Biogeochemistry **43:** 1–15, 1998.

Inorganic nitrogen and microbial biomass dynamics before and during spring snowmelt

PAUL D. BROOKS[1], MARK W. WILLIAMS[2] & STEVEN K. SCHMIDT[3]
[1]*U.S. Geological Survey – Water Resources Division, 3215 Marine St. Boulder, CO 80303, USA;* [2]*Department of Geography and Institute of Arctic and Alpine Research, Campus Box 450, University of Colorado, Boulder, Colorado 80309-0450, USA;* [3]*Department of EPO Biology, Campus Box 334, University of Colorado, Boulder, Colorado 80309-0340, USA*

Accepted 10 November 1997

Key words: alpine, nitrogen cycling, nitrogen saturation, snowmelt, tundra

Abstract. Recent work in seasonally snow covered ecosystems has identified thawed soil and high levels of heterotrophic activity throughout the winter under consistent snow cover. We performed measurements during the winter of 1994 to determine how the depth and timing of seasonal snow cover affect soil microbial populations, surface water NO_3^- loss during snowmelt, and plant N availability early in the growing season. Soil under early accumulating, consistent snow cover remained thawed during most of the winter and both microbial biomass and soil inorganic N pools gradually increased under the snowpack. At the initiation of snowmelt, microbial biomass N pools increased from 3.0 to 5.9 g N m^{-2}, concurrent with a decrease in soil inorganic N pools. During the latter stages of snowmelt, microbial biomass N pools decreased sharply without a concurrent increase in inorganic N pools or significant leaching losses. In contrast, soil under inconsistent snow cover remained frozen during most of the winter. During snowmelt, microbial biomass initially increased from 1.7 to 3.1 g N m^{-2} and then decreased as sites became snow-free. In contrast to smaller pool sizes, NO_3^- export during snowmelt from the inconsistent snow cover sites of 1.14 ($\pm$0.511) g N m^{-2} was significantly greater ($p < 0.001$) than the 0.27 ($\pm$0.16) g N m^{-2} exported from sites with consistent snow cover. These data suggest that microbial biomass in consistently snow-covered soil provides a significant buffer limiting the export of inorganic N to surface water during snowmelt. However, this buffer is very sensitive to changes in snowpack regime. Therefore, interannual variability in the timing and depth of snowpack accumulation may explain the year to year variability in inorganic N concentrations in surface water these ecosystems.

Introduction

Significant progress has been made in the development of a quantitative description of the N cycle in a range of ecosystems. Over the last decade, an emphasis has been placed on understanding N cycling in headwater catchments where surface water chemistry is closely tied to soil biogeochemical processes (Creed et al. 1996; Williams et al. 1996a). The dominant characteristic of headwater ecosystems in the Rocky Mountains is a long, harsh winter followed by a short, cool growing season. Consequently, biogeochemical

processes during the growing season are strongly constrained by climate, primarily mediated by the timing of seasonal snow cover. Both water availability and soil temperature early in the growing season are affected by the timing and distribution of snowmelt runoff which in turn exhibits significant control over both plant and microbial activity (Oberbauer & Billings 1981; Walker et al. 1993). Seasonal snowpacks also may be a source of N early in the growing season. A number of studies have suggested that inorganic N released from winter snowpacks provides a large pulse of mobile, potentially available N each spring (Bowman 1992). While temperature and moisture control soil N dynamics throughout the growing season (Fisk & Schmidt 1995), the controls on N cycling during snowmelt, when temperatures are buffered by melting snow, soil moisture is high, and the potential for N transport to surface water is greatest, remain unknown.

Although vegetation communities are N limited during the growing season (Bowman et al. 1993), recent observations have identified elevated nitrate (NO_3^-) concentrations in surface waters along the Colorado Front Range (Baron 1991; Baron et al. 1994; Williams et al. 1993) both during spring snowmelt and early in the growing season. These increases in surface water NO_3^- concentrations appear to be related to increased atmospheric N deposition (Grant & Lewis 1982; Lewis et al. 1984; Bowman 1992; Sievering et al. 1992), suggesting these systems are experiencing N saturation (Williams et al. 1996b). The apparent contradiction between N limited vegetation and an N saturated system is due, at least partly, to temporal discontinuity between the period of high N availability during snowmelt, and high vegetative N demand during the growing season. A significant fraction of the annual atmospheric N deposition is stored in seasonal snowpacks (Sievering et al. 1992) and released in an ionic pulse during the first portion of snowmelt (Williams & Melack 1991). At Niwot Ridge in the Colorado Front Range the N released from the seasonal snowpack may account for as much as 30% of the net N mineralization from soil organic matter during the growing season (Bowman 1992; Fisk & Schmidt 1995), yet this N enters the soil many weeks before the sites become snow free (Brooks et al. 1995a; Williams et al. 1996a). While some plant species are known to end senescence under the melting snowpack (Mullen & Schmidt 1993), recent research suggests that the majority of plant species at these sites obtain N later in the season (Fisk 1995). This suggests that the physical and biogeochemical environment within the soil immediately before and during snowmelt is a major control on ecosystem scale N cycling and export.

The controls on mineralization, nitrification, and immobilization in subnivian soils are unknown. Seasonal snowpacks insulate the soil surface from harsh environmental conditions above the snow surface and allow soil

to thaw before snowmelt (Sommerfeld et al. 1991, 1993; Brooks et al. 1995b, 1996; Cline 1995). During this period, we have identified high levels of heterotrophic activity (Brooks et al. 1996, 1997) and over-winter net N mineralization before melt (Brooks et al. 1995b, 1996) equal to or greater than estimates of growing season net N mineralization (Fisk & Schmidt 1995). Similarly, nitrification under seasonal snowpacks apparently is responsible for elevated stream water NO_3^- concentrations in a northeastern US watershed (Rascher et al. 1987). In contrast, Zak et al. (1990) identified microbial N immobilization as the dominant process during early spring. This is consistent with NO_3^- concentrations in stream water from an alpine/montane watershed adjacent to our study site that were inversely related to winter snow depths within the catchment (Lewis & Grant 1980). We recently have found that winter and spring trace gas fluxes are very sensitive to changes in snowpack regime (Brooks et al. 1997), and postulate that soil N cycling may be similarly affected by snow cover.

The evidence of active microbial populations under seasonal snow cover suggests that an important portion of the annual N cycle for these systems occurs before the growing season. To examine this possibility, and to identify potential controls on winter/spring N cycling, we followed soil N dynamics under two snowpack regimes during the winter and spring of 1994. Specifically, we examined the relationship between the timing and depth of snow cover and soil inorganic N, microbial biomass N, and inorganic N export under seasonal snowpacks at Niwot Ridge in the Colorado Front Range. The two primary questions we asked were: 1) How are soil and microbial N pools during the winter-spring period affected by snowpack regime?, and 2) Is microbial biomass a significant sink for N during the snowmelt period?

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 kilometers east of the Continental Divide. 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. 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. 1996b), the majority of which falls as snow (Greenland 1989). Sites were located at an elevation of 3510 m. Vegetation at these sites is characteristic of moist meadow communities on Niwot Ridge containing a mixture of the gramminoid *Kobresia myosuroides* and the forb *Acomostylis rossii* with patchy occurrence of communities dominated by the gramminoid *Deschampsia caespitosa* in

protected microsites (Walker et al. 1993). Above-ground primary production over a nine year period averaged 222.8 g (sd 6.6) phytomass m^{-2} at ten moist meadow sites on Niwot Ridge (Walker et al. 1994). Soils are Cryochrepts and vary in depth from approximately 0.3 to 2.0 m overlying granitic parent material (Burns 1980). Soil pH in a 1:1 (weight:volume) DI slurry ranges from 4.6–5.0 (Fisk & Schmidt 1995). The soil organic horizon varies from 80–100 mm in depth, with soil carbon ranging from 150–190 g kg^{-1} and soil N ranging from 11–22 g kg^{-1} (Burns et al. 1980; Brooks et al. 1995a).

The re-deposition of snow by wind characterizes the pattern of snow distribution with a continuous snow cover usually developing in October at the early accumulating, deep snowpack sites and in January at the shallow sites used in this study. Although the sites have different patterns of snow accumulation, melt water from adjacent, uphill areas subsidizes soil moisture at the shallower snowpack sites resulting in similar communities. Soils typically freeze in late autumn before a consistent snow cover develops and gradually warm under the snowpack during the winter (Brooks et al. 1995a). Thawed soil before melt appears when soil temperatures reach −5°C and is generally restricted to the upper, organic soil horizon (Brooks et al. 1995b, 1996), apparently resulting from a bottleneck in the transfer of geothermal energy under snow (Cline 1995). The dominant hydrologic event is spring snowmelt which is the primary control on soil moisture during the growing season.

Methods

Soil N dynamics were followed throughout the winter and spring of 1993–1994 at six, 25 m^{-2}, sites which were located to correspond with concurrent measurements of CO_2 and N_2O flux from the seasonal snowpack (Brooks et al. 1997). Three sites were located in areas characterized by relatively shallow (<1.0 m maximum accumulation), late accumulating snowpacks and three sites were located in areas characterized by deeper (maximum accumulation 1.5–2.0 m), earlier accumulating snowpacks. Six snow pits, one within each of the 25 m^{-2} sites, were dug to the soil surface on each of 10 sampling dates and three soil samples were collected (provided thawed soil was present) from each pit yielding a total of 18 soil samples, 9 from each snowpack regime, per date. Soil samples, 5 cm in diameter and 8 cm deep, were returned to the lab to be analyzed for extractable NO_3^-, NH_4^+, and microbial biomass N. Soil temperatures were measured both manually at the bottom of snowpits using a portable Omega temperature probe (±0.1 °C) and from thermisters installed at the soil surface in October.

Inorganic N fluxes to and from the upper soil horizon (8 cm depth) during the melt period were measured with 8 paired, ion exchange collectors (4

surface and 4 subsurface) placed at each site between 27 December and 4 January and collected immediately after sites became snow-free. This yielded a total of 24 surface and 24 buried collectors (12 under deep snow and 12 under shallow snow for each collector type). Surface resin collectors 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 in an attempt to minimize inputs from overland flow. A silicone plug was placed at the bottom of each tube to exclude N inputs from underlying soil. Open only to the snowpack, these collectors were designed to estimate exchange at the saturated snowpack – soil interface during melt. Subsurface resin collectors were placed in acid washed, 35-mm diameter radiator hose and placed under intact soil blocks which were immediately recovered with snow (Williams et al. 1996a). Within each collector, 20 mL (wet volume) of mixed cation and anion (16–50 mesh) exchange resins were placed in acid washed, permeable nylon bags. Resins were obtained from Baxter Scientific loaded with H^+ or OH^- with a total exchange capacity of 0.57 meq mL^{-1}. These resin collectors are similar to those used in mineralization tubes (DiStefano & Gohlz 1986; Hart & Gunther 1989) and are described in more detail elsewhere (Fisk & Schmidt 1995; Brooks et al. 1996).

Laboratory analyses

To minimize any changes in N pools resulting from disturbance and warming, all soil samples were stored on ice and processed completely within 12 hours of collection. In order to maintain this schedule, it was necessary to pool the three soil samples from each snowpit beginning in March. Immediately upon return from the field, fresh soils were homogenized using a 2 mm sieve, and subsamples were taken for inorganic N and microbial N measurements. Subsamples of freshly sieved 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 (Davidson et al. 1989).

Microbial biomass N in freshly sieved soil was determined using a chloroform fumigation – extraction method (Brookes et al. 1985). For each field soil, paired subsamples (approximately 10 g each) were taken from freshly sieved soil. One subsample (initial) was extracted with 100 ml 0.5 M K_2SO_4 on an orbital shaker at 125 rpm for 30 minutes. The second subsample (final) was fumigated under chloroform vapor following three vacuum/release purge cycles in a desiccator for 5 days, and then extracted with K_2SO_4 as described above. Extracts were digested by persulfate oxidation and analyzed for NO_3^-. A correction factor of 0.54 (Brookes et al. 1985) was applied to the difference in total extractable N between paired initial and final subsamples to estimate microbial biomass N.

Ion exchange resin bags from surface and subsurface were air dried in the laboratory and extracted with 2N KCl as for soil. Extracts from both soils and resins were filtered through preleached, Whatman #1 filter paper and analyzed on a LACHAT flow injection autoanalyzer (FIA, LACHAT Instruments, Mequon). Potassium chloride or K_2SO_4 blanks were run with all samples, and standards were made in the appropriate solutions. Before use, 3 to 5 subsamples from each batch of resins were analyzed for inorganic N contamination.

Data analyses

Differences in soil inorganic N and microbial biomass N pools were evaluated using a repeated measures ANOVA with snowpack regime and sampling date as variables. Because soil at the discontinuous snowpack sites refroze resulting in no values for some sampling dates, we could not evaluate snowpack vs. sampling date differences for all 10 dates. Consequently, we chose four sampling dates when data from all sites were available. These sample dates were: 1) the first time thawed soil was observed in mid-winter, 2) immediately before melt, 3) one week after snowmelt began, and 4) the day sites became snow-free. Differences in soil N pools on individual dates, inorganic N leachate in resin collectors, and soil temperature were evaluated with paired, two-tail *t*-tests.

Results

Snowpack dynamics

The seasonal snowpack at the shallow snowpack sites began to develop in January, but a dry, windy period in March resulted in a decrease in snow depth before the pack redeveloped in late March and early April 1994 (Figure 1). In contrast, the snowpack at the deep sites developed in October and did not decrease significantly during the winter. Maximum snow depths of 0.50 meters for the shallow, inconsistent snow cover sites, and 1.65 meters for the deep snowpack sites occurred in the end of April 1994. Snowmelt began during the last week in April at the shallow sites and during the first week in May at the deeper sites. The shallow sites were snow free by 15 May, while the deep snow cover sites were not snow free until 5 June.

The depth and especially the timing of snowpack accumulation had a significant effect on soil temperature. Continuous snow cover at the deep sites insulated the soil surface from extreme air temperatures resulting in a mean minimum soil temperature of -5.0°C which was significantly ($p < 0.05$)

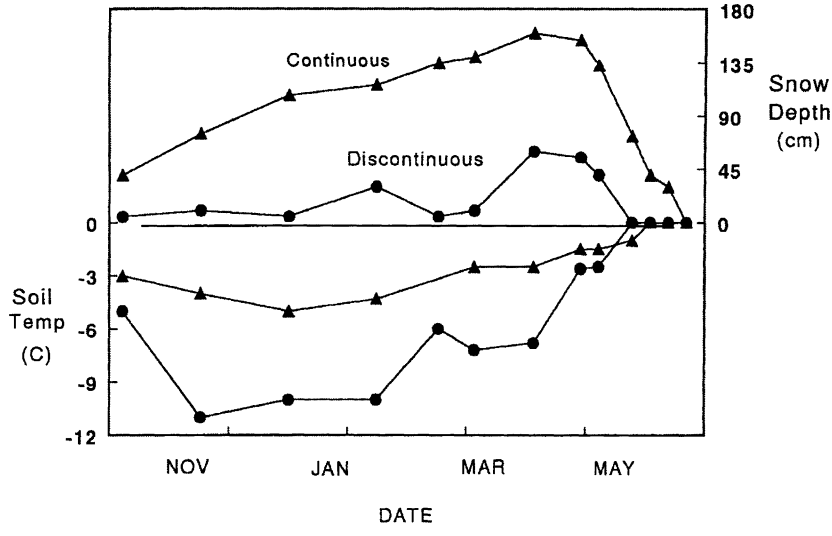

Figure 1. Snow depth (top) and soil surface temperature (bottom) under shallow, discontinuous and deep, continuous snowpacks, 1994. (n = 3, SE is smaller than size of symbol).

warmer than the −11.0°C mean minimum temperature at the shallow, discontinuous snowpack sites. While soils warmed between January and March at the shallow sites, the decrease in snow depth in March allowed the soil to cool (Figure 1), suggesting that a minimum snow depth of approximately 30 cm was necessary to effectively insulate these sites. Consistent with observations made in previous years, thawed soil was observed when the soil temperature reached −5°C and generally was limited to the top 8 cm of the soil. Thawed soil was present under the deep, consistent snowpacks at the first sampling date in early January. In contrast, soil thaw first was observed at shallow sites on one sampling date in March, but soil refroze as temperatures cooled with the decrease in snow cover. Soil at these sites did not thaw again until late April shortly before melt. At all sites soils thawed first in the organic surface horizon with deeper soil remaining frozen until snowmelt began.

Soil N pools

The two ANOVAs indicate that both microbial biomass N and soil inorganic N exhibited significant ($p < 0.001$) variability over time (Table 1). Microbial biomass N values on 4 January 1994 were similar at the three deep, continuous snowpack sites with a grand mean of 1.52 (sd = 0.31, n = 9) g N m^{-2} (Figure 2a). Biomass N at these three sites increased slowly through the winter and then rapidly at the initiation of snowmelt peaking at 5.87 g N m^{-2} on 4 May, which was significantly ($p < 0.05$) higher than the mid-winter values. During

Table 1. F ratios and significance levels from analysis of variance for microbial biomass N and soil inorganic N values (2-way ANOVA with replication).

Variable	Source	F ratio	Significance
Microbial biomass N	Snowpack regime	13.46	$p < 0.01$
	Date	23.05	$p < 0.001$
	Snowpack × Date	5.82	$p < 0.01$
Soil inorganic N	Snowpack regime	29.74	$p < 0.001$
	Date	22.79	$p < 0.001$
	Snowpack × Date	20.90	$p < 0.001$

the latter portion of snowmelt, microbial biomass N decreased rapidly as sites became snow free. Soil inorganic N pools under continuous snow cover increased slowly during the early portion of the winter, peaked on 4 March at 3.05 g N m^{-2}, and then decreased gradually until sites were snow-free. Nitrate constituted 5–10% of the total soil inorganic N pool on all dates with no significant differences between snowpacks or dates.

Similarly, there were significant differences in both microbial N ($p < 0.01$) and soil N ($p < 0.001$) between the two snowpack regimes. In contrast to the deeper snowpack sites, soil under the shallow, discontinuous snowpack was frozen early in the winter and no samples were collected. Soil at these sites thawed briefly in March and microbial biomass N values of 1.35 g N m^{-2} were similar to the January values at the deep sites (Figure 2b). Soil refroze with the decrease in snow cover and samples were not collected until soil again thawed shortly before melt in late April. Similar to the pattern observed at the deep sites, microbial N increased and soil inorganic N decreased during the initial period of melt. However, the peak in microbial biomass N of 3.10 g N m^{-2} was roughly half the value measured under the deep, continuous snowpacks. Soil inorganic N pools in March also were similar to the mid-winter values at the deeper snowpack sites, however soil inorganic N decreased much more sharply at the initiation of melt. For both microbial N and soil inorganic N the interaction between snowpack and date results from a similar pattern of increasing microbial N and decreasing soil inorganic N at the initiation of melt.

The immobilization of 4.34 g N m^{-2} in microbial biomass during the winter and spring at the continuous snow cover sites was much greater than the 1.7 g N m^{-2} immobilized at sites with shallow, inconsistent snow cover (Figure 3). Similarly, the decrease in microbial biomass during the later stages of melt was larger at the continuous snow-cover sites. Under both snowpack regimes, the increase in microbial N during the spring and early portion of snow melt was approximately equal to the decrease during the latter stages of

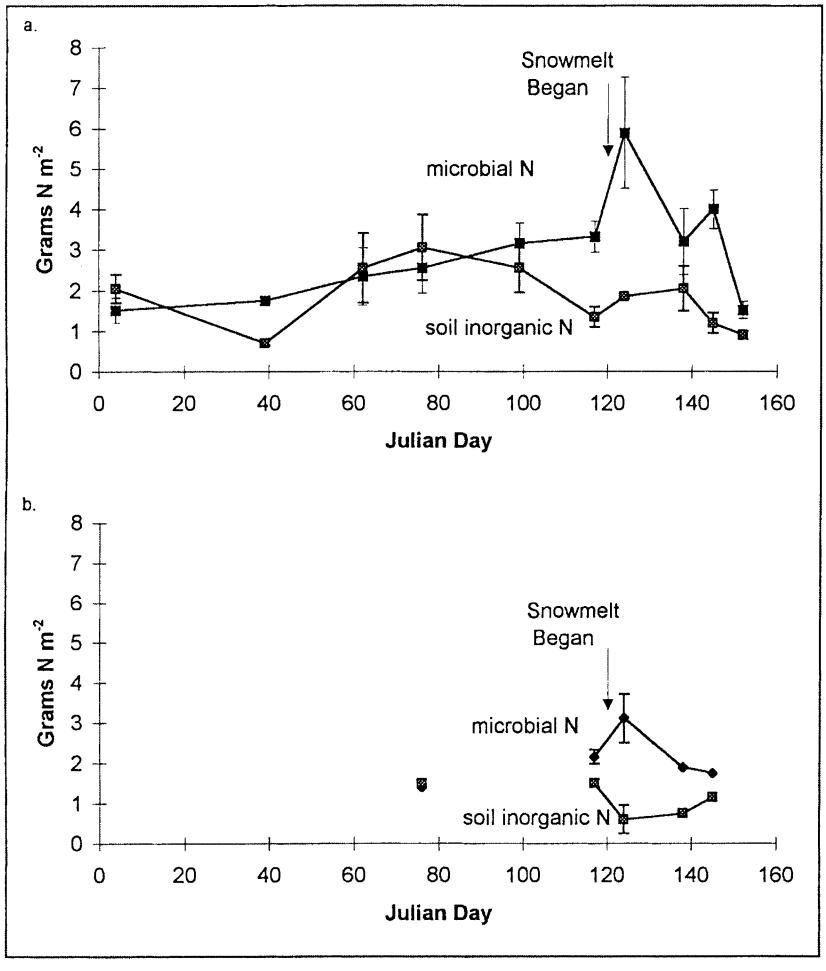

Figure 2. Microbial biomass N and soil inorganic N in soil under deep, continuous snowpacks (a) and under shallow, discontinuous snowpacks (b). (Mean ± SE; $n = 3$).

snow melt. While there were significant changes in both microbial and soil inorganic N pools under snow cover, there were no significant differences in either pool between snowpacks when sites became snowfree.

Inter-system nitrogen fluxes

Surface resin collectors demonstrated a high degree of spatial heterogeneity in N inputs to soil at any one site. Estimates of inorganic (both NO_3^- and NH_4^+) N inputs using the surface resin bags ranged from 367 to 496 mg N m^{-2} across all sites and were not related to snow depth, the timing of

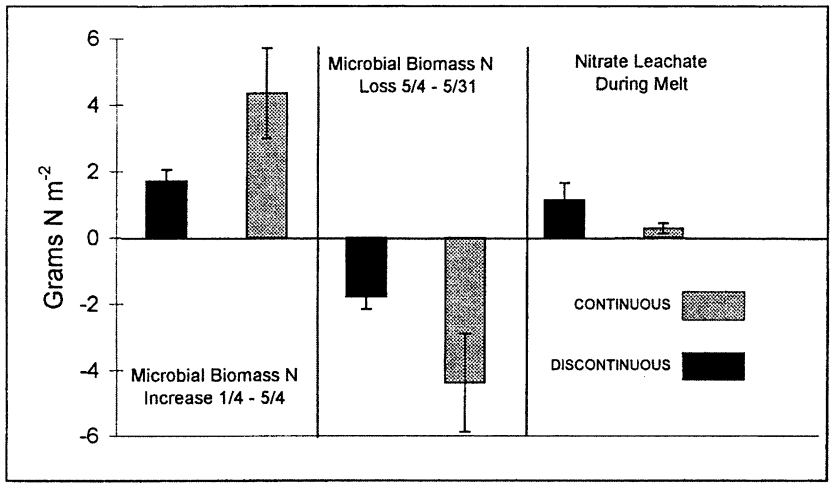

Figure 3. Net immobilization of N in microbial biomass before and during the early stages of snowmelt (left), loss of microbial biomass N during the latter stages of snowmelt (right), and nitrate leachate from the top 8 cm of soil during snowmelt. (mean ± SE; n = 3 for microbial N; n = 12 for leachate).

Table 2. Inorganic nitrogen inputs to the soil surface from resin collectors and from snow chemistry (mg N m^{-2}) (mean (SE)).

	Resin collectors (n = 12)		Snow chemistry (a)	
Site	NH_4^+	NO_3^-	NH_4^+	NO_3^-
Shallow, discontinuous	94 (67)	273 (414)	68	19
Deep, continuous	125 (104)	371 (369)	225	64

(a) from Williams et al. 1996b

snowpack development, or snowpack loading (Table 2). In general, resin collector inputs were higher than snowpack N loading from atmospheric deposition even though an effort was made to exclude soil N from the surface collectors.

However, there was a significant difference ($p < 0.001$) in N leachate measured using the subsurface resin bags. Net N leachate (defined as the difference between inorganic N in subsurface and surface resin bags) from sites with shallow snow cover was 1.14 g N m^{-2}, approximately four times greater than the export of 0.27 g N m^{-2} from sites with deep, continuous snow cover (Figure 3). Although there was no significant difference in soil NO_3^- pools between sites, the higher export is consistent with the sharp decrease in total soil inorganic N pools at melt (Figure 2b).

Discussion

Under both snowpack regimes internal transformations of N in the soil dominated the spring N cycle. Inorganic N loading in the snowpack was less than 10% of the soil inorganic pool at the initiation of snow melt, similar to the 5% (Schimel et al. 1994) to 25% (Williams et al. 1995) reported for arctic and alpine sites, respectively. Previous work using ^{15}N labeled tracers indicates most of this N enters the soil inorganic N pool with snow melt (Brooks et al. 1995b; Williams et al. 1996a). Similarly, isotopic analyses of NO_3^- in stream water during snow melt indicate surface water N export is a mixture of both snowpack and soil sources (Kendall et al. 1995). Although we attempted to exclude soil N from the surface resin collectors, our estimates of N input to the soil from the surface resin collectors were much higher than atmospheric N loading. This suggests that mixing of soil and snowmelt N occurs within the snowpack during melt, and the amount of N entering the soil at any site is a mixture of both atmospheric N deposited in the snowpack and soil N from other nearby locations. Therefore, the controls on the size and mobility of the much larger soil N pool before and during the early portion of melt are the primary factors affecting the balance between N immobilization and export in surface water.

The timing and depth of snow cover had a large effect on both the size of soil inorganic N pools and the magnitude of the fluxes between pools during melt. These controls were mediated primarily through control on soil temperature and the timing of soil thaw. Thawed soil under the deeper snowpacks allowed microbial biomass to become active, increasing slowly before melt and then rapidly immediately after snowmelt began. This pattern suggests the long duration of soil thaw allowed the development of microbial populations which were capable of a rapid, immediate response to snowmelt. This pattern is consistent with CO_2 flux measurements from these and other locations in the Rocky Mountains which decrease in late winter and then increase rapidly at the initiation of melt (Brooks et al. 1996, 1997; Sommerfeld et al. 1993, 1996). The reason for these relatively large increases in both microbial biomass and CO_2 flux while temperature remains buffered at 0 °C during melt are unclear. A possible explanation is that a long period of heterotrophic activity under early developing snowpacks results in a substrate limited environment late in the winter. Infiltrating melt water during the spring mixes the soil solution increasing substrate availability both through mass transport and diffusion.

Because the development of an active microbial biomass under snow appears to be a primary mechanism controlling N export during melt, the interannual variability in the timing of snow cover may have a large effect on N export during the spring. Even though both microbial and soil inorganic N

pools indicate significantly more N is actively cycling under the deeper, more consistent snowpacks, during the early portion of melt the rapid increase in microbial biomass immobilizes N resulting in lower N export from these sites. The timing of this increase in microbial N is consistent with the timing of the highest streamwater NO_3^- concentrations during the spring (Williams & Melack 1991). Measurements made at these shallow snowpack sites during the winter of 1993 (Brooks et al. 1996) also indicate that N export is sensitive to the presence of active microbial communities determined by snowpack regime. In contrast to 1994, both subsurface resin collectors and surface water NO_3^- concentrations in ephemeral streams draining the site identified very little inorganic N export from these soils (Brooks et al. 1996). The difference between the two years appears to be in the timing of snowpack accumulation. The maximum snow depth at these sites was only slightly greater in 1993 than in 1994, but there was no period of ablation in mid-winter in 1993. With a continuous, insulating snow cover in 1993, soil thawed under the snow much earlier in the winter and soil inorganic N concentrations were similar to the deep snowpack sites in 1994 (Brooks et al. 1996). Although we do not have microbial biomass N data from 1993, CO_2 fluxes from co-located sites in 1993 were much higher than in 1994 suggesting a larger, active heterotrophic community under the consistent snow cover in 1994 (Brooks et al. 1997). This combination of higher CO_2 fluxes and low N export is consistent with microbial immobilization of N during melt. Scaling to the catchment, our data suggest that the inverse relationship between mean snow depth and surface water NO_3^- concentrations observed in a multi-year solute budget for a neighboring sub-catchment (Lewis & Grant 1980), was due to an enhanced ability of microbial biomass to immobilize soil N in high snow years, rather than an increase in soil N pools in low snow years. Because much more N is in rapidly cycling pools under deeper snow, this subtle difference in interpretation is important when considering plant available N and annual N budgets in seasonally snow-covered systems.

The large decrease in microbial biomass N as sites became snow free without a concurrent increase in inorganic N pools suggests that N initially immobilized in microbial biomass is transferred to vegetation. The magnitude of N lost from microbial biomass is much larger than both hydrologic export from overlying soils identified by resin collectors and gaseous N fluxes (Brooks et al. 1997) leaving plants as the likely sink for this N. A potential mechanism for this transfer of N may be freeze/thaw events under a waning snowpack when snow depth is no longer sufficient to insulate soil from diurnal temperature fluctuations. Soil exposed to freezing temperatures at night may result in the lysis of microbial cells. As soils warm during the day, N released from the completion of this freeze/thaw cycle is potentially available to plants

which are better able to survive the freeze-thaw. Fisk (1995) recently found that growing season net N mineralization provides only 20% of the total annual vegetation N demand on Niwot Ridge. The decrease in microbial N during the latter stages of melt occurs as many tundra plants are beginning to acquire N in the spring (Mullen & Schmidt, submitted), and may represent a significant fraction of the missing vegetation N demand.

In general, N cycling during the spring snowmelt period is controlled by microbial communities in snow-covered soil which, in turn, are controlled by the timing of snowpack accumulation earlier in the year. We have seen similar results in our measurements of CO_2 and N_2O fluxes from snow covered soil (Brooks et al. 1996, 1997), where small changes in the timing of snowpack accumulation result in an order of magnitude change in over-winter gas fluxes. While climate is still the driver for these processes, there is not a simple relationship between temperature or moisture and these fluxes. Instead, the timing of snow cover earlier in the winter controls the magnitude of soil N fluxes by allowing the development of active microbial communities under the snow. Since spring snowmelt is both the most likely time for hydrologic N export as well as the period of high vegetation N demand, a major component of the annual N cycle in this system is determined by processes which occur under snow before the beginning of the growing season.

Acknowledgements

We thank C. Seibold, T. Bardsley, B. Cress, and M. Fisk for assistance with laboratory analyses and field work; and M. Fisk, S.C. Hart, and an anonymous reviewer for valuable comments on the manuscript. Funding was provided by the National Biological Service, NASA/EOS (NAGW-2602), the Niwot Ridge Long-Term Ecological Research Project (NSF DEB 9211776) and EPA grant #R819448-01-1.

References

Baron JS (1991) Biogeochemistry of a Subalpine Ecosystem: Loch Vale Watershed, Ecological Studies Ser. 90. Springer-Verlag

Baron JS, Ojima DS, Holland EA & Parton WJ (1994) Analysis of nitrogen saturation potential in Rocky Mountain tundra and forest: Implications for aquatic systems. Biogeochemistry 27: 61–82

Bowman WD, TA Theodose, JC Schardt & RT Conant (1993) Constraints of nutrient availability on primary production in two alpine communities. Ecology 74: 2085–2097

Bowman WD (1992) Inputs and storage of nitrogen in winter snowpack in an alpine ecosystem. Arctic and Alpine Res. 24: 211–215

Brookes PC, Landman A, Pruden G & Jenkinson DS (1985) Chloroform fumigation and the release of soil nitrogen: A rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biol. Biochem. 17: 837–842

Brooks PD, SK Schmidt & MW Williams (1995a) Snowpack controls on soil nitrogen dynamics in the Colorado alpine. In: Tonnessen K, Williams M & Tranter M (Eds) Biogeochemistry of Snow-Covered Catchments (pp 283–292). International Association of Hydrological Sciences Publication 228, Wallingford, UK

Brooks PD, Schmidt SK, Walker, DA & Williams MW (1995b) The Niwot Ridge snow fence experiment: Biogeochemical responses to changes in the seasonal snowpack. In: Tonnessen K, Williams M & Tranter M (Eds) Biogeochemistry of Snow-Covered Catchments (pp 293–302). International Association of Hydrological Sciences Publication 228, Wallingford, UK

Brooks PD, Williams MW & Schmidt SK (1996) Microbial activity under alpine snow packs, Niwot Ridge, CO. Biogeochemistry 32: 93–113

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

Burns SF (1980) Alpine Soil Distribution and Development, Indian Peaks, Colorado Front Range. PhD Dissertation, University of Colorado, Boulder, CO

Cline D (1995) Snow surface energy exchanges and snowmelt at a continental alpine site. In: Tonnessen K, Williams M & Tranter M (Eds) Biogeochemistry of Snow-covered Catchments (pp 157–166). International Association of Hydrological Sciences Publication 228, Wallingford, UK

Creed IF, Band LE, Foster NW, Morrison IK, Nicholson JA, Semkin RS & Jeffries DS (1996) Regulation of nitrate-N release from temperate forests: A test of the N flushing hypothesis. Water Resour. Res. 32: 3337–3354

Davidson EA, Eckert RW, Hart SC & Firestone MK (1989) Direct extraction of microbial biomass nitrogen from forest and grassland soils of California. Soil Biol. Biochem. 21: 773–778

DiStephano JF & Gholz HL (1986) A proposed use of ion exchange resins to measure nitrogen mineralization and nitrification in intact soil cores. Comm. Soil Sci. Plant Anal. 17: 989–998

Fisk, MC (1995) Nitrogen dynamics in an alpine landscape. PhD Dissertation, University of Colorado, Boulder, CO

Fisk MC & Schmidt SK (1995) Nitrogen mineralization and microbial biomass N dynamics in three alpine tundra communities. Soil Sci. Soc. Am. J. 59: 1036–1043

Grant MC & Lewis WM (1982) Chemical loading rates from precipitation in the Colorado Rockies. Tellus 34: 74–88

Greenland D (1989) The climate of Niwot Ridge, Front Range, Colorado. Arctic and Alpine Research 21: 380–391

Hart SC & Gunther AT (1989) In situ estimates of annual net mineralization and nitrification in a subarctic watershed. Oecologia. 80: 284–288

Kendall C, Campbell DH, Burns DA, Shanley JB, Silva RA & Chang CC (1995) Tracing sources of nitrate in snowmelt runoff using the oxygen and nitrogen isotopic concentrations of nitrate: Pilot studies at three catchments. In: Tonnessen K, Williams M & Tranter M (Eds) Biogeochemistry of Snow-covered Catchments (pp 339–348). International Association of Hydrological Sciences Publication 228, Wallingford, UK

Lewis WM & Grant MC (1980) Relationship between snow cover and winter losses of dissolved substances from a mountain watershed. Arctic and Alpine Research 12: 11–17

Lewis WM Jr, Grant MC & Saunders JF III (1984) Chemical patterns of bulk atmospheric deposition in the State of Colorado. Water Resour. Res. 20: 1691–1704

Mullen RB & Schmidt SK (1993) Mycorrhizal infection, phosphorus uptake, and phenology in *Ranunculus adoneus*: Implications for the functioning of mycorrhizae in alpine systems. Oecologia 94: 229–234

Oberbauer S & Billings WD (1981) Drought tolerance and water use by plants along an alpine topographical gradient. Oecologia 50: 325–331

Rascher CM, Driscoll CT & Peters NE (1987) Concentration and flux of solutes from snow and forest floor during snowmelt in the West-Central Adirondack region of New York. Biogeochemistry 3: 209–224

Schimel JP, Kielland K & Chapin FS III (1994) Nutrient Availability and Uptake by Tundra Plants. In: Reynolds JF & Tenhunen JD (Eds) Landscape Function: Implications for Ecosystem Response to Disturbance: A Case Study in Arctic Tundra (pp 203–221). Springer-Verlag

Sievering H, Burton D & Caine N (1992) Atmospheric loading of nitrogen to alpine tundra in the Colorado Front Range. Global Biogeochemical Cycles. 6: 339–346

Sommerfeld RA, Musselman RC, Ruess JO & Mosier AR (1991) Preliminary measurements of CO_2 in melting snow. Geophysical Research Letters 18: 1225–1228

Sommerfeld RA, Mosier AR & Musselman RC (1993) CO_2, CH_4, and N_2O flux through a Wyoming snowpack. Nature 361: 140–143

Sommerfeld RA, Massman WJ & Musselman RC (1996) Diffusional flux of CO_2 through snow: Spatial and temporal variability among alpine-subalpine sites. Global Biogeochemical Cycles 10: 473–482

Walker DA, Halfpenny JC, Walker MD & Wessman CA (1993) Long-Term studies on snow-vegetation interactions. Bioscience 43: 287–301

Walker MD, Webber PJ, Arnold EH & Ebert-May D (1994) Effects of inter-annual climate variation on above ground phytomass in alpine vegetation. Ecology 75: 393–408

Williams MW & Melack JM (1991) Solute chemistry of snowmelt and runoff in an alpine basin, Sierra Nevada. Water Resources Research. 27: 1575–1588

Williams MW, Caine N, Baron J, Sommerfeld RA & Sanford RL (1993) Regional assessment of nitrogen saturation in the Rocky Mountains. EOS, Transactions of the American Geophysical Meeting, 1993 Fall Meeting 74(Supplement): 257

Williams MW, Bales RC, Brown AD & Melack JM (1995) Fluxes and transformations of nitrogen in a high-elevation catchment, Sierra Nevada. Biogeochemistry 28: 1–31

Williams MW, Brooks PD, Mosier AR & Tonnessen KA (1996a) Mineral N transformations in and under seasonal snow in a high-elevation catchment, Rocky Mountains, USA. Water Resources Research 32: 3175–3185

Williams MW, Losleben M, Caine N & Greenland D (1996b) Changes in climate and hydrochemical responses in a high elevation catchment, Rocky Mountains. Limnol. Oceanogr. 41: 939–946

Zak DR, Groffman PM, Pregitzer KS, Chreistensen S & Tiedje JM (1990) The vernal dam: Plant-microbe competition for nitrogen in northern hardwood forests. Ecology 7: 651–656