁻³) of air corrected for pressure and temperature, V is the chamber volume (m³), A is the chamber area (m²), and $(d[\text{CO}_2]/dt)$ is the concentration change ($\mu\text{mol mol}^{-1} \text{s}^{-1}$), which is obtained from:

$$d[\text{CO}_2]/dt = k(C_S - C_0).$$

The parameters k [s⁻¹] and C_S [$\mu\text{mol mol}^{-1}$] were estimated using the simplified exponential model proposed by Welles et al. (2001).

Data analysis

Daily fluxes for every combination of inlets were calculated by averaging the fluxes from the 80-min cycles through the tower gradient. For closer analysis of the patterns within and between years, the daily fluxes for the 30–60 cm inlets were chosen because they represented the longest record measured in both years. Environmental variables (snow depth, air temperature, and soil surface temperature) in both years, as well as soil volumetric water content in 2007, were tested as predictors of the daily mean flux using simple linear regressions. The mean daily fluxes in winter 2006 and 2007 were compared with a one-way ANOVA. The total carbon emitted during the snow-covered season was determined by calculating an unweighted mean flux during the sampling period (December 20–May 24) and applying this flux to the entire snow-covered season from November 1–May 31 (212 days). The total carbon emitted in the growing season was quantified by calculating a time-weighted average during the sampling period (July 24–October 3) and applying this flux to the entire snow-free season from June 1–October 31.

Results

Snowpack characteristics

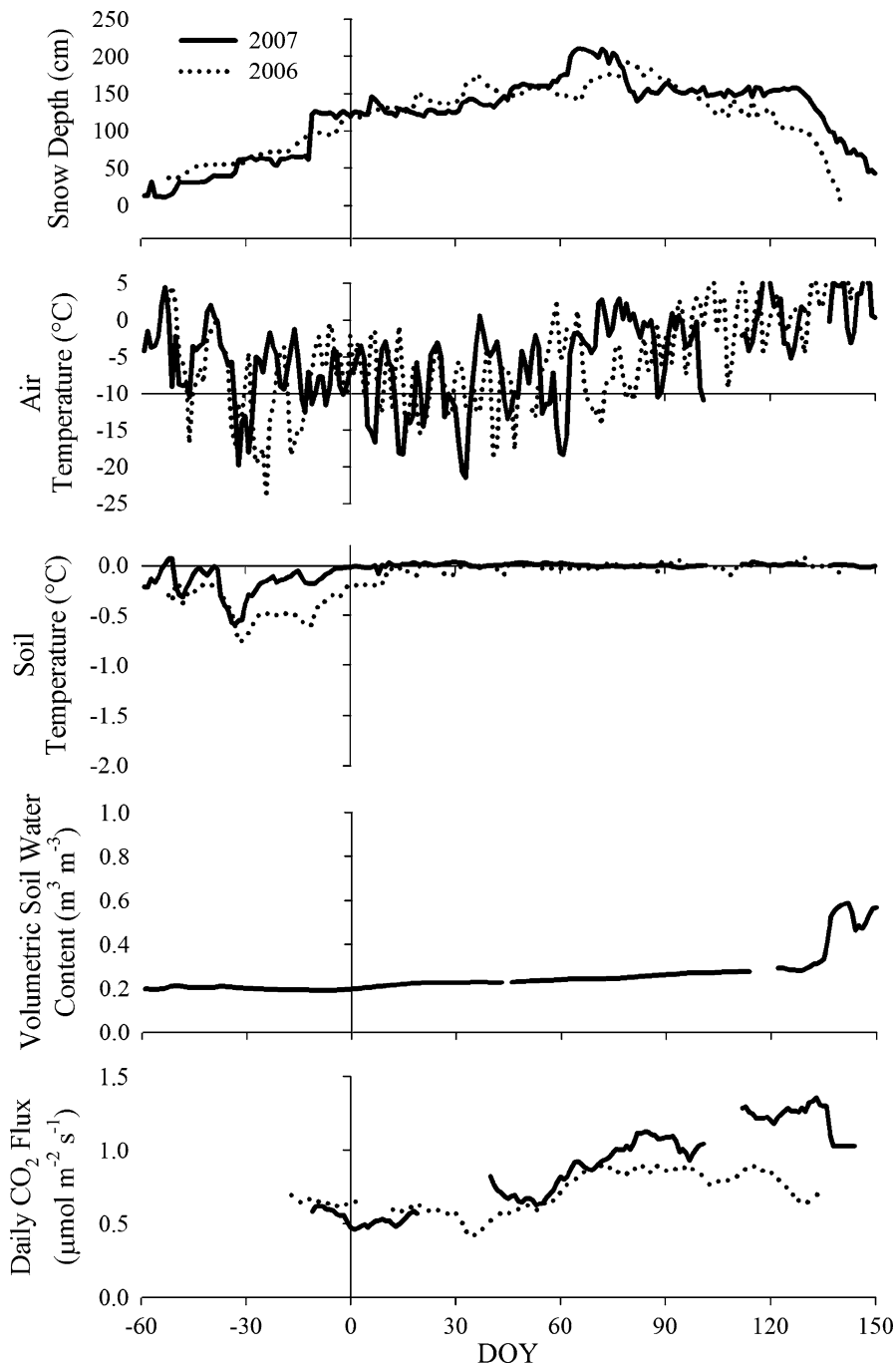
A continuous snowpack developed in late October or early November in both years (Fig. 1a). Maximum snow depth was reached on Day of Year (DOY) 79 in 2006 (194 cm) and DOY 65 in 2007 (220 cm). The mean snow density increased from $\sim 200 \text{ kg m}^{-3}$ early in the season to a maximum of 500 kg m^{-3} near the time of snowmelt. Air temperature followed approximately the same trend during both winters, with minimum values of about -22°C in mid-winter, and an increasing trend in late winter (Fig. 1b). The average air temperature during the snow-covered period was $\sim -5^\circ\text{C}$ for both years. The minimum soil surface temperatures occurred in November for both years, when the snow was still too shallow for flux measurements. By the time the snowpack reached a depth of $\sim 120 \text{ cm}$ (late December 2007 and early January 2006), the soil temperatures had warmed to $\sim 0^\circ\text{C}$ and remained essentially unchanged for the rest of the snow-covered season (Fig. 1a, c). In winter 2007, when soil volumetric water content was recorded, there was a small but steady increase in soil moisture starting soon after DOY 1, i.e., coinciding with soil surface temperature reaching $\sim 0^\circ\text{C}$. Concurrent with the main flush of snowmelt in early May, volumetric water content increased from $\sim 0.25 \text{ m}^3 \text{ m}^{-3}$ on DOY 133 to $\sim 0.60 \text{ m}^3 \text{ m}^{-3}$ on DOY 143 (Fig. 1d).

Winter CO₂ concentration profile and fluxes

The concentration of CO₂ was highest near the soil–snow interface and decreased linearly towards ambient atmospheric values above the snow surface (Fig. 2; Seok et al. 2009). The CO₂ concentration in the snowpack increased as the snowpack developed, reaching a maximum of 8,400 ppm in March 2006 and over 10,000 ppm in May 2007 at the 30 cm inlet (Fig. 2).

Using the CO₂ concentrations and the snowpack characteristics, we calculated a flux for all combinations of inlets (6 in 2006, 21 in 2007). Our estimate of the mean winter CO₂ flux for 2006 based solely on the diffusion calculation ranged from 0.66 to 1.09 $\mu\text{mol m}^{-2} \text{s}^{-1}$ depending on the combination of inlets used. In 2007, the range of seasonal means was similar, 0.58–1.08 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3). However,

Fig. 1 Seasonal course of **a** daily snow depth, **b** daily mean air temperature, **c** daily mean soil surface temperature, **d** daily mean volumetric water content, **e** 14-day moving average of daily CO₂ flux calculated for 30–60 cm inlet data during winter 2007



of the twenty-one inlet combinations, sixteen of them were between 0.7 and $0.9 \mu\text{mol m}^{-2} \text{s}^{-1}$. For further analyses we used the CO₂ flux calculated from the gradient measured with the 30 and 60 cm inlets. In both years, the snowpack was deep enough to cover these inlets in December. Flux values from these inlets were found to be in close agreement to the median flux

values that were derived from the whole array of flux values calculated from different inlet combinations. Furthermore, measurements from these heights represented the longest available dataset. The mean flux using these inlets was $0.71 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 2006, and $0.86 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 2007, significantly higher in 2007 ($p < 0.0001$). These fluxes resulted in the

Fig. 2 Contour plots showing CO₂ mixing ratio (ppm) in snowpack air during the winters of 2006 and 2007. The upper line depicts the height of the snowpack

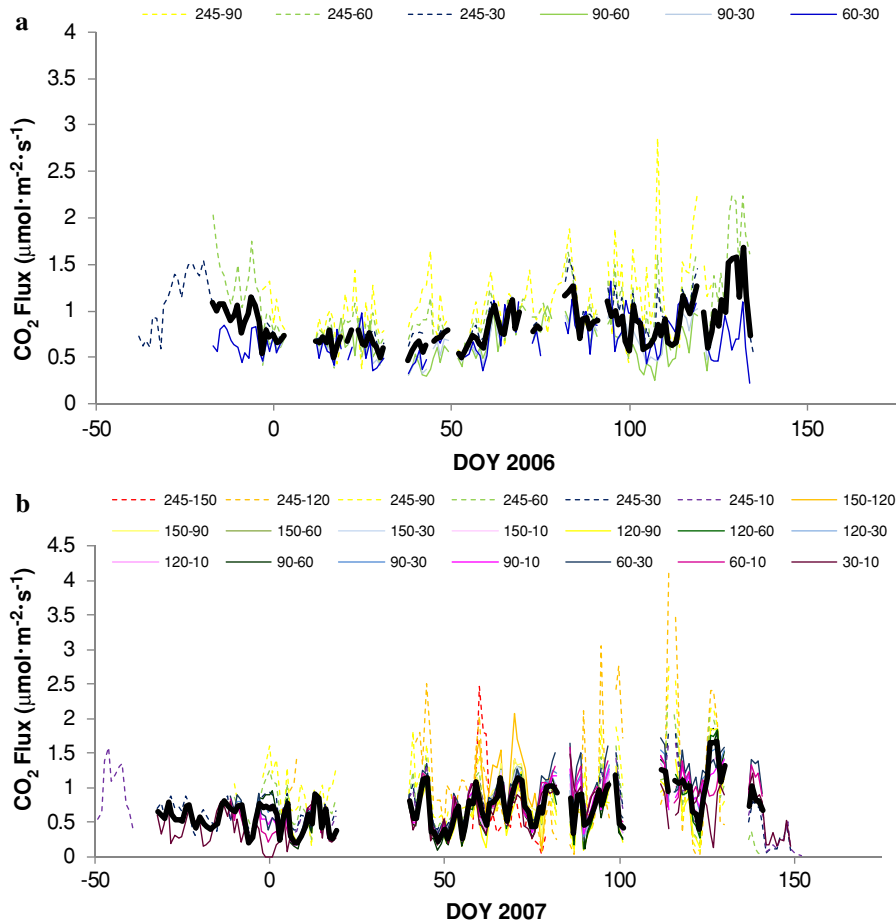
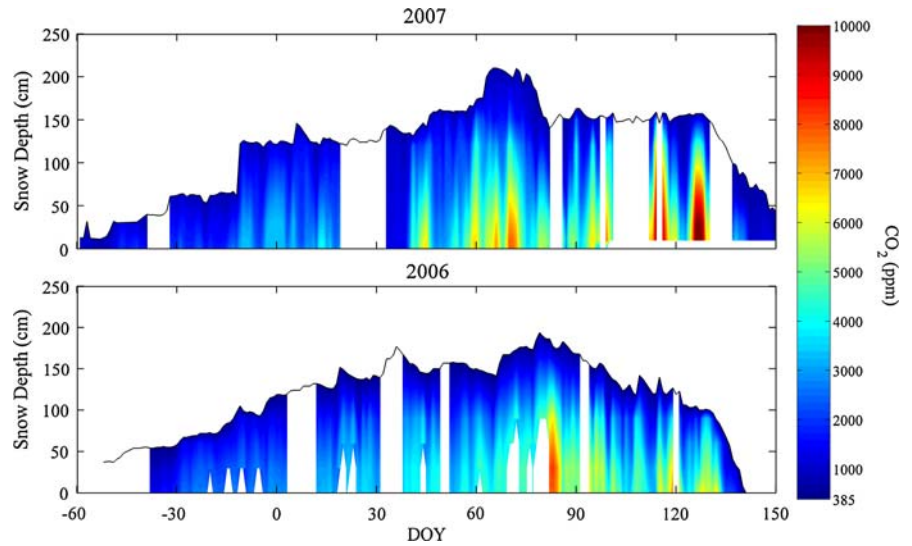


Fig. 3 Seasonal course of daily mean CO₂ fluxes in winters 2006 (a) and 2007 (b), as derived from the available inlet combinations. The *thick black line* depicts the median of the dataset. *Solid colored lines* are for fluxes calculated with both

inlets within the snowpack. *Dashed lines* are fluxes where the inlet at 245 cm was used as an estimate of CO₂ concentration at the snowpack surface

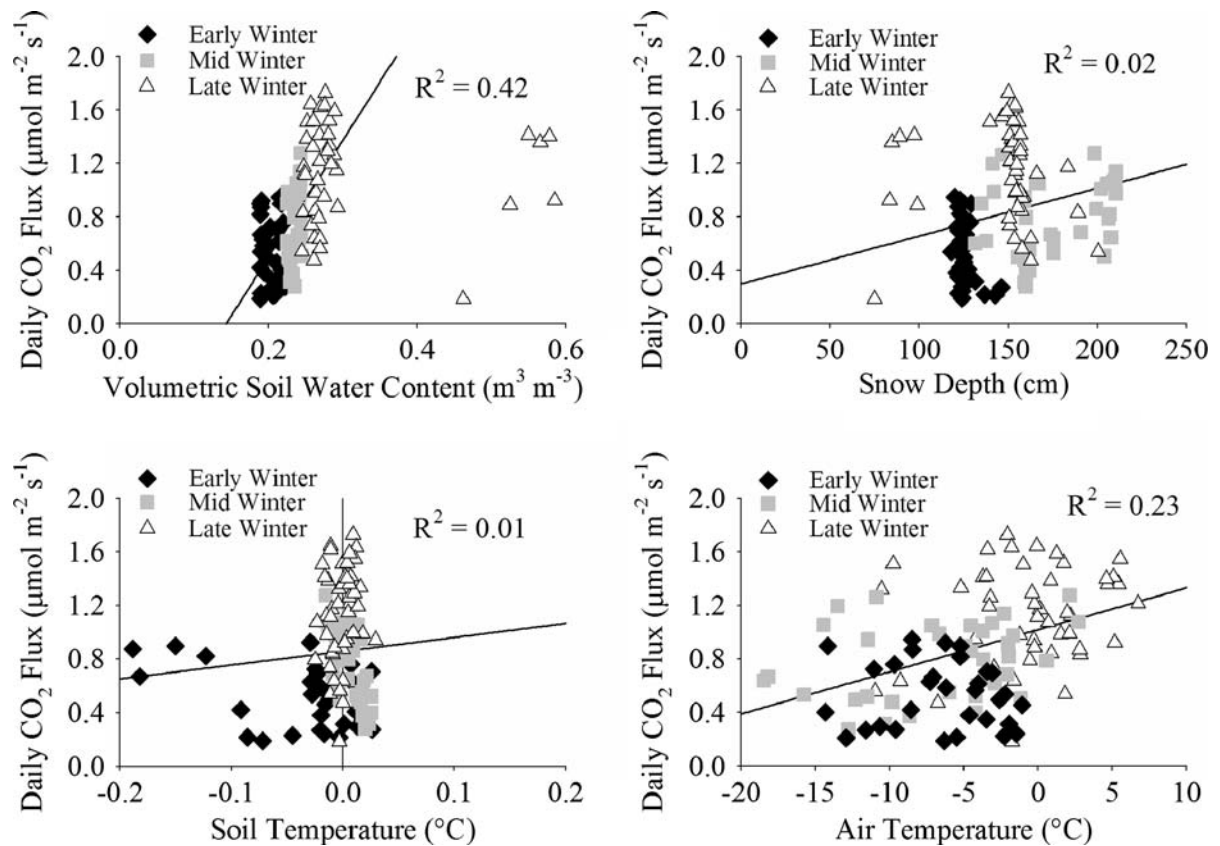


Fig. 4 Relationship between CO₂ flux calculated from the 30 and 60 cm inlets and selected environmental variables in 2007. The snow-covered season was divided into early (Dec–Jan), mid (Feb–March 15), and late (Mar 16–May 30) winter to

highlight the seasonal pattern but the regression analysis used the data from the entire snow-covered season. Maximum snow depth occurred ~March 15th (DOY 74)

emission of 156 g C m⁻² in 2006 and 189 g C m⁻² in 2007 during the snow-covered period.

The relationships between the CO₂ flux and environmental variables over the entire snow-covered season were tested by linear regression analyses. Both the CO₂ flux and volumetric water content increased gradually from early to mid to late winter (Fig. 1d, e). There was a significant ($p < 0.0001$) positive relationship between volumetric water content and CO₂ flux during winter 2007 (Fig. 4). Excluding the 6 days after the onset of snowmelt when the soil moisture was markedly higher, the volumetric water content explained 42% of the variance in CO₂ flux ($p < 0.0001$). Air temperature was also a significant ($R^2 = 0.23$, $p < 0.0001$ in 2007; $R^2 = 0.14$, $p < 0.0001$ in 2006) predictor of CO₂ flux. The regressions of CO₂ flux with snow depth and soil temperature were not significant in either year.

However, this analysis did not include the period early in the snow-covered season when soil temperature ranged from -1 to 0°C because the snow cover was not deep enough to cover the 60 cm inlet sufficiently.

One notable difference between 2006 and 2007 was the seasonal pattern in flux (Fig. 1e). In 2006, a large increase in flux occurred on March 1st (DOY 60), just after a rapid warming of the snowpack to isothermal conditions, followed by the highest observed daily mean flux on March 17th (DOY 76). Although volumetric water content was not measured that year, meltwater was measured in snow lysimeters in the same meadow suggesting that there was an early pulse of snowmelt that reached the soils (Niwt Ridge LTER database). The fluxes increased gradually in 2007 reaching a maximum on May 7th (DOY 127), just before the soil moisture began to increase rapidly indicating snowmelt.

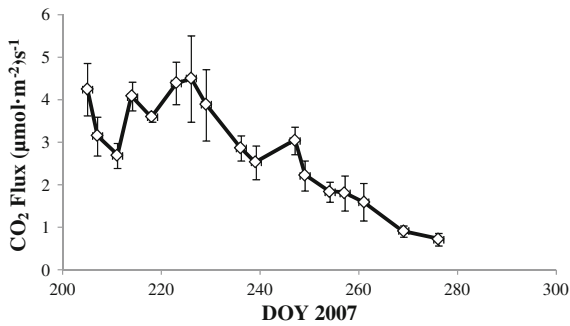


Fig. 5 Seasonal course for summer 2007 CO₂ fluxes (mean \pm 1 SE) based on closed chamber measurements

Summer CO₂ flux

Both the magnitude of the fluxes and the variability over the course of the season was greater during the growing season compared to the snow-covered season. The flux from the soils was highest in July and August with a maximum flux of $4.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ measured on August 14th (DOY 226) (Fig. 5). The flux then declined gradually to $0.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ in October, similar in magnitude to the fluxes measured during the snow-covered season. Integrating under the curve of these seasonal measurements, the time-weighted mean CO₂ flux was $2.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ between DOY 205 and 276. Extending this mean flux to the entire 5-month snow-free season, a total of 413 g C m^{-2} was emitted, $\sim 70\%$ of the annual soil CO₂ flux.

Discussion

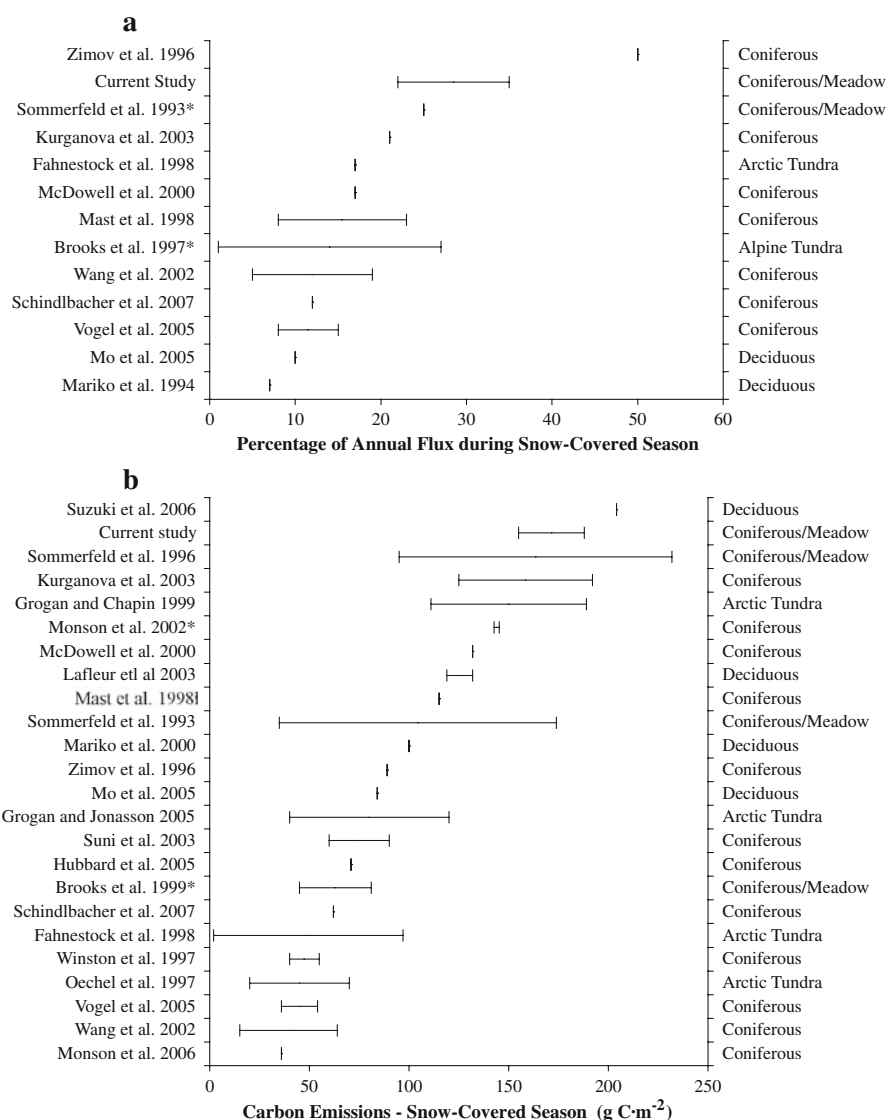
The maximum concentrations of 8,000–10,000 ppm of snowpack air CO₂ measured in these experiments appear to be among the highest reported for seasonally snow-covered areas. These CO₂ concentrations are at least twice the maximum levels reported for a lower elevation subalpine forest on Niwot Ridge (Monson et al. 2006a), and subalpine forest/meadow sites in Wyoming (Sommerfeld et al. 1993; Musselman et al. 2005), and Colorado (Mast et al. 1998; Brooks et al. 2005), but are only slightly higher than those reported by Sommerfeld et al. (1996) for subalpine ecosystems in Wyoming. Several factors likely contributed to these high snowpack CO₂ levels. The maximum snow depth we report of $\sim 2 \text{ m}$ is about twice that of the lower-elevation subalpine

forest at C-1 on Niwot Ridge (Monson et al. 2006a). Because the movement of CO₂ through the snowpack is limited by the rate of diffusion, concentrations at the base of snowpack increase with increasing snow depth. Secondly, our site was very productive, with an annual aboveground NPP of 750 g m^{-2} . Third, soils were at 0°C for most of the snow-covered season. Thus, there is an extended period of time at a constant temperature for heterotrophic microbes to be active in the soils at this fertile site.

While the observed higher concentrations are partly a function of the relatively deep snowpack at the Soddie site, the calculated fluxes were also quite high compared to most of the reported values in the literature. The fluxes calculated using all combinations of inlet pairs suggest that the concentration gradients were roughly linear and did not depend on the depth of sampling. Based on the 30–60 cm inlets the seasonal mean CO₂ fluxes of $0.71 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 2006 and $0.86 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 2007, the integrated seasonal carbon loss of 156 and 189 g C m^{-2} , and the $\sim 30\%$ contribution of the wintertime CO₂ release to the annual flux in 2007 are among the highest reported for snow-covered sites (Fig. 6). Even so, our calculated flux of CO₂ through the seasonal snowpack likely underestimates the actual flux. Seok et al. (2009) show that the flux calculated based solely on diffusion were 36% lower than the total flux when advective loss was included during mid-winter at the Soddie site. These authors also concluded, based on the observed negative relationship between wind speed and CO₂ flux, that the advective flux associated with wind pumping explained much of the day to day variability in gas concentration gradients and diffusion-only fluxes. Despite this recognized bias in the flux calculation, for comparisons to other studies which omit this advective component, here we discuss flux results calculated only based on the diffusion method. However, sites that vary considerably in wind speeds may be difficult to compare without taking advection into consideration.

In 2007, the CO₂ flux increased gradually over the entire winter reaching a maximum around the onset of snowmelt. This pattern has been observed at several other sites with deep snowpacks where soil moisture also increased during the snow-covered season (Sommerfeld et al. 1996; Mast et al. 1998). One source of liquid water to the soil during winter

Fig. 6 Summary of literature values of (a) the relative contribution of the snow-covered seasonal flux to the annual CO₂ flux and (b) the total carbon emitted as CO₂ during the snow-covered season. A symbol (*vertical line*) was used when the mean was reported and *horizontal bars* were used when a range for multiple sites or years was reported. Studies are arranged in ascending order of decreasing flux results with ecosystem type listed



may be snowmelt from the bottom of the snowpack. Feng et al. (2001) report that meltwater was generated from the bottom of the snowpack in the Sierra Nevada of California where soil temperatures were also $\sim 0^{\circ}\text{C}$ for most of the snow-covered season. Another mechanism proposed for increasing soil moisture under the snowpack is the transport of water vapor from the snowpack to the soil because of temperature gradients (Sommerfeld et al. 1996). In 2006, the maximum CO₂ flux occurred during March at a time when meltwater was observed in snow lysimeters at the site, following a warming trend in air temperatures. Once snowmelt had saturated the

soils, the CO₂ fluxes at this site actually decreased slightly, similar to the results of Mast et al. (1998). Fluxes were not measured in the first month of snow cover in the autumn because the snow was not consistently deep enough to cover multiple inlets. At this time, when the temperature at the snow/soil interface was below 0°C , the emission of CO₂ may have been related to temperature instead of moisture. However, once the snow was sufficiently deep, the temperature at the snow–soil interface was at 0°C for many months while the CO₂ fluxes and volumetric water content clearly increased. Thus, at our site, CO₂ flux appears to increase with increasing soil moisture.

Similarly, the N₂O flux through the seasonal snowpack at the Soddie site was linked to soil moisture (Filippa et al. 2009).

Three other seasonal patterns in CO₂ flux have been described from other snow-covered sites. First, at sites that experience freeze–thaw events, pulses of CO₂ can be emitted periodically from soils (Matzner and Borken 2008). Because these events occur on an irregular schedule they may only be detected with frequent sampling. Intermittent releases of trace gases have also been documented in laboratory experiments (Teepe and Ludwig 2004; Kurganova et al. 2007). Second, a mid-winter minimum in CO₂ flux occurs at some sites. In the Arctic, low snow accumulation and subzero air temperatures result in a significant period in mid-winter when soil water is frozen (Olssen et al. 2003). Fluxes of CO₂ in the Arctic tend to be highest in early winter before soils have frozen and during spring once soils have thawed enough for liquid water to be present (Zimov et al. 1996). This mid-winter minimum has also been observed in lower latitude sites. At the C-1 Ameriflux site at Niwot Ridge with a shallower snowpack than the Soddie, the lowest fluxes of CO₂ occurred in midwinter when the near-surface soil temperature was lowest. During the period prior to snowmelt these authors found an exponential relationship between soil temperature and respiration (Monson et al. 2006a). In areas of the alpine tundra on Niwot Ridge with shallow snowpack, no CO₂ emissions were measured when soil temperatures were below -5°C during winter; as the soils thawed and became wetter in spring, an exponential increase in flux rates was observed (Brooks et al. 1997). Finally, a gradual decrease in CO₂ flux during the snow-covered season has been documented at some sites, possibly related to substrate limitation (Vogel et al. 2005; Schindlbacher et al. 2007).

These four seasonal patterns in CO₂ flux (pulsed, mid-winter minimum, increasing, and decreasing) appear to occur in areas that differ in seasonal snow cover. The depth, duration, and timing of the seasonal snowpack have been suggested to modulate indirectly the microbial activity beneath the snow by affecting the soil microclimate (Brooks and Williams 1999). Manipulating these snowpack characteristics has been found to alter many aspects of the carbon and nitrogen cycles (Williams et al. 1998; Groffman et al. 2006; Freppaz et al. 2008). Changes in snow density can also influence nutrient cycling (Rixen et al.

2008). While soil temperature and moisture (e.g., Suzuki et al. 2006) and carbon availability (Brooks et al. 1999, 2005) are most commonly discussed as the controls on CO₂ flux, other variables like air temperature have also been found to be related (Musselman et al. 2005). However, as the values of these variables generally increase during the snow-covered season, they appear to be correlative with and not causative of the seasonal pattern of CO₂ flux. While the seasonal patterns of CO₂ fluxes among sites have been attributed to the indirect effects of the snowpack on microbial activity, there is not a general framework for *a priori* predicting this seasonal pattern as a function of environmental parameters.

We use these previously described temporal patterns of CO₂ flux to develop a conceptual model of how snow controls the seasonal pattern of CO₂ fluxes from snow-covered soils. Similar to the model proposed by Brooks and Williams (1999), this model is based on the concept that subnival microbial activity is controlled by the development of the seasonal snowpack. Snow cover insulates soils from cold air temperatures and, once sufficiently deep, allows the near-surface soil environment to warm towards 0°C. The Brooks and Williams (1999) model described the relative magnitude of heterotrophic activity, using N availability and losses as an example, across a snow depth gradient in alpine catchments; our model focuses on the seasonal pattern of CO₂ fluxes during the winter at snow-covered sites. We hypothesize that there are four zones based on snow cover regimes that are associated with the distinct temporal patterns of CO₂ flux during the snow-covered season (Fig. 7). As snow cover increases from zone I to zone IV, the factor determining the seasonal pattern of CO₂ flux shifts from freeze–thaw events to soil temperature to soil moisture and finally to carbon availability. Although factors like site productivity affect the absolute magnitude of winter CO₂ fluxes, we propose that these four patterns encompass the spectrum of temporal patterns at seasonally snow-covered sites. This model addresses the dominant property of the site controlling the CO₂ flux, and provides information regarding the sampling needed to capture seasonal dynamics.

Sites in zone I are characterized by relatively shallow or inconsistent snowpacks and are associated with frozen soils and freeze–thaw cycles and the

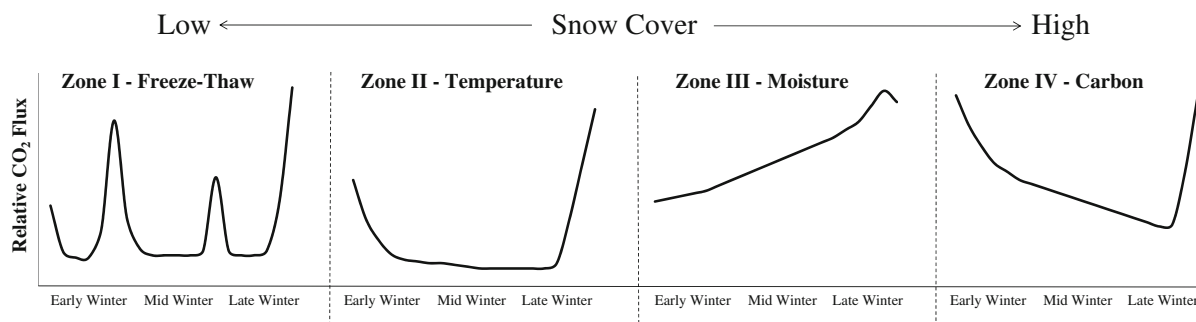


Fig. 7 Conceptual model of the seasonal pattern of CO₂ flux. Four distinct zones are identified based on snow cover regime. The factor controlling the seasonal pattern shifts from freeze–

thaw cycles (*zone I*) to soil temperature (*zone II*) to soil moisture (*zone III*) to carbon availability (*zone IV*) as snowpack depth increases

episodic release of CO₂ from soils. The near-surface soil environment reflects diurnal and synoptic fluctuations in air temperatures. Laboratory experiments have suggested that large pulses of CO₂ can be released during periods when the soils are thawed (Teepe and Ludwig 2004; Kurganova et al. 2007). Because of the unpredictable seasonal pattern of CO₂ fluxes at sites in zone I, frequent sampling would be required to capture any pulses of gas emissions (c.f. Groffman et al. 2006). While field manipulations in natural ecosystems are still relatively rare, pulses of CO₂ release and differences in seasonal carbon emissions have been documented in soils that have experienced freeze–thaw processes (Matzner and Borken 2008). Even if the total amount of carbon emitted does not necessarily change with freeze–thaw cycles, the quality of soil carbon may change as the carbon substrates utilized during freeze–thaw events was found to differ in N content from the plant detritus that typifies the background mineralization of soil carbon (Schimel and Clein 1996). Thus, both the quantity and quality of soil carbon can be altered in sites with shallow snowpacks.

Sites in zone II occur in areas with consistent but relatively shallow snowpacks and are characterized by a mid-winter minimum in CO₂ flux. A snow depth of 30 cm was suggested by Brooks et al. (1997) as sufficient to insulate the soils in Colorado and prevent large diurnal fluctuations in temperature and freeze–thaw cycles. The exact snow depth for this insulation to occur will depend on the local air temperatures. The snow depths that characterize in zone II result in subzero soil temperatures for a significant fraction of the snow-covered season when air temperatures are coldest. Here, fluxes are highest early and late in the

winter when the soil temperatures are warmest. During soil thaw and snowmelt in the spring, the relatively warmer temperatures co-occur with increases in soil moisture and carbon availability. However, the strong non-linear relationships between soil temperature and CO₂ flux suggest temperature limitation for most of the snow-covered season (Brooks et al. 1997; Monson et al. 2006a). Most arctic sites would be classified in zone II because of the cold air temperatures in mid-winter. During the coldest parts of the winter the soils remain frozen at temperatures well below 0°C and the fluxes are minimal. In contrast, in the early stages of winter and during thaw, the microbial activity can be quite high (Olsson et al. 2003).

Sites in zone III, like the Soddie, with relatively deep and long-lasting snowpacks exhibit gradually increasing CO₂ flux. While 30 cm of snow may be sufficient to dampen the influence of the atmosphere, a deeper snowpack is required to completely decouple the soil temperature from the air temperature resulting in soils consistently at 0°C. Based on the soil temperatures at the Soddie site, we suggest that a snow depth of ~120 cm was required to fully insulate the soil beneath the snowpack. When the snowpack reached this depth at the Soddie site, the soil surface temperature had warmed to 0°C and then remained essentially constant until after the snowpack melted. The gradual increase in CO₂ flux at sites in this zone co-occurs with a gradual change in moisture while temperature remains at ~0°C. The small decline in flux observed during snowmelt at the Soddie and other sites (Mast et al. 1998) may be related to the large changes in the soil environment. The diffusion of gases from the soil may slow considerably as water replaces air in the pore space in

the soil. The CO₂ production rates likely decrease when soils become saturated and more anaerobic. Changes in the efflux of CO₂ from soils during snowmelt will reflect the net result of large changes in physical, chemical, and biological environment co-occurring in the soil at this time.

Finally, sites in zone IV are characterized by a relatively long snow-covered season and low net primary productivity. These sites are predicted to have a gradual decline in CO₂ flux during the snow-covered season. Such observed decreases in CO₂ flux have been attributed to carbon limitation (Schindlbacher et al. 2007). These types of sites have rarely been studied but likely occur in snowfields in the alpine tundra where wind redistribution creates deep snowpacks or in areas with high snowfall like the Sierra Nevada of California. Sites in zone IV are similar to zone III in that soil temperatures are consistently at ~0°C which precludes a temperature control on CO₂ flux. Whereas the zone III sites exhibit an increase in flux related to increases in soil moisture, the zone IV sites should be relatively insensitive to soil moisture because carbon limitation increases as the snow-covered season progresses. While most soils may respond to labile carbon additions by increasing CO₂ production (i.e., Brooks et al. 2005), sites in zone IV are distinct because the flux is predominantly related to carbon availability. Production rates of CO₂ may increase at snowmelt because of the flush of nutrients and labile carbon into the soil as is seen when dry soils are rewetted (e.g., Miller et al. 2005). Rapid shifts in microbial biomass observed during snowmelt at sites across the spectrum of snow regimes suggest that rates of heterotrophic activity also fluctuate dynamically at this time of year (Brooks et al. 1998; Lipson et al. 2000). With the exception of zone III, CO₂ efflux from soils should increase at snowmelt because the temperatures are relatively warm (~0°C), there is a pulse of nutrients and carbon, and microbial biomass is at a maximum.

While our conceptual model describes the temporal pattern of CO₂ flux, it does not predict *per se* the magnitude of the carbon emitted during the snow-covered season. Sites with snow depths similar to zone III have been hypothesized to have the greatest heterotrophic activity (Brooks and Williams 1999). As the number of sites with measured CO₂ fluxes is small and the number of studies with multiple years of data is an even smaller subset of these sites, it is difficult to generalize how carbon emissions vary

among the zones or among years within zones. Within a given year, the spatial variability in CO₂ flux at the scale of meters has been reported to be relatively small (Sommerfeld et al. 1996). At sites in zone II, the variability among years in CO₂ flux clearly depends on the timing and depth of the snowpack development with lower snow depths and lower temperatures associated with lower carbon emissions (Monson et al. 2006b). Variability in carbon availability and NPP likely play a role as well. One of the few studies to examine similar sites that differed in productivity found higher CO₂ flux at the more productive site (Hubbard et al. 2005). At an arctic site, winter carbon emissions were related to substrate quality differences between vegetation types (Grogan and Jonasson 2005). While a growing number of studies have measured CO₂ emissions during multiple snow-covered seasons (e.g., Sommerfeld et al. 1996; Mast et al. 1998; Hubbard et al. 2005), our understanding of the relationship between interannual variability in growing season productivity and winter carbon emissions is still limited.

Sites in these four zones may respond differently to interannual and directional changes in climate. The timing and frequency of freeze–thaw events are predicted to vary among years and should control carbon emissions in zone I. Interannual variability in snow depth and air temperatures, because of their influence on soil temperatures, should affect carbon emissions at sites within zone II. A strong non-linear relationship has been observed at the lower elevation C-1 site on Niwot Ridge between soil temperatures and NEE corresponding to interannual variability in snow cover (Monson et al. 2006b). Variability at sites in zone III may be most related to interannual differences in soil moisture when the snowpack first develops. Mast et al. (1998) found that the seasonal pattern of CO₂ flux did not vary across a gradient of soil moisture, but the magnitude of the CO₂ flux depended on the soil moisture. At the Soddie site the interannual variability may be related to the mid-winter snowmelt event in March 2006 when the maximum CO₂ flux occurred well before snowmelt. Similar patterns may occur at warmer sites with deeper snowpacks, where mid-winter thaw or rain-on-snow events could provide a small pulse of moisture to soils. While the magnitude of carbon emissions at all sites should be affected by the length of the snow-covered season, the duration of snow cover may be the dominant control for sites in

zone IV. Years with an earlier snowmelt may be associated with higher growing season productivity resulting in greater carbon availability in the subsequent snow-covered season.

If the interannual variability in snow depth is not sufficient to shift a site between snow regime zones, the seasonal pattern of CO₂ flux should not vary among years. At sites like the Soddie and nearby tundra on Niwot Ridge, where snow depth is largely a function of wind redeposition of snow, changes of snow cover zone would be uncommon. However, where snow depth is predominantly a function of snowfall, sites may shift among zones from year to year. Relatively small changes in snow depth and soil insulation may result in large changes in the seasonal pattern of flux. The relationships among snow cover, soil temperature, and carbon emissions suggest that such a shift between zones II and III occurs at the lower elevation C-1 site on Niwot Ridge (Monson et al. 2006b). Directional changes in snowpack properties (Rixen et al. 2008) may permanently shift the snow regime, seasonal patterns in CO₂ flux, and the magnitude of carbon emissions at a site. These changes in carbon cycling may be magnified by the changes in other nutrient cycling processes that are also predicted with climate change in snow-covered ecosystems (Edwards et al. 2007).

Conclusions

The Soddie site has among the highest CO₂ fluxes reported from snow-covered areas at 0.71 μmol m⁻² s⁻¹ in 2006 and 0.86 μmol m⁻² s⁻¹ in 2007, resulting in 156 and 189 g C m⁻² emitted over the winter. These calculated fluxes likely significantly underestimate the total CO₂ emissions because they ignore the advective flux associated with wind pumping (Seok et al. 2009). The winter flux accounted for ~30% of the annual CO₂ flux at this site. These high fluxes may be due in part to the high aboveground productivity measured at the site (~750 g m⁻²), contributing labile organic matter to the soil. This site may represent the location with maximum CO₂ flux rate on Niwot Ridge as a result of the high NPP, long snow-covered season, and soil temperatures consistently at ~0°C. Other microbial processes, e.g., the production of N₂O, also appear to be quite high at this site (Filippa et al. 2009). With the soil temperatures

near zero, the increasing CO₂ flux during the snow-covered season appears to be related to changes in soil moisture. This temporal pattern occurs in many sites with early developing and deep snowpacks in the region. Changes in snow cover at this site resulting in a shallower snowpack are expected to change the seasonal pattern to one associated with variability in soil temperatures as documented at lower elevations on Niwot Ridge (Monson et al. 2006b). Such directional changes in snow regime at seasonally snow-covered sites may result in a dramatically different seasonal pattern and magnitude of CO₂ flux.

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