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Winter production of CO_2 and N_2O from alpine tundra: environmental controls and relationship to inter-system C and N fluxes

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Abstract Fluxes of CO_2 and N_2O were measured from both natural and experimentally augmented snowpacks during the winters of 1993 and 1994 on Niwot Ridge in the Colorado Front Range. Consistent snow cover insulated the soil surface from extreme air temperatures and allowed heterotrophic activity to continue through much of the winter. In contrast, soil remained frozen at sites with inconsistent snow cover and production did not begin until snowmelt. Fluxes were measured when soil temperatures under the snow ranged from –5°C to 0°C, but there was no significant relationship between flux for either gas and temperature within this range. While early developing snowpacks resulted in warmer minimum soil temperatures allowing production to continue for most of the winter, the highest CO_2 fluxes were recorded at sites which experienced a hard freeze before a consistent snowpack developed. Consequently, the seasonal flux of CO_2—C from snow covered soils was related both to the severity of freeze and the duration of snow cover. Over-winter CO_2—C loss ranged from 0.3 g C m^{-2} season^{-1} at sites characterized by inconsistent snow cover to 25.7 g C m^{-2} season^{-1} at sites that experienced a hard freeze followed by an extended period of snow cover. In contrast to the pattern observed with C loss, a hard freeze early in the winter did not result in greater N_2O—N loss. Both mean daily N_2O fluxes and the total over-winter N_2O—N loss were related to the length of time soils were covered by a consistent snowpack. Over-winter N_2O—N loss ranged from less 0.23 mg N m^{-2} from the latest developing, short duration snowpacks to 16.90 mg N m^{-2} from sites with early snow cover. These data suggest that over-winter heterotrophic activity in snow-covered soil has the potential to mineralize from less than 1% to greater than 25% of the carbon fixed in ANPP, while over-winter N_2O fluxes range from less than half to an order of magnitude higher than growing season fluxes. The variability in these fluxes suggests that small changes in climate which affect the timing of seasonal snow cover may have a large effect on C and N cycling in these environments.

Key words Trace gas flux · Carbon dioxide · Nitrous oxide · Snow cover

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Introduction

Identifying the sources and sinks of both CO_2 and N_2O has been the focus of considerable research over the last decade. Notably absent from this work has been a concerted effort to quantify non-growing season fluxes from seasonally snow-covered systems. Approximately 50% of the Northern Hemisphere experiences a significant snow-covered season, including both high-elevation and high-latitude ecosystems which are dominated by extended periods of snow cover. Recent work from a number of locations has identified significant fluxes of CO_2 from beneath snowpacks in arctic (Zimov et al. 1991), alpine (Brooks et al. 1995, 1996), and forested ecosystems (Sommerfeld et al. 1993; Wickland et al. 1995; Winston et al. 1995). These studies suggest that subnivian heterotrophic activity may be a significant component of the annual carbon cycle in seasonally snow covered systems. Similarly, global models of atmospheric CO_2 concentrations suggest soils continue to produce CO_2 throughout the winter, contributing to the observed winter CO_2 maximum (Raich and Potter 1995). However, the spatial and temporal variability as well as the environmental controls on these fluxes are unknown.

The timing and depth of snowfall in areas characterized by extended periods of snow cover are known to exert significant controls on species composition, primary production, and biogeochemical cycles during the growing season (Oberbauer and Billings 1981; Walker et al. 1993b). Similarly, seasonal snowpacks have the potential to affect biogeochemical processes by insulating the soil surface from extreme air temperatures and allowing soil microbial activity to continue while vegetation is dormant (Fahey 1971; Sommerfeld et al. 1993; Brooks et al. 1996). Microbial activity is known to occur within the range of temperatures found under seasonal snowpacks (Benoit et al. 1972; Coxson and Parkinson 1987), and most microbial exoenzymes remain structurally intact after freezing and have the ability to remain active at these temperatures (McClaugherity and Linkins 1990).

While soil microbial activity during the growing season is strongly related to soil moisture and temperature (VanCleve et al. 1983; Fisk and Schmidt 1995), the controls on heterotrophic activity during the winter are unknown. Seasonal and diurnal variations in the physical environment of soil (e.g., temperature and moisture) that characterize the growing season are absent during the winter. Snow cover greatly reduces energy exchange at the soil/snow interface (Cline 1995), and soil moisture remains relatively constant until the initiation of snowmelt (Cline 1995; Brooks et al. 1996). As free water becomes available in the soil, temperature is buffered within a narrow range slightly below 0°C, potentially for many months (Edwards and Cresser 1992; Sommerfeld et al. 1993). In systems characterized by extended periods of snow cover, this relatively homogenous environment may last significantly longer than the growing season.

Very little work has been done to quantify N_2O flux from these environments during the snow-covered season. Williams et al. (1995) have suggested that N_2O flux is not a significant component of alpine N cycling in the Sierra Nevada. In contrast, winter N_2O fluxes from both alpine (Sommerfeld et al. 1993) and subalpine (Mosier et al. 1993) sites in Wyoming are similar to growing season fluxes, and may equal 25% of atmospheric NO_3—N deposition. We have measured similar fluxes on Niwot Ridge (Brooks et al. 1996), yet none of these studies have described the natural variability or identified controls on this flux.

This study was designed to identify the spatial and temporal variability of both CO_2 and N_2O flux from beneath seasonal snow packs, and to evaluate the controls on this activity with respect to the depth and timing of snowpack accumulation. Specifically, CO_2 and N_2O fluxes from beneath natural and experimentally augmented snowpacks were measured for two years in an experiment designed to answer two questions.

1. How are fluxes of CO_2 and N_2O related to the depth and timing of snowpack accumulation?
2. Are winter fluxes of these gases a significant fraction of the annual fluxes of C and N in these systems?

Materials and methods

Study site

This work was conducted at Niwot Ridge, Colorado (40°03′N, 105°35′W), located in the Front Range of the Rocky Mountains approximately 5 km east of the Continental Divide. This site is a UNESCO Biosphere Reserve and an NSF-funded long-term ecological research site with long-term records of climate, hydrology, primary production, and trace gas flux. The climate is characterized by long, cold winters and short, cool growing seasons. Mean annual temperature is –3°C, annual precipitation is 1050 mm (Williams et al. 1996), the majority of which falls as snow (Greenland 1989). All sites were located on Niwot Saddle, an area of intensive research at an elevation of 3510 m. Soils are cryochrepts and vary in depth from approximately 0.3 to 2.0 m overlying granitic parent material (Burns 1980). Soil pH ranges from 4.6 to 5.0 and all sites are completely above treeline. Vegetation at the shallow snowpack and snow fence augmented sites is dominated by the gramminoid *Kobresia myosuroides* with patchy occurrence of communities dominated by the forb *Acomostylis rossii* and the gramminoid *Deschampsia caespitosa* in protected microsites (Walker et al. 1993a). Vegetation at the naturally deep snowpack sites is dominated by *A. rossii* and *D. caespitosa*, with patchy occurrence of *K. myosuroides*.

Soils typically freeze in early winter before a continuous snowpack develops (Brooks et al. 1996). The scouring and redeposition of snow by wind characterizes the pattern of snowpack accumulation with a continuous snow cover typically developing in October or November at the naturally deep snowpack sites and in January at the naturally shallow snowpack sites used in this study.

Methods

Flux measurements were made at two naturally shallow snowpack sites (maximum depth less than 1 m) during the winter of 1992–1993 (referred to as the 1993 season), and three naturally shallow, three naturally deep (maximum depth 1.5–2.0 m), and three experimentally deepened snowpack sites during the winter of 1993–1994 (referred to as the 1994 season). The experimentally deepened snowpack resulted from a 2.6 m by 60 m snow fence constructed during October 1993 and described in detail elsewhere (Walker et al. 1993a; Brooks et al. 1995). One of the shallow snowpack sites in 1993 was in an area expected to be within the snow fence drift and the other was established in area well outside the expected drift. Each site was approximately 10 m^2 and contained three gas collectors at the soil surface for replicate measurements. One shallow site from the 1993 season was within the snow fence drift in 1994 and was used as one of the three snow fence sites. The second site from the 1993 season was outside the drift in 1994 and was included as one of the three shallow sites.

Carbon dioxide flux, N_2O flux, snowpack depth and density, soil surface temperature, and depth of thawed soil were measured monthly during January and February, and then bi-weekly to weekly until sites were snow free during the winters of 1993 and 1994. Gas samples were collected for CO_2 and N_2O concentrations in the atmosphere above the snowpack and at the soil-snow interface using the method of Sommerfeld et al. (1993). After a continuous snowpack developed at each site a snow pit was dug to the soil surface and gas collectors were placed at the base of the snowpack in an undisturbed area of snow at the edge of the pit and the pit was refilled. Collectors were constructed from 10-mm thick sections of stainless steel pipe (100 mm diameter). The open ends of these short sections of pipe were covered with 50-µm stainless steel mesh designed to exclude snow but permit the passage of gases (Sommerfeld et al. 1991). Each collector was connected to a sampling valve located above the snow surface by 1.6 mm (internal diameter) teflon tubing. Valves were closed between sample collection to prevent mixing of atmospheric and snowpack air. Collectors were not sampled for the first 30 days after installation to avoid effects from soil or snowpack disturbance or during the final days of snow melt when the snowpack became saturated and collectors filled with water. All samples were collected in glass syringes and analyzed by gas chromatography (Hewlett-Packard 5880A) at the University of Colorado Mountain Research Station within 24 h. Soil temperature was measured using thermistors installed during the autumn as the seasonal snowpack developed. The depth of thawed soil and gravimetric soil moisture were measured at the base of snowpits dug in areas of similar snow depth 5–10 m from the gas collectors.

Fluxes of CO_2 and N_2O through the snowpack were calculated using Fick's law.

$$J_g = D_g(d[g]/dz)tf$$

where: J_g is the gas flux, D_g is a diffusion coefficient, $[g]$ is measured gas concentration, z is the depth of the snowpack, t is tortuousity, and f is the snowpack porosity. The diffusion coefficient D_g for both CO_2 and N_2O in air is 0.139 $cm^2\ s^{-1}$, consistent with previous research on trace gas flux through snow (Solomon and Cerling 1987; Sommerfeld et al. 1993). Gas concentrations above the snowpack and at the snow/soil interface were used to calculate the vertical concentration gradient. Fluxes were calculated only when gas concentrations at the soil surface and the snow surface were significantly different from each other. Flux was assumed to be zero when concentrations were not significantly different. Snow depth was measured manually at each sampling site using a graduated snow probe. Snow density was obtained from snowpits dug at biweekly intervals and measured in 10-cm increments from the top to the bottom of the snowpack (Williams et al. 1996). Porosity was calculated as the inverse of snowpack density. Tortuousity varies weakly as a function of density and was estimated as $f^{1/3}$ (Striegl 1993).

While gas transport may be expected to vary with changes in snow density, the absence of melt freeze cycles during the winter in these ecosystems results in snow density that varies over a relatively narrow range. Consistent with this observation, a number of studies in the Rocky Mountains have shown that measured CO_2 and N_2O concentration gradients within the snowpack are not significantly different from diffusional gradients calculated using gas concentrations at the snowpack-atmosphere and snowpack-soil interface (Mast and Clow 1994; Massman et al. 1995). Perhaps more important than snowpack density in controlling gas flux through the snowpack are short-term pressure fluctuations at the snowpack surface. Recent research has suggested that the simple diffusion model may under-estimate flux by as much as 30%, primarily due to these pressure fluctuations at the snow surface (Massman et al. 1995). In the absence of independent confirmation of these effects we have chosen to use the more conservative model in our calculations. Recently, Sommerfeld et al. (1996) have suggested the accuracy of this method for flux calculation through snow is ± 11%.

Most statistical analyses were performed using BLSS, the Berkeley Interactive Statistical System (release 4.1, 1989) run on a Sun workstation. Differences between the snowpack regimes were determined using a one-way ANOVA followed by protected t-tests. Regressions were performed using Quattro Pro and Slidewrite + on a personal computer.

Results

The natural inter-annual variability in snowpack accumulation between the two years, together with the construction of the snow fence, resulted in four different snowpack regimes for this study: (1) shallow snowpack, moderate duration (1993); (2) shallow snowpack, short duration (1994); (3) naturally deep snowpack, long duration (1994); and (4) artificially deep snowpack, long duration (1994) (Table 1). The two shallow, moderate duration sites in 1993 had a consistent snow cover lasting 155 days. In contrast, the natural snowpack developed much later and melted earlier in this area in 1994 and the three shallow, short duration sites had a consistent snow cover for only 61 days. The sites behind the snow fence (artificially deep, long duration) in 1994 had consistent snow cover for 201 days, while the naturally deep sites were snow-covered for 208 days. At both naturally deep snowpack and snowfence sites the longer period of snow cover was due to earlier accumulation rather than delayed melt.

Snowpack density gradually increased over the course of each winter season, however these changes were relatively small until the latter portion of snow melt when gas collectors flooded and measurements were not made. Mean snowpack density during the period when fluxes were measured was 0.379 g cm^{-3} (SD 0.047) in 1993 and 0.404 g cm^{-3} (SD 0.060).

Although soil at all sites was frozen by 1 November in both years, the timing of snow cover controlled the severity of soil frost. The minimum soil surface temperature of −14°C at the shallow sites in 1993 was much colder than the minimum temperatures of −6.5°C to −7.5°C at the deep and snow fence sites in 1994, or −11°C at the shallow sites in 1994 (Table 1). Once covered by a consistent snow cover, soils gradually warmed and thawed soil was observed when soil temperatures reached −5°C. Soil temperatures remained between −5°C and −0.5°C until snowmelt when all soils reached 0°C. At all sites, thawed soil before melt was restricted to the upper, organic soil horizons, resulting in a 3- to 8-cm layer of thawed soil over frozen, mineral soils. This condition persisted until after snowmelt began when soils thawed completely. Gravimetric soil moisture ranged from 0.90 to 1.10 g H_2O/g soil (dry weight) until snowmelt, when soils became saturated with melt water.

Carbon dioxide concentrations at the soil-snow interface during the 1993 season were not significantly

Table 1 Physical characteristics and gas concentrations of the four snowpack regimes in this study

Site	Maximum Snow Depth	Snow Cover Duration	Minimum Soil Temperature	CO_2 Concentrations Mean	CO_2 Concentrations Range	N_2O Concentrations Mean	N_2O Concentrations Range
Shallow 1993	80	155	−14	999	447–1732	346	338–352
Shallow 1994	50	61	−11	393	375–428	334	326–345
Deep 1994	165	208	−7.5	629	382–915	366	334–420
Fence 1994	170	201	−6.5	566	383–1080	359	334–414

different than atmospheric concentrations until 4 March when the mean concentration of the six samples collected from the two shallow snowpack, moderate duration sites was 446 ppm. Concentrations increased throughout the winter reaching 1732 ppm approximately two weeks before sites were snow free (Table 1), and then decreased on the last sample date when soils were saturated with melt water. Concentrations of N_2O at the soil-snow interface were not significantly different than atmospheric concentrations until 4 April, and then increased throughout the snow-covered season (Table 1). In contrast, soil surface CO_2 concentrations of 670 ppm (snow fence) to 738 ppm (naturally deep) on 4 February 1994 already were significantly greater than atmospheric. Similarly, soil surface N_2O concentrations were above atmospheric at snow fence and deep sites on the first sample date in 1994. While mean soil surface CO_2 concentrations under both of the long duration snowpacks in 1994 were lower than under the moderate duration snowpack the previous year, mean N_2O concentrations at these sites were higher (Table 1). Both CO_2 and N_2O concentrations at the shallow site in 1994 were not significantly greater than atmospheric until after snow melt began.

Snowpack controls on flux

Within the narrow range of temperature that thawed soil was present under these snowpacks, there was no significant relationship between soil temperature and the flux of either gas (Fig. 1). However, CO_2 production was not observed when soil surface temperatures were below –5°C, the temperature at which soil began to thaw and free water became available for heterotrophic activity. This suggests that the heterotrophic activity responsible for the observed fluxes occurs in this upper soil horizon. In general, fluxes were much more variable at the warmer end of this temperature range with both the largest and smallest positive fluxes occurring between −2°C and 0°C. This suggests that factors other than temperature are important in controlling flux within this environment.

Fluxes of CO_2 from the two shallow, moderate duration snowpacks in 1993 were observed after the soil had been snow-covered for approximately 74 days, and then increased throughout the remainder of the winter until approximately 2 weeks before the sites were snow-free. While there was no significant relationship between flux and temperature, there was a significant ($P < 0.01$, $r^2 = 0.927$), exponential relationship between CO_2 flux and the number of days thawed soil was present under the snow (Fig. 2a). The lowest flux during this period, 16.4 mg C m^{-2} day^{-1}, occurred in early March, and the highest flux, 873.6 mg C m^{-2} day^{-1} occurred in May shortly after snowmelt began. The mean CO_2 production over the 81 days on which fluxes were observed at these sites was 316.7 mg C m^{-2} day^{-1} (Table 2). The flux of N_2O from these shallow, moderate snowpack duration sites began approximately 1 month after CO_2 flux was observed from the snowpack. Similar to the pattern observed with CO_2 flux, there was a significant ($P < 0.05$, $r^2 = 0.607$), exponential relationship between the mean daily N_2O flux from the snowpack and

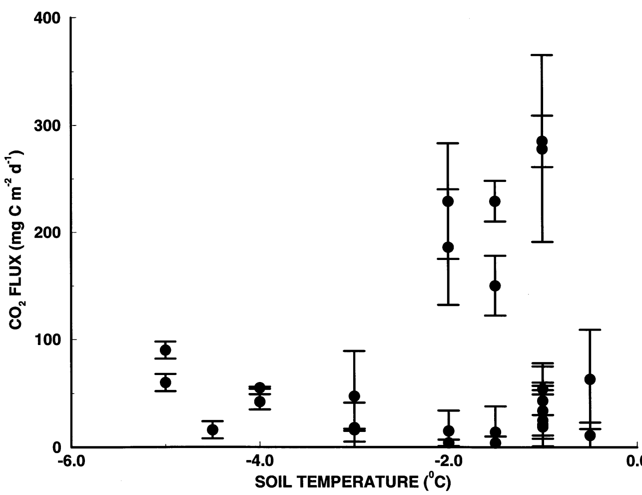

Fig. 1 Mean daily CO_2 flux and soil surface temperature for all sample dates and all sites where flux occurred before the beginning of snowmelt

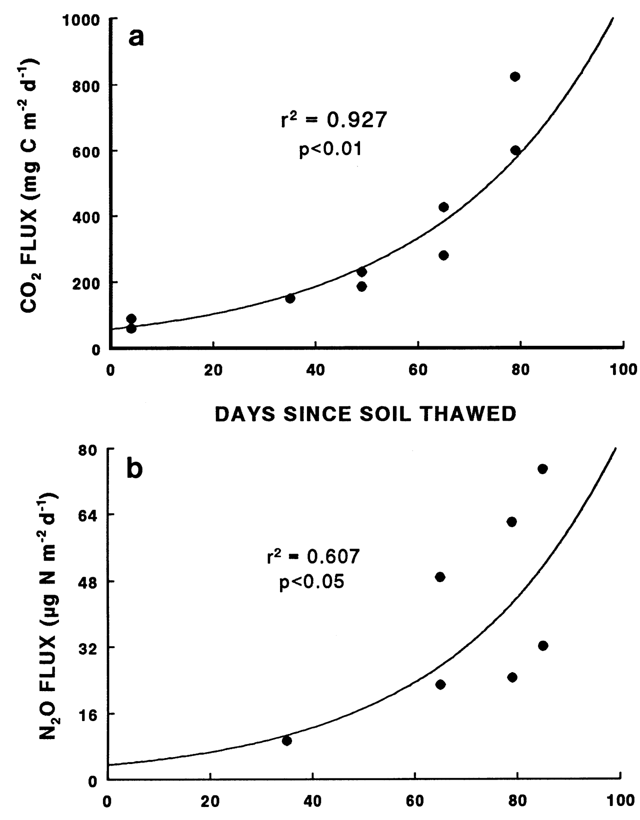

Fig. 2 Relationship between **a** the mean daily CO_2 flux and **b** mean daily N_2O flux and the number of days thawed soils were present under shallow, moderate duration snowpacks in 1993, $n = 6$

Table 2 A comparison of carbon dioxide flux estimates during the snow-covered season from Niwot Ridge, Colorado, and Glacier Lakes Ecosystem Experiments Site (GLEES), Wyoming. Seasonal flux is the product of mean daily flux and duration. Estimates of carbon inputs during the growing season are provided for comparison

Site	*Daily flux* ($mg\ C\ m^{-2}\ day^{-1}$) Mean	Range	*Seasonal Flux* ($g\ C\ m^{-2}$)	*Source*
Snow-covered Season				
Niwot Ridge				
Shallow Snowpack 1993	316.7	0–873.6	25.7	This Study
Shallow Snowpack 1994	29.6	0–36.1	0.3	This Study
Fence Snowpack 1994	59.6	1.4–355.2	11.9	This Study
Deep Snowpack 1994	86.7	15.5–475.5	16.9	This Study
GLEES				
Alpine 1991	174.0	96–444	40.9	Sommerfeld et al. 1993
Alpine 1992	204.0	84–516	47.9	Sommerfeld et al. 1993
Subalpine 1991	648.0	216–1644	152.3	Sommerfeld et al. 1993
Subalpine 1992	468.0	168–660	109.9	Sommerfeld et al. 1993
Growing Season Inputs				
Niwot Ridge Above Ground Net Primary Production				
All alpine sites	1054	88.9–2856	94.9	Walker et al. 1994
GLEES (litter fall)				
Subalpine	566	424–708	71.3	Sommerfeld et al. 1993

Table 3 A comparison of snow-covered and growing season nitrous oxide flux estimates from Niwot Ridge, Colorado, and Glacier Lakes Ecosystem Experiments Site (GLEES), Wyoming. Seasonal flux is the product of mean daily flux and duration

Site	*Daily flux* ($\mu g\ N\ m^{-2}\ day^{-1}$) Mean	Range	*Seasonal Flux* ($mg\ N\ m^{-2}$)	*Reference*
Snow-covered Season				
Niwot Ridge				
Shallow Snowpack 1993	39.7	0–78.0	2.0	This Study
Shallow Snowpack 1994	37.6	0–39.7	0.2	This Study
Fence Snowpack 1994	82.5	5.3–395.6	16.6	This Study
Deep Snowpack 1994	111.9	11.9–471.7	23.3	This Study
GLEES				
Alpine 1991	10.1	−0.8–52.6	2.5	Sommerfeld et al. 1993
Alpine 1992	9.4	−6.4–11.2	2.2	Sommerfeld et al. 1993
Subalpine 1991	23.8	6.7–65.5	5.6	Sommerfeld et al. 1993
Subalpine 1992	15.4	5.3–43.9	3.6	Sommerfeld et al. 1993
Growing Season				
Niwot Ridge				
Dry Meadow (control)	16.8	0–52.8	1.5	Neff et al. 1994
Dry Meadow (fertilized)	336.0	24–2037.6	31.1	Neff et al. 1994
Moist Meadow	24.0	0–93.4	2.2	S. Schmidt unpublished
Wet Meadow (control)	19.2	0–170.4	1.7	Neff et al. 1994
Wet Meadow (fertilized)	823.0	89–2580.0	74.1	Neff et al. 1994
GLEES				
Subalpine 1992	49.2	−19.2–864.0	6.2	Mosier et al. 1993

the number of days thawed soils were present under snow (Fig. 2b). Measured fluxes increased from 9.2 μg N_2O—N m^{-2} day^{-1} to a maximum flux of just under 78 μg N_2O—N m^{-2} day^{-1} shortly before the sites were snow-free (Table 3). The mean flux over the 50 days production was observed at these sites was 39.7 μg N_2O—N m^{-2} day^{-1}.

Although the shallow, short duration snowpacks in 1994 were in the same area as the shallow, moderate duration sites the previous year, the absence of an insulating snowpack throughout much of the winter season prevented heterotrophic activity before snowmelt. Soil at these sites did not thaw, and CO_2 flux did not occur until the spring melt. Subnivian CO_2 production was present for only 10 days until the sites were snow-free. The mean flux over this period, 29.6 mg C m^{-2} day^{-1}, was significantly lower than fluxes measured in this area the previous year. Nitrous oxide production was observed at only one of these shallow sites and, similar to CO_2, flux did not begin until after snowmelt, continuing for approximately 6 days before the sites were snow free. The measured flux at this site, 37.6 μg N_2O—N m^{-2} day^{-1}, was similar to the mean flux at shallow sites during the 1993 season, but half of the highest fluxes measured from beneath shallow snowpacks during snowmelt the previous year.

The development of a consistent snow cover early in the winter season at the snow fence and naturally deep sites allowed fluxes of both gases to begin much earlier in the snow covered season than in 1993. When collectors were installed at both snow fence and naturally deep sites between 28 December and 4 January thawed soils were observed, suggesting that CO_2 production had begun. When the first gas samples were collected on 4 February the mean CO_2 fluxes of 46.9 mg C m^{-2} day^{-1} at the naturally deep sites and 42.2 mg C m^{-2} day^{-1} at the snow fence sites were 2.5–3 times higher than the first fluxes measured during the previous season. In contrast to the pattern observed at the two sites during the 1993 season, an exponential increase in CO_2 flux was not observed over the remainder of the snow-covered season (Fig. 3a). Carbon dioxide production at both naturally deep and snow fence sites decreased between 50 and 90 days after thawed soil was first observed, and then increased dramatically shortly before and during the snowmelt season.

Nitrous oxide flux from both the naturally deep snowpack and snow fence sites in 1994 also began much earlier in the winter than in 1993. By 4 February, the mean N_2O flux was greater than 50 μg N_2O—N m^{-2} day^{-1} at both the naturally deep and snow fence sites. Production decreased in late winter, and then increased dramatically shortly before and during snowmelt (Fig. 3b). While this pattern is similar to that seen with CO_2, the decrease in N_2O flux began 3–4 weeks later in the snow-covered season than the decrease in CO_2 production. This suggests that the lower flux of both gases was due to decreased production rather than a change in the rate of transport through the snowpack. Even with the mid-winter decrease, mean fluxes for the 1994 season, 82.5 μg N_2O—N m^{-2} day^{-1} at the snow fence sites and 111.9 μg N_2O—N m^{-2} day^{-1} at the deep snowpack sites, were significantly higher than those measured in 1993 (Table 3).

Over-winter losses of CO_2 and N_2O

The total winter CO_2—C loss was controlled by both the duration and timing of snowpack accumulation. While sites characterized by shallow, short duration snowpacks exhibited the smallest seasonal C loss, the over-winter C flux from sites with longer periods of snow cover was variable with the largest seasonal loss from sites characterized by the lowest minimum soil temperature early in the winter followed by an extended period of snow cover. Multiplying the mean daily CO_2 flux for a site by the duration of flux yields estimates of the amount of carbon mineralized under snow of 0.3 g C m^{-2} for the shallow, short duration snowpack sites, 11.9 g C m^{-2} for the snow fence sites, 16.9 g C m^{-2} for the naturally deep snowpack sites, and 25.7 g C m^{-2} for the shallow, moderate duration snowpack sites (Fig. 4).

Unlike C loss, the hard freeze in 1993 did not result in an increase in over-winter N_2O—N loss. In contrast, the over-winter N_2O—N loss from these sites was more closely related to the length of time soils remained covered by a consistent snowpack than was CO_2—C loss. Multiplying the mean daily N_2O flux by the duration of

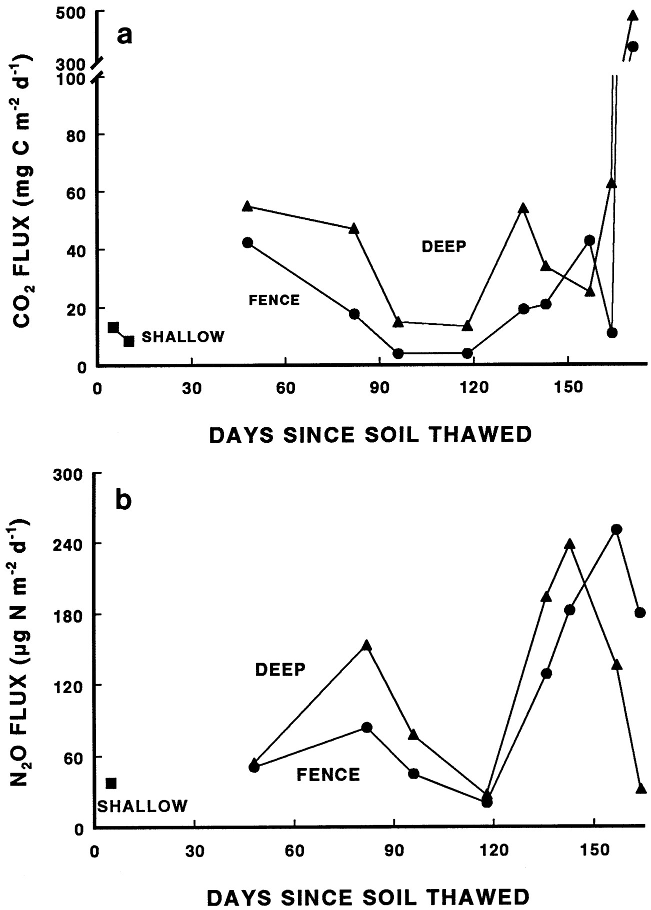

Fig. 3 Relationship between **a** the mean daily CO_2 flux and **b** mean daily N_2O flux and the number of days thawed soils were present under shallow snowpack, snow fence, and naturally deep snowpack sites in 1994, $n = 9$

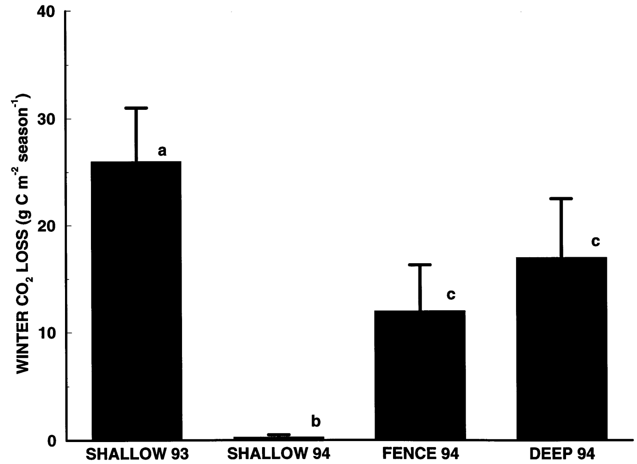

Fig. 4 Over-winter CO_2—C loss from the four snowpack regimes

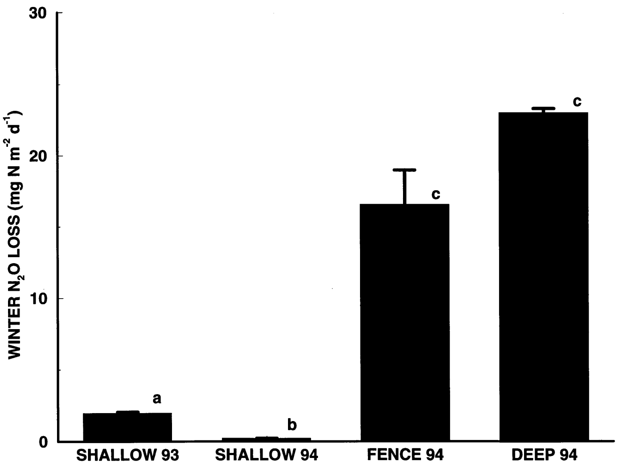

Fig. 5 Over-winter N_2O—N loss from the four snowpack regimes

flux yields winter N losses of 0.2 mg N m^{-2} for the shallow, short duration snowpack sites, 2.0 mg N m^{-2} for the shallow, moderate duration snowpack sites, 16.6 mg N m^{-2} for the snow fence sites, and 23.3 mg N m^{-2} for the naturally deep snowpack sites (Fig. 5).

Discussion

Snowpack controls on flux

A number of studies have identified CO_2 fluxes through seasonal snow cover (Solomon and Cerling 1987; Zimov et al. 1991; Sommerfeld et al. 1993, 1996; Winston et al. 1995; Brooks et al. 1996), yet the controls on heterotrophic activity under snow and even the location within the soil where this activity occurs remain unclear. Identifying the depth within the soils where this production occurs is the first step in describing controls and evaluating the importance of these fluxes to ecosystem processes. The absence of flux from our sites before surface soil thawed suggests the majority of flux from this system originates in a thin organic layer at the soil surface. In contrast, Winston et al. (1995) have suggested the source of CO_2 flux measured through snow in the boreal forest is heterotrophic activity in deeper soils. Sommerfeld et al. (1996) suggest that the early winter fluxes at two sites in Wyoming result from activity relatively deep in the soil, while production later in the snow-covered season occurs in the upper soil layers. These reports suggest that there may be at least two very different under-snow environments, and it is important to consider the major differences between these systems. Deeper soils are less subject to temperature fluctuations than surface soils and the carbon pools for heterotrophic activity are generally smaller and of lower quality, both of which suggest production rates in these layers should be relatively stable. In contrast, surface soil layers are insulated only by the seasonal snow cover and are characterized by annual fresh carbon inputs in litter fall, suggesting that fluxes originating in this layer may be much more variable. Because fluxes at these sites appear to originate only in near-surface soil, this paper deals with controls on flux that may affect the active, rapidly cycling C and N pools in these soils.

Soil temperatures under consistent snow cover were effectively decoupled from atmospheric temperature. Even though soil at all sites used in this study froze early in the winter season, continuous snow cover allowed soil to thaw long before spring snow melt. This insulating effect of snow cover has been noted by a number of researchers (Thorud and Duncan 1972; Edwards and Cresser 1992) with a 30 cm snow depth being important in controlling the severity of soil freeze (Crawford and Legget 1957). Similarly, Sommerfeld et al. (1993) have found that soil remained unfrozen throughout the winter under both subalpine and alpine snowpacks following an early, heavy snowfall, yet the observation of previously frozen soil thawing without a melt event is unusual. The energy required to warm these soils before melt appears to be geothermal. Recent energy balance measurements at Niwot Ridge have identified a bottleneck in the transfer of geothermal energy at the soil-snow interface which develops once the snowpack reaches a depth of approximately 30 cm (Cline 1995). We previously have identified thawed soil in the organic soil horizon under snow before melt and suggested that organic solutes act to suppress the freezing point in this layer (Brooks et al. 1995). Similarly, solute depression of the freezing point by ion diffusion as soils begin to freeze may result in thawed soil at temperatures below 0°C (Edwards and Cresser 1992). In these soils thaw occurs, and free water becomes available, only when soil temperatures are above –5°C. Earlier-developing snowpacks, both natural and experimentally deepened, result in warmer minimum soil temperatures, a smaller temperature gradient over which soils must be warmed before they thaw, and longer periods when heterotrophic activity can occur under the snowpack.

Although relatively cold, the thawed upper soil layer is not subject to diurnal temperature fluctuations and intermittent wet/dry cycles that characterize the growing season. Once soil begins to thaw the presence of both liquid water and ice buffers temperatures within a narrow range between –5°C and 0°C, soil moisture remains relatively stable before melt (Mosier et al. 1993; Brooks et al. 1995), and the upper soil layer becomes a relatively cold, but constant environment. Net N mineralization rates before snowmelt within this environment are higher than rates during the growing season (Brooks et al. 1996), suggesting the presence of an active heterotrophic community. While a number of alpine plant species are known to end senescence before they are snow free (Mullen and Schmidt 1993) and may contribute to the observed CO_2 fluxes after snowmelt begins, it is unlikely that vegetation at these sites remains active throughout the winter. These observations suggest that an active microbial community in snow-covered soil is the primary source of CO_2 in this system.

The absence of a significant relationship between temperature and CO_2 production within this unique environment suggests that temperature, controlled by snowpack accumulation, serves primarily as a switch controlling when, and if, heterotrophic activity begins. This switch occurs at approximately –5°C when soil thawed and CO_2 production was first observed. The large variability in measured flux at the warmer temperatures suggests other factors, most likely substrate availability, are important in controlling the magnitude of heterotrophic activity once the soil thaws. The exponential increase in the flux of both gases observed at the shallow, moderate duration sites is similar to the relationship observed when microorganisms are grown in a substrate rich environment (Schmidt 1992), and suggests the presence of an actively growing microbial population in snow-covered soils (Fig. 2a). Freeze/thaw cycles are known to increase labile C substrates (Ivarson and Snowden 1966; White 1973; Edwards and Cresser 1992), and high fluxes of CO_2 have been attributed to the pulse of available carbon as soils thaw (Soulides and Allison 1961; Skogland et al. 1988; Schimel and Clein 1996). The low soil temperatures at the shallow, moderate duration snowpack sites during the winter of 1993 indicate these soils experienced a severe freeze before a consistent snowpack developed. This freeze/thaw event, along with labile carbon compounds leached from litter fall, presumably provided a large pool of carbon substrates for heterotrophic activity. When soils thawed under the snowpack microorganisms began exploiting these C compounds several months before snowmelt. Similarly, the mid-winter decrease in production at the longer lasting snowpacks is consistent with substrate limitation. A number of other studies have suggested that similar mid-winter decreases in CO_2 flux from seasonal snowpacks are due to decreased production within the soil (Sommerfeld et al. 1993, 1996; Winston et al. 1995).

Just as the exponential increase in CO_2 production may represent a growing heterotrophic community, the exponential increase in N_2O flux at the two shallow, moderate duration snowpack sites in 1993 is consistent with a population of denitrifiers growing in a substrate rich environment (Fig. 2b). Consistent with this explanation is the observation that N_2O production began approximately one month after CO_2 production, suggesting that an initial period of heterotrophic activity may be important in reducing oxygen availability at microsites within the soil to a point that favors denitrification. A number of studies have identified N_2O production within the range of temperatures found under these snowpacks as long as a significant carbon source is available (Mahli et al. 1990; Dorland and Beauchamp 1991). Similarly, a significant pulse in N_2O production has been identified as soils thaw in the spring (Bremner et al. 1980; Goodroad and Keeney 1984; Christensen and Tiedje 1990). In contrast to production beginning in mid-winter, Christensen and Tiedje (1990) observed a pulse of N_2O only when soils thawed in the spring. A possible explanation for these differences may be that their soils experience a number of freeze/thaw cycles throughout the winter while our sites do not. Multiple freeze/thaw events may "reset the clock" by reducing microbial populations several times through the winter season so that conditions are not favorable for denitrification until snowmelt. Sequential freeze/thaw cycles have been shown to decrease the surviving microbial population in soil, resulting in lower total heterotrophic activity with each subsequent freeze event (Schimel and Clein 1996).

It is difficult to evaluate whether our failure to observe an exponential increase in fluxes at the naturally deep snowpack and snow fence sites was due to our sampling schedule or to the absence of such an increase. The observation that soil already had thawed when collectors were installed in January at all of these sites indicates that the earlier snow cover allowed heterotrophic activity to begin much sooner than we anticipated and that an exponential increase in flux, if it occurred, may have been present earlier in the snow-covered season. If this explanation is correct, the increase in N_2O fluxes between the first two sampling dates at the snow fence and naturally deep snowpack sites (Fig. 3b) may be the latter portion of an exponential increase similar to that observed the previous year. Alternatively, the earlier snow cover resulted in warmer minimum soil temperatures at these sites and may have precluded a hard freeze. Consequently, the pool of labile C substrates within the soil may have been significantly smaller than during the previous season. This possible explanation is supported by the lower CO_2 fluxes at these sites throughout the snow-covered season. In contrast to the lower CO_2 fluxes, N_2O production in these soils was significantly higher than under the shallow, moderate duration snowpacks in 1993. Whether this difference was related to reduced oxygen availability, higher nitrate availability, both favoring denitrification, or a longer season for facultative anaerobes to become established is unclear. These differences do, however, suggest a complex series of controls on microbial activity in these soils.

The decrease in the production of both gases observed late in the snow-covered season at naturally deep snowpack and snow fence sites is consistent with the idea that substrate availability is the primary control on heterotrophic activity within this environment. Such a decrease could be due to a decrease in labile carbon sources late in the season or to a decrease in oxygen availability in these relatively moist soils after an extended period of heterotrophic activity. The observation that N_2O fluxes continued to increase for several weeks after the decrease in CO_2 fluxes is consistent both with oxidant limitation and the lag between CO_2 flux and N_2O flux observed at moderate snowpack sites in 1993. More detailed soil data, as well as experimental manipulations, are needed to evaluate the relative controls of different substrates on heterotrophic activity in these systems.

While heterotrophic activity in consistently snow-covered soils appears to be controlled by substrate availability, the shallow snowpack sites in 1994 demonstrate the dominant control snowpack accumulation has on over-winter activity. Although low soil temperatures indicate that the shallow sites in 1994 experienced a hard freeze which may have resulted in a large pool of labile C substrates, the lack of consistent snow cover prevented soil thaw before snow melt and precludes an evaluation of substrate controls on heterotrophic activity at these sites. Comparing these sites to the moderate duration snowpacks in the same area the previous year, however, demonstrates the strong control that relatively small changes in seasonal snow cover (50 cm in 1994 vs. 80 cm in 1993, Table 1) have on determining when or if an environment which allows heterotrophic activity in these systems develops.

The important of over-winter fluxes to ecosystem C and N fluxes

The depth and timing of snow cover determined whether the over-winter CO_2 fluxes were a significant component of annual C fluxes. Based on annual above ground primary production (ANPP) of approximately 95 g C m^{-2} for alpine tundra on Niwot Ridge (Walker et al. 1994) subnivian heterotrophic activity mineralized 27% ANPP at the shallow, moderate duration sites in 1993, but less than 1% under shallow, short duration snowpacks in this same area the following year. This suggest that the natural year to year variability in over-winter heterotrophic activity may be very large in areas characterized by shallow snow cover. Although both the snow fence and naturally deep sites experienced longer periods of snow cover than the shallow, moderate duration sites, over-winter heterotrophic activity mineralized only 13% and 18% of ANPP, respectively, at these sites. While it is possible we missed a portion of flux early in the snow-covered season, the large difference in mean daily fluxes indicates that over-winter heterotrophic activity at these sites was significantly lower than at the moderate snowpack duration, hard freeze sites. Similarly, the large differences in seasonal C loss from the snow fence, naturally deep snowpack, and shallow snowpack sites in 1994 indicates a high level of spatial heterogeneity in over-winter activity. Just as mean daily flux seems to be limited by available substrate, it appears that over-winter carbon loss may be controlled by freeze/thaw cycles which release labile C substrates in the soil. Small changes in climate, therefore, may have a significant impact on the total winter CO_2—C flux from these systems by affecting both the severity of soil freeze and the length of time heterotrophic activity is present in snow-covered soils.

Sommerfeld et al. (1993) have identified larger over-winter carbon fluxes from the Glacier Lakes Ecosystem Experiment Site (GLEES), approximately 150 km from Niwot Ridge (Table 2). The mean daily flux at their alpine sites was lower than the flux from the moderate duration, hard freeze site in 1993 but greater than any of the sites in 1994 (Table 2). Their sites are relatively sheltered compared to ours resulting in a longer period of consistent snow cover which leads to higher seasonal carbon loss from their sites. Although they have fewer sites, the long term record from the GLEES location demonstrates that these fluxes are a consistently important portion of annual C fluxes (Sommerfeld et al. 1996).

The affect this over-winter heterotrophic activity has on growing season biogeochemical cycles is unknown. The utilization of a large portion of labile carbon compounds under snow potentially may limit heterotrophic activity later in the year. Therefore, both the spatial and inter-annual variability in snowpack accumulation may have a significant impact on nutrient availability during the growing season. This suggests that some of the variability in vegetation communities in alpine tundra which has been associated with snowpack regime (Oberbauer and Billings 1981; Walker et al. 1993b) may be due to processes under snow rather than during the growing season. While this hypothesis needs to be validated by further research, the idea should not be surprising given the potentially high levels of heterotrophic activity under snow and the long period of snow-cover relative to the growing season in these systems.

Evaluating over-winter N_2O—N loss was somewhat simpler than over-winter C loss. Even though the variability in production increased under longer duration snowpacks, the seasonal N_2O—N loss generally increased as the duration of thawed soil under the snowpack increased (Table 3). The extended period of snow cover provided by the snow fence in 1994 increased the winter N_2O—N loss by a factor of eight compared to the same area in 1993, before construction of the fence (Fig. 5). This increase was due not only to a longer period of production, but to significantly higher mean daily flux rates. Mean N_2O flux rates at the shallow sites during the 1993 season were higher than fluxes measured from both dry and wet meadows on Niwot Ridge during the growing season (Neff et al. 1994). Slightly lower fluxes have been measured during the winter from both forested and alpine sites in Wyoming (Sommerfeld et al. 1993). Mean fluxes from the naturally deep snowpacks and snow fence sites in 1994, however, were much higher than growing season fluxes reported for either alpine or forested sites in the Rocky Mountains (Neff et al. 1994; Mosier et al. 1993; Matson et al. 1992).

While the magnitude of both the mean daily and the annual N_2O fluxes measured in this study is not large compared to fluxes measured from many temperate or tropical sites, these fluxes are a significant component of inter-system N fluxes on Niwot Ridge. The combination of higher flux rates and a longer season of production under consistent snowpacks suggests the annual N_2O flux from these systems is dominated by production during the snow covered season (Table 3). Our estimates of N inputs to these sites from the snowpack during melt range from 150 to 250 mg N m^{-2} (Brooks et al. 1996), suggesting that N_2O flux from the deep and fence sites during the snow-covered season were 7% to 15% of inputs. It is likely that most, if not all, of these fluxes result from denitrification within these relatively wet soils. This suggests that the total over-winter N flux from these systems may be significantly higher depending on the ratio of N_2 to N_2O produced.

In summary the timing of snowpack development is the most important factor controlling when and if production of both CO_2 and N_2O will occur in snow covered soils. Consistent snow cover insulates the soil from extreme air temperatures and allows heterotrophic activity to continue in a relatively homogeneous environment throughout much of the winter. Small changes in the timing of seasonal snow cover control both the duration and magnitude of this activity. More research is needed to determine how the observed variability in winter soil microbial activity may affect a wide range of ecosystem processes from nutrient availability during the growing season to soil carbon storage.

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