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Microbial activity under alpine snowpacks, Niwot Ridge, Colorado

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Abstract. Experiments were conducted during 1993 at Niwot Ridge in the Colorado Front Range to determine if the insulating effect of winter snow cover allows soil microbial activity to significantly affect nitrogen inputs and outputs in alpine systems. Soil surface temperatures under seasonal snowpacks warmed from -14 °C in January to 0 °C by May 4th. Snowmelt began in mid-May and the sites were snow free by mid June. Heterotrophic microbial activity in snow-covered soils, measured as CO_2 production, was first identified on March 4, 1993. Net CO_2 flux increased from 55 mg CO_2-C m^{-2} day^{-1} in early March to greater than 824 mg CO_2-C m^{-2} day^{-1} by the middle of May. Carbon dioxide production decreased in late May as soils became saturated during snowmelt. Soil inorganic N concentrations increased before snowmelt, peaking between 101 and 276 mg kg^{-1} soil in May, and then decreasing as soils became saturated with melt water. Net N mineralization for the period of March 3 to May 4 ranged from 2.23 to 6.63 g N m^{-2}, and were approximately two orders of magnitude greater than snowmelt inputs of 50.4 mg N m^{-2} for NH_4^+ and 97.2 mg N m^{-2} for NO_3^-. Both NO_3^- and NH_4^+ concentrations remained at or below detection limits in surface water during snowmelt, indicating the only export of inorganic N from the system was through gaseous losses. Nitrous oxide production under snow was first observed in early April. Production increased as soils warmed, peaking at 75 μg N_2O-N m^{-2} day^{-1} in soils saturated with melt water one week before the sites were snow free. These data suggest that microbial activity in snow-covered soils may play a key role in alpine N cycling before plants become active.

Introduction

The long residence time of nutrients in plants relative to microbes has led to the assumption that vegetation provides the primary buffer controlling the output of nutrients in surface water (Stoddard 1994). Dormant vegetation, cold temperatures, and extensive snow cover in alpine areas suggest little or no interaction between inorganic nitrogen (N) in snowmelt and basin

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soils and biota. However, immobilization of N in soil microbial biomass has been shown to play a critical role in limiting the hydrologic export of N in surface water both during the spring (Zak et al. 1990) and following disturbances (Vitousek & Andariese 1986). Although snow cover generally minimizes photosynthetic activity during the early stages of snowmelt, consistently snow-covered soils are insulated from extreme air temperatures and may be unfrozen under the snowpack (Sommerfeld et al. 1993; Brooks et al. 1993). These thawed soils provide an environment where microorganisms may remain active. In general, microbial activity can continue as long as free water is available, typically down to -5 °C (Schimel et al. 1995), although activity has been reported at temperatures as low as -6.5 °C (Coxson & Parkinson 1987).

Microbial activity under seasonal snowpacks has been shown to affect the N cycle in a number of ecosystems. Sommerfeld et al. (1993) identified significant losses of N_2O through winter and spring snowpacks in Wyoming. Microbial immobilization was presumably responsible for immobilization of $^{15}NH_4^+$ applied to the snow surface during the winter in British Columbia (Preston et al. 1990). Lewis & Grant (1980) reported that NO_3^- concentrations in stream water from an alpine/montane watershed in Colorado were inversely related to winter snow depths within the catchment. This relationship also was true for other biologically active compounds (e.g. phosphorus and potassium), which led the authors to suggest that snow cover could prevent soils from freezing and allow biological activity to modify surface water chemistry. Similarly, mineralization of organic matter followed by nitrification under seasonal snowpacks is apparently responsible for elevated stream water NO_3^- concentrations in eastern North America (Rascher et al. 1987).

A significant fraction of system N inputs to Niwot Ridge result from a combination of wet and dry deposition in seasonal snowpacks (Bowman 1992; Sievering et al. 1992). An increase in N deposition rates observed along the Colorado Front Range (Lewis & Grant 1980; Grant & Lewis 1982; Lewis et al. 1984) is apparently driven by an increase in anthropogenic N in Colorado over the last two decades (Fahey et al. 1986). A significant fraction of this N is stored in seasonal snowpacks and released in an ionic pulse during the first portion of snowmelt (Williams & Melack 1991a). This temporal asynchrony between N deposition in snow and release during snowmelt apparently results in episodic elevation of N concentrations in alpine basin surface waters during the early stages of snow pack runoff throughout the Front Range (Reddy & Caine 1990; Baron 1991; Williams et al. 1993a). These elevated NO_3^- concentrations may indicate N saturation (Baron et al. 1994), and may serve as a potential early indicator of surface water acidification (Williams et al. 1995).

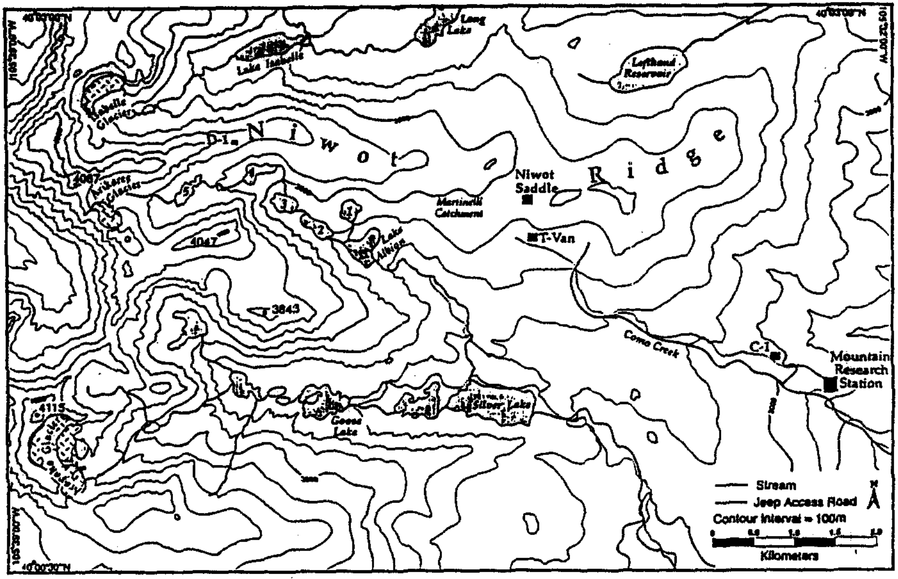

Fig. 1. Location of Niwot Ridge International Biosphere Reserve along the Colorado Front Range.

This study examined the relationship between snow cover, microbial activity, and N cycling in alpine soils at an elevation of 3510 m in the Colorado Front Range. Physical and chemical properties of both snow and soil were measured throughout the winter and spring of 1993. Carbon dioxide flux from seasonal snowpacks was measured to provide an estimate of microbial activity. Inorganic N inputs were measured from both the snowpack and soil organic pools. Nitrogen losses were followed in surface and groundwater as well as gaseous forms. The resulting data allow us to evaluate: 1) the distribution of subnivean microbial activity; 2) nitrogen inputs to the terrestrial system from the snowpack; and 3) sources of NO_3^- in surface waters during snowpack runoff.

Study site

All experiments were conducted on Niwot Ridge, Colorado (40°03′ N, 105°35′ W) located in the Front Range of the Rocky Mountains 5 km east of the Continental Divide (Fig. 1). This site is an UNESCO Biosphere Reserve and has been the location of extensive research by the University of Colorado's Long-Term Ecological Research program. Three sites, each approximately 10 m^2, were established in moist meadow communities as described by

Walker et al. (1994). Two alpine sites were located at an elevation of 3510 m. The third site, established to provide preliminary information on the effect of earlier snowpack accumulation on microbial activity, was located at treeline at an elevation of 3400 m. Soils are Cryochrepts and vary in depth from approximately 0.3 to 2.0 m overlying granitic parent material (Burns 1980). Soil C in the top 100 mm ranges from 130–200 g kg^{-1}, and soil N pools range from 9–15 g kg^{-1} (Burns 1980). Soil pH in the autumn of 1992 ranged from 4.6 to 5.0 (Fisk & Schmidt 1995).

The climate is characterized by long, cold winters and short (1 to 3 months), cool growing seasons. Mean annual temperature is -3 °C, annual precipitation is 900 mm, the majority of which falls as snow (Greenland 1989). Wind velocities during winter average 10 to 13 m s^{-1}. A continuous snowpack generally begins to accumulate in November at the treeline site, and in December or January at the alpine sites.

Methods

Sampling schedule

Sites were established in October 1992 and monitored monthly until soils thawed and net CO_2 efflux from the snowpack was observed. Thereafter, gas and soil samples were collected every other week until snowmelt began and then weekly until the sites were snow free. Snow chemistry samples were collected weekly from mid-April until sites were snow free in mid-June. Collection of surface water began shortly after the initiation of snowmelt (mid-May) and continued through the summer.

Atmospheric inputs

Inorganic N loading to each site was calculated from volume weighted mean NO_3^- and NH_4^+ concentrations in melted snow multiplied by snow water equivalence (SWE) at each site. Snow samples for chemical content were collected using the protocol of Williams & Melack (1991b). Snow was collected using beveled PVC tubes (50-mm diameter, 500-mm long), which had been soaked in 10% HCl and then rinsed at least five times with deionized water. Vertical, contiguous cores were collected, in increments of 400-mm, from the snow-air interface to the snow-ground interface. Snow density measurements were made using a 1 L stainless steel cutter (Elder et al. 1991). Snow water equivalence (SWE) was calculated as depth times density. Snow temperatures were taken every 100mm (±1.0 °C). Surface water samples were collected at about weekly intervals during snowpack runoff in acid-washed, polyethylene bottles that were copiously rinsed with deionized water, and then rinsed again with sample water. Samples were then treated the same as melted snow.

To assess the spatial heterogeneity of N inputs to soil, PVC tubes containing mixed bed ion exchange resins in permeable nylon bags were placed at the soil surface. Resin bags contained 20 mL (wet volume) of mixed cation and anion (16–50 mesh) exchange resins (Hart & Gunther 1989). Resins were obtained from Baxter Scientific loaded with H^+ or OH^- with a total exchange capacity of 0.57 meq mL^{-1}. These bags were placed in 50-mm long, 35-mm diameter PVC tubes located at the soil surface and allowed to extend 30 mm above the soil surface to minimize inputs from overland flow. A silicone plug was placed at the bottom of each tube to exclude N inputs from underlying soil. Nine of these tubes were placed at the soil surface at each site on 22 October and were collected immediately after the sites became snow free (between 3 and 10 June).

Gas fluxes

Carbon dioxide and nitrous oxide fluxes were estimated using the method of Sommerfeld et al. (1993). Gas collectors, constructed of 100-mm diameter by 10-mm thick stainless steel disks covered with 50 mm stainless steel mesh, were placed at the soil surface after the snowpack had begun to develop. Three collectors were located within each 10 m^2 site. Collectors were connected to sampling ports located above the snow surface by 1/16 inch teflon tubing. Gas samples from under the snowpack were collected monthly through February, every other week in March and April, and weekly during May and June. Samples were collected in 10 cc glass syringes at each sample date from the snow/soil surface as well as from the snow/atmosphere interface. Fick's law was used to calculate flux rates,

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

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, and f is the snowpack porosity (calculated as the inverse of snowpack density). The diffusion coefficient (D_g) was assumed to be 0.139 cm^2 s^{-1} for both CO_2 and N_2O, and is the same as that used by Sommerfeld et al. (1993).

Soil nitrogen

Mineralization tubes (35 × 100 mm), similar to those described by DiStefano & Gohlz (1986) and Hart & Gunther (1989) were used to estimate net over-winter mineralization rates. Six paired soil cores (35 × 100-mm) were collected at each site when ion exchange resin bags were installed in October. Three cores, one from each pair, were returned to the laboratory and analyzed for soil inorganic N, the second core of each pair was incubated in the field throughout the winter and collected when the sites were snow free. Ion exchange resin bags (described above) were sealed in the bottom of each tube to collect leached N. Net over-winter N mineralization was calculated as difference in inorganic N concentrations in paired soil cores plus N extracted from the resin bags at the bottom of each tube, minus snowmelt N inputs.

In addition to over-winter measurements, net N mineralization/immobilization between sampling dates during the snow covered season was estimated from the change in KCl extractable N over time. At each sampling date, snow pits were dug to the soil surface and three soil samples were collected from each plot and returned to the lab to be analyzed for extractable NO_3^- and NH_4^+. Soils samples, approximately 50-mm in diameter, were collected only from thawed soils which varied in depth from 30–80 mm. Net N mineralization was calculated as the difference in soil inorganic N concentrations in these soil cores between sampling dates. After snow melt, inputs from surface resin bags were substracted from these values. A layer of frozen soil under thawed surface soils was present throughout the snow-covered season, suggesting little or no subsurface N loss. Soil surface temperatures and thaw depth were taken manually at the bottom of snowpits using either an Omega temperature probe (±0.1 °C) or a Tel-Tru thermometer (±0.2 °C).

Laboratory analyses

Snow samples were transferred to new polyethylene bags after collection. Samples were stored frozen (−20 °C) for three to nine months until analysis. Blank samples of distilled, deionized water were stored in the bags for the same amount of time and showed no significant contamination from the bags (Williams et al. 1992). Snow samples were placed in covered polyethylene buckets and melted at 4 °C to minimize chemical changes. Subsamples were then filtered through pre-rinsed, 47-mm Gelman A/E glass fiber filters with ca. 1-micron pore size. Filtered samples were stored in the dark at 4 °C for subsequent analyses. Ammonium was determined colorimetrically within 24 hrs of melting, on a LACHAT flow injection analyzer (Lachat Instruments, Mequon, Wisconsin) using a phenolate reaction enhanced by nitroprusside (detection limit 9.8 mg L^{-1}, precision 2.7%). Nitrate was measured by ion chromatography (Dionex Model 2010i) employing chemical ion suppression and conductivity detection (detection limit 1.4 mg L^{-1}, precision 1.5%).

Soil samples were processed within 12 hours of returning from the field. Fresh soils were sieved and homogenized using a 2 mm sieve. Subsamples of this soil were extracted with 2N KCl (1:5, weight:volume) by shaking at

250 rpm for 60 minutes and allowed to sit at room temperature for 18 hours. Samples were then filtered through Whatman #1 filter paper and aliquots of the extracts were analyzed on a LACHAT flow injection autoanalyzer. Nitrate was analyzed using a sulfanilamide reaction following reduction to nitrite on a cadmium column. Ammonium was analyzed as in snow. Soil moisture was determined gravimetrically following drying to constant weight in a 60 °C oven and expressed as grams water divided by grams dry soil and multiplied by 100% (values may exceed 100%). Ion exchange resin bags from surface collectors and mineralization tubes were air dried in the laboratory and extracted with 2N KCl. Nitrate and NH_4^+ were analyzed using the same methods as the soils. Potassium chloride blanks were run with all samples, and standards were made in 2N KCl. Before use, 3 to 5 subsamples from each batch of resins were analyzed for inorganic N.

All gas samples were analyzed on a Hewlit-Packard 5890A gas chromatograph. Carbon dioxide was separated on a 2 m Porapak-Q column (80–100 mesh), converted to methane in a nickel catalyst tube at 375 °C and measured on a Flame Ionization Detector (FID) at 400 °C. Nitrous oxide was measured on a ^{63}Ni Electron Capture Detector (ECD) at 350 °C following separation on 0.6 m and a 3.0 m Porapak-Q columns connected in series to allow backflushing between samples. Measured fluxes were converted to N loss per square meter using an N_2:N_2O production ratio of 9:1 (Ryden et al. 1979).

Results

Physical characteristics

The two alpine sites were characterized by discontinuous snow cover from October through December. A continuous snowpack began to accumulate in the beginning of January 1993 (Fig. 2). Maximum snow depth of 0.8 m at the alpine sites, and 1.27 m for the treeline site occurred in the end of April. Snowmelt began between May 4 and May 19 and all sites were snow free the first week in June. Volume-weighted mean concentrations of inorganic N at maximum snow accumulation were 71 μg L^{-1} for NH_4^+ and 135 μg L^{-1} for NO_3^-.

Intermittent snow cover from October until January allowed soils at all sites to freeze to a depth greater than 100 mm. Soil temperatures at the two alpine sites followed a similar pattern through the spring. Minimum soil surface temperatures of −14 °C at the alpine sites were measured on January 14 (Fig. 2). Alpine soil temperatures began to warm as a consistent snowpack began to accumulate. By early March soil temperatures had risen above −5 °C and thawed soil appeared under the snowpack. Soil temperatures continued

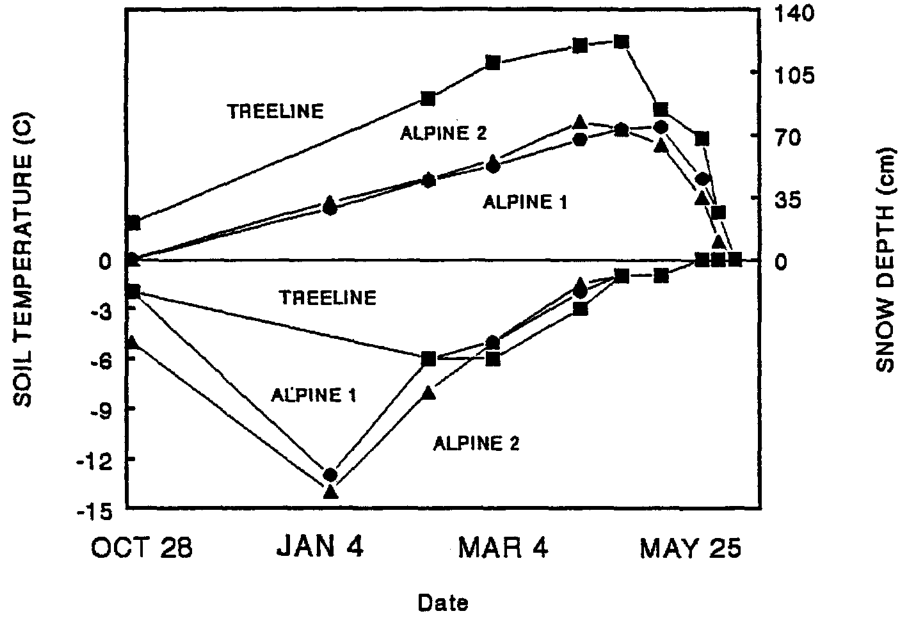

Fig. 2. Relationship between snowpack accumulation (top) and soil surface temperatures (bottom) at three sites on Niwot Ridge during the winter/spring of 1992–1993 (*n* = 3 for each date, sd is smaller than symbol). Treeline (■), Alpine 1 (●), Alpine 2 (▲).

to rise reaching 0 °C when snowmelt began during the first week of May. In contrast, soils at the treeline site reached a minimum temperature of −8 °C, yet remained frozen until snowmelt, which began approximately one week earlier than at the alpine sites. Soils at all sites thawed from the surface down creating an active layer at the snow/soil interface which was isolated from deeper soils or subsurface hydrological flowpaths (Table 1).

Gravimetric soil moisture at each of the two alpine sites remained relatively constant until snowmelt began and then increased significantly at both sites. Soil moisture before snowmelt was lower at Alpine 1 (64–88%), which is on a slight southerly aspect, than at Alpine 2 (112–126%) which is comparatively flat. Soil moisture increased rapidly at both sites with the onset of snowmelt (Table 1). Soils were frozen at the treeline site and no soil samples were collected from before melt began.

CO_2 flux

There was no measurable CO_2 flux at any of the three sites from December 1992 through February 1993. The mean temperature of the soil surface was between −5 °C and −14 °C during this time (Fig. 2). By March 4, surface temperatures had warmed above −5 °C and CO_2-C production of 55 to

Table 1. Soil properties from Niwot Ridge, 1993. mean (sd), $n = 3$

Date	Soil temperature (C)	Gravimetric soil moisture (%)	Nitrate soil mgN/kg	Ammonium mgN/kg	Depth of thaw (cm)
			TREELINE		
March 4	a	a	a	a	0
April 4	a	a	a	a	0
April 18	a	a	a	a	0
May 4	−1	170 (2)	3.9 (1.0)	276.3 (15.1)	0–2
May 18	0	128 (6)	1.7 (0.3)	43.3 (2.0)	0–5
May 24	0	104 (3)	1.0 (0.1)	31.0 (3.1)	>10
			ALPINE 1		
March 4	−5	88 (9)	3.1 (0.2)	50.1 (22.6)	5–6
April 4	−1	88 (8)	1.9 (0.1)	50.6 (10.6)	5–6
April 18	−1	64 (2)	1.8 (0.2)	89.2 (16.0)	5–6
May 4	−1	68 (6)	1.1 (0.4)	101.3 (60.6)	4–10
May 18	0	122 (1)	1.2 (0.2)	48.7 (5.9)	6–10
May 24	0	146 (2)	0.6 (0.4)	69.6 (18.1)	>10
			ALPINE 2		
March 4	−5	126 (2)	2.3 (0.5)	107.3 (11.3)	5–6
April 4	−1.5	112 (2)	3.1 (0.3)	118.8 (10.1)	6
April 18	−1	124 (6)	2.9 (1.0)	214.5 (16.8)	5–6
May 4	−1	114 (5)	3.1 (0.9)	256.8 (52.8)	2–5
May 18	0	182 (5)	0.1	0.9 (0.3)	6–8
May 24	0	156 (3)	0.5 (0.1)	62.2 (6.7)	>10

a = soil frozen and no sample collected
ND = Not Detected

90 mg m^{-2} d^{-1} was observed at the alpine sites (Fig. 3). Carbon dioxide production at these sites increased as soil surface temperatures warmed through the beginning of May, peaking at 824 mg CO_2-C m^{-2} d^{-1} immediately before snowmelt. In contrast, CO_2 production was not observed at the treeline site until snow melt began during the first week of May. Estimates of flux indicated CO_2 production under the snowpack exhibited microsite heterogeneity (Fig. 3), with coefficients of variation in the range of 20–25%. There was no significant difference in CO_2 flux from the two alpine sites before snowmelt. Carbon dioxide flux decreased significantly (t-test, $p < 0.01$) at Alpine 1 as soils became saturated with snowmelt (Table 1). No significant decrease in CO_2 production was observed during melt at the other two sites.

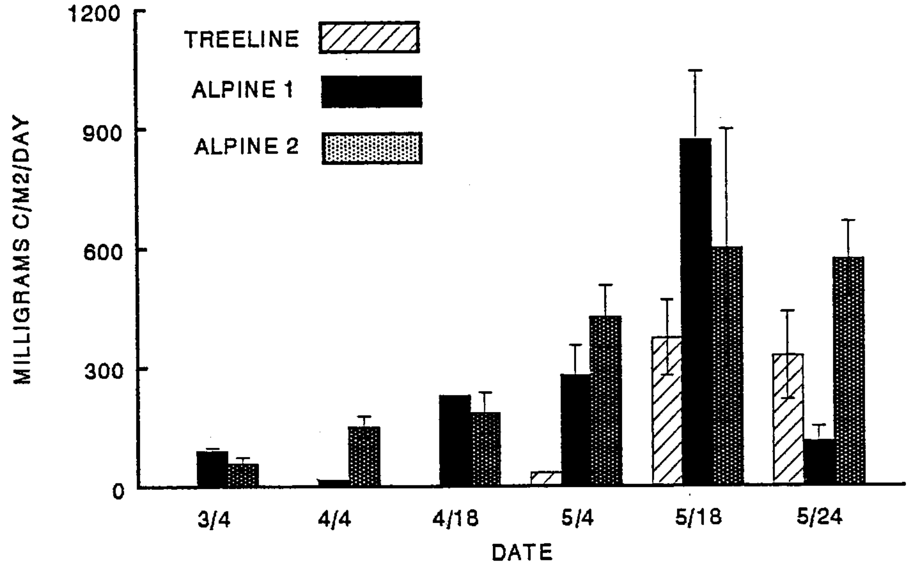

Fig. 3. Carbon dioxide flux from snow covered soils on Niwot Ridge during the spring of 1993. (mean ±sd, $n = 3$).

Table 2. Winter atmospheric nitrogen inputs to Niwot Ridge estimated from ion exchange resins at the soil/snow interface. Input estimates from snowpack concentrations at maximum accumulation are provided for comparison. (Values are mean ±sd)

	Resin Bag Inputs (mg N/m^2) $n = 6$	
Site	**Nitrate**	**Ammonium**
Treeline	60.2 (±65.5)	192.1 (±181.2)
Alpine 1	205.6 (±123.9)	100.3 (±9.3)
Alpine 2	14.2 (±9.6)	88.7 (±78.6)
	Snowpack Estimates (mg N/m^2)	
Site	**Nitrate**	**Ammonium**
Treeline	148.2	76.9
Alpine 1	94.8	49.1
Alpine 2	97.2	50.4

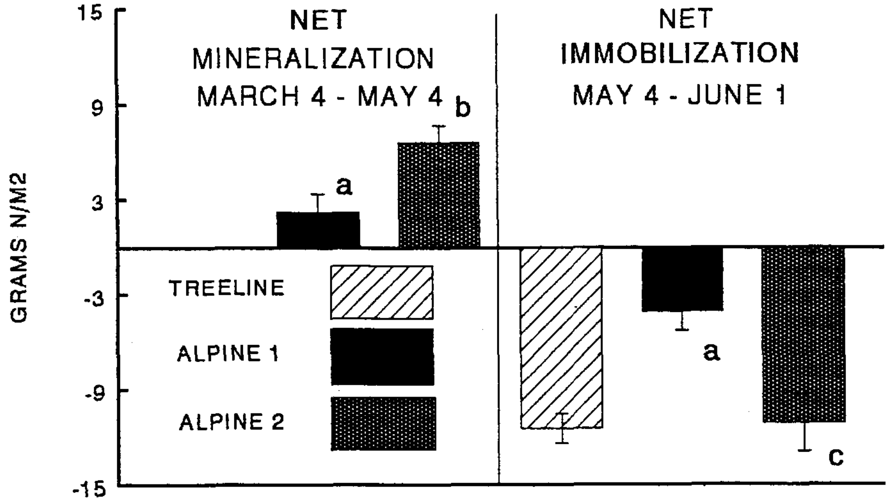

Fig. 4. Net N mineralization inputs calculated from the change in soil inorganic N concentrations in KCl extracts before snow melt (left). Net N immobilization estimated from decrease in soil inorganic N concentrations in KCl extracts after snow melt (right) (mean ±sd, *n* = 3). Mineralization/Immobilization pairs which share the same letter are not significantly different.

N inputs and transformations

Atmospheric inputs

Loading of inorganic N to the alpine sites, calculated from snowpack concentrations multiplied by the Snow Water Equivalent (SWE), was 50.4 mg N m^{-2} for NH_4^+ and 97.2 mg N m^{-2} for NO_3^-. The resin tubes at the soil surface estimated N inputs of 14.2 and 205.5 mg N m^{-2} for NO_3^- and 88.7 and 100.3 mg N m^{-2} for NH_4^+ at the alpine sites (Table 2). Inorganic N loading in the snowpack at the treeline site was 76.9 mg N m^{-2} for NH_4^+ and 148.2 mg N m^{-2} for NO_3^-. Resin tube estimates of NH_4^+ inputs were higher at the treeline site, 192.1 mg N m^{-2}, while NO_3^- inputs of 62.0 mg N m^{-2} were intermediate between the two alpine sites. The coefficients of variation for estimates of N inputs ranged from 10% to greater than 100% (Table 2).

Soil N mineralization

The increases in soil inorganic N concentrations under the snowpack from 4 March through 3 May indicate a two month period of significant mineralization beneath snow. Mean net N mineralization inputs during this two month period, calculated as the difference between soil inorganic N concentrations on each date, were 2.23 g N m^{-2} for Alpine 1 and 6.63 g N m^{-2} for Alpine 2 (Fig. 4). These inputs were more than an order of magnitude greater than N inputs from snowmelt. Thawed soils were not observed at the treeline site

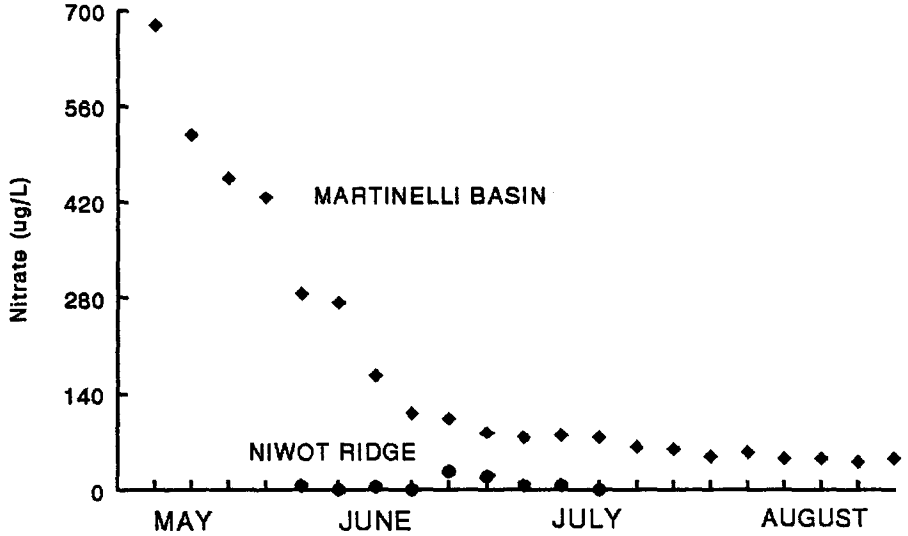

Fig. 5. Surface water NO_3^- concentrations from ephemeral streams draining alpine sites on Niwot Ridge (●) and from perennial streams in Martinelli Basin (◆).

before snowmelt, and net N mineralization inputs could not be calculated for this site. Soil inorganic N concentrations decreased rapidly during May as soil temperatures reached 0 °C, indicating re-immobilization of mineralized N under the melting snowpack (Table 1, Fig. 4). This is consistent with the resin cores installed in October and collected at the end of snowmelt which failed to indicate net over-winter mineralization. There was no significant difference in soil inorganic N concentrations in paired soils cores between the beginning of the incubation on 22 October 1992 and collection on 3 June 1993 (data not shown). Nitrogen concentrations in resin bags located at the bottom of the resin cores were not significantly greater than sample blanks. At collection, soil within the resin cores was frozen below a depth of 50 mm, apparently isolating resin bags from mineralized N in the upper portion of the soil.

Nitrogen outputs

Hydrologic losses

No significant export of inorganic N from the system occurred in surface or ground water draining the alpine sites. Concentrations of ammonium in surface waters remained below detection limits throughout the spring and summer. Nitrate concentrations remained below detection limits during the early stages of runoff, increased to approximately 25 μg N L^{-1} during mid-

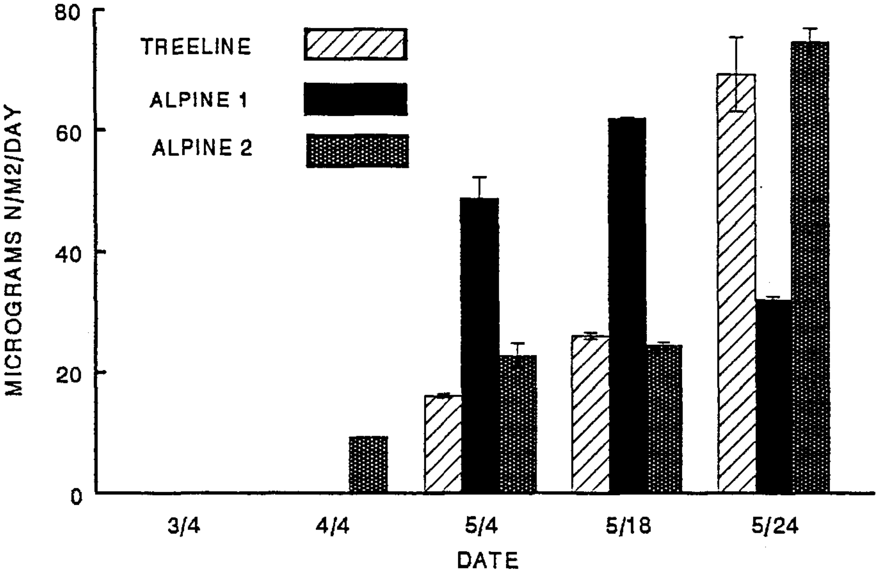

Fig. 6. Denitrification N flux (N_2O-N) from snow covered soils on Niwot Ridge during the spring of 1993.

summer after sites were snow free, and then decreased below detection limits (Fig. 5). The resin bags located in the bottom of the resin cores designed to estimate N mineralized failed to accumulate any leached N at a depth of 100 mm, suggesting no loss of inorganic N to subsurface hydrological flow during melt at any of the three sites (data not shown).

Gaseous losses

Nitrous oxide production was first observed on April 4 when the soil surface temperature was −1.5 °C (Fig. 2). Production increased throughout May, peaking after snowmelt began when soils were fully saturated and soil temperatures were 0 °C (Fig. 6, Table 1). The maximum flux measured at Alpine 1, 62.04 (±0.13) μg N m^{-2} d^{-1}, was significantly lower ($p < 0.05$) than those measured at either Alpine 2 (74.84 ± 2.24 μg N m^{-2} d^{-1}), or Treeline (69.34 ± 6.16 μg N m^{-2} d^{-1}). Unlike CO_2, N_2O production within a site appeared to be relatively uniform under the snowpack, with coefficients of variation ranging from 1 to 10%. Integrating these fluxes over the snow covered period yields an estimated loss of 30–50 mg N m^{-2} from the system which is approximately 30% to 50% of spatially averaged NO_3^- N loading from the snowpack at these sites.

Discussion

Physical characteristics

Although subject to freezing temperatures for several months, soils under continuous winter/spring snowpacks on Niwot Ridge warm enough to support significant levels of microbial activity. Thawed soils under seasonal snowpacks have been noted by a number of researchers (Fahey 1971; Sommerfeld et al. 1993; Brooks et al. 1993). Williams et al. (1993b) report that alpine soils at Emerald Lake Watershed in the Sierra Nevada, which froze in early winter, warm to 0 °C prior to the initiation of snowmelt. Sommerfeld et al. (1993) found that soils in the Medicine Bow mountains of Wyoming remained unfrozen throughout the winter following an early, heavy snowfall. The depth and timing of snow cover appear to be the most important factors regulating this thaw. The high initial soil moisture at the treeline site together with the observation that soils at the treeline site thawed later than alpine soils at a higher elevation suggests that the thermal inertia provided by soil moisture also may play an important role in determining the timing and extent of soil thaw. Although Alpine 1 is located on a slight southerly slope, the timing of thaw was similar to the flat site, Alpine 2, indicating the source of energy warming these soils prior to snow melt was probably ground heat flux rather than insolation. The fact that soils thawed from the surface is possibly due to a depression in the eutectic point caused by higher organic matter content.

CO_2 flux

Soil respiration began immediately after soils thawed under the seasonal snowpack while soils were still well below 0 °C. This is similar to the pulse of respiratory activity as soils thaw identified by Skogland et al. (1988). Estimates of CO_2 lost from soils under snowpacks during March, April, and May are approximately 20% of the carbon fixed annually in above ground primary production for these communities (Bowman et al. 1993; Walker et al. 1994). This is somewhat less than has been reported for forested sites in Wyoming where flux estimates from soils which remain unfrozen throughout the winter suggest subnivean respiration may mineralize up to 50% of yearly litter fall (Sommerfeld et al. 1993). The presence of evergreen vegetation at the sites used by Sommerfeld et al. (1993) indicate a potential contribution of root respiration to the fluxes measured in that study. In contrast, the absence of vegetation above the snow at the alpine sites in this study suggests that the majority of the CO_2 flux measured at these sites before snowmelt began was due to soil microbial respiration. It is possible that a portion of the increase in CO_2 flux observed immediately after snowmelt began was due to the contribution of root respiration.

Relatively few studies have directly addressed soil microbial activity at temperatures below zero, although significant subnivean microbial activity has been suggested by other work. Kelley et al. (1968) reported elevated CO_2 concentrations under an Alaskan snowpack and suggested heterotrophic microbial activity as a possible carbon dioxide source. Similarly, subnivean decomposition and respiration rates in the subarctic (Moore 1986; Taylor & Jones 1990) suggest the presence of heterotrophic microbial activity under snow. At these sites on Niwot Ridge the highest CO_2 fluxes were measured when soils were at 0 °C, and no production was observed below −5 °C. This cutoff is within the range at which free water becomes available in the soil (Schimel et al. 1995) yet slightly higher than the minimum temperature of −6.5 °C reported for soil microbial activity *in situ* (Coxson & Parkinson 1987). The spatial heterogeneity in production observed in this study, however, suggests that soil temperature was not the sole constraint on microbial activity under snow.

N inputs and transformations

Atmospheric

Inorganic N inputs from snowmelt were approximately 3 to 6% of net N mineralization during the snow-covered season. This is similar to the 5% reported by Schimel et al. (1995) for arctic tundra. However, these inputs of inorganic N from the snowpack to the soil during melt exhibit a great deal of spatial heterogeneity. Bowman (1992) has reported soil N inputs may range from 14% to 101% of the spatially averaged inputs due to heterogeneous patterns of snow distribution. Additionally, meltwater flowpaths through snow are highly variable at both temporal and spatial scales (Bales et al. 1993), and result in a great deal of variation in the quantity of N which reaches the soil surface at any location (Williams & Melack 1991a). While the resin bags at the soil surface were designed to evaluate this heterogeneity, the spatially averaged N inputs estimated from the resin bags at the surface were higher than what would be expected based on volume weighted mean snowpack concentrations. Since these resins were isolated from direct contact with the soil, this suggests that N from the soil solution travelled laterally at the base of the snowpack. Although this method does not appear to be suitable for estimating the variability of snowmelt N inputs to the soil at a particular site, it does indicate the variability in inorganic N inputs at any location and suggests a potentially mobile pool of inorganic N at the soil surface.

Mineralization

Mineralization of organic matter was the dominant source of N soil inorganic N before and during the spring thaw. Net N mineralization inputs of 2–6 g N m^{-2} snow-covered-season^{-1} measured in this study are considerably higher than inputs of 0.9 to 1.2 g N m^{-2} growing season^{-1} (Fisk & Schmidt 1995) and may contribute to plant growing season demands estimated by Fisk & Schmidt (1995) at 4–6 g N m^{-2} season^{-1}. While many microbially derived soil exoenzymes have activation energies which allow them to remain active at the low temperatures characteristic of these soils (McClaugherty & Linkins 1990), CO_2 flux data indicates the presence of an active microbial population which began to grow after soils thawed under the snow. Taken together, the high net N mineralization and high levels of heterotrophic respiration suggest a period during the snow covered season when microbes are utilizing labile carbon sources and mineralizing N in the process. If vegetation remains dormant before melt begins, assimilation of N lags behind gross N mineralization resulting in the high net N mineralization measured in this study.

This pattern of net N mineralization observed on Niwot Ridge in early spring is similar to the flush of mineralized soil N reported in arctic tundra and bog soils as they thaw during the spring (Kielland 1990). Williams et al. (1995) reported that mineralization of soil organic matter N in an alpine basin with relatively poor soil development was approximately four times greater than atmospheric N inputs. While net nitrification rates were generally lowest in the winter, approximately half of the net mineralized N was converted to nitrate in over-winter incubations (Williams et al. 1995). Similarly, in thawed soils under an Adirondak snowpack, nitrate concentrations in soil water increased relative to snowpack concentrations suggesting net N mineralization followed by nitrification in snow-insulated soils (Rascher et al. 1987; Peters & Driscoll 1989). On Niwot Ridge, however, soil inorganic nitrate concentrations did not increase, suggesting relatively low nitrification rates. This may be due to the high levels of heterotrophic activity in relatively wet soils reducing the oxygen concentrations below levels required for nitrification.

Although temporal patterns in soil N concentrations suggest significant net N mineralization took place before snowmelt began, the resin cores incubated for the entire snow-covered season did not identify over-winter net N mineralization. The absence of N in resin bags at the bottom of over-winter resin cores apparently was due to the resins being isolated from the microbially active layer at the soil surface by ice within the soil core. Soils in the bottom half of the cores were still frozen when collected after the sites became snow-free. This suggests that N mineralized under the snow was re-immobilized in the soil during snow melt.

Nitrogen outputs

Hydrologic losses

Surface water inorganic N concentrations indicated no loss of N from Niwot Ridge in overland flow during the early stages of snowmelt and only limited export later in the summer. While NH_4^+ concentrations in surface waters are often below detection limits (Williams et al. 1993a), the low levels of NO_3^- in surface waters during snowmelt at Niwot Ridge are unusual. Surface waters in Martinelli Basin, 500 m from the alpine sites, show a pronounced pulse of NO_3^- in stream water (Fig. 5.) during the early stages of runoff (Reddy & Caine 1990; Williams et al. 1993b). Similarly, other sites along the Front range experience elevated stream water N concentrations each spring. This has been shown at both the Loch Vale watershed in Rocky Mountain National Park (Baron 1991) and the Glacial Lakes Ecosystem Experiments Site in Wyoming (Williams et al. 1993b).

The absence of N in buried resin bags, together with no loss of N in overland flow, indicates that both snowpack N inputs and mineralized soil N were retained within the system. The ability of cold soils to rapidly immobilize large quantities of N during snowmelt is supported by work of Preston et al. (1990) who reported that greater than 50% of inorganic N added as ammonium to snow during the winter was recovered in the soil organic fraction immediately after snowmelt. Presumably, N immobilization on Niwot Ridge is greater due to higher levels of microbial biomass in the relatively well developed soils at this site compared to poorly developed soils in glaciated valleys. This immobilization could be due either to a higher microbial biomass or a higher level of microbial activity in these well developed soils. The ability of this system to immobilize the increased levels of N stored in the seasonal snowpack probably depends on three factors: 1) the degree of infiltration and spatial heterogeneity of snowmelt N inputs to the soil; 2) the size of the active microbial population; and 3) the amount of N mineralized under the snow.

Gaseous losses

Nitrous oxide fluxes measured in this study suggest that any inhibition of denitrification activity by low temperatures is partially overcome by high substrate availability. This hypothesis is supported by a number of studies which have identified a pulse of denitrification activity in early spring from previously snow covered soils, when substrate concentrations presumably are high (Groffman & Tiedje 1989; Goodroad & Keeney 1984). Hixson et al. (1988) reported N_2O flux from saturated soils at 0 °C were not significantly different from saturated soils between 5 ° and 10 °C, while N_2O production has been reported at temperatures as low as -4 °C with relatively small rate increases up to 4 °C (Struwe & Kjoller 1990; Mahli et al. 1990).

Winter N_2O fluxes from Niwot Ridge are similar in magnitude to those measured by Sommerfeld et al. (1993) from spring snowpacks at the Glacial Lakes Experimental Ecosystem Site (GLEES) in Wyoming. The maximum flux measured from these sites during the snow-covewred season is only slightly lower than fluxes measured at adjacent sites during the growing season (Schmidt et al. 1993, unpublished data). The extended period of snow cover in alpine areas suggests these fluxes may play a major role in the spring alpine N cycle. Preliminary calculations, using a 9:1 N_2:N_2O ratio from the literature (Ryden et al. 1979), indicate that the winter/spring N loss through denitrification is approximately equal to the atmospheric NO_3^--N inputs in snowmelt and may comprise as much as 50% of the annual gaseous N loss. This is significantly higher than in the Sierra Nevada of California where both atmospheric loading and denitrification activity are lower (Williams et al. 1995). Williams et al. (1995) estimated gaseous N loss was approximately 5% of deposition inputs in that system. This difference is probably due to the presence of highly developed soils at Niwot Ridge, while the Sierra Nevada sites are dominated by exposed bedrock and talus, with soils comprising approximately 20% of the basin surface area.

Conclusions

Consistent snow cover on Niwot Ridge allowed soils to thaw in late winter resulting in an environment where soil microorganisms became active long before snow melt. Soil thawed from the surface downward isolating microbial activity from deeper soils and groundwater. Microbial mineralization of soil organic matter in this layer resulted in a large soil inorganic N pool shortly before snowmelt. The majority of inorganic N stored in the seasonal snowpack entered this soil pool during melt. While most of this N was reimmobilized, a significant fraction, approximately equal to NO_3^--N loading in the snowpack, was lost through denitrification under the snowpack. These data suggest that microbial activity under seasonal snowpacks may play an important role in controlling N export, both in surface water and as gaseous N losses. Additionally, the large decrease in soil inorganic N during snowmelt when vegetation is becoming active suggests microbial activity during the winter may contribute to plant available N as sites become snow-free.

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