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The contribution of beneath-snow soil respiration to total ecosystem respiration in a high-elevation, subalpine forest

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[1] The respiratory loss of CO_2 from soil microbes beneath winter snow in forests from cold climates can significantly influence the annual carbon budget. We explored the magnitude of winter soil respiration using continuous measurements of beneath-snow CO_2 concentration within the footprint of a flux tower in a subalpine forest in the Rocky Mountains. We used eddy covariance measurements from the tower to obtain estimates of total wintertime ecosystem respiration and compared them to the calculated beneath-snow CO_2 flux. Soil respiration in the winter was estimated to contribute 35–48% of the total wintertime ecosystem respiration, and 7–10% of the total annual ecosystem respiration. The largest increase in soil respiration occurred in the late winter following an earlier-than-normal initiation of snowmelt and increase in snow density. Following this melt event, respiration rates increased approximately sixfold, despite an increase in soil temperature of only 0.3°–0.5°C. We interpret the late-winter surge in soil respiration to be triggered by a strong response of beneath-snow microbes to the pulse of meltwater coupled with extremely high sensitivity of the microbial biomass to increases in soil temperature.

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1. Introduction

[2] In forest ecosystems from cold climates the mineralization of soil organic matter (SOM) during the winter can potentially occur at high rates [*van Bochove et al.*, 2000; *Groffman et al.*, 2001; *Wickland et al.*, 2001; *Brooks et al.*, 2005; *Schimel et al.*, 2004; *Hirano*, 2005; *Hubbard et al.*, 2005; *Monson et al.*, 2005, 2006]. The recognition that winter processes can make an important contribution to annual biogeochemical budgets has challenged the traditional view of winter as a season of suppressed activity [*Campbell et al.*, 2005]. In a high-elevation subalpine forest of Colorado, we have previously shown that the amount of respired carbon lost during the winter can be as much as 50–90% of the carbon gained the previous summer [*Monson et al.*, 2005]. In this ecosystem, interannual dynamics in winter snow cover have been correlated to interannual dynamics in ecosystem respiration, with winters of low snowpack exhibiting lower soil temperatures (due to less thermal insulation) and lower ecosystem respiration rates [*Monson et al.*, 2006]. In these past studies, we hypothesized that much of the seasonal and interannual variation in winter ecosystem respiration is due to variation in the beneath-snow soil respiratory component. To date, however, it has been difficult to obtain measurements that would isolate the soil component from the overall ecosystem respiration rate.

[3] Several past studies have shown that microbial activity beneath snow can be high. In the alpine tundra ecosystem, soil microbial biomass reaches a maximum during the winter [*Brooks et al.*, 1996; *Lipson et al.*, 2000; *Schadt et al.*, 2003]. Measurements of beneath-snow respiration in subalpine forest ecosystems have shown that winter CO_2 fluxes can be significant in magnitude [*Sommerfeld et al.*, 1993, 1996; *Mast et al.*, 1998; *McDowell et al.*, 2000, *Musselman et al.*, 2005], and studies are just now emerging that address the processes that drive these high fluxes. *Brooks et al.* [2005] showed that addition of labile carbon substrates to microbial communities beneath the snow of

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subalpine forest and alpine tundra ecosystems stimulated soil respiration. *Hubbard et al.* [2005] showed that beneath-snow respiration rates from young and old subalpine forests in the Rocky Mountains of Colorado nearly doubled as the winter progressed from January through the beginning of May, and there was a slight trend toward higher respiration rates in an older forest stand (300 years) compared to a younger stand (50 years). Recently, studies in Japan have suggested that beneath-snow soil respiration is stimulated during the melt period by the downward diffusion of carbon substrates [*Hirano*, 2005], and that the mixing of ambient air into snowpacks during windy conditions is an important determinant of the overall rate of CO_2 flux into the atmosphere [*Takagi et al.*, 2005].

[4] In this study, we deployed a novel instrument for the near-continuous measurement of beneath-snow CO_2 concentration. The instrument allowed us to calculate beneath-snow soil respiration rates and observe the magnitude and seasonal dynamics of winter soil respiration at eleven sites simultaneously. By deploying the instrument within the footprint of tower-based eddy covariance measurements, we were able to evaluate the relative importance of beneath-snow versus above-snow components of winter respiration. We focused on the question: what are the magnitude and dominant seasonal dynamics in winter soil respiration in this ecosystem? We were less interested in the detailed mechanisms of CO_2 transport through the snowpack, which has been the focus of several past studies [e.g., *Massman et al.*, 1997; *Takagi et al.*, 2005; *Swanson et al.*, 2005].

2. Study Site

[5] The studies were conducted at the Niwot Ridge AmeriFlux site located at 3050 m above sea level in a subalpine forest just below the Continental Divide near Nederland, Colorado (40°1′58″N; 105°32′47″W). The secondary forest surrounding the site is ~100 years old, having regrown after early twentieth-century logging. The forest is dominated by subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*). The understory is relatively sparse, containing tree seedlings from all three species and patches of *Vaccinium myrtillus* (25% average understory coverage). Annual precipitation for the site averages 800 mm (approximately 65% falling as snow) and the mean annual temperature is 1.5°C. General characteristics of turbulent fluxes of CO_2, H_2O and sensible heat were reported by *Turnipseed et al.* [2003, 2004] and energy budget characteristics were reported by *Turnipseed et al.* [2002]. Overall dynamics in forest carbon uptake have been previously reported by *Monson et al.* [2002, 2005] and *Huxman et al.* [2003]. Patterns of growing-season soil respiration were reported by *Scott-Denton et al.* [2003, 2006] and *Sacks et al.* [2006].

3. Methods

3.1. Eddy Covariance Measurements of Ecosystem Respiration Rate

[6] Turbulent fluxes were measured at 21.5 m from a scaffolding-type tower. Details of the flux measurements have been reported previously [*Monson et al.*, 2002; *Turnipseed et al.*, 2002, 2003, 2004]. Briefly, the eddy covariance method was used to measure the eddy flux for CO_2, H_2O and temperature (see *Baldocchi* [2003] for a review of the eddy covariance method). Wind velocity was measured with a 3-dimensional sonic anemometer (model CSAT-3, Campbell Scientific, Logan) and [CO_2] was measured with a closed-path infrared gas analyzer (model 6262, LiCor, Inc., Lincoln). Density corrections due to changes in H_2O vapor concentrations were made according to *Webb et al.* [1980]. Wind coordinates were rotated according to *Kaimal and Finnigan* [1994] for the data of 1999–2001, and according to *Wilczak et al.* [2001] for the data of 2002–2004, to force the mean crosswind and vertical wind speeds to zero. We have conducted extensive analyses of these coordinate rotation methods at our site, compared them to other rotation methods, and estimated potential errors in the calculated eddy flux due to low-frequency filtering, all of which is reported in a previous publication [*Turnipseed et al.*, 2003]. The storage of CO_2 within the canopy was measured using a vertical profile system as described by *Monson et al.* [2002]. The change in stored CO_2 was added to the calculated eddy flux of CO_2 to provide net ecosystem CO_2 exchange (NEE) as described by *Goulden et al.* [1996a]. Advective CO_2 fluxes can be significant at this study site, although our detailed studies of this issue show that the fluxes are extremely small during the winter when mean CO_2 gradients are small, and over the entire year cause on average a 5–10% error in the annual cumulative NEE when considered without consideration of advection (C. Yi et al., University of Colorado, unpublished results, 2006). By convention, NEE is considered negative in sign when the net CO_2 flux is from the atmosphere to the forest and positive when the net flux is from the forest to the atmosphere.

3.2. Beneath-Snow Measurements of Soil Respiration Rate

[7] Beneath-snow [CO_2] was measured using a multiinlet air-sampling system combined with a single LI-7000 IRGA gas analyzer (Li-Cor Inc, Lincoln, Nebraska). Eleven chambers (2.5 L volume) were set on the ground in autumn and allowed to be covered by snow during the subsequent winter. Four chambers were located within 10 cm of tree boles and seven chambers were located in the open area between trees (at least 1.5 m to the nearest tree). An additional three inlets were placed above the snow to obtain the atmospheric [CO_2]. Air from the soil and atmospheric inlets was pumped ($1.4\ l\ min^{-1}$) to independent glass buffer volumes (2 L) from which samples were drawn and sent to the IRGA for analysis. Each buffer volume was sampled for 80 s every 30 min and only data from the final 20 s of the sampling time were used. Data on [CO_2] was continuously recorded at 1-s intervals during each sampling period. Because the buffer volumes were filled at the same time, all measurements of [CO_2] can be traced to the same times of collection. We conducted preliminary experiments in which air was pumped at different rates and volumes to the IRGA and found no effect on the observed CO_2 concentration. The IRGA was automatically calibrated at

3- to 5-hour intervals. Calibration was obtained from three gases of a known [CO_2] (413, 504 and 749 ppmv) and calibrated accuracy to within ±2%. The maximum beneath-snow [CO_2] we observed in 2004 was 3295 ppmv. This concentration exceeded that for our highest calibration gas and introduced the possibility of error due to nonlinearity. We conducted analyses during the winter of 2005 to determine the linearity of signals across the range 0–3000 ppmv using three calibration gases in the same range as those used during 2004, plus a fourth mixture of 5000 ppmv. In the latter analysis, we ran the same chambers used in 2004, under the same winter conditions, but at a different site and with all four calibration gases. We calculated a systematic error of ~5% at an observed value of 3000 ppmv if the calibration was limited to the lower three gases alone.

[8] At one of the 11 measurement sites, we installed two additional inlets, one at 10 cm above the ground and one at 50 cm above the ground, in order to characterize the vertical profile of [CO_2] within the snowpack. When combined with the chamber on the ground and the inlet above the snowpack, these additional inlets provided us with a potential profile of four heights. The inlet at 10 cm was covered with snow as of 20 November, and therefore we have information on the vertical profile at three heights (0, 10 and 120 cm, the latter being ambient air) through the entire winter. The inlet at 50 cm was covered with snow on 7 February, and therefore we have information for all four heights (0, 10, 50 and 120 cm, the latter being ambient air) from that date until the end of snowmelt (6 May 2004). In one analysis, we calculated the storage flux for CO_2 within the snowpack at the site where we had access to the vertical gradient in [CO_2]. This was done in the same way that the storage flux is calculated for a canopy; the vertical profile of [CO_2] was used to calculate the integral of [CO_2] as a function of height and thus assess day-to-day changes in total stored CO_2 within the snowpack. The storage flux was not added to the estimates of the soil respiration rate (R_s) for each chamber site because we only had values of the storage flux at a single site. However, it does provide some evidence of the magnitude of this term and its potential influence on our estimates of R_s.

[9] Measurements of snow depth were conducted at 1–2 week intervals using wooden rods with calibrated height marks planted within 10 cm of each respiration chamber. Soil temperatures were measured using platinum resistance thermometers (model STP-1, Radiation Balance Energy Systems, Inc., Seattle, Washington) embedded next to five of the chambers and copper-constantan thermocouples embedded next to the remainder. Air temperature was measured at 2 m above the ground using a single ventilated platinum resistance thermometer (model HMP-35D, Vaisala, Inc., Vantaa, Finland), and a second set of soil temperatures were measured as the integrated value from 0–10 cm using the average of five platinum resistance thermometers (model STP-1, Radiation Balance Energy Systems, Inc., Seattle, Washington), at a site located 15 m from the soil chambers. Soil moisture was measured using the average of seven time domain reflectometer probes (model CS-615, Campbell Scientific, Logan, Utah) distributed near the chamber site and installed at a 45° angle to 15 cm depth.

3.3. Flux Model of CO_2 Diffusion Through the Snowpack

[10] The flux of CO_2 through the snowpack was calculated using a steady state diffusion model with driving variables being the [CO_2] gradient, atmospheric pressure, air temperature, and snowpack depth, porosity and tortuosity [*Sommerfeld et al.*, 1993; *Brooks et al.*, 1997]. Several past studies have discussed the foundations for this model and likely causes of uncertainty [*Massman et al.*, 1997; *Mast et al.*, 1998; *Hubbard et al.*, 2005], and a number of studies have used similar models to estimate CO_2 diffusion through snow [*Sommerfeld et al.*, 1993; *Williams et al.*, 1996; *Zimov et al.*, 1996; *Sommerfeld et al.*, 1996; *Brooks et al.*, 1997; *Massman et al.*, 1997; *Mast et al.*, 1998; *Fahnestock et al.*, 1998; *McDowell et al.*, 2000; *Welker et al.*, 2000; *Hubbard et al.*, 2005; *Musselman et al.*, 2005; *Swanson et al.*, 2005]. The greatest uncertainty lies in the determination of snowpack structure and its effect on diffusional paths. The porosity and tortuosity of the snow are generally not measured directly, but rather scaled to snowpack density, which is measured directly. We determined snowpack density at 10-cm vertical intervals on a weekly basis after manually digging snow pits. Snow water equivalence (SWE), snow temperature, grain type, size, and snowpack stratigraphy were measured following previously published protocols and used to calculate snow density [*Williams et al.*, 1996]. Mean snow density (ρ) was calculated using the mean integral density with respect to height,

$$\overline{\rho} = \frac{1}{z_s}\int_0^{z_s} \rho_z dz, \tag{1}$$

where z_s is the depth of the snowpack and ρ_z is the density at a given depth.

[11] The flux model that we used was originally derived from the general biophysical principles governing diffusion through porous media [see *Millington*, 1959; *Millington and Shearer*, 1971]. On theoretical grounds, diffusion through a porous medium can be defined according to

$$\mathrm{F_j} = \mathrm{D_j}\,\theta\,\tau\frac{\partial \overline{\mathrm{c}}_\mathrm{j}}{\partial z}, \tag{2}$$

where F_j is the flux rate for scalar j, D_j is the diffusion coefficient in air, θ is porosity, τ is tortuosity, and $\overline{c}_j$ is time-averaged concentration. Thus, a diffusion transfer function can be defined that is dependent on the product among D_j, θ, and τ. The value for D_j for the diffusion of CO_2 through air at 0°C was assumed to be 0.139 $cm^2\ s^{-1}$. Values for θ were calculated as a function of snow density (ρ) according to: $\theta = 1 - (\rho/973\ kg\ m^{-3})$, where 973 $kg\ m^{-3}$ is the density of ice [*Hubbard et al.*, 2005]. Tortuosity is a function of snow particle size, sorting and packing. Theoretical models of pore space distribution [*Millington*, 1959; *Millington and Shearer*, 1971], and empirical measurements with various porous media have shown universal convergence toward a

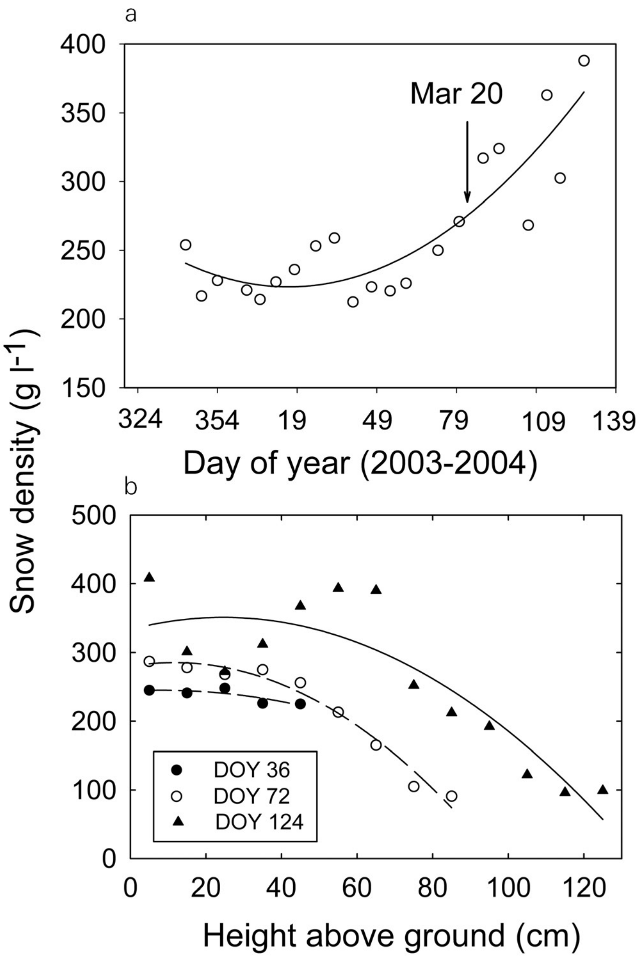

Figure 1. (a) Change in snow density as a function of date. The line represents the best-fit, second-order polynomial equation ($y = ax^2 + bx + c$; a = 0.0115, b = −1.30, c = 260.3, $r^2 = 0.78$, $P < 0.0001$). (b) Changes in snow density as a function of depth in the snowpack on three representative dates. The line for each date represents the best-fit, second-order polynomial equation ($y = ax^2 + bx + c$) (DOY 124; a = −0.0292; b = 1.439, c = 333.491, $r^2 = 0.78$) (DOY 72; a = −0.0391; b = 0.9028, c = 280.016, $r^2 = 0.97$) (DOY 36; a = −0.0164; b = 0.2714, c = 243.77, $r^2 = 0.73$).

relationship that is bounded by $\tau = \theta^{2/3}$ to $\tau = \theta^{1/3}$ [*Millington*, 1959; *Millington and Shearer*, 1971; *Striegl and Ishii*, 1989]. We used the relationship of $\tau = \theta^{1/3}$ as has been used in past studies [*Hubbard et al.*, 2005]. Equation (2) carries the assumption that CO_2 fluxes in the horizontal coordinates are negligible. It is likely that some CO_2 diffuses laterally through the snowpack as there is a measurable [CO_2] gradient from open areas between trees to areas next to trees. However, this gradient is typically smaller (15–27% difference in [CO_2] between open spaces and trees across a distance of 1.5–5 m) than the vertical gradient (41–78% difference in [CO_2] between the soil surface and the atmosphere across a distance of 0.1–1.5 m). Errors in our model due to the assumption of negligible horizontal transport are greatest for sites next to trees, where the horizontal path between the chamber and the atmosphere next to the tree bole is short.

4. Results

[12] Snow density remained relatively constant at 200–250 g H_2O L^{-1} between 20 November, the date when the snow first completely covered the surface chambers, and 20 March, the date when unseasonably warm temperatures triggered the first seasonal melt event (Figure 1a). (The week of 20 March was characterized by a mean air temperature of 2.7°C, which was higher than the mean temperature of −2.1 ± 0.8°C observed for the same week during the previous five years.) After 20 March, the mean density of the snowpack increased to a seasonal maximum of 385 g L^{-1} on 6 May. Snow density within the vertical profile of the snowpack varied in nonlinear fashion on any given date (Figure 1b). Prior to the 20 March melt event, snow density varied continuously from higher densities deeper in the snowpack to lower densities near the upper surface. After the 20 March melt event (e.g., Day 165 after 20 November 2003), we observed discontinuities in the profile of snow density. Density was highest in the lowest snow layer, followed by a decrease in density for the layers between 15 and 35 cm, a secondary increase in the layers between 35 and 65 cm, and a final continuous decrease from 65 cm to the top of the snowpack. These discontinuities probably reflect the deposition and secondary freezing of meltwater as it percolates downward, as has been reported at other sites in the Rocky Mountains [*Mast et al.*, 1998; *Swanson et al.*, 2005].

[13] Despite progressive increases in the depth of the snowpack between late November and 20 March (Figure 2a), the [CO_2] beneath the snowpack was fairly constant, ranging between 150 and 250 ppmv above ambient (Figure 2b). Coincident with the 20 March snowmelt, the [CO_2] beneath the snow began to increase, slowly at first, then sharply after a few days. There was a period of several days near the beginning of April when snow depth and density appeared to decrease (depth decreased proportionately more than density; see Figures 1a and 2a), and there was a small decrease in the [CO_2] beneath the snow (Figure 2b). Otherwise, the [CO_2] during the late spring period exhibited continuous increases until early May. The 20 March initiation of melt was clearly observed in the long-term records of daily average air temperature and soil moisture (Figure 2c). A pulse of water entered the upper layers of the soil on 20 March. The March snowmelt lasted approximately 18 days, with air temperatures fluctuating slightly above and below 0°C. Following the 18-day melt period, new snow was deposited and air temperatures decreased; although soil moisture remained relatively high through the remainder of the snow-covered season. The seasonal snow pattern of deposition and melting at the C1 study site, located 500 m from the soil chamber site, paralleled that for the chamber site, although absolute amount of snow was higher at the C1 site, probably due to local effects of canopy structure (Figure 2a). The broad range in snow depth for the chamber site shown in Figure 2a

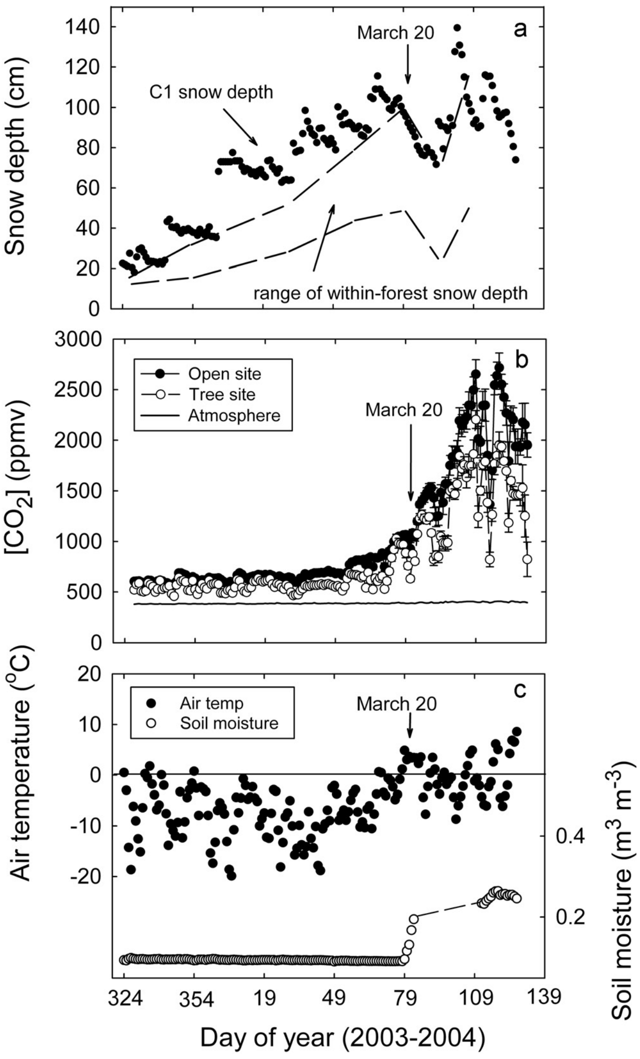

Figure 2. (a) Change in snow depth through the winter of 2003–2004 measured at the C1 Experimental Site at Niwot Ridge (an open area 500 m from the tower flux site) using an optical sensor, and at the 11 chamber sites located at the tower flux site using visual survey at 2-week intervals. For the optical data, mean daily values are shown. We only show the overall range of values for the visual survey. (b) The mean CO_2 concentration beneath the snowpack for seven chambers located in the open areas between trees and for four chambers located next to tree boles. The mean CO_2 concentration in the atmosphere just above the snowpack is also shown. Points represent the mean ± S.E., except for the atmospheric values where the trend is shown with a single line. (c) The mean daily air temperature and mean daily volumetric soil moisture content through the winter of 2003–2004. During the period between 23 March and 19 April 2004 we were not able to obtain soil moisture data owing to instrument malfunction.

is attributable to the fact that our sampling scheme covered locations next to tree boles (where the snow depth was generally shallower) to open, between-tree locations (where the snow depth was deeper).

[14] The daily mean air temperature, measured above the snowpack (at 2 m height), varied by approximately 25°C, with a high near 5°C and a low near −20°C (Figure 3a). The soil temperature at 0–10 cm varied as a function of air temperature, but with the total variation occurring over a considerably narrower range; soil temperatures varied over a total range of 2.5°C (a factor of 10 lower than the variation in air temperature), ranging from a high of approximately 0.1°C to a low of approximately −2.4°C. Soil temperatures remained at or below 0°C until the middle of April, when soil temperature remained relatively constant (at approximately 0.15°C), irrespective of air temperature; this coincided with a second major melt event. When the daily mean R_s was expressed as a function of air temperature (at 2 m) a weak, but significant, exponential relationship could be described (Figure 2b). Variation in air temperature only explained 9% of the variance in R_s. The first-order temperature coefficient (R_T; analogous to the Q_{10} used in metabolic studies) for the response of R_s to air temperature was 1.26. When R_s was expressed as a function of soil temperature measured at the soil chambers, a stronger exponential relationship could be described; in this case, 67% of the variance in R_s could be explained by variation in soil temperature. The value of R_T for the case of soil temperature was extremely high, at 5.76×10^5. Once again, it should be emphasized that the values for R_T reflect temperature dependence across the entire season, which is fundamentally different than the instantaneous timescale traditionally used for calculating the Q_{10}.

[15] Soil temperature was lower for the chambers located next to tree boles, compared to chambers in open spaces (Figure 4a). Calculated R_s decreased through the autumn and into the middle of winter, followed by a sharp increase following the 20 March snowmelt (Figure 4b). The total seasonal cumulative CO_2 loss (calculated as the sum of the daily totals) was 2.69 mol m^{-2} for tree sites and 4.03 mol m^{-2} for open sites. The seasonal flux calculated in Figure 4b represents the steady state diffusion flux, which carries the assumption of no change in CO_2 storage within the snowpack. We did not have the potential to test this assumption at each of the eleven measurement sites, although we were able to test it at the one site where we installed additional inlets (Figure 4c). Up to the 20 March snowmelt, the storage flux was of the same magnitude as the diffusion flux, but it tended to change sign frequently, such that the residual sum of the mean daily storage flux on 20 March was only 0.28 μmol m^{-2} s^{-1}. When calculated over the entire period from 24 November to 20 March, this resulted in an average contribution of the mean daily storage flux to the mean daily total CO_2 flux of only 0.0035 μmol m^{-2} s^{-1}. Following the 20 March initiation of snowmelt, the measured storage flux became large in magnitude, though still erratic in sign. The residual sum of the mean daily storage flux from 20 March to 6 May was −2.1 μmol m^{-2} s^{-1}; when calculated over the entire period, this resulted in an average contribution of the mean daily storage flux to the mean daily total CO_2 flux of −0.034 μmol m^{-2} s^{-1}.

[16] In order to determine the percentage contribution of R_s to the total ecosystem respiration rate (R_{eco}), we calculated total daily net ecosystem CO_2 exchange (24 hour total)

and compared it to the total R_s (also 24 hour total) (Figure 5). The net daily NEE was positive for all periods in this analysis, indicating net CO_2 loss to the atmosphere (i.e., net ecosystem respiration), up to the final week. During the final week, the forest exhibited net daily CO_2 uptake as reflected in the negative values in Figure 5a. When calculated for the entire winter, daily R_s was, on average, 35% of R_{eco} (Figure 5a). We hypothesized that some daytime photosynthesis could have influenced R_{eco}, even before the forest exhibited net daily CO_2 uptake; so, we repeated the analysis using only nighttime NEE data (standardized to the hours between 1800 and 0600), and the 12-hour sum of R_s (Figure 5b). Once again, we found that the daily R_s calculated for only the nighttime period was, on average, 35% of the nighttime R_{eco}.

[17] We examined two aspects of the flux model to assess possible errors in the calculation of R_s. First, we looked for evidence that "pressure pumping" caused the invasion of ambient air into the snowpack, dilution of the [CO_2] at the snow-soil interface, and underestimation of R_s. Pressure-pumping has been defined as the forced transport of ambient air into a snowpack as drag occurs when the mean or turbulent wind passes over the snow surface [*Kelley et al.*, 1968; *Sommerfeld et al.*, 1996; *Massman et al.*, 1997; *Takagi et al.*, 2005]. We looked for evidence of pressure-pumping by analyzing beneath-snow [CO_2] as a function of above-canopy wind speed in 10-day bins from 20 November 2003 through 30 March 2004 (Figure 6a). (We ceased the analysis on 30 March because the increased frequency of data gaps prevented us from fulfilling the criterion of 80% intact 30-min averaging periods.) In 12 out of 13 ten-day periods we observed evidence of pressure pumping, as the [CO_2] at the ground surface was negatively correlated with the mean wind speed ($\overline{u}$). Two representative binned periods are presented in Figure 7. Although there was variability among successive 10-day measurement bins, statistically significant negative slopes (at $P < 0.05$) characterized each set of observations. The tendency for pressure pumping to dilute the beneath-snow [CO_2] increased as the winter progressed, and the depth of the snowpack increased (Figure 6a). We used the y intercept of the correlations from each of the 10-day bins to estimate the beneath-snow [CO_2] that existed in the absence of pressure-

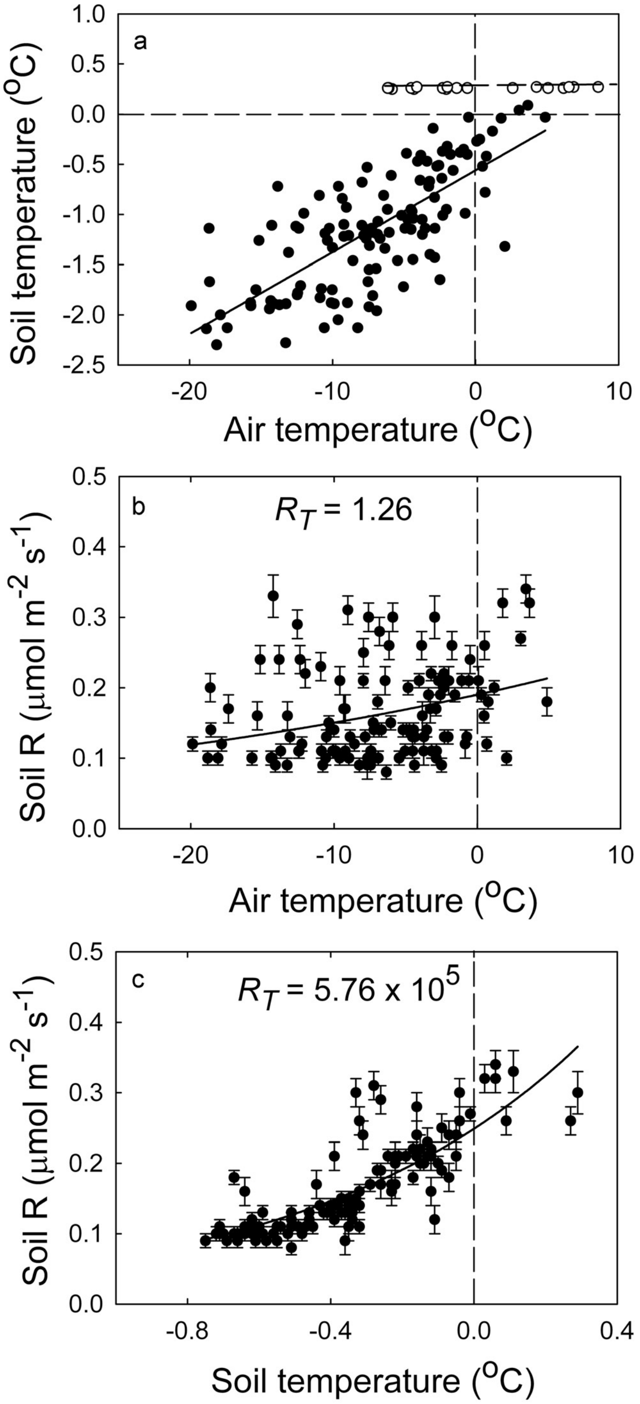

Figure 3. (a) The relation between air temperature above the snowpack and soil temperature beneath the snowpack. Solid circles indicate data collected prior to isothermality in the snowpack and the initiation of snowmelt. Open circles indicate data collected after the initiation of snowmelt on 20 March. The correlation between the two variables was significant for the presnowmelt data: $y = 0.082x - 0.56$; $r^2 = 0.54$; $F = 140.7$; $p < 0.0001$. (b) The relation between air temperature and beneath-snow respiration rate (R_s). The line describes the relation between the two variables according to: $y = a \exp^{bx}$; a = 0.190; b = 0.024; $R^2 = 0.09$; F = 12.18; p = 0.0007. (c) The relation between soil temperature and R_s. The line describes the relation between the two variables according to: $y = a \exp^{bx}$; a = 0.249; b = 1.326; $R^2 = 0.67$; F = 246.28; $p < 0.0001$. Values for R_s in B and C represent mean ± S.E. (n = 11). The term R_T represents the first-order exponential temperature coefficient, analogous to the Q_{10}. Air and soil temperature for A and B were taken from a site near the main AmeriFlux tower where both air and soil temperature are measured and represent data from the primary AmeriFlux database. Soil temperature data for C were taken as the mean of soil temperature probes located next to each of the 11 soil chambers and include both sites in the open and next to trees.

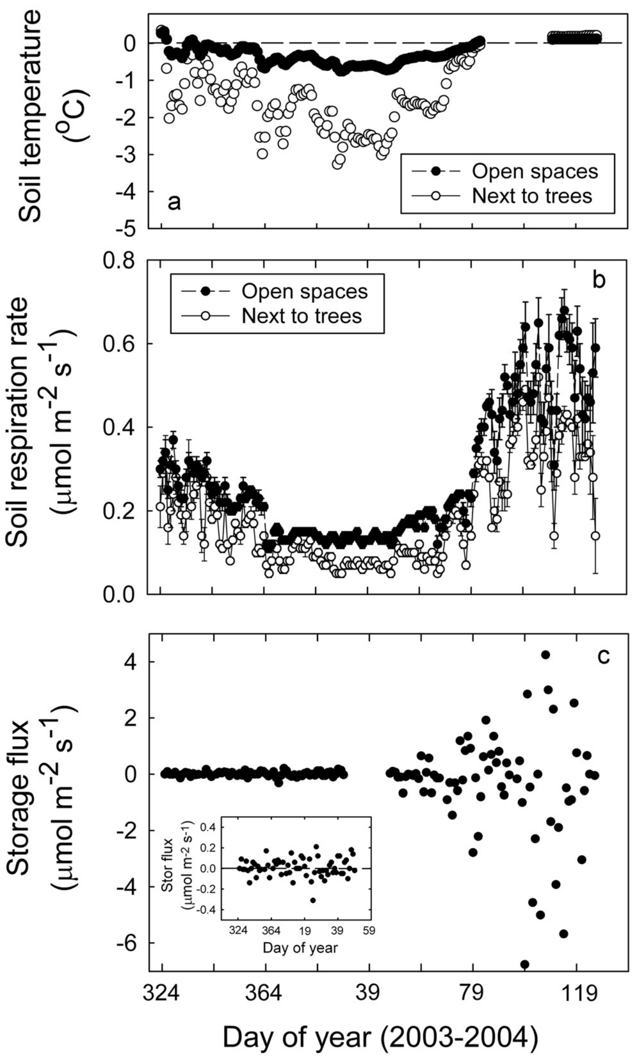

Figure 4. (a) Seasonal pattern of soil temperature as a function of date. Values are the mean (n = 7 for the open sites and n = 4 for the tree sites). (b) Calculated R_s as a function of date. Values are mean ± S.E. (n = 7 for the open sites and n = 4 for the tree sites). (c) The calculated storage flux of CO_2 in the snowpack as a function of date. The inset shows an expanded version of the storage flux for the "premelt phase."

pumping (Figure 6b). Compared to the observed mean [CO_2] in each 10-day bin, the [CO_2] in the absence of pressure pumping increased by 0.9 to 7.2%, with an overall mean of 3.0% (S.E. = 0.66%). We observed similar trends in [CO_2] at heights other than 0 cm, as a function of $\bar{u}$, although the variance in the data was too great to discern depth-dependent differences in the degree of pressure pumping.

[18] In a second test of the modeling procedures, we examined the accuracy of the model with regard to predicting the vertical profile of the snowpack [CO_2]. In past studies, nonlinearities in the [CO_2] gradient have been resolved by choosing a portion of the gradient that approaches linearity and is characterized by relatively constant snow density [e.g., *Mast et al.*, 1998], or using numerical approaches to adjust the gradient for depth-dependent changes in snow density [e.g., *Ishii et al.*, 1989]. We used an alternative approach. We modeled the vertical profile in [CO_2] using calculated R_s and observed snow densities, and compared it to the observed [CO_2] profile at the one site where we had access to multiple inlets. We reasoned that the mismatch between these profiles would reflect error in the model's ability to predict R_s from the two-point concentration gradient, or the transfer of snow density information into diffusive resistance. In Figure 8, the "modeled" values reflect the expected [CO_2] profile using observed values of snow density and the steady state assumption of constant flux across the snowpack. The "no wind observed" values reflect the mean [CO_2] obtained from the *y* intercept of 10-day bins of the relationship between [CO_2] and above-snow wind speed.

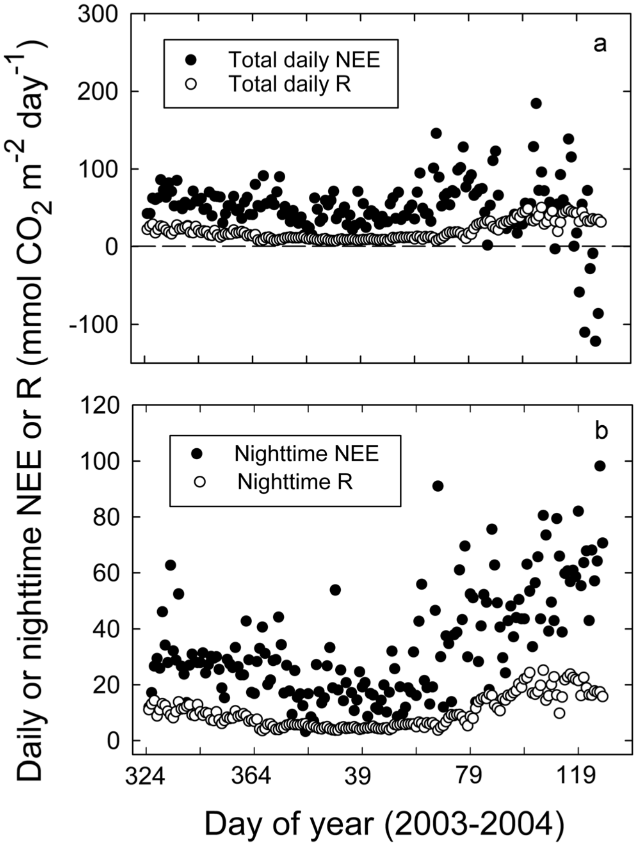

Figure 5. (a) Total daily ecosystem NEE and total daily beneath-snow soil respiration rates during the winter months of 2003–2004. (b) Nighttime NEE and nighttime beneath-snow soil respiration rates during the winter months of 2003–2004. The negative values late in the season for the total daily NEE show the influence of photosynthesis as the growing season was initiated.

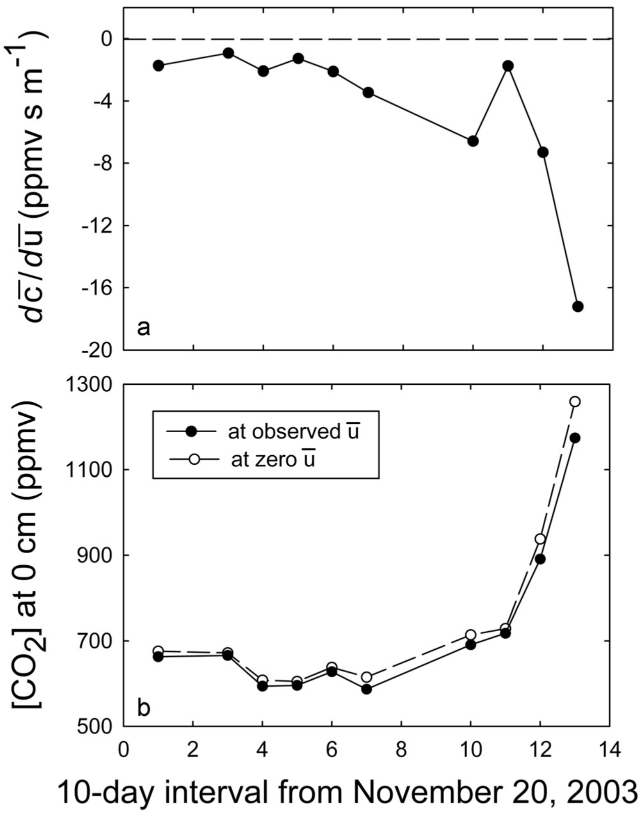

Figure 6. (a) The linear slope of the relationship between the [CO$_2$] beneath the snowpack and the mean wind speed (ū) above the canopy (at 21.5 m height) for 10-day binned data collected between 20 November 2003 and 30 March 2004. Data for each binned period were the 30-min means of both [CO$_2$] and ū for the entire period, except for gaps due to calibration periods or instrument malfunction. We only used bin periods in which at least 80% of the 30-min averaging periods were intact, which required us to drop three of the 10-day bins from the analysis (bins 2, 8 and 9) and all bins after 30 March. All slopes were significantly different from 0 at $P < 0.05$ (from ANOVA), and negative in sign. (b) The mean observed [CO$_2$] for each 10-day bin and the [CO$_2$] taken as the *y* intercept of the regressions for each bin. The *y* intercept value represents the [CO$_2$] at ū = 0, and thus in the absence of pressure pumping.

When the modeled and observed [CO$_2$] were integrated across the vertical profile, we estimated 35% and 32% overestimates in the modeled values for the periods 0–76 days and 77–135 days after 20 November, respectively.

5. Discussion

[19] Our observations support a number of past studies which have shown winter carbon cycling beneath the snowpack of high-elevation ecosystems to be active and significant to the determination of local carbon budgets [*Brooks et al.*, 1996; *Lipson et al.*, 2000; *Brooks et al.*, 2005; *Schadt et al.*, 2003; *Hirano*, 2005; *Hubbard et al.*, 2005; *Monson et al.*, 2005, 2006]. Within the assumptions of our diffusive flux model, R$_s$ was influenced by seasonal changes in snow depth and density, the timing of snowmelt, and the presence of an active soil microbial biomass. We interpret our observations to indicate two distinct phases, controlled by different factors, in the seasonal response of R$_s$. The "premelt phase" was reflected in the observations from 20 November to 20 March. During this phase, the beneath-snow [CO$_2$] increased (to approximately 10% of the total seasonal increase), along with an approximate fivefold increase in snow depth. The fact that the [CO$_2$] increased at all during this period, in the face of decreasing soil temperature, reflects the importance of the increase in

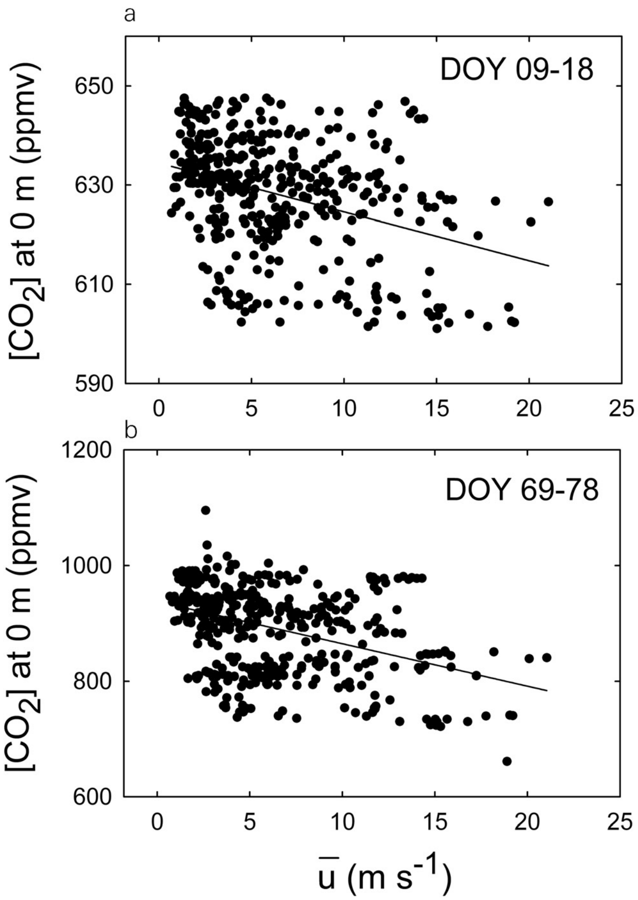

Figure 7. Two representative regressions illustrating the relationship between the [CO$_2$] beneath the snowpack and the mean wind speed (ū) above the canopy (at 21.5 m height). The periods were chosen to illustrate a 10-day period (a) early in the winter and (b) late in the winter. Note the higher beneath-snow [CO$_2$] for the late-winter period. The linear relationships are described by $y = mx + b$, with the relevant coefficients being $m = -2.11$, $b = 637.9$ ($R^2 = 0.29$; $F = 163.61$; $P < 0.001$) for the DOY 09–18 data, and $m = -7.30$, $b = 937.6$ ($R^2 = 0.14$, $F = 65.81$, $P < 0.0001$) for the DOY 69–78 data. Each point represents 30-min means of both [CO$_2$] and ū for the entire period, except for gaps due to calibration periods or instrument malfunction.

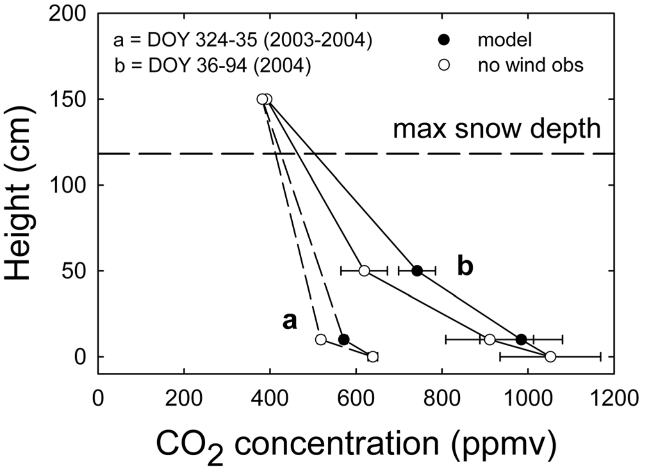

Figure 8. The modeled and observed (with no wind) vertical profiles of the mean [CO_2] for the period between 20 November 2003 and 5 February 2004 (when snow depth dictated that two heights in the profile could be used), and between 5 February 2004 and 6 May 2004 (when three heights could be used). The observed values were taken as the *y* intercept of the binned analyses depicted in Figures 6 and 7. Values are mean ± S.E. for all days in the indicated intervals.

snow depth and concomitant increase in diffusive resistance. During this period, declining soil temperature and increasing snow depth appear to compensate for each other, causing the [CO_2] to increase, despite declining R_s, but not to increase as much as predicted by the increase in snow depth alone. The "postmelt phase" was reflected in the observations from 20 March to 6 May. During this phase, we conclude that R_s was controlled by soil moisture and soil temperature. To reach this conclusion, we first had to acknowledge, and then analyze, the change in snow structure that accompanied the initiation of snowmelt. With the onset of the 20 March melt event, snow density increased (Figure 1). The formation of high-density snow or ice lenses in a snowpack can impede the upward diffusion of respired CO_2 [*Winston et al.*, 1995; *Mast et al.*, 1998; *Swanson et al.*, 2005]. Thus our initial inclination was to conclude that the postmelt build-up of CO_2 in the snowpack (Figure 2b) was due to the accompanying increase in snow density. We note, however, that in addition to causing an increase in snow density, the 20 March melt episode caused liquid water to be delivered to the underlying soil (Figure 2c). The melt-induced increase in soil moisture, likely caused an increase R_s due to the increased activity of soil microbes. The question we asked is: can the increase in snow density alone account for the observed increase in [CO_2], or must we invoke changes in R_s as a contributing cause. At steady state, a 32% increase in snow density, as occurred after 20 March, should cause a 53% increase in the [CO_2] at the base of the snowpack if R_s and snow depth remain constant (calculated using equation (2)). In reality, the depth of snowpack decreased by 25% following 20 March. When we combined this decrease with the observed 32% increase in snow density, and started the analysis from the CO_2 concentration that existed beneath the snowpack immediately prior to 20 March, we predicted that the beneath-snow [CO_2] should have decreased by 7% during the melt phase. During the 3 weeks after 20 March, however, we observed a 131% increase in the beneath-snow [CO_2]. The large increase in beneath-snow [CO_2] cannot be explained by the increase in snow density. Rather, the large increase must be due to higher rates of R_s. This led us to the conclusion that the effects of soil moisture and soil temperature on microbial respiration are more important than the effects of snowpack structure on the postmelt build-up of [CO_2].

[20] *Hirano* [2005] also observed strong dependence of R_s on soil moisture during the postmelt phase in a snowpack in Japan. He concluded, however, that this response was not a direct response of R_s to moisture, but rather an indirect response to the leaching of carbon substrates that had accumulated in the litter layer during the winter. The observations that he used to reject a direct response to soil moisture included the fact that the soil at his site was relatively moist during the premelt period, yet R_s was low. At the Niwot Ridge site, the soils are frozen during the winter and moisture availability is relatively low. There is a clear point of transition in the moisture and temperature condition of the soil after the initiation of snowmelt (Figure 2c), and so we cannot rule out a direct response of the soil to soil moisture, as was done in the Japanese study. It might be true that along with the initial pulse of meltwater there is an increase in carbon substrate availability. In fact, we have shown in a previous study that there is a large pulse of sucrose that enters the upper layers of the soil during the winter [*Scott-Denton et al.*, 2006]; this pulse could be dispersed during snowmelt. However, at the present time, we cannot distinguish between moisture and substrate effects on the stimulation of R_s. In a related subalpine ecosystem, *Musselman et al.* [2005] observed a large increase in subsnow [CO_2] at the onset of snowmelt, similar to what we observed in the current study, indicating general control by soil moisture over R_s at this critical transition between winter and spring.

[21] The one factor that appeared to influence R_s during both seasonal phases was temperature. Our observations showed that variations in air temperature above the snowpack had the potential to affect R_s beneath the snowpack (Figures 3a and 3b). The overlying snow did not completely buffer soil temperature from day-to-day changes in air temperature; on average, a 10°C change in air temperature translated to a 0.8°C change in soil temperature. Once snowmelt had commenced with regularity, however, soil surface temperature became completely uncoupled from air temperature, remaining slightly above 0°C. Although the coupled, but muted, response of soil temperature to changes in air temperature, at least for the premelt phase, means that it is possible to predict R_s as a function of air temperature, the variance in R_s was poorly explained by air temperature alone (Figure 3b). Variation in soil temperature near the measurement chambers explained considerably more of the variance in R_s (Figure 3c). In fact, R_s was extremely sensitive to small changes in soil temperature, particularly

when temperatures were less than 0°C. The first-order temperature coefficient for R_s as a function of soil temperature was unprecedented at 5.76×10^5. High temperature coefficients have been reported previously for R_s measured at subzero temperatures in laboratory studies [e.g., *Mikan et al.*, 2002], and they have been explained by small changes in the fraction of liquid water as temperature varies below 0°C [e.g., *Patterson and Smith*, 1981]. Small increases or decreases in the thickness of liquid water films on soil particles could influence substrate diffusion rates or microbial growth rates that, in turn, could influence R_s on the timescale of days-to-weeks. In support of the coupled influences of temperature and soil moisture, we observed the strongest response of R_s to changes in soil temperature following 20 March, when meltwater appeared in the soil and R_s increased sharply (Figure 2c).

[22] We commonly observed reductions in the [CO_2] beneath the snowpack during periods of high wind (Figures 6 and 7). We interpret these reductions as evidence of "pressure pumping" whereby quasistatic pressure fields are created in the snowpack as the wind blows across the surface [e.g., *Massman et al.*, 1995, 1997]. Some past studies have revealed these pressure effects to cause mixing of air within snowpacks, and potentially influence short-term gas fluxes. Takagi and coworkers [*Takagi et al.*, 2005] observed that wind-induced changes in the CO_2 storage of the snowpack, combined with the diffusion flux, explained a higher fraction of the 30-min averaged total CO_2 flux, than diffusion alone. Using a 3-D transport model, however, Massman and coworkers [*Massman et al.*, 1997] showed that the short-term influence of pressure-pumping tends to be averaged out over longer time intervals. We calculated the mean daily storage flux at Niwot Ridge using the one site where we had access to within-snowpack measurements of [CO_2] (Figure 4c). The storage flux often varied from day-to-day between CO_2 loss and gain and, for the period up to 20 March, the net storage flux approached zero. Following 20 March, storage fluxes were greater in magnitude, presumably because R_s was also greater in magnitude. The negative sign to the storage flux during the post-melt period is consistent with higher net CO_2 storage in the snowpack. Even during this postmelt phase, however, the positive and negative storage fluxes tended to compensate for each other over time, and the residual flux at the end of the period only accounted for 11% of the average diffusion flux. Thus the diffusion flux was more important than the storage flux in determining the seasonally integrated R_s.

[23] Beyond forcing high-CO_2 air out of the snowpack, the infusion of ambient air during pressure-pumping has the potential to dilute the [CO_2] gradient and thus reduce R_s. We assessed the degree to which pressure pumping influences the 30-min, time-averaged R_s as the difference in [CO_2] in the presence of both diffusion and pressure pumping (the actual observed CO_2 concentration) and the absence of pressure pumping (the *y* intercept of the regressions of CO_2 concentration versus wind speed). Dilution of the [CO_2] gradient should influence R_s in linear, proportional fashion. From this analysis, we concluded that, on average, the [CO_2] beneath the snowpack was reduced by 3% owing to winds at the site; this is a relatively small effect. Wind-dependent dilution of the beneath-snow [CO_2] was highest during mid to late March, when the snowpack was deepest. This was also the time when the beneath-snow [CO_2] was highest among those bins used in the analysis (Figure 6b), and the relative increase in the importance of pressure-pumping could be a consequence of the higher absolute [CO_2].

[24] We tested the accuracy of our diffusional flux model by assessing its ability to predict the vertical [CO_2] gradient through the snowpack. Using data from either early or late in the winter, we estimated a 30–35% error in the model's predictions (Figure 8). The principal sources for error in this test of the model are the measurement of snow density, the translation of snow density into a diffusive transfer coefficient, and the estimation of R_s. The snow densities that we reported are similar to those reported from past studies in this ecosystem and the methods used to measure snow density carry relatively low potential for error (i.e., the measurement of snow mass per unit volume is relatively straightforward). There might be some error in estimating R_s with a two-point, linear model of the [CO_2] gradient, rather than a multiple-point, non-linear model. We checked this possible source of error by comparing estimates of R_s using two-point, three-point and four-point concentration gradients at the one site where we had multiple sample inlets. In no case, through the entire season, did we detect a difference of more than 10% between the flux estimated from a linearized profile versus the actual profile (data not shown). It is our conclusion that the greatest source of error in our estimate of the [CO_2] gradient is the accuracy of determining the diffusive resistance from the snow density measurement. The translation of snow density into snow porosity and tortuosity, and the use of the product among porosity, tortuosity and diffusivity to represent the diffusive resistance, do not appear to be entirely adequate. In this case, the error appears to work in the direction of decreasing the estimated R_s, compared to the true flux. That is, the actual [CO_2] gradient is steeper than that predicted by the flux model.

[25] One of the principal aims of this study was to determine the percentage of R_{eco} that can be accounted for by R_s. On average, the cumulative R_s (for the entire season) was ~3 mol m^{-2}, which represents 35% of the total wintertime R_{eco}. This estimate reflects the simple averaging of all eleven beneath-snow chambers, and is not weighted for the relative cover of "open" versus "near-tree" sites. As noted above, uncertainty exists in this estimate; the true value for R_s could be in the range of 30–35% higher than that predicted by the model. Thus our best estimate of the contribution of R_s to R_{eco} is 35–48%. The highest values for R_s that we observed were approximately 10–14% the rates observed during the middle of the summer [*Scott-Denton et al.*, 2003], and the cumulative R_s for the 2003–2004 winter season was 7–10% the cumulative ecosystem respiration [see *Monson et al.*, 2005]. Thus, while the winter soil CO_2 flux is small relative to growing season CO_2 fluxes, it is persistent and a significant component of the annual carbon budget.

[26] The carbon loss from beneath the snowpack at Niwot Ridge is less than that observed for a mountain snowpack in Japan [*Hirano*, 2005]. In that study, $\sim$6 mol m^{-2} was lost from R_s, and that was with only 4 months of snow cover, compared to $\sim$3 mol m^{-2} lost in 5 months of snow cover from the Niwot Ridge site. The site in Japan is at a lower elevation with a higher annual temperature (6.5°C at the site in Japan versus 1.5°C at Niwot Ridge). Additionally, the soils do not freeze during the winter at the Japanese site, as they do at the Niwot Ridge site. In our study, the range of daily R_s was 7.4–47.6 mmol C m^{-2} d^{-1}, with a seasonal average of 17.7 mmol C m^{-2} d^{-1}. These values are lower than the average of 42.3 mmol C m^{-2} d^{-1}, which was observed for dry soils in a different subalpine forest in the Rocky Mountains of Colorado [*Mast et al.*, 1998], and $\sim$50 mmol C m^{-2} d^{-1} from winter forest soils in a subalpine site in the Snowy Range of Wyoming [*Sommerfeld et al.*, 1996]. At the Niwot Ridge site, the cumulative observed R_s for the 5-month snow-covered period represents 16–22% of the net CO_2 uptake observed for the photosynthetic tissues of the forest during the growing season [*Monson et al.*, 2005]. Once again, this is slightly less than the value of 25% estimated for the subalpine forest in the Snowy Range of Wyoming [*Sommerfeld et al.*, 1996].

[27] Given our observations, we must conclude that the greatest fraction of wintertime R_e originates from aboveground portions of the forest. This conclusion may be surprising at first because the trees at the site have been shown to be photosynthetically inactive during the winter [*Monson et al.*, 2005], and aboveground temperatures are extremely cold (Figure 3b). However, the wintertime aboveground biomass is probably much larger than the belowground biomass. Although the anchoring tree roots at this site can be woody and deep, the fine root biomass is relatively sparse and shallow. Soils at the site are shallow, which restricts the depth occupied by soil microbial biomass. The aboveground tissues are evergreen and thus, despite low photosynthetic rates, they require some degree of maintenance respiration. Past measurements of needle respiration in the trees at our site during the late winter, before the snow had completely melted revealed rates between 0.1 and 0.3 μmol m^{-2} s^{-1}; albeit these rates were determined immediately following the spring upregulation of photosynthetic capacity in the forest [*Huxman et al.*, 2003]. If we take the seasonally averaged nighttime NEE for the winter of 2003–2004, which was measured as 34 mmol m^{-2} d^{-1} (taken from the data in Figure 5), and assume that 60% is due to aboveground respiration, all of which is needles (a conservative assumption given that some unknown fraction of the respiration will be from woody tissues), with an average leaf area index of 4.2 [see *Monson et al.*, 2002], we estimate a winter-averaged needle respiration rate of 0.11 μmol m^{-2} s^{-1}. This is admittedly a rough calculation, and it is likely too high because we did not account for woody respiration during the winter. However, it at least informs us that the residual aboveground respiration during the winter, after accounting for soil respiration, is within reasonable bounds compared to our past measurements on the needles.

[28] We have not conducted an analysis of the percentage of R_{eco} represented by R_s during the snow-free months. However, on the basis of extensive soil chamber measurements made over three growing seasons [*Scott-Denton et al.*, 2003] and comparisons to nighttime NEE measurements made over two growing seasons [*Monson et al.*, 2002], we estimate that approximately 70% of the snow-free R_{eco} is represented by R_s. In a coniferous forest in Maine, the midsummer percentage of R_{eco} represented by R_s is 65% [*Davidson et al.*, 2005], a value which is not too different from that for other temperate and northern-latitude forests [*Goulden et al.*, 1996b; *Law et al.*, 1999; *Lavinge et al.*, 1997]. Thus the estimate of R_s/R_{eco} that we have obtained for the snow-covered season is lower than that typically observed during the growing season.

[29] Monson and coworkers [*Monson et al.*, 2006] recently reported that interannual variation in winter R_{eco} is sensitive to interannual variation in late-winter snow depth; years with high amounts of late-winter snow, have higher soil temperatures and higher rates of R_{eco}, compared to years with lower amounts of late-winter snow and lower soil temperatures. The results of our current analysis indicate that the interannual influence of snow depth occurs despite the fact that R_s only accounts for a modest fraction of R_{eco}. We assume that this is in part due to the high temperature sensitivity of the winter microbial biomass. The microbial communities that exist beneath the snow are capable of exponential growth and substrate-induced growth respiration at temperatures far lower than those in summertime soils, and they appear to have uniquely low growth yields in response to added substrate [*Monson et al.*, 2006]. Our continuing studies at the Niwot Ridge AmeriFlux site are aimed at understanding the unique qualities of the beneath-snow microbial communities, with a special emphasis on why these organisms confer such a high level of temperature sensitivity to the winter beneath-snow respiration rate.

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