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Seasonal patterns in soil surface CO_2 flux under snow cover in 50 and 300 year old subalpine forests

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Abstract. Soil CO_2 flux can contribute as much as 60–80% of total ecosystem respiration in forests. Although considerable research has focused on quantifying this flux during the growing season, comparatively little effort has focused on non-growing season fluxes. We measured soil CO_2 efflux through snow in 50 and ~300 year old subalpine forest stands near Fraser CO. Our objectives were to quantify seasonal patterns in wintertime soil CO_2 flux; determine if differences in soil CO_2 flux between the two forest ages during the growing season persist during winter; and to quantify the sample size necessary to discern treatment differences. Soil CO_2 flux during the 2002–2003 and 2003–2004 snow season averaged 0.31 and 0.35 μmols m^{-2} s^{-1} for the young and old forests respectively; similar to the relative difference observed during summer. There was a significant seasonal pattern of soil CO_2 flux during the winter with fluxes averaging 0.22 μmols m^{-2} s^{-1} in December and January and increasing to an average of 0.61 μmols m^{-2} s^{-1} in May. Within-plot variability for measurements used in calculating flux was low. The coefficients of variation (CV) for CO_2 concentration, snowpack density, and snow depth were 17, 8 and 14%, respectively, yielding a CV for flux measurements within-plot of 29%. A within plot CV of 29% requires 8 sub-samples per plot to estimate the mean flux with a standard error of ±10% of the mean. Variability in CO_2 flux estimates among plots (size = 400 m^2) was similar to that within plot and was also low (CV = ~28%). With a CV of 28% among plots, ten plots per treatment would have a 50% probability of detecting a 25% difference in treatment means for α = 0.05.

Introduction

CO_2 fluxes from soil can account for 60–80% of total ecosystem respiration in forests (Law et al. 1997; Janssens et al. 2001; Milyukova et al. 2002). Understanding the seasonal dynamics of this flux is important for constructing annual carbon budgets, for modeling the effects of climate change on soil carbon storage and CO_2 release to the atmosphere (Chapin et al. 1996), and for estimating belowground carbon allocation by plants (Giardina and Ryan 2002). Although considerable research has focused on quantifying this flux during the growing season, comparatively little effort has focused on non-growing season fluxes.

Approximately 50% of terrestrial ecosystems in the northern hemisphere experience significant snow cover during the winter months (Sommerfeld et al. 1993). Historically, most annual estimates of soil CO_2 flux have assumed soil CO_2 flux in winter is zero (Fahnestock et al. 1998). However, a significant body of work has emerged over the past 10 years showing soil CO_2 fluxes under snow can account for as much as 20% of the annual soil CO_2 budget because winter snow packs can prevent significant soil freezing allowing for continued microbial activity (e.g. Brooks et al. 1996; Brooks et al. 1997). Most measurements of soil CO_2 flux through snow packs have been conducted in tundra and alpine ecosystems because these systems have been the focus of increased interest in the contribution of high latitude ecosystems to the global carbon budget (Chapin et al. 1996; Oechel et al. 2000). Significant soil surface flux under snow packs also occurs in the more productive subalpine forested ecosystems (Sommerfeld et al. 1996; Mast et al. 1998; McDowell et al. 2000) but we have almost no information on the variability of these fluxes over a winter season and virtually no information on the effects of forest age (Winston et al. 1995).

The few studies quantifying soil respiration in winter relative to the growing season results not only from the historical assumption that wintertime fluxes were close to zero but also from the methodological difficulties of measuring soil CO_2 flux through snow packs. Quantifying this flux requires accurate estimates of CO_2 concentrations, depth and snow pack properties (density, porosity and tortuosity). Because access to snow-covered environments and measurement conditions can be difficult, most studies measuring soil CO_2 flux through snow have relied on few samples and treatment or site replicates. Although some effort has been made towards standardizing methodologies (McDowell et al. 2000), we have little information on the sub-sampling intensity needed within-plots or the number of plots necessary to evaluate treatment differences for CO_2 efflux through snow. Improving our estimates of the contribution of wintertime soil CO_2 flux will require replicated studies addressing these questions.

Our objective in this study was to quantify soil surface CO_2 flux in winter for a Rocky Mountain subalpine forest. We designed a replicated experiment to address three questions: (i) does CO_2 flux under snow vary within the winter season, and does any seasonal pattern differ among forests of different ages (50 and $\sim$300 year old); (ii) do differences in soil surface CO_2 flux that are apparent between these different aged forests during the growing season persist during the winter; (iii) what is the sample size necessary to accurately estimate soil CO_2 flux through snow within a 400 m^2 plot, and how many plots are necessary to detect treatment differences for $\alpha = 0.05$?

Methods

Our study site is located in the Fool Creek watershed in the Fraser Experimental Forest (FEF) near Fraser Colorado, USA, (39° 4′ N 105° 52′ W)

(Figure 1). Average annual temperature at the experimental forest is 2 °C. The forest receives an average of 740 mm precipitation each year, with approximately two-thirds falling as snow. During the mid 1950s, 50% of the timbered area in the Fool Creek watershed was harvested to examine the effects of timber removal on water yield. The harvest consisted of alternating cut and unharvested strips resulting in forest strips ranging from 20 to 110 m wide (Troendle and King 1985). As part of a larger study to examine the effects of nutrition and forest age on below ground carbon allocation, we installed five replicates (blocks) each in a subset of the cut and unharvested strips in the upper Fool Creek Watershed. The blocks were located along an elevation gradient spanning approximately 300 m and each block faces a general northerly aspect. Stand age in the cut and uharvested strips is about 50 and 300 years old, respectively. Each block consists of two cut and unharvested pairs for a total of four measurement plots (400 m^2 each) per replicate (10 plots total for each treatment). Two plots per treatment per block were installed because one plot from each cut and unharvested strip will be fertilized at a later date. For this study, the block was considered the replicate for estimating differences in soil CO_2 flux between the 50 and 300 year old stands (n = 5). Total basal area in each treatment is distributed among three dominant tree species; Engelmann spruce (*Picea englemanii* Parry), Subalpine fir (*Abies lasiocarpa* (Hook) Nutt.) and lodgepole pine (*Pinus contorta* var. *latifolia*). Engelmann spruce occupies 45% of the basal area in the 300 year old stands, followed by lodgepole pine (30%) and subalpine fir (25%). In the 50 year old stands, subalpine fir occupies 52% of the basal area followed by Engelmann

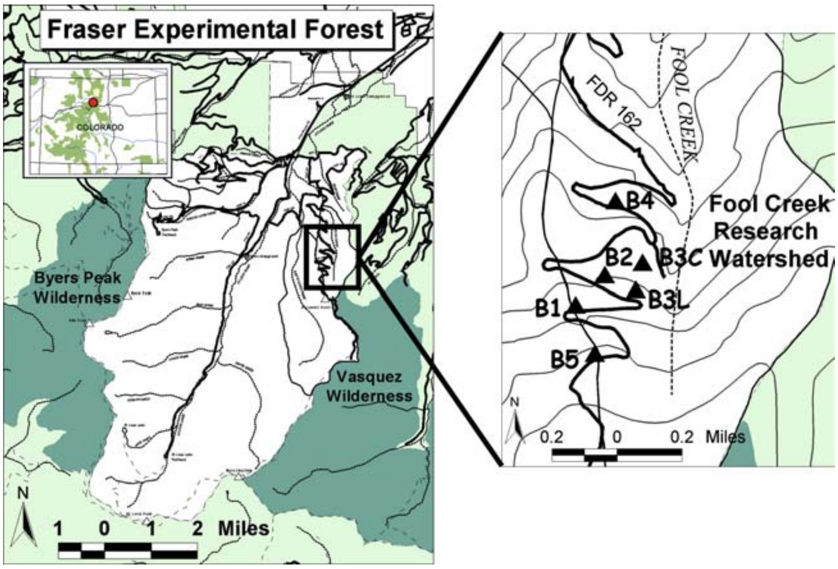

Figure 1. Study site location.

Table 1. Plot (400 m^2) characteristics for the 300 and 50 year +old stands

Treatment	*N*	Diameter (cm)	Basal area (m^2 ha^{-1})	LAI
300	10	15.54 (0.63)	60.44 (2.99)	4.53 (0.39)
50	10	9.36 (0.34)	18.31 (1.66)	1.51 (0.13)

Values are means for each parameter. Values in parentheses are ± 1 SE. LAI was estimated using allometric equations derived at Fraser Experimental Forest for each species (Troendle and King 1985).

spruce (33%) and lodgepole pine (15%). Average tree diameter, basal area and leaf area index for the 50 and 300 year old stands are given in Table 1.

CO_2 flux

We estimated soil surface CO_2 efflux through snow using Fick's first law, following Massman et al. (1995) as

$$J_g = f\tau D \frac{P_o}{RT_0}\left(\frac{T}{T_0}\right)^{0.81}\frac{d[g]}{dz} \tag{1}$$

where $J_g =$ the gas flux (μmols m^{-2} s^{-1}), D is the diffusion coefficient for CO_2 in air (0.139 cm^2 s^{-1}), P_o/RT_0 is the molecular density of CO_2 at STP (44.63 mol m^{-3}), f is snow pack porosity (unitless), t is tortuosity (unitless), [g] is the measured difference in gas concentration between the soil and snow surface (μmols mol^{-1}), T is the average snowpack temperature (K), and z is depth of the snow pack.

CO_2 concentration

For this study, we report data from the 2002–2003 and 2003–2004 snow years. For 2002–2003, we sampled soil CO_2 flux under snow in January, April and March. For the 2003–2004 snow year, our sample dates were December 2003 and January 2004. In January 2003, our sampling design followed that of Sommerfeld et al. (1993). We constructed CO_2 samplers from 4.2 cm diameter PVC tube covered on both ends by a fine mesh stainless steel screen. During the fall of 2002, three samplers were placed along a transect in the middle of each 20 m × 20 m plot, approximately 5 m apart. Bev-a-line tubing (0.32 cm ID) connected each sampler to a central location and each tube was secured to a tree above the expected maximum snow depth (~3 m). The tubes and samplers were sealed using a stopcock to prevent air exchange between the soil–snow interface and the atmosphere. In 2003, on day of year (DOY) 23 and 24, CO_2 concentration at the soil–snow interface was estimated by first removing a volume of air equal to the volume of the tubing to flush any air not in equilibrium with the surrounding pore space. A second sample was then extracted using a gas tight syringe and stored in a 20 ml evacuated exetainer (Labco, LTD, Houston, TX) with a gas tight septum. Samples were analyzed for CO_2 concentration the same day (<8 h after sampling) in the FEF laboratory on a LICOR 6262 infrared gas analyzer configured as a closed system. We also measured ambient CO_2 concentration at the snow surface immediately before sampling each plot by drawing volume of air into the gas tight syringe and storing it in an exetainer.

Because with-in plot variability was high during our first sample date, we elected to change our sampling scheme to include more sub-samples per plot. All samples for the remainder of the sampling dates were obtained using a portable infrared gas analyzer (EGM 4, PP Systems, Haverhill, MA) and a modified snow depth probe (Snowmetrics, Fort Collins, CO) (Brooks et al. 1999; Welker et al. 2000). The probe is outfitted with a drilled pointed tip attached to 0.32 cm diameter Bev-a-line tubing. The tubing runs inside the length of the probe and attaches to the gas analyzer. A sample is obtained by inserting the probe vertically into the snow pack to ground level. The gas analyzer pulls air through the tubing and a CO_2 concentration is obtained when the reading is stable ($\sim$30–45 s). Sample dates using this method were DOY 93-94, 142-143, 351-352 for 2003 and DOY 27–28 for 2004.

Snow pack properties

We estimated snow pack density and porosity from snow pits along the elevation gradient of our 5 replicates. For the January 2003 sample, we dug five snow pits, four were located in 300 year old stands (all adjacent to our measurement plots) and one was located in a 50 year old stand. For the rest of the sample dates, we dug six pits, three each in the 50 and 300 year old stands located at the top, middle and bottom of the elevational gradient for our replicates. At each pit, we measured total depth as well as density and temperature in 10 cm increments for the entire depth of the snow pit. Mean density (kg m^{-3}) for the snow pack was estimated from a weighted average of the 10 cm layers. Porosity (f) was calculated from mean density (ρ) as

$$f = 1 - (\rho/973\,\mathrm{kg\,m^{-3}}) \tag{2}$$

where 973 kg m^{-3} = the density of ice.

For all of our sampling dates, snow depth was estimated from 10 evenly spaced samples obtained with a depth probe along a diagonal transect through each 400 m^{-2} plot. For all but the January 2003 samples, the depth measurement was obtained at the exact location of the CO_2 sample. In January 2003, an average depth was used for the three CO_2 samplers installed on each plot.

The tortuosity coefficient is a time consuming and difficult parameter to estimate (e.g. Massman et al. 1997; Winston et al. 1995); however, studies examining gas diffusion through porous media (mostly soils) suggest that tortuosity may be estimated as a function of density (Millington 1959; Millington and Shearer 1971; Striegl and Ishii 1989). Here, we estimate tortuosity as

$$t = f^{1/3} \tag{3}$$

Statistical analysis

We evaluated the seasonal pattern and treatment differences of soil surface CO_2 efflux through snow using repeated measures analysis Proc Mixed, SAS (SAS Institute, 1999). We averaged CO_2 flux in each plot, for each treatment, and considered the block as our basic sampling unit ($n = 5$ per treatment).

Sample and sub-sample analysis

We evaluated the sub-sample size (n) necessary to estimate soil CO_2 flux within a plot with a standard error of ±10% of the mean as

$$n = (\mathrm{CV}/10)^2 \tag{4}$$

where CV = the average CV within plot. We used the same analysis for snow depth and density.

Our sample plots were 400 m^2 and we used the Power Analysis and Sample Size Software Package (www.ncss.com/pass.html) to estimate how many plots per treatment would be needed to detect differences with the measured range of among-plot variability.

Results

Soil CO_2 flux

Soil surface CO_2 flux varied during winter months at our site ($p < 0.01$, Figure 2). Values ranged from a low of 0.19 μmols m^{-2} s^{-1} in January 2003 to 0.67 μmols m^{-2} s^{-1} in May 2003. This pattern did not differ between forest ages but soil CO_2 efflux under snow was 13% lower in the younger forest ($p = 0.005$) during the winter months (Figure 2).

Within-plot CV's ranged from 20 to 31%, and CV's were similar across the winter and for the two forest ages. Eight sub-samples per plot were necessary to estimate soil CO_2 efflux with a standard error within 10% of the actual mean (Figure 3a). Doubling the sample size to 16 increases the precision only slightly, yielding standard errors within 7% of the mean.

CV among plots in the same age class ranged from 13% to 28% of the mean flux, with no discernable pattern in CV throughout the winter. This low plot-

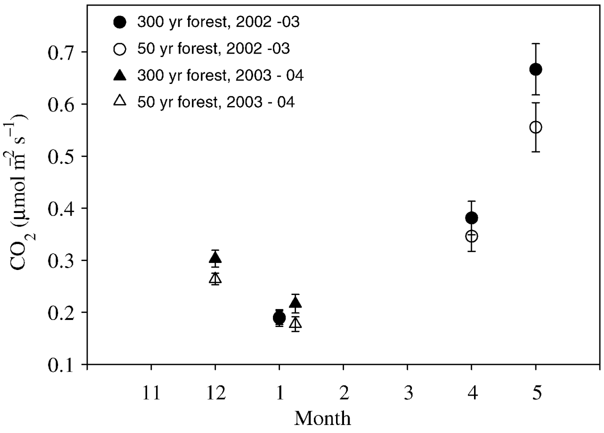

Figure 2. Mean soil CO_2 flux through snow pack in 50 year old (open symbols) and 300 year old (closed symbols) stands during the 2002–2003 and 2003–2004 snow seasons. There was a significant seasonal trend in soil CO_2 flux ($p < 0.01$). Fluxes between treatments were also significantly different ($p < 0.01$). Error bars are ±1 standard error.

to-plot variability indicates that 10 plots per treatment would have a 50% probability (β or power) of detecting a difference in treatment means of 25% for $\alpha = 0.05$. Larger differences between treatments can be detected with fewer sample plots. For example, for a treatment difference of 50%, five plots per treatment would have a >79% probability of detecting that difference for a CV ≤ 28% (Figure 3b).

Snow pack properties

Mean density in sampled snow pits ranged from 224.4 kg m^{-3} in December 2003 to 402.5 kg m^{-3} in May 2003. In general, density appeared higher in the 50 year old stands but differences were relatively small (less than 10%) for any given date (Table 2). The average CV for all pits throughout the winter was 8%. Our sample size analysis indicates that our snow pit sampling scheme accurately estimates the mean snow pack density at our site. Measuring six snow pits allows us to estimate density with a standard error of 3% of the mean. Doubling the sample size does not appreciably increase precision (SE = ±2%).

Discussion

Seasonal patterns and treatment differences in soil CO_2 flux

Our results show a definitive seasonal pattern of winter soil CO_2 flux rates in different age subalpine forests at FEF. Most studies evaluating seasonal trends

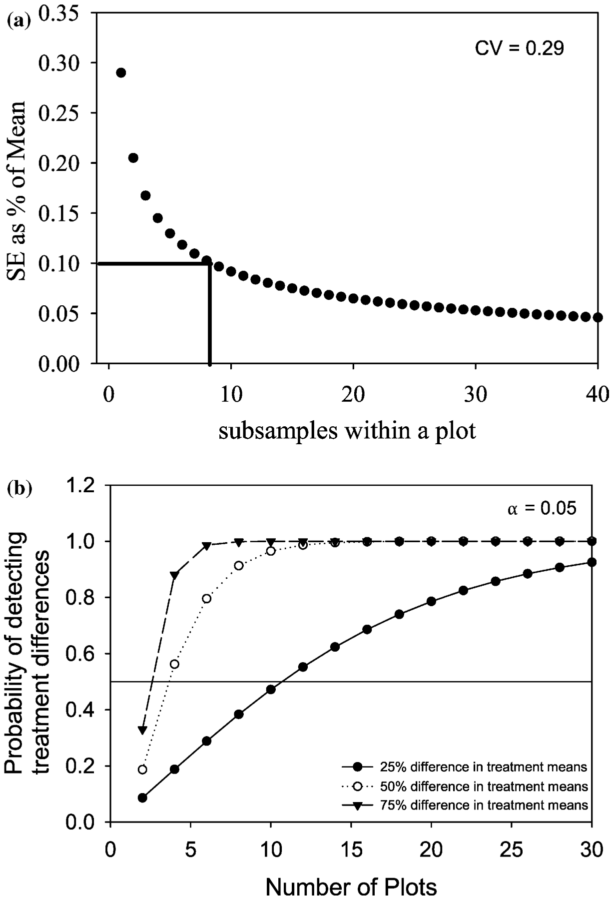

Figure 3. (a) Standard errors as a percentage of the mean (CV/√n) versus sub-sample size. Solid lines indicate sample size necessary for a standard error ± 10% of the mean. (b) The probability of detecting significant treatment differences of 25, 50 and 75% for a given number of plots.

in soil CO_2 flux through snow have focused on tundra (Zimov et al. 1996; Brooks et al. 1997; Fahnestock et al. 1998) and wetland (Wickland et al. 2001; Roehm and Roulet 2003) ecosystems, but some have investigated seasonal trends in soil CO_2 fluxes through snow in forests (Sommerfeld et al. 1993; Winston et al. 1995; Sommerfeld et al. 1996; Kurganova et al. 2003). Only one of these examined fluxes for different aged forests (Winston et al. 1995) but their values were too variable to discern differences. In general, seasonal patterns we observed are similar to those observed in other studies with fluxes low and relatively stable through the early to mid winter months and a gradual increase late in the snow year as snow melt begins.

Daily fluxes for the 300 and 50 year old stands averaged 30.2 and 26.8 mmols m^{-2} d^{-1} respectively over the course of the winter. These are

Table 2. Snow pit characteristics for each sampling date for the 300 and 50 year old stands

Treatment		January 2002–2003	April 2002–2003	May 2002–2003	December 2003–2004	January 2003–2004
300	Density (kg m^{-3})	255.8 (4.4) $n = 5$	264.3 (13.8) $n = 2$	402.5 (18.3) $n = 3$	224.4 (14.0) $n = 3$	228.6 (4.7) $n = 3$
	Temperature (°C)	− 7.1 (0.1)	− 3.2 (0.2)	0.1 (0.1)	− 7.2 (0.1)	− 9.0 (0.46)
50	Density (kg m^{-3})	282.6 (na) $n = 1$	282.2 (22.2) $n = 2$	368.4 (10.6) $n = 3$	228.9 (6.7) $n = 3$	241.1 (6.5) $n = 3$
	Temperature (°C)	− 6.8 (na)	− 2.1 (0.5)	0.1 (0.02)	− 7.6 (0.4)	− 7.4 (0.08)

Sample size is equal for density and temperature for each sampling date and treatment. Values in parentheses are ± 1 SE.

similar to, but lower than those found in a mixed conifer forest in Washington state, (58 mmols $m^{-2} d^{-1}$; McDowell et al. 2000), and an Engelmann spruce forest in Wyoming (45 mmols $m^{-2} d^{-1}$; Sommerfeld et al. 1996). Some of the difference results from how soil CO_2 flux through the snow pack was calculated between studies. Our flux calculation (Eq. 1) differs from that used in McDowell et al. (2000) and Sommerfeld et al. (1993) in that Eq. 1 is derived considering conservation of mass; i.e. flux is a function of the difference in CO_2 mass above and below the snowpack rather than a difference in mixing ratio above and below the snowpack. This difference is important for fluxes measured at high altitudes because in the derivation of Eq. 1, the pressure correction terms cancel (Massman, personal communication). For this study, the use of Eq. 1 to calculate flux yields 30% lower fluxes than the equation used by Sommerfeld et al. (1993) and McDowell et al. (2000).

The higher fluxes in the 300 year old relative to the 50 year old stands (Figure 1) are similar in magnitude on a percentage basis to those observed during the summer (approximately 13%, unpublished data). Differences during winter between the stands are not related to soil temperature because soil temperatures (10 cm) in the two age classes were virtually identical ($p = 0.7$) on all of our sampling dates (−0.46 and − 0.50°C respectively). Soil moisture may explain some of the difference but we did not collect the data necessary to adequately address this possibility.

A possible contribution to the differences in soil CO_2 flux between treatments at our site is the large difference in GPP and consequent larger standing stocks of roots in the older plots. To examine this, we assumed that leaf area and total below ground carbon allocation are relatively proportional (Litton et al. 2004) and plotted mean soil CO_2 flux versus leaf area for each of our sample dates (Figure 4). Leaf area was estimated from allometric equations for each species derived at FEF (Kaufmann et al. 1982). During December, January and April, the slope of this relationship was not significant ($p > 0.1$). The relationship improved for our May measurements and with a significant slope ($p < 0.01$) and higher R^2 (0.16). Analysis of the CO_2 flux versus leaf area relationship during summer months does not indicate any further improvement, but slopes and R^2 values are similar to those observed for the May sample. Since treatment differences are still apparent during the early winter months, its possible that the microbial community and or microbial resources differ between the 300 and 50 year old stands and contribute to the differences observed during the winter and growing seasons.

Numerous studies show that soil CO_2 efflux under snow can be a significant portion of the carbon budget for a variety of ecosystems (e.g. Mast et al. 1998; Welker et al. 2000; Wickland et al. 2001). Total carbon efflux during winter (estimated from 15 November to 31 May) for the subalpine forests we studied was approximately 71 g cm^{-2}. This corresponds to about 8% of annual GPP found in lower elevation subalpine forests at FEF or roughly 80% of the carbon allocated to annual wood production (Ryan and Waring 1992). Our results indicate the importance of understanding the seasonal pattern of soil

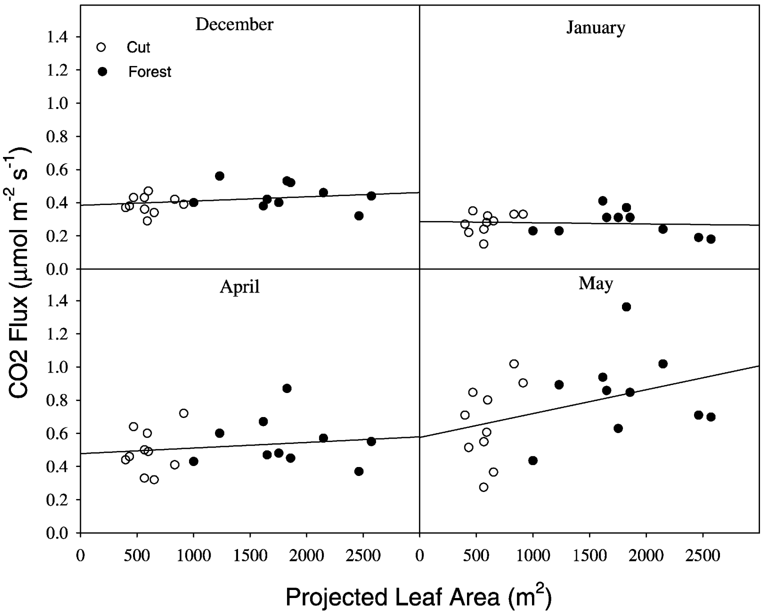

Figure 4. Plot mean Soil CO_2 flux versus total plot projected leaf area index (LAI) during four separate sampling dates. Mean soil CO_2 flux was not related to LAI for any month except May 2003. The slope of soil CO_2 flux versus LAI was significant ($p < 0.01$) during May with an R^2 of 0.16.

surface CO_2 flux when calculating seasonal estimates. For example, using the average flux obtained in January would result in a 50% underestimation of soil CO_2 flux for the season and using May values would result in 50% overestimation.

Sample size estimates within and among plots

Because of the difficulties in accessing snow covered sites and measuring CO_2 fluxes through snow, most studies use small sample sizes and few replicates to quantify soil CO_2 flux in winter. Our analysis indicates that eight sub-samples are required to estimate plots means for soil CO_2 flux for our 400 m^2 plots with a standard error ± 10% of the mean in the subalpine forests we studied. Larger areas would likely require a larger sample size.

Sampling transects through our plot were systematically placed along plot diagonals and did not differentiate between gaps or tree wells. It's possible that in more homogenous landscapes, fewer samples would be necessary to estimate a mean flux and conversely, a more heterogeneous landscape may require more. Because there are few winter estimates of soil CO_2 flux compared to the growing season, including sample size analysis in future studies should improve winter estimates and annual carbon budgets in ecosystems that experience significant snow cover.

CO_2 flux estimates and potential errors

Methods for measuring soil CO_2 flux through snow include dynamic chamber methods at the snow or soil surface (e.g. Winston et al. 1995; Kurganova et al. 2003) and static estimates using the CO_2 concentrations at the soil and snow surface with a diffusional model that accounts for depth, porosity and tortuosity of the snow pack (Sommerfeld et al. 1993; Sommerfeld et al. 1996). McDowell et al. (2000) evaluated these methods finding the most reliable estimates were obtained using CO_2 concentrations and the diffusional model. Most studies using this method employ gas samplers that maintain a snow free void at the soil/snow interface. A syringe is used to extract a sample and CO_2 concentrations are measured back in a laboratory using a gas chromatograph (e.g. Brooks et al. 1997; Roehm and Roulet 2003). Using a portable infrared gas analyzer and sampling probe (e.g. Brooks et al. 1999; Welker et al. 2000) to obtain CO_2 concentrations reduces sampling time, increases spatial sampling and allows for increased numbers of sample replicates. Although there are no direct comparisons of this method with the more traditional gas sampler and syringe technique, our similar January estimates obtained in 2003 (gas samplers) and 2004 (irga samples) (Figure 2) suggests that they are comparable.

A potential error in measuring CO_2 fluxes through snow packs may occur if the diffusion of CO_2 through the snow pack is accompanied by significant advection from turbulence driven pressure pumping (Massman et al. 1995). A met station in a 50 year old stand near our sampling locations recorded wind speeds at 3 and 10 m above ground level (Elder, unpublished data). Wind speeds near the snow surface during our sampling dates averaged about 0.5 m s^{-1} from 0800 to 1700 and never exceeded 3.7 m s^{-1} for any given sampling day. Low wind speeds in general result in minimal turbulence driven pressure pumping (Massman et al. 1997). In the absence of data to determine if pressure pumping affected our results, we suggest that low average wind speed during our flux sampling makes it unlikely that our results were affected by pressure pumping.

Reliable estimates of soil CO_2 flux using the diffusional model of Sommerfeld et al. (Sommerfeld et al. 1993) require accurate characterization of the snow pack (Eq. 1). The most difficult parameter to estimate is tortuosity, a measure of the "connectedness" of snow pore spaces. Because tortuosity is a multiplicative factor in Eq. 1, errors in this parameter scale directly to the CO_2 flux estimate. Studies using the diffusional model have accounted for this parameter differently, including measuring it directly (Winston et al. 1995; Massman et al. 1997), modeling it as a function of porosity (Brooks et al.; McDowell et al. 2000; Roehm & Roulet 2003), or assuming unity and ignoring it (Sommerfeld et al. 1996). Our estimates of tortuosity (Eq. 3) ranged from

0.84 to 0.92 which are within the range for those found by direct measurement in snow packs with similar depth and density profiles (Massman et al. 1997, 0.75–0.94). Because the diffusional model appears to have become the standard for wintertime estimates of soil CO_2 fluxes, more research is needed on tortuosity effects on gas diffusion through snow packs.

The remaining two parameters that are critical for accurate estimates of CO_2 diffusion through snow are porosity and depth. Most studies using the diffusional model for CO_2 flux derive porosity from density (e.g. Eq. 1). The degree that actual porosity measurements deviate from those derived from density has yet to be determined but deserves more research to improve or validate the accuracies of estimates of gas diffusion through snow packs. Since porosity estimates currently rely on density of the snow profile, accurate density measurements are necessary on spatial and temporal scales that correspond with the flux sampling. In general snow pack densities are relatively conservative over small spatial scales and on slopes of similar aspect Elder et al. (1991). This is reflected in the low variation in snow pack density between our snow pits (CV $\approx 8\%$). We also compared our density estimates with those associated with the NASA Cold Land Processes Field Experiment (CLPX) (Cline et al. 2002). For the CLPX study, 16 snow pits on two sampling dates were established over a 1 km^2 area that included our sampling sites. Density profiles for these samples were remarkably similar to ours ($\pm 5\%$) and had a CV of about 3%. In contrast to density, snow depth can vary considerably even within a 400 m^2 area. Differences of more than 70 cm between minimum and maximum depths in our 20×20 m plots were not uncommon. Therefore, accurate depth measurements at the point of CO_2 measurement are critical to accurate estimates of CO_2 flux through snow.

Acknowledgments

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References

Brooks P.D., Campbell D.H., Tonnessen K.A. and Heuer K. 1999. Natural variability in N export from headwater catchments: snow cover controls on ecosystem N retention. Hydrol. Process. 13: 2191–2201.

Brooks P.D., Schmidt S.K. and Williams M.W. 1997. Winter production of CO_2 and N_2O from Alpine tundra: environmental controls and relationship to inter-system C and N fluxes. Oecologia 110: 403–413.

Brooks P.D., Williams M.W. and Schmidt S.K. 1996. Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. Biogeochemistry 32: 93–113.

Chapin F.S., Zimov S.A., Shaver G.R. and Hobbie S.E. 1996. CO_2 fluctuation at high latitudes. Nature 383: 585–586.

Cline D., Elder K., Davis B., Hardy J., Liston J.E., Imel D., Yeueh S.H., Gasiewski A.J., Koh G., Armstrong R.L. and Parsons M. 2002. Overview of the NASA cold land processes field experiment (CLPX-2002). Microwave and Remote Sensing of the Atmosphere and Environment III. International Society of Optical Engineering, Hangzhou, China, pp. 361–372

Elder K., Dozier J. and Michaelsen J. 1991. Snow accumulation and distribution in an Alpine Watershed. Water Resour. Res. 27: 1541–1552.

Fahnestock J.T., Jones M.H., Brooks P.D., Walker D.A. and Welker J.M. 1998. Winter and early spring CO_2 efflux from tundra communities of northern Alaska. J. Geophys. Res.-Atmos. 103: 29023–29027.

Giardina C.P. and Ryan M.G. 2002. Total belowground allocation in a fast rowing *Eucalyptus* plantation estimated using a carbon balance approach. Ecosystems 5: 487–489.

Janssens I.A., Lankreijer H., Matteucci G., Kowalski A.S., Buchmann N., Epron D., Pilegaard K., Kutsch W., Longdoz B., Grunwald T., Montagnani L., Dore S., Rebmann C., Moors E.J., Grelle A., Rannik U., Morgenstern K., Oltchev S., Clement R., Gudmundsson J., Minerbi S., Berbigier P., Ibrom A., Moncrieff J., Aubinet M., Bernhofer C., Jensen N.O., Vesala T., Granier A., Schulze E.D., Lindroth A., Dolman A.J., Jarvis P.G., Ceulemans R. and Valentini R. 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biol. 7: 269–278.

Kaufmann M.R., Edminster C.B. and Troendle C.A. 1982. Leaf area determinations for subalpine tree species in the central Rocky Mountains. Research Paper RM-238.

Kurganova I., De Gerenyu V.L., Rozanova L., Sapronov D., Myakshina T. and Kudeyarov V. 2003. Annual and seasonal CO_2 fluxes from Russian southern taiga soils. Tellus Ser. B-Chem. Phys. Meteorol. 55: 338–344.

Law B.E., Ryan M.G. and Anthoni P.M. 1997. Seasonal and annual respiration of a ponderosa pine ecosystem. Global Change Biol. 5: 169–182.

Litton C.M., Ryan M.G. and Knight D.H. 2004. Effects of tree density and stand age on carbon allocation patterns in postfire lodgepole pine. Ecol. Appl. 14: 460–475.

Massman W.J., Sommerfeld R.A., Mosier A.R., Zeller K.F., Hehn T.J. and Rochelle S.G. 1997. A model investigation of turbulence-driven pressure-pumping effects on the rate of diffusion of CO_2, N_2O, and CH_4 through layered snowpacks. J. Geophys. Res.-Atmos. 102: 18851–18863.

Massman W.J., Sommerfeld R.A., Zeller K., Hehn T., Hudnell L. and Rochelle S.G. 1995. CO_2 flux through a Wyoming seasonal snowpack: diffusional and pressure pumping effects. Biogeochemistry of snow-covered catchments. International Association of Hydrological Sciences, Wallingford, pp. 71–79.

Mast M.A., Wickland K.P., Striegl R.T. and Clow D.W. 1998. Winter fluxes of CO_2 and CH_4 from subalpine soils in Rocky Mountain National Park, Colorado. Global Biogeochem. Cyc. 12: 607–620.

McDowell N.G., Marshall J.D., Hooker T.D. and Musselman R. 2000. Estimating CO_2 flux from snowpacks at three sites in the Rocky Mountains. Tree Physiol. 20: 745–753.

Millington R.J. 1959. Gas diffusion in porous media. Science 130: 100–102.

Millington R.J. and Shearer R.C. 1971. Diffusion in aggregated porous media. Soil Science 111: 372.

Milyukova I.M., Kolle O., Varlagin A.V., Vygodskaya N.N., Schulze E.D. and Lloyd J. 2002. Carbon balance of a southern taiga spruce stand in European Russia. Tellus Ser. B-Chem. Phys. Meteorol. 54: 429–442.

Oechel W.C., Vourlitis G.L., Hastings S.J., Zulueta R.C., Hinzman L. and Kane D. 2000. Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. Nature 406: 978–981.

Roehm C.L. and Roulet N.T. 2003. Seasonal contribution of CO_2 fluxes in the annual C budget of a northern bog. Global Biogeochem. Cyc. 17: 1029, doi:10.1029/2002GB001889.

Ryan M.G. and Waring R.H. 1992. Maintenance respiration and stand development in a subalpine lodgepole pine forest. Ecology 73: 2100–2108.

Sommerfeld R.A., Massman W.J. and Musselman R.C. 1996. Diffusional flux of CO_2 through snow; spatial and temporal variability among alpine-subalpine sites. Global Biogeochem. Cyc. 10: 473–482.

Sommerfeld R.A., Mosier A.R. and Musselman R.C. 1993. CO_2, CH_4 and N_2O flux through a Wyoming snowpack and implications for global budgets. Nature 361: 140–142.

Striegl R.G. and Ishii A.L. 1989. Diffusion and consumption of methane in an unsaturated zone in North-Central Illinois, United-States. J. Hydrol. 111: 133–143.

Troendle C. and King R.M. 1985. The effect of timber harvest on the Fool Creek watershed, 30 years later. Water Resour. Res. 21: 1915–1922.

Welker J.M., Fahnestock J.T. and Jones M.H. 2000. Annual CO_2 flux in dry and moist arctic tundra: field responses to increases in summer temperatures and winter snow depth. Climatic Change 44: 139–150.

Wickland K.P., Striegl R.G., Mast M.A. and Clow D.W. 2001. Carbon gas exchange at a southern Rocky Mountain wetland, 1996–1998. Global Biogeochem. Cyc. 15: 321–335.

Winston G.C., Stephens B.B., Sundquist E.T., Hardy J.P. and Davis R.E. 1995. Seasonal variability in CO_2 transport through snow in a boreal forest biogeochemistry of snow-covered catchments. International Association of Hydrological Sciences, Wallingford, pp. 61–70.

Zimov S.A., Davidov S.P., Voropaev Y.V., Prosiannikov S.F., Semiletov I.P., Chapin M.C. and Chapin F.S. 1996. Siberian CO_2 efflux in winter as a CO_2 source and cause of seasonality in atmospheric CO_2. Climatic Change 33: 111–12.