Carbon limitation of soil respiration under winter snowpacks: potential feedbacks between growing season and winter carbon fluxes

P A U L D . B R O O K S *, D I A N E M C K N I G H T † and K E L L Y E L D E R ‡

Hydrology and Water Resources, University of Arizona, Tucson, AZ 85716, USA, †INSTAAR, University of Colorado, Boulder, CO 80309, USA, ‡USFS, Rocky Mountain Research Station, Ft Collins, CO 80526, USA

Abstract

A reduction in the length of the snow-covered season in response to a warming of high-latitude and high-elevation ecosystems may increase soil carbon availability both through increased litter fall following longer growing seasons and by allowing early winter soil frosts that lyse plant and microbial cells. To evaluate how an increase in labile carbon during winter may affect ecosystem carbon balance we investigated the relationship between carbon availability and winter CO_2 fluxes at several locations in the Colorado Rockies. Landscape-scale surveys of winter CO_2 fluxes from sites with different soil carbon content indicated that winter CO_2 fluxes were positively related to carbon availability and experimental additions of glucose to soil confirmed that CO_2 fluxes from snow-covered soil at temperatures between 0 and $-3\,°C$ were carbon limited. Glucose added to snow-covered soil increased CO_2 fluxes by 52–160% relative to control sites within 24 h and remained 62–70% higher after 30 days. Concurrently a shift in the $\delta^{13}C$ values of emitted CO_2 toward the glucose value indicated preferential utilization of the added carbon confirming the presence of active heterotrophic respiration in soils at temperatures below $0\,°C$. The sensitivity of these winter fluxes to substrate availability, coupled with predicted changes in winter snow cover, suggests that feedbacks between growing season carbon uptake and winter heterotrophic activity may have unforeseen consequences for carbon and nutrient cycling in northern forests. For example, published winter CO_2 fluxes indicate that on average 50% of growing season carbon uptake currently is respired during the winter; changes in winter CO_2 flux in response to climate change have the potential to reduce substantially the net carbon sink in these ecosystems.

Keywords: carbon cycle, climate change, CO_2 flux, soil respiration, winter biogeochemistry

Received 7 May 2004; revised version received 12 July 2004 and accepted 13 September 2004

Introduction

The northern hemisphere terrestrial carbon sink has been estimated at $1.5\,\text{GtC\,yr}^{-1}$ with the majority of this sink located in ecosystems north of $40°$ latitude (Schimel *et al.*, 2001). A warming of these northern latitudes over the last several decades has lengthened the growing season and increased carbon fixation (Black *et al.*, 2000; Kimball *et al.*, 2000). Similarly, increasing atmospheric CO_2 concentrations may further enhance photosynthetic carbon uptake (Schlesinger & Lichter, 2001; Luo *et al.*, 2003). The fate of the additional fixed carbon is not known, but to act as a long-term carbon sink, any increase in primary production must be stored in long-lived biomass or preferably

Correspondence: Paul D. Brooks, e-mail: brooks@hwr.arizona.edu

transferred to a slowly degrading soil organic matter pool. Between 50% and 80% of carbon uptake under elevated CO_2 or during longer growing seasons is allocated to short-lived tissues (e.g., foliage and litter) and exudates (Schlesinger & Lichter, 2001; Liski *et al.*, 2002; Lloyd *et al.*, 2002) and a large proportion of these relatively labile carbon compounds enters the soil with litter fall and senescence providing a fresh carbon source to the soil heterotrophic community. Freeze–thaw events before a consistent snow cover develops may increase the lability of this carbon by promoting cell lysis (Schimel & Clein, 1996), but low soil temperatures in winter suggest limited heterotrophic processing until spring. However, recent findings indicate that soil microbial biomass may actually peak in winter (Brooks *et al.*, 1996; Lipson *et al.*, 2000; Schadt *et al.*, 2003) suggesting the

presence of a soil heterotrophic community with an unknown capability of utilizing this carbon.

The efflux of CO_2 from soils to the atmosphere continues throughout the winter with recent measurements indicating that 60% or more of growing season carbon uptake can be lost during the winter (Sommerfeld *et al.*, 1993; Winston *et al.*, 1997; Oechel *et al.*, 2000; Monson *et al.*, 2002). Winter CO_2 fluxes originally were attributed to the abiotic release of CO_2 that accumulated in the soil during the previous growing season, but this mechanism alone does not explain the spatial and temporal variability observed in fluxes suggesting an active heterotrophic component to winter CO_2 efflux. In general, however, the controls on soil respiration, especially at the low temperatures that characterize these soils in winter, are not as well understood as those on photosynthetic C uptake. However, the variability in respiration may determine the magnitude and even the direction of net ecosystem carbon exchange (NEE) (Oechel *et al.*, 2000; Valentini *et al.*, 2000).

There is not a direct relationship between soil temperature and winter CO_2 flux, but there does appear to be a critical threshold for active respiration, typically between -7 and $-5\,°C$, below which a lack of free water limits contemporaneous heterotrophic contributions to winter CO_2 loss (Edwards & Cresser, 1992; Schimel & Clein, 1996; Brooks *et al.*, 1997). Consistent snow cover effectively decouples soil temperatures from the atmospheric and soil temperatures above this critical threshold characterize many environments with greater than 30 cm of snow. Several studies suggest that labile carbon substrate controls heterotrophic activity if free water is present (Schimel & Clein, 1996; Brooks *et al.*, 1997; Lipson *et al.*, 2000), but this has not been demonstrated with experimental manipulations in the field. The potential magnitude of winter CO_2 loss, coupled with a lack of current biogeochemical models to accurately represent heterotrophic activity at low temperatures, motivated our investigation of the effects of carbon availability on winter soil respiration. Specifically, we test the hypothesis that CO_2 flux under snow cover results from *in situ* carbon-limited hetrotrophic activity.

Methods and site description

Over-winter CO_2 flux surveys

Intensive winter CO_2 flux measurements were made along five, 1 km transects in the upper Snake River and Deer Creek catchments in Summit County, Colorado. Elevation varied between 3400 and 3700 m; vegetation along the transects included: one dominated by coniferous forest, two dominated by mixed deciduous (primarily birch and willow) and meadow vegetation, and two dominated by grasses and sedges. Seasonal snow cover begins to develop in October, snowmelt begins in late April or early May, and the transects are snow-free in June. Soils are mixed typic Cryochrepts with the majority of organic carbon in the O-A horizon (80–120 mm deep). Total soil carbon ranges from 3.9 to $11.2\,kg\,C\,m^{-2}$ without a clear pattern based on either vegetation or soil parent material. Snow depth ranged from 90 to 245 cm and soil surface temperatures ranged between -3 and $0\,°C$ when CO_2 fluxes were measured.

CO_2 fluxes were measured at 10 locations along each 1 km transect approximately biweekly between January and May. One to three concentration profiles were obtained at each location. CO_2 concentrations were measured with a portable infrared gas analyzer (IRGA-PP Systems, Amesbury, MA, USA) at the snow surface and at 25 cm depth increments through the snowpack to the soil surface by inserting a stainless steel probe through the snowpack. The lower 5 cm of the probe was perforated to sample gas concentrations within the snowpack and connected to the IRGA with internally routed tygon tubing. Snow pits were dug to the soil surface adjacent to sampling locations to obtain snowpack physical characteristics for flux calculations. Fluxes were calculated using a steady-state diffusion model incorporating vertical concentration gradients through the snowpack and depth, porosity, tortuosity, temperature, and pressure. More detailed information on flux calculation can be found in Sommerfeld *et al.* (1993) and Brooks *et al.* (1999).

Soil carbon amendments

We dug snow pits to the soil surface and established three carbon-amended plots and three snow-removal control plots (approximately $2\,m \times 1.5\,m$) in both deciduous and coniferous forests in mid-February 2003. Three 50 mm diameter soil cores were collected from the O-A horizon of each plot and pooled for bulk carbon content and isotopic analyses. Glucose purchased from a local grocery and purported to be from cane sugar was added to the soil surface of the carbon-amended plots at a loading of $100\,g\,C\,m^{-2}$. Soils were unfrozen and between -1 and $-3\,°C$ at the time of addition. Soils of both snow-removal control and C-amendment plots were exposed for 30–45 min and then recovered with snow. Samples for $\delta^{13}C$-CO_2 were collected and CO_2 fluxes were calculated at 24 h and 30 days after addition of the carbon substrate using the method described above. Measurements were made at a total of nine locations within each forest type: three locations within carbon addition plots, three within control snow-removal plots, and three in an adjacent undisturbed area.

The coniferous forest sites used in the carbon addition experiment were located in Fraser Experi-

mental Forest in Grand County Colorado. The elevation was 3206 m and vegetation is dominated by subalpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta* var. *latifolia*). Two-thirds of annual precipitation of 737 mm falls as snow and seasonal snow cover typically extends from October to May. Soils are classified as Podzols with the majority of carbon in the O-A horizon ($\sim$100 mm). Bulk soil carbon content was 11.6 kg m^{-2}. Soil temperature ranged between -3 and $-1\,°C$ when fluxes were measured.

The deciduous forest sites used in the carbon addition experiment were located in Routt National Forest, Routt County, Colorado at an elevation of 2850 m. Vegetation was dominated by Aspen (*Populus tremuloides*) forest. The majority of 1040 mm mean annual precipitation falls as snow and the snow cover season typically extends from early November until late May. Soils are mixed typic Cryochrepts with an O-A horizon approximately 180 mm and a bulk soil carbon content of 26.1 kg m^{-2}. Soil temperature ranged between -2 and $0\,°C$ when fluxes were measured.

Carbon isotopes and mixing-model analyses

Soil samples were separated in litter, coarse soil organic matter, and bulk soil, and homogenized using a 2 mm sieve and dried at 60 $°C$. Percent soil C and N and ^{13}C of soil, litter, and sugar were measured by EA-MS at the stable isotope laboratory, Department of Geoscience, University of Arizona, Tucson. Four replicate analyses of the added glucose indicated a $\delta^{13}C$ value of $-24.9‰$, indicating a C3 source such as beet sugar rather than the expected C4 cane sugar.

Gas samples for $\delta^{13}C$-CO_2 analyses were collected from the base of the snowpack using the pump on the IRGA and the sampling probe described above. One liter glass collection flasks were filled with helium in the lab and flushed with 1.5 L of gas sample in the field. $\delta^{13}C$-CO_2 analyses were carried out using a Micromass Mass Spectrometer (Waters, Milford, MA, USA) custom-fitted with an Optima dual inlet (Waters, Milford, MA, USA) in the stable isotope laboratory located at the Institute of Arctic and Alpine Research, University of Colorado, Boulder.

A two-component mixing model using the ^{13}C values of observed fluxes, soil carbon, and added glucose was used to calculate the relative contribution of endogenous soil carbon and sugar to the observed fluxes.

$$\% \text{soil carbon} = (\delta^{13}C\text{-}CO_2 - \delta^{13}C\text{-glucose})/(\delta^{13}C\text{-soil}^*$$
$$- \delta^{13}C\text{-glucose}) \times 100,$$

where $\delta^{13}C$-CO_2 is the isotopic signature of the CO_2 emitted from the carbon-amended plots, $\delta^{13}C$-glucose is the isotopic signature of the added glucose, and $\delta^{13}C$-soil* is the isotopic signature of endogenous soil carbon being respired. Because the bulk soil ^{13}C value is not likely to represent the labile fraction of carbon being respired, $\delta^{13}C$-soil* was estimated using the ^{13}C-CO_2 values emitted from the control plots. The contribution of glucose was then calculated by subtraction.

The $\delta^{13}C$ value of the CO_2 collected from the base of the snowpack at all control sites was enriched relative to the native soil C and litter ($-25.07‰$ and $-27.60‰$, respectively). Although micro-organisms may preferentially utilize enriched carbon sources, the primary factor in this enrichment is an increase of approximately 4.4‰ because of the faster diffusion of lighter isotopes out of the snowpack, similar to the enrichment of soil $\delta^{13}C$-CO_2 (Cerling *et al.*, 1991). Additionally, respiration itself may result in a slight fractionation of $\delta^{13}C$ values, but this shift is relatively small and variable in comparison with the enrichment during diffusion. We took a conservative approach and only corrected for enrichment during diffusion. For example, a $\delta^{13}C$ value of $-21.0‰$ measured at the base of the snowpack was assumed to arise from a carbon source with a value of $-25.4‰$.

Results

The biweekly CO_2 flux surveys conducted between January and May indicated that subnivian CO_2 efflux was significantly related to soil carbon content (Fig. 1). Mean daily CO_2 flux rates between January and May ranged from 212 to 386 mg C m^{-2} day^{-1}, placing them in the mid-range of reported CO_2 efflux rates from snow-covered soil (Sommerfeld *et al.*, 1993; Winston *et al.*, 1997; McDowell *et al.*, 2000; Suni *et al.*, 2003). Soil temperatures under the snow were between 0 and $-3\,°C$ and there was no relationship between CO_2 efflux and temperature, consistent with the previous studies of winter soil CO_2 fluxes (Sommerfeld *et al.*, 1993; Brooks *et al.*, 1997; Winston *et al.*, 1997). The lowest fluxes were associated with a coniferous forest site (soil carbon 7.8%; CO_2 flux 212 $\pm$ 37 mg C m^{-2} day^{-1}) and the highest fluxes associated with a deciduous forest/gramminoid site (soil carbon 22.2%; CO_2 flux 386 $\pm$ 40 mg C m^{-2} day^{-1}).

There was an immediate increase in subnivian CO_2 concentrations in response to the addition of labile carbon (glucose) to snow-covered soils in both deciduous and coniferous forests sites. In both ecosystems, subnivian CO_2 concentrations 24 h following the carbon additions were highest at the carbon-amended sites, intermediate at untouched control sites, and lowest at the snow pit control sites (Fig. 2). The decrease in concentrations at the snow pit control sites highlights the effect of the sugar on *in situ* soil respiration. The removal of snow cover both introduced atmospheric air with a
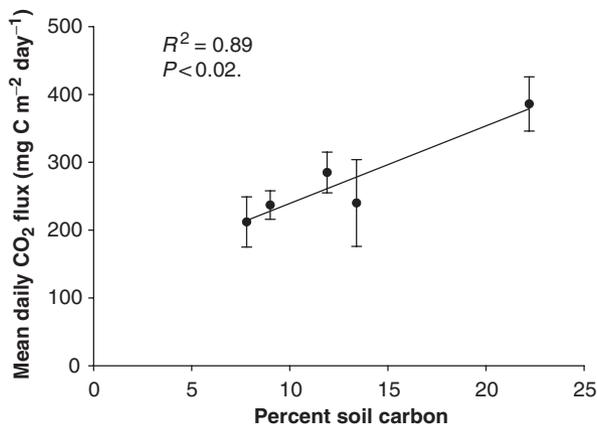
Fig. 1 Relationship between overwinter CO_2 flux and soil carbon content along five 1 km transects in Summit Country, CO. CO_2 fluxes were measured approximately biweekly between January and May at 10 locations along each transect. Error bars represent standard deviation of 10 measurements.
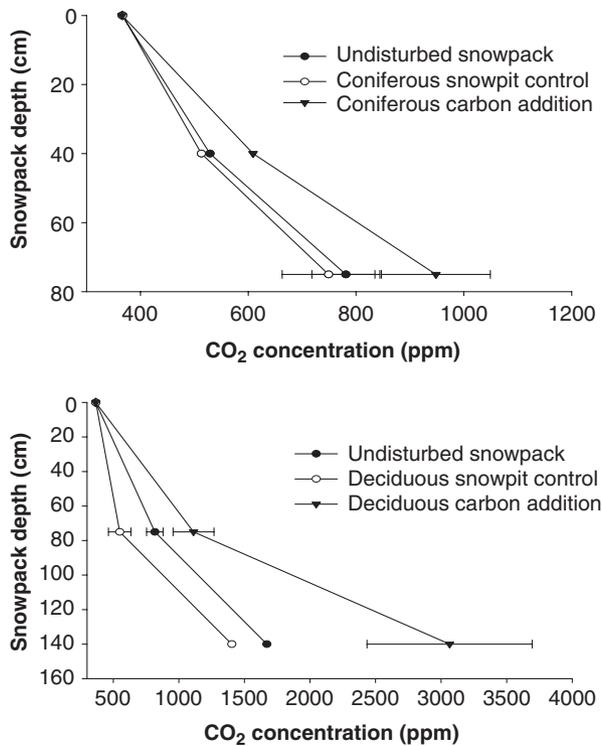
Fig. 2 CO_2 concentration profiles within the snowpack 24 h following carbon addition to subnivian soils in coniferous forest (top) and deciduous forest (bottom).

CO_2 concentration near ambient (approximately 372 ppm) to the soil surface and chilled the soil surface both of which would be expected to reduce CO_2 concentrations at the base of the snowpack. Consequently, the gradients measured after 24 h had to develop within that period and represent the evasion of new CO_2 from the soil into the snowpack.
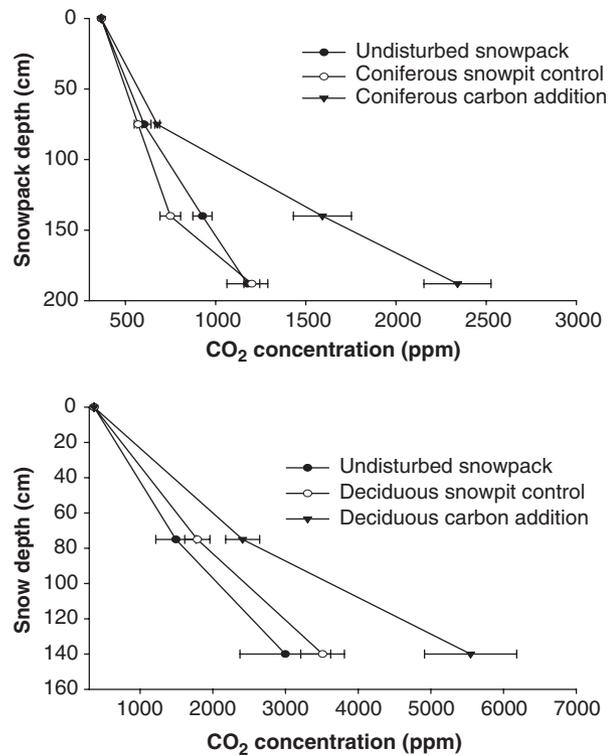
Fig. 3 CO_2 concentration profiles within the snowpack 30 days following carbon addition to subnivian soils in coniferous forest (top) and deciduous forest (bottom).

After 30 days CO_2 concentrations remained elevated at the carbon addition sites while there were no differences in concentrations between snow pit and untouched controls (Fig. 3). The break in slope in the upper portion of CO_2 concentration profiles reflects atmospheric mixing and pressure pumping affecting CO_2 concentrations in the upper 20–40 cm of the snowpack, with concentration gradients in the lower portion of the snowpack resulting from diffusion (Massman *et al.*, 1997). The mass-specific linear diffusion distance for CO_2 is approximately 219 cm day^{-1} for $^{12}CO_2$ and 216 cm day^{-1} for $^{13}CO_2$, which corrected for snowpack properties, yields a vertical transport rate of roughly 100–125 cm day^{-1} for these sites indicating that CO_2 at the base of the snowpack represents from new soil evasion.
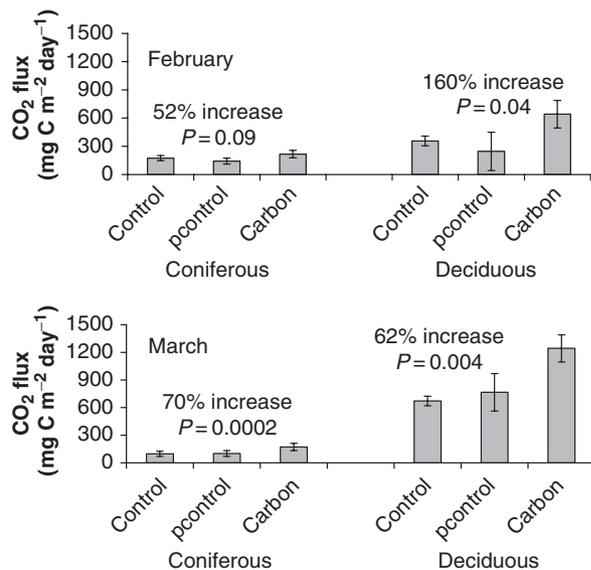
Fluxes of CO_2 from beneath snowpacks in coniferous and deciduous forests sites were 52–160% higher than snow pit control plots 24 h following the addition of carbon (Fig. 4). Snow pit control plots exhibited fluxes that were 18–32% lower than untouched controls reflecting the disturbance of removing and replacing the snow cover. Fluxes at the carbon-amended sites remained 70% higher in the coniferous forest and 62% higher in the deciduous forest than their respective control sites 30 days after addition. Fluxes at the deciduous forest sites were higher in March than in

the same treatment in February. In contrast, fluxes at all coniferous forest sites were lower in March than at the same treatment locations in February.

The isotopic signature of the $\delta^{13}C$-CO_2 measured at the base of the snowpack following carbon addition reflected a shift to active heterotrophic utilization of the added substrate (Table 1). One day after the manipulations there was a slight increase in the $\delta^{13}C$ values at the snow pit control sites but a decrease in $\delta^{13}C$ values at the carbon addition sites when compared with values from the base

Fig. 4 The response of subnivian soil respiration to experimental additions of carbon top panel is 24 h after addition; bottom panel is 30 days after addition; control refers to undisturbed natural snowpacks, pcontrol refers to snow-removal control, carbon refers to the soil that received carbon additions; values are the mean and standard deviation of three measurements. P-values refer to significant differences between snow-removal control and carbon-amended plots. The decreases at the snow-removal control sites after 24 h was not significant.

of a natural snowpack. The small increase at the snow pit control sites may be because of a shift in substrate utilization following disturbance, or more likely the short-term entrainment of a small amount of ambient air (with a $\delta^{13}C$ of approximately -8‰) in the disturbed snow-pack. In contrast, $\delta^{13}C$ values at the carbon-amended sites were 2.75–4.0‰ lower, reflecting utilization of the added carbon. After 30 days there was no difference between the $\delta^{13}C$ of the CO_2 at the base of the undisturbed and snow pit control sites, but the carbon-amended sites both had values shifted toward the added glucose reflecting the contribution of the added carbon to CO_2 flux.

We calculated the contribution of the added carbon substrate to the observed fluxes with a two-component mixing model that used the $\delta^{13}C$ of the added carbon and the $\delta^{13}C$ of natural soil carbon source in the control plot (calculated by subtracting the 4.4‰ fractionation factor from the measured $\delta^{13}C$-CO_2) as end members. These analyses indicated that the added carbon was the source of 53% of the CO_2 efflux 24 h after substrate addition at the coniferous forest sites, and 70% (coniferous) to 79% (deciduous) of the total CO_2 flux after 30 days (Table 1). The increasing utilization of glucose over the 30 days may indicate either growth of *in situ* organisms or a switch of subnivian community composition.

Discussion

These results provide conclusive evidence that active respiration in soils at or below $0\,^\circ C$ contributes to winter CO_2 efflux. This should not be surprising in that patterns of CO_2 flux in response to freeze events, changes in microbial biomass over winter, laboratory experiments, and isotopic tracers all provide strong circumstantial evidence for active, *in situ* respiration (Brooks *et al.*, 1996, 1997, 1999; Schimel & Clein 1996; Winston *et al.*, 1997). Winter CO_2 fluxes have been documented in a range of ecosystems, but it was not known if this carbon loss resulted from CO_2 trapped within the soil, root respira-

Table 1 $\delta^{13}C$ values of CO_2 emitted from snow-covered soils (corrected for fractionation because of diffusion as described in methods) and contributions to measured CO_2 flux from the added glucose and from soil organic matter (SOM); contributions were calculated using a two component mixing model with the $\delta^{13}C$ values of the added glucose (-24.9‰) and of snow pit control CO_2 as end members

	$\delta^{13}C$-CO_2 undisturbed control plots	$\delta^{13}C$-CO_2 snow pit control plots	$\delta^{13}C$-CO_2 amended plots	% CO_2 flux from glucose	% CO_2 flux from SOM
24 h after C addition					
Coniferous	-21.07 (0.80)	-19.50 (0.29)	-22.25 (0.12)	53	47
Deciduous	-25.15 ()	-22.19 (0.03)	-26.21 (0.28)	??	??
30 days after C addition					
Coniferous	-23.01 (0.11)	-22.81 (0.03)	-24.28 (0.13)	71	30
Deciduous	-25.43 (0.01)	-25.58 (0.02)	-25.01 (0.01)	79	21

?? cannot be calculated because the $\delta^{13}C$-CO_2 value from the amended plot is outside of the range of the two end members.
Values are mean (standard deviation).

tion, *in situ* active heterotrophic respiration, or a combination of all three. The large, rapid, and sustained increase in CO_2 fluxes in response to the carbon addition can only be explained by increased soil respiration. Similar to reports for the growing season (Melillo *et al.*, 2002), this winter soil respiration is carbon limited and can respond rapidly to increased labile carbon availability. The decrease in CO_2 fluxes in response to a short-term removal of the snowpack supports the suspected importance of consistent snow cover to winter biogeochemical cycling (Brooks *et al.*, 1997; Groffman *et al.*, 2001) and provides an additional mechanism (timing of snow cover) for incorporating winter respiration into biogeochemical models.

Three processes explain the enriched (relative to soil) $\delta^{13}CO_2$ values from winter respiration. Preferential utilization and respiration of labile, isotopically heavier carbon compounds in soil organic matter result in an enrichment on the order of 2–4‰ (Kaiser *et al.*, 2001; Cleveland *et al.*, 2004); water stress in surrounding trees may enrich the $\delta^{13}C$ of root respiration and finally, widespread mixing or entrainment of atmospheric CO_2 with CO_2 at the base of the snowpack. Mixing of atmospheric air is unlikely because of the strong CO_2 concentration gradients (4–52 ppmv cm^{-1}) through the snowpack coupled with evidence that pressure and wind-driven fluctuations in snowpack gas concentrations do not propagate to the depths of these snowpacks (Massman *et al.*, 1997). Similarly, entrainment is unlikely except for immediately following snow pit excavation. Comparison between the untouched controls and the snow-removal controls indicates that after 24 h there was a 1.5–2.9‰ enrichment at the snow pit control plots relative to untouched controls that could be because of entrainment of atmospheric air. Irrespective of the causes for the enriched $\delta^{13}C$-CO_2

Table 2 Reported values of net ecosystem carbon exchange (NEE) for seasonally snow-covered forests at sites with at least 12 months of continuous measurements; negative values indicate a net uptake of carbon by the ecosystem

Location	Ecosystem	NEE (g C m^{-2} yr^{-1})	Citation
Colorado, Niwot	Coniferous	−58	Monson *et al.* (2002)
		−81	
Finland*	Coniferous	−235	Suni *et al.* (2003)
		−233	
		−186	
		−157	
Canada, Boreas	Coniferous	19	Goulden *et al.* (1998)
		19	
		−40	
		72	
Germany 1	Coniferous	−77	Valentini *et al.* (2000)
Sweden 2	Coniferous	−190	Valentini *et al.* (2000)
Finland 1	Coniferous	−245	Valentini *et al.* (2000)
Sweden 1	Coniferous, mixed	90	Valentini *et al.* (2000)
		−5	
		80	
Canada, Mer Bleue	Deciduous/bog	278	Lafleur *et al.* (2003)
		−254	
		−251	
		−37	
Canada, Camp Borden	Mixed/deciduous	−60	Barr *et al.* (2002)
		−240	
		−170	
Canada, Old Aspen	Deciduous	−70	Barr *et al.* (2002)
		−120	
		−270	
Maine, Howland	Mixed	−210	Hollinger *et al.* (1999)
Wisconsin, Willow Creek	Deciduous	−167	Curtis *et al.* (2002)
Michigan, UMBS	Mixed	−220	Curtis *et al.* (2002)
France 1	Deciduous	−220	Valentini *et al.* (2000)
		−260	
Denmark 1	Deciduous	−90	Valentini *et al.* (2000)
		−170	
		−130	
Iceland 1	Deciduous	−100	Valentini *et al.* (2000)

*Calculated based on growing season uptake and average winter release.

Table 3 Reported values of winter CO_2 flux from seasonally snow-covered forests

Location	Ecosystem	Winter CO_2 efflux ($g\,C\,m^{-2}\,yr^{-1}$)	Citation
Colorado, Niwot	Coniferous	143	Monson *et al.* (2002)
		145	
Finland	Coniferous	60–90	Suni *et al.* (2003)
Colorado	Coniferous	45	Brooks *et al.* (1999)
Wyoming, GLEES	Coniferous	110	Sommerfeld *et al.* (1993)
Canada, Boreas	Coniferous	40–55	Winston *et al.* (1997)
Idaho	Coniferous	132	McDowell *et al.* (2000)
Canada, Mer Bleue	Deciduous/bog	119	Lafleur *et al.* (2003)
		89	
		132	
		127	
Colorado	Deciduous/meadow	81	Brooks *et al.* (1999)
Wyoming, GLEES	Deciduous/meadow	152	Sommerfeld *et al.* (1993)

values, the physical factors that affect the δ^{13}C-CO_2 values in the substrate-amended plots also affect the snow pit control plots allowing direct comparisons between the treatment and snow-removal controls.

Combined with recent research that has demonstrated that both fungal (Schadt *et al.*, 2003) and bacterial (Brooks *et al.*, 1996; Lipson *et al.*, 2000) biomass values are higher in snow-covered soils than in summer, these findings complicate predictions of how climate change in northern latitudes will affect ecosystem carbon balance. The primary control on winter soil heterotrophic activity is the presence of a snow cover of sufficient depth to insulate soils from extreme atmospheric temperatures (Brooks *et al.*, 1997). Climate variability drives a complex relationship between snowpack depth, extent, and duration, which are coupled to winter soil temperature regimes, free water, and the potential for winter heterotrophic activity. If an insulating snowpack is present, the secondary control on heterotrophic activity appears to be carbon availability. This activity is of sufficient magnitude and variability to warrant inclusion into biogeochemical models to improve future predictions of carbon balance.

To provide context for the potential importance of increased winter CO_2 efflux on the terrestrial carbon cycle in northern forests, we compiled recently published values for winter CO_2 fluxes and annual (12 months rather than growing season only) NEE values for coniferous and deciduous forests subject to seasonal snow cover (Table 2). Mean NEE for primarily deciduous forests ($-165\,g\,C\,m^{-2}\,yr^{-1}$, SD = 78, $n = 19$) was larger and less variable than for primarily coniferous forests ($-79\,g\,C\,m^{-2}\,yr^{-1}$, SD = 119, $n = 17$). Similarly, winter CO_2 fluxes were larger and less variable in deciduous forests ($117\,g\,C\,m^{-2}\,yr^{-1}$, SD = 27, $n = 6$) than in coniferous forests ($88\,g\,C\,m^{-2}\,yr^{-1}$, SD = 38, $n = 11$) (Table 3). On average, failing to account for winter CO_2 fluxes would result in an overestimation of annual NEE of 71%

in deciduous forests (-244 vs. $-165\,g\,C\,m^{-2}$) and 111% in coniferous forests (-167 vs. $-79\,g\,C\,m^{-2}$). Too little is known about respiration at temperatures below 0 °C to predict with any certainty that longer growing seasons or more severe autumn soil frosts will promote increases in winter respiration similar to the results observed with carbon additions in this study. However, the high levels of activity and sensitivity to substrate availability suggest that the subnivian heterotrophic community has the potential to affect ecosystem carbon exchange directly through the mineralization of organic matter or indirectly through changes in timing of heterotrophic activity, carbon mineralization and associated nutrient cycling.

Ultimately, understanding the effects of climate change on carbon balance in northern forests will require identifying feedbacks between growing season and winter biogeochemical cycles. Both longer growing seasons and more frequent or severe soil frosts have the ability to increase carbon availability going into the winter. Low temperatures and the absence of a temperature–CO_2 flux relationship present difficulties in incorporating the effects of increased carbon availability into current biogeochemical models. Measurements and modeling of snow cover, soil temperature, and free water availability during the winter can determine the potential for active respiration to occur, while the strong relationship between soil carbon and CO_2 efflux and the immediate response of subnivian respiration to added carbon provide starting points for developing a mechanistic understanding of feedbacks between growing season processes and the magnitude of winter soil respiration.

References

Barr AG, Griffis TJ, Black TA *et al.* (2002) Comparing the carbon budgets of boreal and temperate deciduous forest stands. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **32**, 813–822.

Black TA, Chen WJ, Barr AG *et al.* (2000) Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophysical Research Letters*, **27**, 1271–1274.

Brooks PD, McKnight DM, Bencala KE (1999) The relationship between soil heterotrophic activity, soil dissolved organic carbon (DOC) leachate, and catchment-scale DOC export in headwater catchments. *Water Resources Research*, **35**, 1895–1902.

Brooks PD, Schmidt SK, Williams MW (1997) Winter production of CO_2 and N_2O from alpine tundra: environmental controls and relationship to inter-system C and N fluxes. *Oecologia*, **110**, 403–413.

Brooks PD, Schmidt SK, Williams MW (1996) microbial activity under alpine snowpacks, Niwot Ridge, Colorado. *Biogeochemistry*, **32**, 92–113.

Cerling TE, Solomon DK, Quade J *et al.* (1991) On the isotopic composition of carbon in soil carbon-dioxide. *Geochimica Et Cosmochimica Acta*, **55**, 3403–3405.

Cleveland CC, Neff JC, Townsend AR *et al.* (2004) Composition, dynamics, and fate of leached dissolved organic matter in terrestrial ecosystems: results from a decomposition experiment. *Ecosystems*, **7**, 275–285.

Curtis PS, Hanson PJ, Bolstad P *et al.* (2002) Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agricultural and Forest Meteorology*, **113**, 3–19.

Edwards AMC, Cresser MS (1992) In *Advances in Soil Science* (ed. Stewart BA), pp. 59–79. Springer-Verlag, New York, NY.

Goulden ML, Wofsy SC, Harden JW *et al.* (1998) Sensitivity of boreal forest carbon balance to soil thaw. *Science*, **279**, 214–217.

Groffman PM, Driscoll CT, Fahey TJ *et al.* (2001) Colder soils in a warmer world: a snow manipulation study in a northern hardwood forest ecosystem. *Biogeochemistry*, **56**, 135–150.

Hollinger DY, Goltz SM, Davidson EA *et al.* (1999) Seasonal patterns and environmental control of carbon dioxide and water vapour exchange in an ecotonal boreal forest. *Global Change Biology*, **5**, 891–902.

Kaiser K, Guggenbergre G, Zech W (2001) Isotopic fractionation of dissolved organic carbon in shallow forest soils as affected by sorption. *European Journal of Soil Science*, **52**, 585–597.

Kimball JS, Keyser AR, Running SW *et al.* (2000) Regional assessment of boreal forest productivity using an ecological process model and remote sensing parameter maps. *Tree Physiology*, **20**, 761–775.

Lafleur PM, Roulet NT, Bubier JL, Frolking S, Moore TR (2003) Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. *Global Biogeochemical Cycles*, **17**, 1036, doi: 10.1029/2002GB001983.

Lipson DA, Schmidt SK, Monson RK (2000) Carbon availability and temperature control the post-snowmelt decline in alpine soil microbial biomass. *Soil Biology & Biochemistry*, **32**, 441–448.

Liski J, Perruchoud D, Karjalainen T (2002) Increasing carbon stocks in the forest soils of western Europe. *Forest Ecology and Management*, **169**, 159–175.

Lloyd J, Shibistova O, Zolotoukhine D *et al.* (2002) Seasonal and annual variations in the photosynthetic productivity and carbon balance of a central Siberian pine forest. *Tellus Series B – Chemical and Physical Meteorology*, **54**, 590–610.

Luo YQ, White LW, Canadell JG *et al.* (2003) Sustainability of terrestrial carbon sequestration: a case study in Duke Forest with inversion approach. *Global Biogeochemical Cycles*, **17**, art. no. 1021, doi: 10.1029/2002GB001923.

Massman WJ, Sommerfeld RA, Mosier AR *et al.* (1997) A model investigation of turbulence-driven pressure-pumping effects on the rate of diffusion of CO_2, N_2O, and CH_4 through layered snowpacks. *Journal of Geophysical Research-Atmospheres*, **102**, 18851–18863.

McDowell NG, Marshall JD, Hooker TD *et al.* (2000) Estimating CO_2 flux from snowpacks at three sites in the Rocky Mountains. *Tree Physiology*, **20**, 745–753.

Melillo JM, Steudler PA, Aber JD *et al.* (2002) Soil warming and carbon-cycle feedbacks to the climate system. *Science*, **298**, 2173–2176.

Monson RK, Turnipseed AA, Sparks JP *et al.* (2002) Carbon sequestration in a high-elevation, subalpine forest. *Global Change Biology*, **8**, 459–478.

Oechel WC, Vourlitis GL, Hastings SJ *et al.* (2000) Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. *Nature*, **406**, 978–981.

Schadt CW, Martin AP, Lipson DA *et al.* (2003) Seasonal dynamics of previously unknown fungal lineages in tundra soils. *Science*, **301**, 1359–1361.

Schimel DS, House JI, Hibbard KA *et al.* (2001) Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature*, **414**, 169–172.

Schimel JP, Clein JS (1996) Microbial response to freeze–thaw cycles in tundra and taiga soils. *Soil Biology & Biochemistry*, **28**, 1061–1066.

Schlesinger WH, Lichter J (2001) Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO_2. *Nature*, **411**, 466–469.

Sommerfeld RA, Mosier AR, Musselman RC (1993) CO_2, CH_4, and N_2O flux through a Wyoming snowpack. *Nature*, **361**, 140–142.

Suni T, Berninger F, Markkanen T *et al.* (2003) Interannual variability and timing of growing-season CO_2 exchange in a boreal forest. *Journal of Geophysical Research-Atmospheres*, **108**.

Valentini R, Matteucci G, Dolman AJ *et al.* (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.

Winston GC, Sundquist ET, Stephens BB *et al.* (1997) Winter CO_2 fluxes in a boreal forest. *Journal of Geophysical Research – Atmospheres*, **102**, 28795–28804.