

The Temporal Dynamics of Carbon Dioxide under Snow in a High Elevation Rocky Mountain Subalpine Forest and Meadow

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Abstract

Carbon dioxide (CO₂) concentration under snow was examined through two winter seasons at a 3100 m elevation subalpine site in the Snowy Range of Wyoming. CO₂ was monitored every half hour at the soil/snow interface, and at about –25 cm soil depth the second year, in a meadow and in an adjacent forest. CO₂ under snow in the meadow was significantly higher than that in the forest. CO₂ at –25 cm depth in the soil was significantly higher than soil surface CO₂. The CO₂ under snow increased rapidly as snow melted and snowmelt began in the spring. CO₂ concentration under snow depended primarily on amount occurring during the previous 24 or 48 h. However, CO₂ concentration was related to snow depth and soil temperature, and indirectly to several seasonal environmental factors, especially solar radiation. Solar radiation, snow depth, and CO₂ under snow all increase concurrently as the winter season progresses. CO₂ flux was consistently higher in the meadow than in the forest and increased in late winter for both sites. Snow covered subalpine meadows and forests contribute considerable amounts of CO₂ to the atmosphere in the winter.

Introduction

Research has shown that biological production of CO₂ under snow in winter in temperate regions can be significant, and a major contributor to the global CO₂ balance (Sommerfeld et al., 1993; Koizumi et al., 1996; Zimov et al., 1996; Welker et al., 2000; Mariko et al., 2000). Little is known about the temporal or spatial variability of this CO₂.

Thermal insulation of deep snow can result in thawing soils and microbial and tree root respiration throughout the winter (Mariko et al., 2000). Zimov et al. (1996) suggest that this respiration produces heat sufficient to warm soils to above freezing. Thawing soils can result in rapid changes in CO₂ efflux (Skogland et al., 1988; Elberling, 2003; Elberling and Brandt, 2003). Because of changes in available nitrogen, populations of soil surface microorganisms can change throughout the winter causing subsequent changes in respiration and resultant changes in soil surface CO₂ (Brooks et al., 1993).

Data from the Glacier Lakes Ecosystem Experiments Site (GLEES) ecosystem, an alpine/subalpine ecosystem at 3180 m elevation in the Snowy Range of southeastern Wyoming, indicates that soil surface temperature is near 0°C after the snowpack accumulates, light is extremely low under the snowpack occurring at this site (typically 1–2 m deep), and soil moisture is generally low. Since the snowpack temperature is not isothermal and does not melt before early spring (May), there is little reason to expect much change in water or nutrient movement to the soil at this site. Thus, it is assumed that with constant light, moisture, nutrient input, and temperature, CO₂ under snow should be relatively constant throughout the snow-covered period, particularly under deep snow. Ice lenses do occasionally and somewhat randomly form in the snow from surface heating as the snowpack accumulates, limiting the CO₂ diffusion to the surface and thus affecting CO₂ concentration under snow. Also, there is evidence that soil mineralization, nitrification, and ammonification occur under snowpacks (Brooks et al., 1997; Williams et al., 1996).

Wind and atmospheric pressure can cause changes in the gradient of CO₂ from the soil/snowpack interface to the snowpack surface

(Winston et al., 1995; Massman et al., 1997; Massman et al., 2002; Albert and Shultz, 2002). The spatial and temporal dynamics of these changes and their effects on CO₂ dynamics of the soil/snowpack interface are largely unknown. These changes may be critical in quantifying the contribution of CO₂ in snow-covered terrain to the global CO₂ balance.

Snowpack characteristics differ in meadow and forests, with snow water equivalent and melt rates higher in meadows than that in adjacent forest (McCaughy and Farnes, 2001). These differences of lower density yet slower melt under canopies likely affect transfer of CO₂ to the snow surface and concentration of CO₂ under the snow at the soil surface.

Soil temperature is expected to remain relatively constant under a snowpack until snowmelt. Soil temperature had a large effect and soil moisture had little effect on forest floor CO₂ in a temperate Douglas fir forest not snow covered (Drewitt et al., 2002). CO₂ was more closely related to temperature at 5 cm than at other depths. Similarly, Hirano et al. (2003) reported topsoil CO₂ production was more closely related to temperatures at 7 cm depth than at 2, 10, or 15 cm. Mariko et al. (2000) found CO₂ flux more closely related to 3–30-cm-deep soil temperatures under snow than to soil surface temperatures. Drewitt et al. (2002) point out that soil temperature at a single depth will not identify the flux-temperature relationship of the soil profile.

Most measurements of CO₂ in winter under snow have been made from samples collected at a few sites on an infrequent basis (Sommerfeld et al., 1993; van Bochove et al., 1996; Mast et al., 1998; Jones et al., 1999; Fahnestock et al., 1999), thus these data are limited on spatial and temporal variability throughout a winter season. There have been a few more intensive observation programs. Hirano et al. (2003) monitored CO₂ at half-hour intervals from May to December, but did not indicate any snowcover at the site. CO₂ under snow was measured at daily intervals under an arctic snowpack up to 40 cm deep (Kelley et al., 1968). They found changes in CO₂ concentration throughout the season, with most change early and late in the season, and they reported a relationship of CO₂ to wind speed above the snowpack. The relationship to wind speed is likely a result of pressure

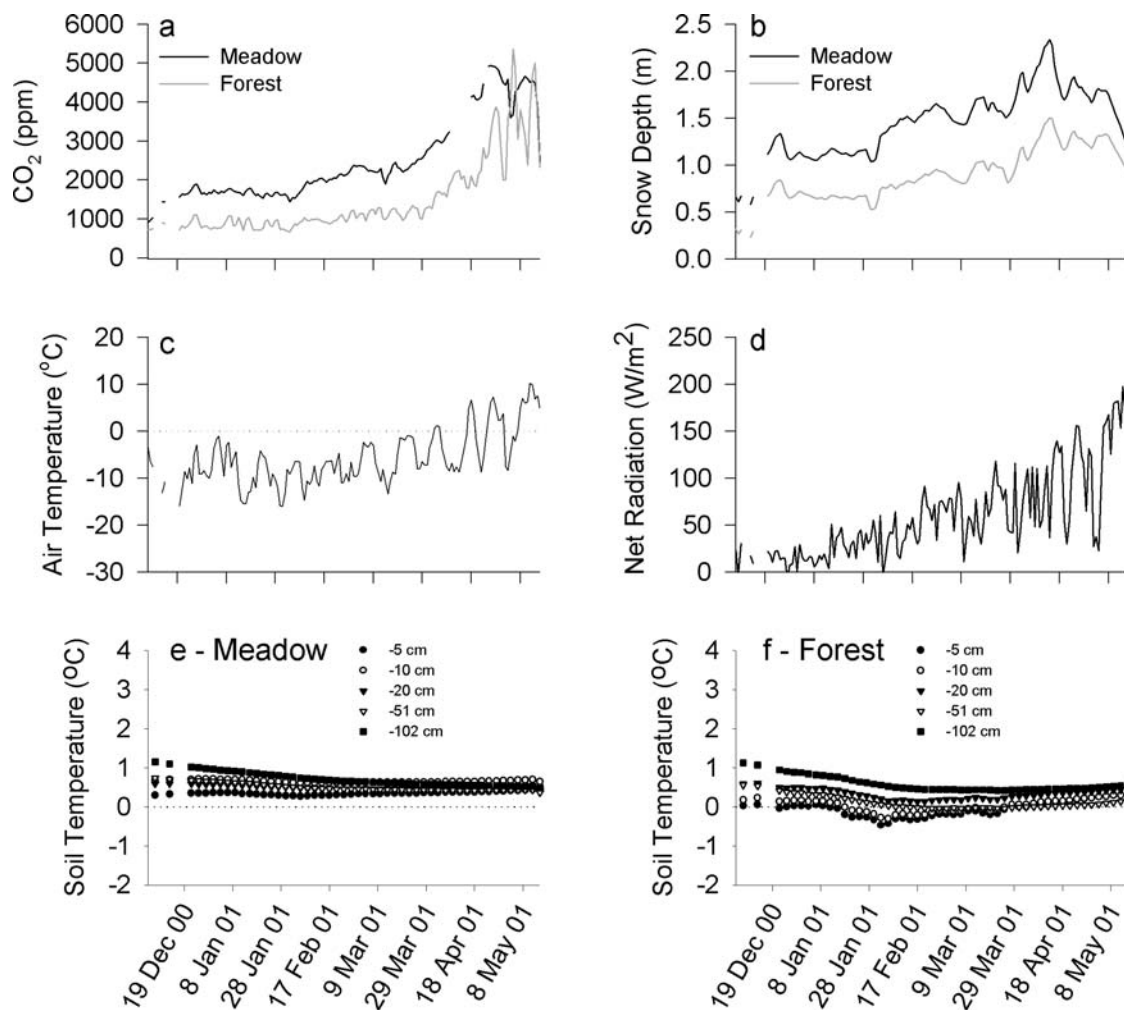


FIGURE 1. 2000–2001 winter mean daily values ($n = 48$ half-hour readings per day) for (a) CO₂ under snow, (b) snow depth, (c) air temperature, (d) net radiation, (e) meadow soil temperature, and (f) forest soil temperature. CO₂ samples were collected from +5 cm to –5 cm at the soil surface/snowpack base interface. Missing CO₂ data were due to frozen sample lines.

pumping (Massman et al., 1997). Available data suggest that there are large spatial and temporal variations in CO₂ under snow at the GLEES (Sommerfeld et al., 1996). This may be due to biological activity of roots and microorganisms in the soil. Fungal biomass in high-elevation Rocky Mountain soils reaches maximum levels in late winter (Schadt et al., 2003). Even diurnal changes in CO₂ can occur under snow in alpine environments (Welker et al., 1999).

The primary objective of this study was to examine temporal changes in carbon dioxide concentration under snow. The study intensively monitored CO₂ at an adjacent meadow and forest site throughout two winter seasons, providing data on the temporal dynamics of CO₂ under snow in these two subalpine environments. The relationship of CO₂ under snow and environmental and meteorological parameters was examined. It was expected that CO₂ at the soil/snowpack interface should increase throughout the winter season with the increasing depth of the snowpack, a physical barrier for CO₂ diffusion from the soil surface to the atmosphere. A secondary objective of this study was to provide preliminary estimates of CO₂ flux from the meadow and forest site, to examine their difference in contribution to winter-time flux.

Methods

The study was conducted during two winters (2000–2001 and 2001–2002) at the GLEES Brooklyn monitoring site at 3100 m

elevation in the Snowy Range of southeastern Wyoming (Musselman, 1994). The site is seasonally snow covered from November through May, with maximum snow accumulation generally between 1.5 and 2.5 m. Two monitoring sites were selected, a small, 50-m-diameter meadow and the adjacent closed canopy Engelmann spruce/subalpine fir forest. The two sampling sites were less than 20 m apart. Ten-cm-diameter by 1-cm-thick gas collector disks (Sommerfeld et al., 1991) were installed vertically at the soil surface (0 to –10 cm depth in year 1, +5 cm to –5 cm in year 2) in the meadow and in the forest. The trees in the forest were irregularly spaced, and the sample site was about 1 m from the base of the nearest tree. The first year two collector disks were installed 0.5 m distant from each other in the meadow and similarly in the forest. In the second year, collector disks from each site were installed 6–8 m from each other. The sample site location in the first year (and also used in year 2) was designated Meadow A and Forest A, while the second 6- to 8-m-distant site monitored in year 2 was designated Meadow B and Forest B. Also in the second year, an additional collector disk was placed vertically at –20 to –30 cm depth (10-cm disk centered at –25 cm depth) under each surface sampler. This depth was sampled to determine if soil surface and deeper soil CO₂ differed. CO₂ was monitored using sampling lines from each sampler disk for a short period of time once every half hour throughout the winter.

Sample lines 0.6-cm i.d. (0.25 inch) and 15-m (meadow) or 37-m (forest) long were installed along the ground from the collectors to an

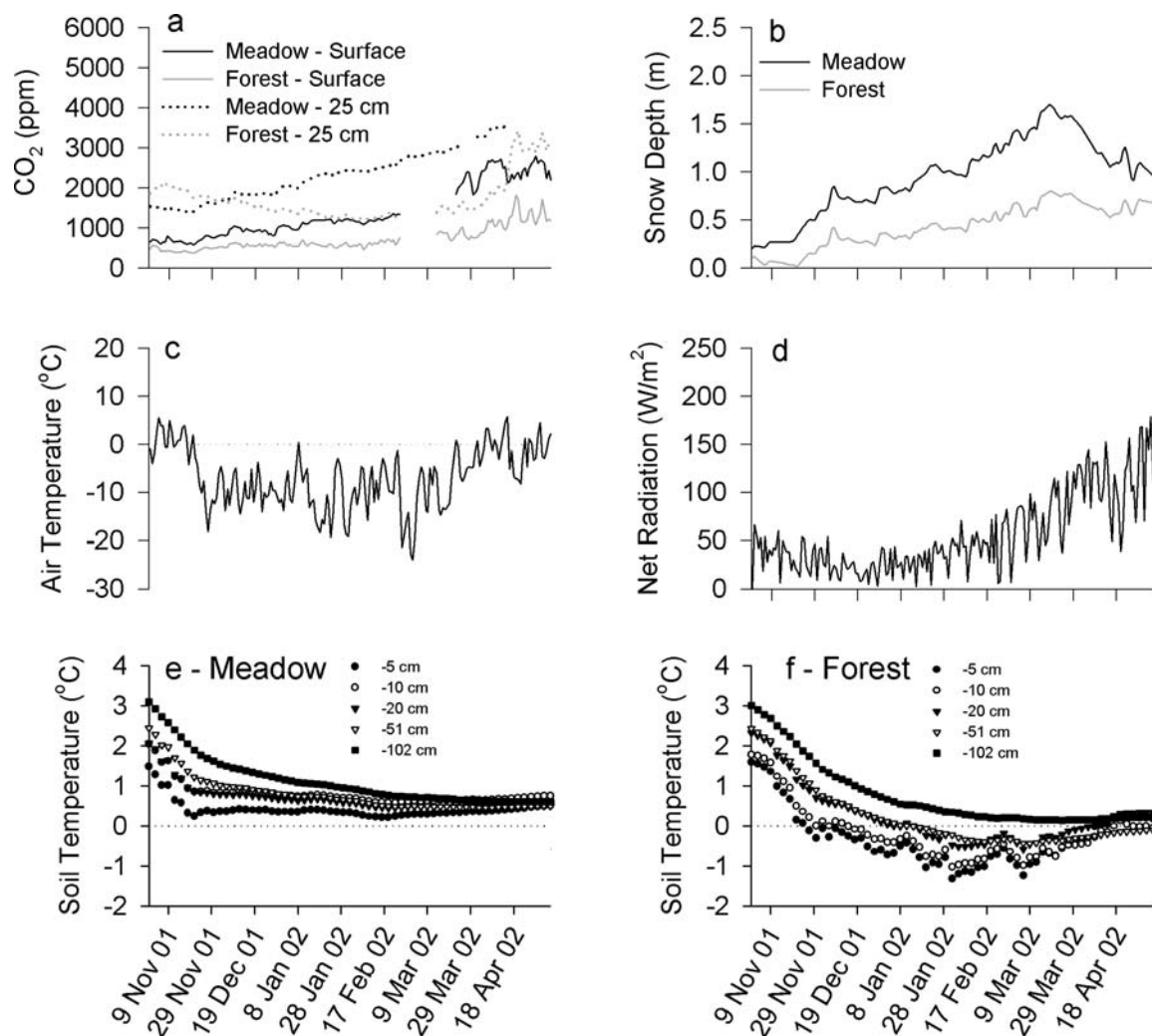


FIGURE 2. 2001–2002 winter mean daily values ($n = 48$ half-hour readings per day) for (a) CO_2 under snow, (b) snow depth, (c) air temperature, (d) net radiation, (e) meadow soil temperature, and (f) forest soil temperature. CO_2 samples were collected at the soil surface at the base of the snowpack, and at -25 cm deep underground.

instrument shelter. Air samples were collected from each disc at the beginning of every half hour throughout the season. Samples were pulled sequentially from each of the four samples discs at 8 L min^{-1} to a LiCor 6262 for CO_2 measurement. The analyzer was calibrated periodically (weekly 2001, monthly 2002) using 0 ppm and 1940 ppm CO_2 standards. The typical time to purge the line was 6 s for the meadow, and 12 s for the forest. After purging, air pulled from the soil was analyzed for about 18 s in the meadow and 12 s for the forest. Pumping times were held constant so that both the meadow and the forest had the same volume of air pulled from the soil into the line (approximately $8 \text{ L min}^{-1} \times 24 \text{ s}$, just over 3 L total volume). This maintained similar treatments of pressure gradients and recharging effects for both the forest and the meadow. Only the concentration of CO_2 associated with the initial volume contained in the disk sampler was used for analysis. After sampling, the discs were allowed to return to equilibrium until the next half-hour sampling. Given the small volume of air pulled from each disc at each sampling, it was expected that CO_2 returned to equilibrium before the next half-hour sampling period. Pumping was controlled and data were recorded using a Campbell 23X datalogger, and data were downloaded weekly. The experiment was halted when sufficient melt had occurred that water came into the lines.

Several environmental and meteorological parameters were monitored as possible covariates to compare to CO_2 under snow. Soil

temperatures were measured and recorded every 5 min at -5 , -10 , -20 , -51 , and -102 cm depth less than 5 m distance from the CO_2 monitoring sites in both the meadow and the adjacent forest. Soil temperature data indicated little change with depth, so they were averaged by depth for statistical analysis.

Meteorological data (wind speed, wind direction, air temperature, relative humidity, net radiation) were recorded at 28 m height and above the surrounding forest canopy on a tower located 15 m from the meadow site. Meteorological data, measured at 1-s and averaged at half-hour intervals, was compared to the half-hour CO_2 data.

Seasonal snow accumulation at the site typically begins in October. Snow depth was recorded every Tuesday in the meadow and forest, .05–1.0 m from the CO_2 collectors. Half-hour snow depth values were estimated using weekly measurement plus precipitation data recorded on a strip chart at a National Atmospheric Deposition Program (NADP) Belfort rain gauge located in a large meadow less than 100 m from the CO_2 monitoring site. For 2001, half-hour snow depth measurements were inferred by interpolating between the weekly measurements with a waveform related to the data from the NADP Belfort rain gage event recorder. For 2002, half-hour snow depth measurements were inferred by interpolating between the weekly snow depth readings with (1) a waveform related to the NADP Belfort rain gage data and (2) a waveform from data from a continuous snow depth recorder located on the meteorological tower 15 m from the meadow

TABLE 1

Single variable regression analysis, CO₂ under snow vs. snow depth, meteorology, and soil temperature, for meadow and forest, winter of 2000–2001. CO₂ averaged for two samples at each site. Data analyzed for the entire season. OLS = ordinary least squares.

Independent variables	Meadow				Forest			
	OLS		Autoregressive		OLS		Autoregressive	
	R ²	Pr > t	Partial R ²	Pr > t	R ²	Pr > t	Partial R ²	Pr > t
Snow depth	0.487	<0.001	0.000	0.365	0.494	<0.001	0.002	0.017
Air temperature	0.499	<0.001	0.000	0.744	0.431	<0.001	0.001	0.222
Wind speed	0.037	0.021	0.001	0.018	0.032	0.028	0.004	0.025
Net radiation	0.556	<0.001	0.001	0.045	0.479	<0.001	0.002	0.081
Atmospheric pressure	0.150	<0.001	0.000	0.609	0.144	<0.001	0.001	0.436
Ambient CO ₂	0.066	0.002	0.003	<0.001	0.038	0.016	0.006	0.005
Relative humidity	0.076	0.001	0.004	0.800	0.070	0.001	0.005	0.951
Mean soil temperature	0.289	<0.001	0.000	0.348	0.078	0.001	0.000	0.465

CO₂ site. Monitoring continued from October until snowmelt in May of each year.

CO₂ under snow data were initially analyzed independent of the environmental and meteorological covariates. Differences between replicates were first examined using paired-*t* analysis. The level of significance for all our statistical analyses is 0.05. Replicates were not significantly different in 2001. Therefore, where data was available for only one replicate, that value was used; otherwise the replicates were averaged. Significant differences existed between replicates in 2002. Data were averaged when data from both replicates were available; when only one replicate was available, the record was discarded. Data used for analysis were daily means only for days where both forest and meadow had $n > 39$ CO₂ values (out of a possible 48 half-hour values). Further paired-*t* tests compared forest to meadow sites each year and compared surface to underground CO₂ for 2002. Because data were collected at only one meadow and one forest site, results are applicable only to these specific sites.

Relationships between CO₂ and snow depth, soil temperature, and meteorological parameters were initially examined by ordinary least squares (OLS) regression, a method commonly used for this type of data. However, temporal autocorrelation in the response data reduced the validity of OLS regression. Independent of the OLS analysis, the autoregressive analysis provides information on the gradual seasonal progression of CO₂ under snow. Although OLS is commonly used in analyses, autoregressive analysis is the most valid method of analysis for these data, and the autoregressive partial R²s far more accurately represent the explanatory power of the environmental variables. Nevertheless, OLS analyses are discussed here for comparison and to illustrate the limitations of this analysis. In addition, the OLS analysis is included to understand the physical relationship between CO₂ under snow and environmental and meteorological parameters.

An autoregressive model was used which incorporated time lags of 1 and 2 days to examine change over time. Two lags were specified because the first lag term was always highly significant, the second

TABLE 2

Single variable regression analysis, CO₂ under snow vs. snow depth, meteorology, and soil temperature, for meadow and forest, winter of 2000–2001. CO₂ averaged for two samples at each site. Data analyzed separately for early and late season. OLS = ordinary least squares.

Independent variables	7 Dec 2000 to 21 Mar 2001				22 Mar 2001 to 15 May 2001			
	OLS		Autoregressive		OLS		Autoregressive	
	R ²	Pr > t	Partial R ²	Pr > t	R ²	Pr > t	Partial R ²	Pr > t
Meadow								
Snow depth	0.769	<0.001	0.000	0.340	0.017	0.379	0.002	0.280
Air temperature	0.021	0.164	0.000	0.544	0.254	<0.001	0.000	0.823
Wind speed	0.067	0.011	0.001	0.322	0.036	0.195	0.010	0.027
Net radiation	0.415	<0.001	0.001	0.319	0.163	0.005	0.003	0.195
Atmospheric pressure	0.000	0.900	0.000	0.643	0.261	<0.001	0.000	0.529
Ambient CO ₂	0.209	<0.001	0.000	0.524	0.090	0.038	0.024	<0.001
Relative humidity	0.008	0.388	0.000	0.928	0.240	0.001	0.019	0.542
Mean soil temperature	0.515	<0.001	0.004	0.001	0.354	<0.001	0.000	0.663
Independent variables	7 Dec 2000 to 31 Mar 2001				1 Apr 2001 to 15 May 2001			
	OLS		Autoregressive		OLS		Autoregressive	
	R ²	Pr > t	Partial R ²	Pr > t	R ²	Pr > t	Partial R ²	Pr > t
Forest								
Snow depth	0.427	<0.001	0.018	<0.001	0.000	0.948	0.003	0.542
Air temperature	0.061	0.010	0.000	0.784	0.171	0.004	0.015	0.159
Wind speed	0.084	0.003	0.021	0.010	0.025	0.298	0.027	0.047
Net radiation	0.329	<0.001	0.009	0.090	0.156	0.007	0.020	0.086
Atmospheric pressure	0.019	0.154	0.010	0.084	0.237	0.001	0.000	0.802
Ambient CO ₂	0.133	<0.001	0.009	0.093	0.019	0.362	0.028	0.047
Relative humidity	0.010	0.312	0.000	0.961	0.119	0.020	0.026	0.692
Mean soil temperature	0.132	<0.001	0.006	0.112	0.585	<0.001	0.091	<0.001

TABLE 3

Single variable regression analysis, CO₂ under snow vs. snow depth, meteorology, and soil temperature, for meadow and forest, winter of 2001–2002, for surface and underground (–25 cm deep) samplers. CO₂ averaged for two samples at each site. Data analyzed for the whole season, 1 November to 5 May. OLS = ordinary least squares.

Independent variable	Meadow				Forest			
	OLS		Autoregressive		OLS		Autoregressive	
	R ²	Pr > t	Partial R ²	Pr > t	R ²	Pr > t	Partial R ²	Pr > t
Surface								
Snow depth	0.541	<0.001	0.000	0.017	0.494	<0.001	0.000	0.098
Air temperature	0.107	<0.001	0.000	0.825	0.065	<0.001	0.002	0.031
Wind speed	0.002	0.623	0.002	<0.001	0.019	0.070	0.034	<0.001
Net radiation	0.650	<0.001	0.000	0.603	0.468	<0.001	0.001	0.100
Atmospheric pressure	0.001	0.672	0.000	0.885	0.006	0.298	0.000	0.367
Ambient CO ₂	0.149	<0.001	0.000	0.164	0.136	<0.001	0.004	0.007
Relative humidity	0.001	0.706	0.000	0.740	0.004	0.442	0.000	0.336
Mean soil temperature	0.356	<0.001	0.000	0.606	0.096	<0.001	0.000	0.936
25 cm								
Independent variable	Meadow				Forest			
	OLS		Autoregressive		OLS		Autoregressive	
	R ²	Pr > t	Partial R ²	Pr > t	R ²	Pr > t	Partial R ²	Pr > t
Snow depth	0.801	<0.001	0.000	0.385	0.020	0.065	0.001	0.612
Air temperature	0.001	0.712	0.000	0.839	0.213	<0.001	0.001	0.070
Wind speed	0.016	0.113	0.000	<0.001	0.047	0.004	0.006	<0.001
Net radiation	0.487	<0.001	0.000	0.208	0.256	<0.001	0.000	0.349
Atmospheric pressure	0.022	0.063	0.000	<0.001	0.013	0.136	0.000	0.092
Ambient CO ₂	0.001	0.774	0.000	0.009	0.243	<0.001	0.002	0.001
Relative humidity	0.003	0.480	0.000	0.761	0.000	0.817	0.000	0.982
Mean soil temperature	0.540	<0.001	0.000	0.195	0.110	<0.001	0.002	0.001

marginally so, and the third almost always nonsignificant. Use of an autoregressive model permits evaluation of the effects of covariates separately from the effects of the temporal trends in the response data.

Meteorological values examined for relationship to CO₂ under snow were air temperature, wind speed, net radiation, atmospheric pressure, relative humidity, and atmospheric CO₂. Meteorological data analyzed for relationship to CO₂ under snow were the daily mean values of the 48 half-hour readings. Data from early season and late season were analyzed separately after a preliminary analysis of the whole season data.

Snow density was measured using a Federal sampler on 7 February, 4 March, 3 April, and 8 May 2002 to calculate snow porosity as described in Appendix A and to allow estimates of diffusional flux of CO₂ through the snowpack to the atmosphere. CO₂ flux was calculated for these four dates using the equation for flux as derived in Appendix A. Data were analyzed to compare meadow with forest, using paired-*t* analysis. Cumulative flux was then estimated for the period from 7 February to 8 May using linear interpolation of snow porosity between the four data points.

Results and Discussion

MEADOW AND FOREST CO₂ UNDER SNOW

There was no significant difference between the two samplers located 0.5 m from each other at each site the first year. During the second year, the greater separation of the two surface samplers at each site resulted in greater difference between the two. In addition, variability between individual sampler locations was higher underground than at the surface. However, forest and meadow sites still were statistically different as in the first year, with higher CO₂ concentrations in the meadow than in the forest both at the surface and

underground. Considerably less ground surface biomass and soil fine root biomass has been observed at this site in the forest than in the meadow, suggesting less biomass available for decay and respiration in the forest. Underground samplers (–25 cm deep) had significantly higher CO₂ than surface samplers at both sites.

There were somewhat temporally irregular patterns of CO₂ under snow, but CO₂ concentrations under snow in 2001 increased gradually throughout the winter season, particularly after snow accumulation began to increase, and were significantly higher in the meadow than in the forest (Fig. 1). Mid-winter soil temperatures were consistently lower in the forest than in the meadow (Fig. 1). Data from the second year indicate little change in soil surface CO₂ under snow until later in the season, even though snow depth increased gradually throughout the season (Fig. 2). Mid-winter soil temperatures were slightly above zero in the meadow and slightly below zero near the surface in the forest in 2002 (Fig. 2).

REGRESSION ANALYSES OF CO₂ UNDER SNOW

Partial R² values for the independent variables in the autoregressive models are presented in Tables 1–5. These R² values are calculated by first calculating the R² value of a model incorporating the two temporal lags only, and subtracting this value from the R² of a model that includes temporal lag terms and the environmental covariate of interest. The resultant partial R² represents the explanatory value attributable exclusively to the environmental variable (Neter et al., 1989). These analyses found that the CO₂ under snow could best be related to the previous 1- or 2-day readings (Tables 1–5), and that CO₂ under snow was related more closely to the previous day's concentration than to the environmental parameters, reflecting the gradual increase in CO₂ as the winter season progressed. Even though the autoregressive analysis confirms that CO₂ under snow is most

TABLE 4

Single variable regression analysis, CO₂ under snow vs. snow depth, meteorology, and soil temperature, for meadow and forest, winter of 2001–2002, for surface (0 to –10 cm deep) samplers. CO₂ averaged for two samples at each site. Data analyzed separately for early and late season. OLS = ordinary least squares.

Independent variable	1 Nov 2001 to 18 Mar 2002				19 Mar 2002 to 5 May 2002			
	OLS		Autoregressive		OLS		Autoregressive	
	R ²	Pr > t	Partial R ²	Pr > t	R ²	Pr > t	Partial R ²	Pr > t
Meadow—surface								
Snow depth	0.933	<0.001	0.011	<0.001	0.282	<0.001	0.011	0.138
Air temperature	0.245	<0.001	0.001	0.122	0.078	0.064	0.004	0.504
Wind speed	0.033	0.050	0.010	<0.001	0.105	0.030	0.054	0.009
Net radiation	0.011	0.262	0.001	0.027	0.052	0.133	0.000	0.954
Atmospheric pressure	0.090	0.001	0.001	0.201	0.041	0.181	0.002	0.701
Ambient CO ₂	0.143	<0.001	0.002	0.005	0.123	0.018	0.000	0.924
Relative humidity	0.001	0.753	0.000	0.238	0.000	0.947	0.000	0.820
Mean soil temperature	0.585	<0.001	0.001	0.050	0.121	0.019	0.000	0.794
Forest—surface								
Independent variable	1 Nov 2001 to 18 Mar 2002				19 Mar 2002 to 5 May 2002			
	OLS		Autoregressive		OLS		Autoregressive	
	R ²	Pr > t	Partial R ²	Pr > t	R ²	Pr > t	Partial R ²	Pr > t
Snow depth	0.755	<0.001	0.044	<0.001	0.366	<0.001	0.053	0.003
Air temperature	0.213	<0.001	0.013	0.003	0.003	0.723	0.005	0.393
Wind speed	0.028	0.062	0.085	<0.001	0.447	<0.001	0.184	<0.001
Net radiation	0.065	0.005	0.012	0.004	0.003	0.731	0.026	0.047
Atmospheric pressure	0.126	<0.001	0.000	0.834	0.045	0.149	0.008	0.294
Ambient CO ₂	0.062	0.005	0.022	<0.001	0.063	0.084	0.015	0.071
Relative humidity	0.041	0.026	0.000	0.859	0.038	0.183	0.018	0.107
Mean soil temperature	0.387	<0.001	0.006	0.030	0.652	<0.001	0.097	<0.001

highly related to the previous day's CO₂. OLS regression analyses show that CO₂ under snow could also be related to most meteorological parameters when the autoregressive time lag time factors are not considered (Tables 1–5, Figs. 1 and 2).

Snow depth and soil temperature were the environmental parameters that had the highest OLS R² values with CO₂ under snow (Tables 1–5). CO₂ under snow, and its variability, increased more rapidly as daily mean temperature reached above freezing for both years (Figs. 1 and 2). These meteorological and soil temperature parameters reflect seasonal changes coincident with increasing seasonal snow depth. Seasonal changes in air temperatures are related to seasonal changes in solar radiation and these meteorological changes are related to changes in snow depth.

OLS regression analysis R² values indicate that CO₂ at the soil surface and solar radiation were related for the whole season for 2002 (Table 3). When the early season and late season data were analyzed separately, R²s for solar radiation and soil surface CO₂ were considerably lower, and were significant only for early season in the forest (Table 4). CO₂ at –25 cm depth was less related to solar radiation than CO₂ at the surface for the whole season analysis (Table 3), and were not significantly related when early or late season were analyzed separately (Table 5). The high R²s reflect the seasonal change in solar radiation concurrent with change in CO₂ under snow, detected using data throughout the whole season, but not observed within the early or within the late season data (Figs. 3 and 4). Highest partial R² values for temporal lags were for data collected the whole season, with the meadow R² values slightly higher than the forest (Table 6).

OLS regression coefficients for CO₂ under snow and selected environmental parameters are shown in Figures 3 and 4. The results indicate a close relationship of CO₂ under snow and snow depth. Because of the apparent change in relationship of CO₂ under snow and snow depth early and later in the season (Figs. 1a, 2a, 4), the data were

analyzed separately for the early and late season. Early and late season were arbitrarily defined as when this abrupt change appeared to occur (Figs. 1a and 2a). Results for 2001 indicate that the relationship between CO₂ and snow depth and meteorological factors was stronger in the early season data (Table 2). In 2002, early and late season results were similar (Table 4). An exception is for wind speed in the forest for 2002, which was more related to CO₂ later in the season (albeit still accounting for little of the variability) than earlier. Wind speed might be expected to have a more instantaneous relationship to CO₂, perhaps not reflected in the 24-h means analyzed seasonally here. Pressure pumping can rapidly change CO₂ in the snowpack (Massman et al., 1997). Overall, the meteorological data did not show higher regression R²s of CO₂ under snow in the meadow compared to the forest, even though the ambient meteorological data were collected above the meadow.

With the few exceptions discussed here, CO₂ under snow using OLS regression was significantly related to meteorological variables, but, except for solar radiation and air temperature, R²s were low suggesting that little of the variability in CO₂ was accounted for by these parameters. Nevertheless, ambient air relative humidity and atmospheric pressure showed some relationship to CO₂ under snow only for the late season of 2001, but not for early season 2001 or for 2002. Wind speed showed little relationship to CO₂ under snow except for late season surface CO₂ and early season underground CO₂ in the forest in 2002, although these R²s were lower. Ambient CO₂ was not closely related to CO₂ under snow, except for –25 cm deep CO₂ in both the meadow and forest. Ambient CO₂ changes little throughout the winter, typical for remote snow covered sites. Wind speed is expected to be higher in the meadow than in the forest, but snow density was lower in the forest than in the meadow. Since many meteorological parameters are autocorrelated, they are not independent variables, and the similarity in significance (or non-significance) of the

TABLE 5

Single variable regression analysis, CO₂ under snow vs. snow depth, meteorology, and soil temperature, for meadow and forest, winter of 2001–2002, for underground (–25 cm deep) samplers. CO₂ averaged for two samples at each site. OLS = ordinary least squares.

Independent variable	1 Nov 2001 to 18 Mar 2002				19 Mar 2002 to 5 May 2002			
	OLS		Autoregressive		OLS		Autoregressive	
	R ²	Pr > t	Partial R ²	Pr > t	R ²	Pr > t	Partial R ²	Pr > t
Meadow –25 cm								
Snow depth	0.943	<0.001	0.000	0.044	0.945	<0.001	0.008	<0.001
Air temperature	0.240	<0.001	0.000	0.769	0.433	0.001	0.001	0.731
Wind speed	0.035	0.027	0.001	<0.001	0.036	0.384	0.001	0.678
Net radiation	0.192	<0.001	0.000	0.714	0.094	0.155	0.008	0.032
Atmospheric pressure	0.118	<0.001	0.000	0.001	0.005	0.761	0.022	<0.001
Ambient CO ₂	0.094	0.000	0.000	0.003	0.493	0.000	0.003	0.223
Relative humidity	0.004	0.436	0.000	0.644	0.027	0.450	0.001	0.777
Mean soil temperature	0.600	<0.001	0.000	0.196	0.370	0.002	0.000	0.931
Forest –25 cm								
Snow depth	0.581	<0.001	0.001	0.187	0.233	0.001	0.002	0.126
Air temperature	0.295	<0.001	0.001	0.038	0.005	0.621	0.000	0.398
Wind speed	0.185	<0.001	0.014	<0.001	0.119	0.016	0.012	<0.001
Net radiation	0.002	0.674	0.001	0.050	0.009	0.519	0.001	0.191
Atmospheric pressure	0.096	0.001	0.000	0.983	0.034	0.208	0.003	0.049
Ambient CO ₂	0.080	0.002	0.006	<0.001	0.267	0.000	0.002	0.079
Relative humidity	0.001	0.747	0.001	0.177	0.032	0.221	0.001	0.309
Mean soil temperature	0.910	<0.001	0.006	<0.001	0.854	<0.001	0.008	<0.001

relationship of many of the environmental parameters to CO₂ concentrations is not unexpected. The seasonal change in many environmental parameters, coincidental with seasonal changes in snow depth and under snow CO₂, suggests caution when evaluating cause and effect of these parameters and CO₂ under snow. There is likely an indirect relationship of CO₂ under snow with solar radiation and air temperature, reflected in their effect on snowpack.

SEASONAL CHANGES IN CO₂ UNDER SNOW

The seasonal increases in CO₂ evident throughout the winter were related to increased snow depth until later in the snow season when CO₂ concentrations and variability increased dramatically. The co-occurring increase in CO₂ under snow and snow depth reflect the snowpack resistance to the transfer of CO₂ through the snowpack to the atmosphere. There was little diurnal variability of CO₂ under snow until later in the season. The change occurred at about 20 March for the meadow and 1 April for the forest in 2001 (Fig. 1). The increased variability in CO₂ occurred sooner in the meadow than in the forest, perhaps because snow rescission started sooner in the open meadow than in the shaded forest site. This increase appears to have begun when mean daily temperature became above freezing at the snow surface (Figs. 1c and 2c), and is associated with seasonal increases in net radiation (Figs. 1d and 2d). CO₂ buildup begins as the snowpack accumulates, and concentrations increase as the snowpack depth increases. The greatest increase in CO₂ occurred as the peak snowpack depth began to recede, suggesting increased snow density inhibited diffusion of CO₂ through the snowpack, water coursing through the snowpack inhibited diffusional paths, or biogeochemical changes occurred in the soil as snowmelt occurred. Late season increases in CO₂ were reported by Mariko et al. (2000), with the increases in CO₂ occurring much later and more closely related to soil temperature than to increases in air temperature and co-occurring decreases in snow

depth. Hardy et al. (1995) reported higher variability in CO₂ flux from snow in the spring, and attributed the higher variability to tree wells, melting snow, and impermeable ice layers.

Soil temperatures followed typical seasonal progressions, with soil surface temperatures initially higher and responding quicker than deep soils to above soil temperature changes (Figs. 1 and 2). Temperatures near the soil surface decreased until there was little difference in soil temperature with depth near the end of the winter season. Since maximum soil temperature differences between soil depths was only about 2°C even early in the season when differences were greatest, and relative differences between soil temperatures at the various depths were often less than 1°C, soil temperature data were averaged for analysis. Soil surface CO₂ under snow in our study was closely related to soil temperatures in 2001 (Tables 1 and 2) and in 2002 (Tables 3 and 4). CO₂ at –25 cm depth in the soil under snow was also related to soil temperature (Table 5).

The delay in the late season increase in CO₂ in the forest compared to the meadow suggests that air temperatures and solar radiation reported above the meadow may not reflect impact of those parameters under the canopy in the forest. It would be expected that solar radiation and air temperature would be lower in the forest than in the meadow even though the meteorological parameters monitored at 28 m height in the meadow but above adjacent canopy level would reflect area rather than local meadow or forest conditions.

The increase in late season CO₂ from the soil at both sites suggests increased nutrient input to soil microorganisms from initial melting snow. Snowpack also began to decrease at this time in 2002 (Fig. 2b); however, the snowpack did not decrease in depth before early May for 2001, the result of four spring snowfall episodes during April that year (Fig. 1b). Soil moisture was nearly constant during both winters, at about 10% volumetric water content in the forest and about 30% in the meadow. A sudden increase in soil moisture suggestive of the movement of snowmelt water into soil occurred 13–14 May in the

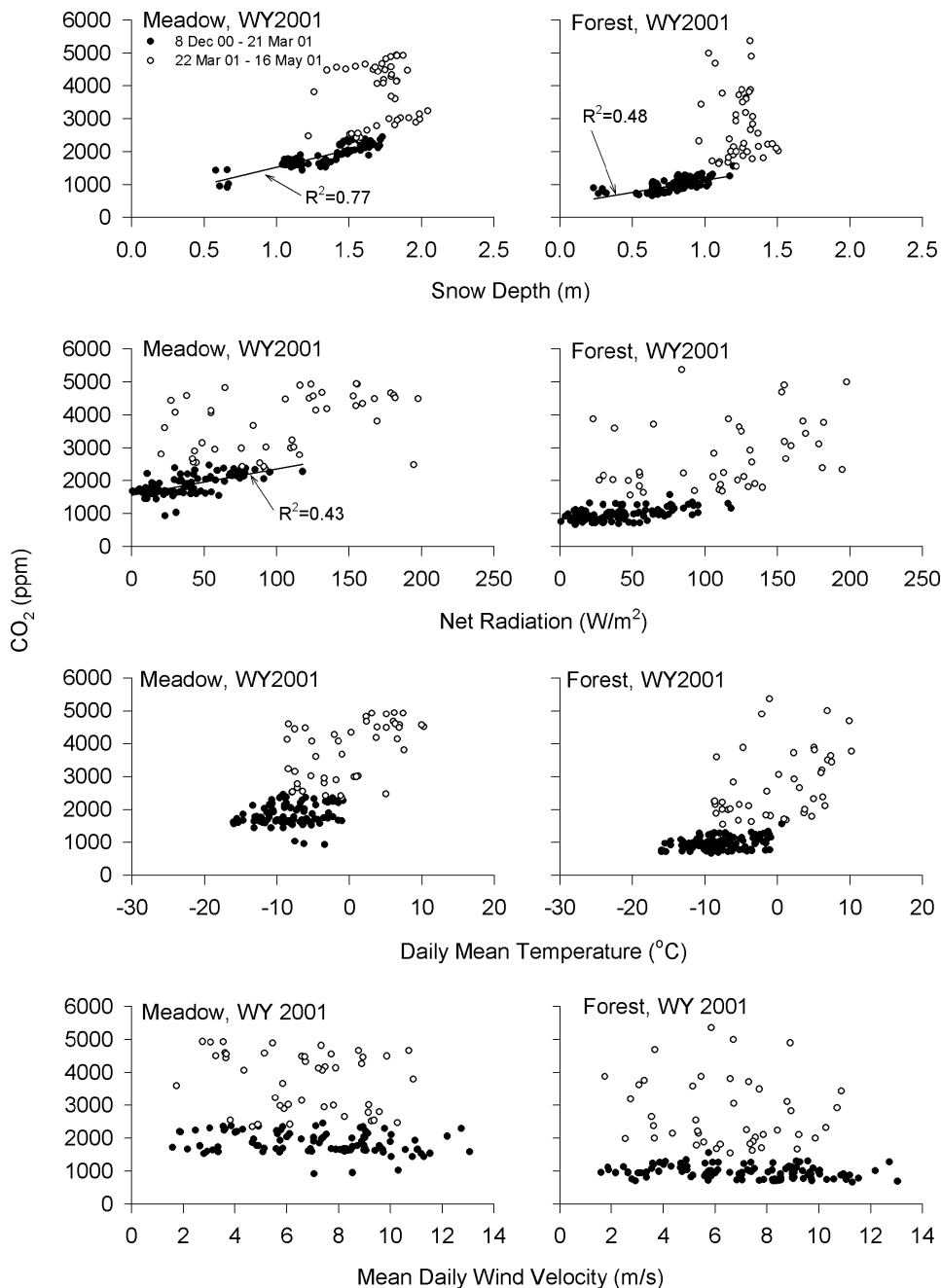


FIGURE 3. Mean ($n = 48$ half-hour readings per day) daily soil surface CO_2 vs. snow depth, solar radiation, air temperature, and wind speed for the meadow and forest for the winter of 2000–2001. Solid circles are early season CO_2 under snow, open circles are late season.

meadow and 15–16 May in the forest for both years of the study, much later than the time of large increases in CO_2 (Figs. 1a and 2a).

Tree physiological activity is likely to be partially responsible for the late winter increased CO_2 concentrations. Ambient air temperature began to increase and exceeded above freezing temperature at the time of increase in soil CO_2 (Figs. 1c and 2c). Photosynthesis is expected to increase with increasing air temperature, and root respiration as well as microbial activity would increase with increasing soil temperature and increasing snowmelt. Transpiration increases in Engelmann spruce at high elevation in Colorado have been reported to occur in early February to late March as air temperature increases (Boyce and Lucero, 1999), suggesting increased physiological activity at this time. Data from a subalpine fir forest at 3050 m elevation about 150 km south of our site (Monson et al., 2002) indicate that trees were dormant during the winter until mid-April to early May, and abrupt shift to springtime CO_2 uptake by trees seemed to be related to rising soil temperature.

There was a highly significant relationship with OLS regression between snow depth and total season soil surface CO_2 under snow for the meadow and the forest in 2001, but only for early season meadow and forest when the seasons were analyzed separately (Fig. 3). Similarly, with OLS regression, total season CO_2 at the soil surface had a highly significant relationship to snow depth in 2002, and more for the early season than late season when analyzing seasons separately (Fig. 4). For CO_2 at -25 cm depth in the soil, similar relationships to those at the surface were evident in the meadow but not in the forest. In the forest, CO_2 when examined throughout the whole season was not related to snow depth (Table 3, Fig. 4). However, CO_2 at -25 cm in the soil did show a high regression coefficient relating to snow depth for early season in the forest (Table 5). This was an inverse relationship suggesting subsurface CO_2 pool depletion at this time. Late season meadow subsurface CO_2 also decreased with increasing snow depth.

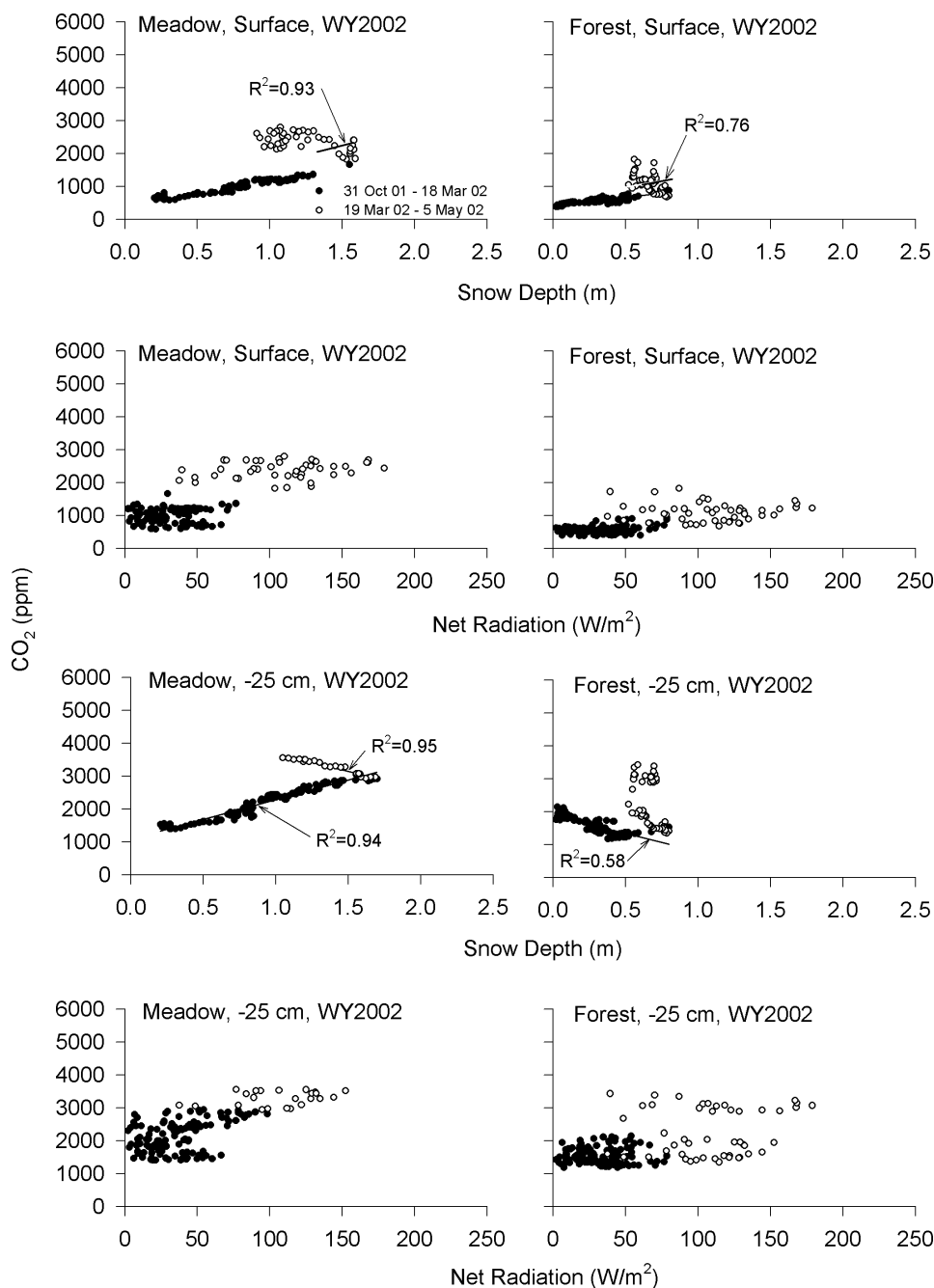


FIGURE 4. Mean ($n = 48$ half-hour readings per day) daily soil surface CO_2 and -25 cm deep CO_2 vs. snow depth and radiation for the meadow and forest for the winter of 2001–2002. Solid circles are early season CO_2 under snow, open circles are late season.

MID-WINTER CO_2 FLUXES THROUGH SNOW

CO_2 flux calculated for four days during the winter of 2002 (Fig. 5) indicates that flux was consistently higher in the meadow than in the forest, and increased from 0.290 to $0.658 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the meadow and from 0.196 to $0.418 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the forest from mid-winter to late winter, more than doubling as the season progressed. Similar winter CO_2 flux values from the GLEES ecosystem have previously been reported, 0.161 – $0.845 \mu\text{mol m}^{-2} \text{s}^{-1}$ for various dates in winter during 1992–1994 (Sommerfeld et al., 1996) and 1.01 – $1.67 \mu\text{mol m}^{-2} \text{s}^{-1}$ on 27 March to 1 April 1997 (McDowell et al., 2000). McDowell et al. (2000) found higher values in the forest than in the meadow. Zeller (1995) reported CO_2 flux from the site for 28 January to 1 February 1993, at $4.2 \mu\text{mol m}^{-2} \text{s}^{-1}$, with an average range of about -0.54 to $+5.68 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Zeller, 1995, their Fig. 8, and personal communication), and the flux was related to wind speed. Mast et al. (1998) reported average winter flux of $0.169 \mu\text{mol}$

$\text{m}^{-2} \text{s}^{-1}$ (saturated soil) to $0.490 \mu\text{mol m}^{-2} \text{s}^{-1}$ (dry soil) from a subalpine site in Colorado, and also observed a wind effect on CO_2 . Estimated flux from 7 February to 8 May at our site, calculated from daily mean values using linearly interpolated porosity data, show higher values (except for one day, 19 April) and generally less temporal variability in the meadow than the forest (Fig. 5). Dynamic changes in porosity would have an effect on CO_2 flux. However, a few days after snowfall and the initial snowpack settling, porosity does not change much over time (Lundy et al., 2002). Any porosity changes for a deep winter snowpack such as that in this study seem to occur rather slowly, except toward melt season when porosity may change quickly. Nevertheless, it is useful to examine what might happen if porosity (or tortuosity) were to change significantly from day to day or week to week. Assuming a constant CO_2 source, then the undersnow CO_2 would change in such a way as to return the fluxes to their original balance between production in the soil and loss to the atmosphere. For example, if porosity (or tortuosity) were to decrease in time (but not by

TABLE 6

Partial R^2 of temporal autocorrelation terms for 2001 and 2002, i.e., correlation of response data to temporal lags. Lag times were 24 and 48 h.

Response dataset	Partial R^2 (2 lags)
2001	
Meadow (WY days 68–228)	0.973
Forest (WY days 68–228)	0.868
Meadow (WY days 68–171)	0.925
Meadow (WY days 172–228)	0.914
Forest (WY days 68–182)	0.647
Forest (WY days 183–228)	0.666
2002	
Meadow, Surface, all days	0.981
Forest, Surface, all days	0.902
Meadow, –25 cm, all days	0.996
Forest, –25 cm, all days	0.976
Meadow, Surface, WY days 31–169	0.965
Meadow, –25 cm, WY days 31–169	0.994
Forest, Surface, WY days 31–169	0.825
Forest, –25 cm, WY days 31–169	0.972
Meadow, Surface, WY days 170–217	0.626
Meadow, –25 cm, WY days 170–217	0.965
Forest, Surface, WY days 170–217	0.707
Forest, –25 cm, WY days 170–217	0.962

so much as to eliminate the flux) then the undersnow CO_2 would increase, thus increasing the gradient, until the former flux had been restored. So the flux tends to be conserved (as long as the CO_2 source remains constant in time), but the balance between the gradient and the porosity (or tortuosity) would change in such a way that their product would remain constant. The same reasoning applies if porosity (or tortuosity) decreases in time, except now the gradient will increase.

Although interpolated data should be used with caution, snow properties at this site change gradually when these measurements were taken (porosity changed from 0.77 to 0.67 in the forest and from 0.74 to 0.66 in the meadow; also see Sommerfeld et al., 1996), suggesting these flux estimates are valid.

We estimate that cumulative flux of CO_2 from 7 February to 8 May 2002 to be 40.82 g C m^{-2} from the meadow site and 30.53 g C m^{-2} from the forest site. Interpolation between four mid-winter data points was considered valid since snow density slowly increases with time (Martinelli, 1971; Lundy et al., 2002), typical for this site during mid-winter, and the change between the four data points was small. These values are for only 3/8 of the mid-October to mid-June snow covered season, indicating that actual CO_2 flux from these ecosystems in winter is considerably higher. Sommerfeld et al. (1996) estimate 232 g C m^{-2} and McDowell et al. (2000) estimate 132 g C m^{-2} for full season wintertime flux for the site. Many of the measurements for the wintertime estimates of Sommerfeld et al. (1996) were in late winter when fluxes are higher. Zeller and Nikolov (2000) used the FORFLUX model (Nikolov and Zeller, 2003) to show a net ecosystem flux of C in the winter of 1996 (Zeller and Nikolov 2000, their Fig. 11), with 7 February to 8 May 1996 accounting for 41.8 g C m^{-2} (N. Nikolov, personal communication), similar to our meadow site values. All of these studies confirm that subalpine forests and meadows can be important sources of CO_2 during winter.

Conclusions

CO_2 concentrations under snow were higher in the meadow than in the adjacent forest. Snow depth, snow density, and soil temperatures were lower in the forest than in the meadow.

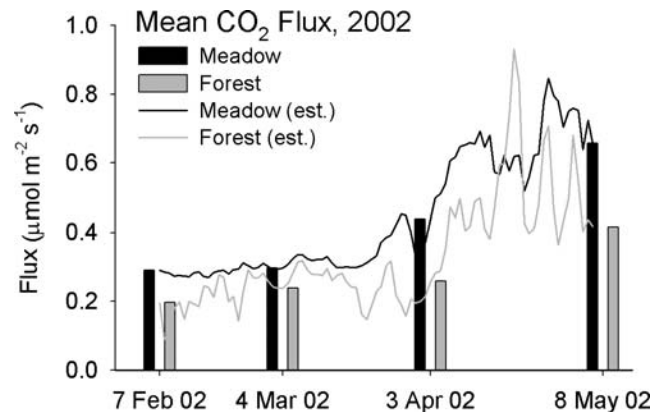


FIGURE 5. Calculated diffusional CO_2 flux for 7 February, 4 March, 3 April, and 8 May 2002 for the meadow and forest sites, and linearly interpolated daily CO_2 flux from 7 February through 8 May.

CO_2 concentrations were higher at –25 cm depth in the soil than at the soil surface, and higher at the surface than ambient CO_2 , reflecting a diffusion gradient from deep soil to the soil surface/snowpack interface, and from the soil surface to the snow pack surface/atmosphere interface.

CO_2 increased at the soil-snow interface throughout the season. A dramatic change occurred at about the time of peak snowpack, when snowmelt began, concurrent with increasing air temperatures. The buildup of soil surface CO_2 prior to snowmelt was likely related to snow depth. Higher and more variable CO_2 concentrations under snow later in the season may be related to snow melt and biological activity.

CO_2 under snow was most closely related to snow depth and soil temperature, and to a lesser extent to solar radiation. Other ambient meteorological parameters monitored were less related to under snow CO_2 , but some of these, particularly air temperature, were related to solar radiation. CO_2 increases throughout the season, as does snow depth, solar radiation, and air temperature. Physical and biological relationships would suggest increased CO_2 under snow with increasing snow depth throughout the season, since respiration continues but snowpack limits diffusion to the atmosphere. The relationship of CO_2 under snow with meteorological parameters such as solar radiation implies an indirect relationship as seasonal changes in solar radiation affect air temperature and subsequent snow depth.

CO_2 flux was higher in the meadow than in the forest, and was considerably higher late in the winter season than during mid-winter. Subalpine forests and meadows contribute considerable amounts of CO_2 to the atmosphere through snow in the winter.

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Appendix A. Derivation of an Equation for Calculation of CO₂ Diffusional Flux through Snow

The expression for the diffusional mass flux of a dilute gas (e.g., CO₂) through a porous media (snow or soil) and into the free atmosphere (air) that is consistent with the conservation of mass reads

$$J_c = -D_e \frac{\partial \rho_c}{\partial z}, \quad (\text{A1})$$

where J_c is the diffusional flux (in units $\text{ML}^{-2} \text{T}^{-1}$, where M = mass, L = length, and T = time, such as $\text{mg m}^{-2} \text{s}^{-1}$), D_e is the effective diffusion coefficient ($\text{L}^2 \text{T}^{-1}$), ρ_c is the mass density (ML^{-3}) of the gas, z is distance or depth of the porous media (L), and $\partial \rho_c / \partial z$ is the gradient of density with respect to z . However, J_c is usually expressed in terms of molar density, thus $J_c^m = J_c / M_c$, where J_c^m is the mass flux expressed in molar units and M_c is the molecular mass of the gas. D_e includes the effects of the porosity and tortuosity of the medium, as well as temperature and pressure effects. Including these adjustments, Equation A1 can be rewritten as

$$J_c^m = -\phi \tau D(0,1) \frac{P_0}{P} \left(\frac{T}{T_0} \right)^\alpha \frac{\partial C}{\partial z}, \quad (\text{A2})$$

where ϕ is porosity of the medium, τ is the tortuosity of the medium, $D(0,1)$ is the diffusivity of the dilute gas in air at STP ($T_0 = 273.15^\circ\text{K}$, and $P_0 = 1 \text{ atm}$), P is the ambient pressure (atm), T is the ambient temperature ($^\circ\text{K}$), $\alpha = 1.81$ (Massman, 1998), and $C = \rho_c / M_c$, is the molar density of the gas. The molar concentration (denoted here as χ_c) can be expressed in terms of mol fraction by dividing C by the total molar density of all gases, C_{total} , therefore, the gradient can be expressed as

$$\frac{\partial C}{\partial z} = \frac{\partial (C_{\text{total}} \chi_c)}{\partial z}. \quad (\text{A3})$$

In general, because the gas is dilute, $C_{\text{total}} \gg C$ or equivalently, $\chi_c \ll 1$. By the ideal gas law, $C_{\text{total}} = P/RT$, where R is the universal gas constant. For the present discussion we can further assume that the variations in P and T with depth are small enough so that C_{total} within and above the medium is constant. Therefore, the gradient can be further expressed as

$$\frac{\partial C}{\partial z} = \frac{P}{RT} \frac{\partial \chi_c}{\partial z}. \quad (\text{A4})$$

Combining Equations (2) and (4) yields

$$J_c^m = -\phi \tau D(0,1) \frac{P_0}{RT_0} \left(\frac{T}{T_0} \right)^{0.81} \frac{\partial \chi_c}{\partial z}. \quad (\text{A5})$$

Equation (5) is used for estimating the diffusional flux of CO₂ through a snowpack. Porosity is determined as $\phi = 1 - (\rho_b / \rho_i)$, where ρ_b is the bulk density of snow and ρ_i is the bulk density of ice (917 kg m^{-3}). The terms τ , $D(0,1)$, and P_0/RT_0 are constants, where $\tau = 0.85$ (Massman et al., 1997), $D(0,1) = 0.1381(10^{-4}) \text{ m}^2 \text{s}^{-1}$ for CO₂ in air (Massman, 1998), and $P_0/RT_0 = 44.613 \text{ mol m}^{-3}$. The gradient function $\partial \chi_c / \partial z$ is often approximated as the finite difference of two measurements taken at the top and the bottom of the snowpack, i.e., $\partial \chi_c / \partial z = \Delta \chi_c / \Delta z$, where $\Delta \chi_c$ denotes the measured difference in χ_c and Δz denotes the distance between the two points of measurements of χ_c .