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Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities

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Abstract

Microbial activity in Arctic tundra ecosystems continues through the winter and is an important component of the annual C budget. This activity is sensitive to climatic variation, particularly snow depth because that regulates soil temperature. The influence of winter conditions on soil N cycling is poorly understood. In this study, we used intact core incubations sampled periodically through the winter and following growing season to measure net N mineralization and nitrification in dry heath and in moist tussock tundra under ambient and experimentally increased snow depths (by use of a snowfence). In dry heath, we sampled soils under *Dryas octopetela* or *Arctostaphylos alpine*, while in tussock tundra, we sampled *Eriophorum vaginatum* tussocks and *Sphagnum* dominated areas between tussocks. Our objectives were to: (1) examine how different winter snow regimes influenced year-round N dynamics in the two tundra types, and (2) evaluate how these responses are affected by dominant species present in each system. In tussock tundra, soils with increased winter snow cover had high net N mineralization rates during the fall and winter, followed by immobilization during thaw. In contrast, N mineralization only occurred during the autumn in soils with ambient snow cover. During the growing season when N immobilization dominated in areas with ambient snow cover, soils with increased winter snow cover had positive net mineralization and nitrification rates. In dry heath tundra, soils with increased snow depth had high late winter net N mineralization rates, but these rates were: (a) comparable to early winter rates in soils under *Arctostaphylos* plants with ambient snow cover; (b) greater in soils under *Arctostaphylos* plants than in soils under *Dryas* plants; and (c) less than the rates found in tussock tundra. Our findings suggest under ambient snow conditions, low soil temperatures limit soil N mineralization, but that deeper snow conditions with the associated warmer winter soil temperatures dramatically increase over-winter N mineralization and thereby alter the amount and timing of plant-available N in tundra ecosystems.

Keywords: Arctic; Tussock tundra; Dry heath tundra; Nitrogen mineralization; Nitrification; Snow; Winter; Cold season; N availability

1. Introduction

Arctic ecosystems are characterized by long winters; soils are frozen and snow-covered much of the year (Chapin and Shaver, 1985; Jones et al., 1999). Despite these apparently harsh conditions, however, soil respiration continues through the winter (Zimov et al., 1996; Oechel et al., 1997; Fahnestock et al., 1998, 1999; Jones et al., 1999; Welker et al., 2000). Even though the bulk of soil water freezes just below 0 °C, soil particles continue to have liquid water films around them down to temperatures of at least −10 °C (Romanovsky and Osterkamp, 2000), and the presence of unfrozen water in soil allows microbial activity to continue (Coxson and Parkinson, 1987; Rivkina et al., 2000; Mikan et al., 2002). Although Arctic wintertime CO_2 flux rates are low, winters are so long that soil respiration during the nongrowing season (defined as the 'cold season' by Olsson et al. (2003)) constitutes an important component of annual C budgets (Fahnestock et al., 1999; Welker et al., 2000). While both the existence and importance of cold season microbial respiration have been demonstrated, few studies have examined soil nutrient dynamics during the cold season. The dynamics of N processes may be especially important because most tundra ecosystems are N limited and changes in N supply may affect leaf development, carbon flux and biomass production (Shaver and Kummerow, 1992; Schimel et al., 1996). Net

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mineralization occurs over the cold season in both the Alaskan (Giblin et al., 1991) and Scandinavian Arctic tundra (Schmidt et al., 1999), and decomposing litter immobilizes N over the cold season (Hobbie and Chapin, 1996). In contrast, net N mineralization rates during the growing season are often low or negative, indicating that microbial N immobilization is the dominant process (Chapin et al., 1988; Kielland, 1990; Giblin et al., 1991; Nadelhoffer et al., 1991; Schmidt et al., 1999; Jonasson et al., 1999). These studies suggest that soil inorganic N dynamics are fundamentally different during the cold season, with a shift from immobilization during the growing season to mineralization during the cold season.

While we know that N mineralization occurs during the Arctic cold season, we know little about the seasonality of the process through the cold season or of what regulates cold season mineralization. Although above ground conditions in the Arctic appear to change little between the fall, when snow first begins to accumulate, and the spring when it melts, soil conditions through this period vary dramatically (Olsson et al., 2003). This 9-month cold season encompasses the period of maximum soil thaw depth in the autumn (even as soil begins to freeze from the surface), a period when soils are completely frozen in the winter, and a period when they begin to thaw at the surface again. Given this range of conditions, soil processes are likely to vary dramatically through the cold season and are likely to be specifically sensitive to climate changes that might only affect one period of the cold season or another. Measurements that encompass the entire cold season will miss processes that occur on shorter time scales.

Two periods of the cold season are most likely to be important biologically within the context of year-round N cycling. During the autumn, soils are warm and at their deepest thaw. Although the above ground portion of plants senesce in the fall, some plants have perennial roots (Billings et al., 1978; Kummerow et al., 1983), while others (such as *Eriophorum vaginatum*) produce new roots in fall (Sullivan et al., 2002). Thus, if autumn N mineralization occurs it may be available for plant uptake. The other potentially important period is the spring, when soils begin to thaw. If N accumulates in the soil under the winter snowpack, it would be available for plants that either have overwintering roots or that produce a new flush of roots in early spring (Billings et al., 1978; Kummerow et al., 1983; Lipson and Monson, 1998; Sullivan et al., 2002). N uptake at snowmelt has been demonstrated in both alpine and Arctic ecosystems (Bilbrough et al., 2000). Uptake at snowmelt may be particularly important for nonvascular species (Bilbrough et al., 2000). Thus, cold season inorganic N dynamics may be important in providing N for plant uptake in arctic ecosystems, but these dynamics are poorly understood. As growth in most tundra plant communities is strongly nutrient limited, understanding when soil resources are available is critical to understanding plant nutrient uptake, community dynamics and the overall C cycle of the tundra (Chapin and Shaver, 1985; Shaver and Kummerow, 1992; Shaver et al., 1992; Rustad et al., 2001).

The potential for the importance of cold season N dynamics in arctic tundra is demonstrated by studies conducted in alpine tundra. Alpine tundra systems at Niwot Ridge, Colorado exhibit higher rates of net mineralization during the winter than during the growing season (Williams et al., 1996; Brooks et al., 1998). However, N mineralization rates depend upon the amount and duration of snow cover, with the nature of nutrient cycling over winter being dependent on the timing and amount of snow (Brooks and Williams, 1999). Brooks et al. (1995) found that areas with earlier and deeper snow accumulation had higher levels of soil N and greater mineralization rates due to warmer soil temperatures. Alpine soils are considerably warmer than Arctic tundra soils (Bilbrough et al., 2000), so Arctic soils may be less active during the winter. However, because climate change is predicted to warm Arctic systems, potentially resulting in greater and prolonged snow cover (Maxwell, 1992), it is important to assess how changes in winter soil temperatures affect soil N processes during the cold season and how these effects may be continued into the growing season.

In this study we measured soil N dynamics at multiple time periods throughout the growing and cold seasons in dry heath and moist tussock tundra systems in northern Alaska. Our objectives were to (1) examine soil N pool sizes and net N mineralization rates during the fall, winter, and spring in order to determine the periods during the cold season that are important in soil inorganic N dynamics; (2) compare these patterns between dry heath and moist tussock tundra, and how they vary with species composition within these tundra types; and (3) assess how changing snow cover affects soil N dynamics during the cold season. We hypothesized that the fall and spring would be important periods of soil activity, but that cold soil temperatures during deep winter would result in low levels of microbial activity in systems with normal snow cover. We also hypothesized the increased winter snow cover would result in warmer winter soil temperatures and increased soil activity during the winter, resulting in a fundamental change in soil inorganic N processes.

2. Materials and methods

2.1. Site description

This research was conducted in dry heath and moist tussock tundra near the Toolik Field Station (68°38′N, 149°38′W, elevation 760 m a.s.l.), located in the northern foothills of the Brooks Range, Alaska, USA. The overall climate is somewhat continental with summer air temperatures reaching 20 °C while winter temperatures are frequently down to −40 °C. Annual precipitation is 318 mm, with 43% falling in the cold season (http://ecosystems.mbl.

edu/ARC). Our discussion of winter climate follows the definitions of Olsson et al. (2003), who divide the winter into five periods: (1) 'early snow', when soils are near 0° but the snowpack is still ephemeral; (2) 'early cold', when snow begins to accumulate but soils are still freezing; (3) 'deep cold',; when soil temperatures drop to very low levels; (4) 'late cold', when temperatures begin to rise again; and finally (5) 'thaw', when the snowpack melts and soils begin to thaw. The timing of the early snow to early cold transition is highly variable depending on regional atmospheric circulation (Olsson et al., 2003) but is typically around the middle of October at Toolik Lake. The end of the 'early cold' period is dependent on snowfall and snow depth, but is typically around early December. The timing of thaw is driven by the rapidly increasing day length and insolation in spring and typically occurs around mid-May. Most of the snow accumulation is during the 'early cold' period, and averages 20–40 cm, though the environment is windy and snow is redistributed, producing deep drifts in places. For convenience, we call the three middle 'cold' periods simply 'deep winter' since some of our measurements integrate across the three.

The soils and vegetation of the sites are described in detail elsewhere (Walker et al., 1999; Michaelson and Ping, 2003, http://ecosystems.mbl.edu/ARC). The dry heath site is on a slight ridge, and is close to level. Vegetation is low stature, with vascular plant canopy coverage of only around 50%; interspaces often contain lichens (Welker et al., 1997). The dominant vascular plant species are *Dryas octopetela*, *Arctostaphylos alpina*, *Loiseleuria procumbens*. *Dryas* and *Arctostaphylos* grow in near monotypic stands 0.25 to several meters across. The soil is a frigid typic Eutrocryept. It is thin, very gravelly, with an organic-rich surface horizon that is 5 cm deep at most. The average bulk density is 0.56 g/cm^3. The active layer is >1 m deep as a result of the coarse textured soils.

The moist tussock site is on a gentle slope (ca. 5°), and is approximately 500 m from the heath site. It is uphill and on a larger ridge. This site is acidic tundra dominated by the tussock-forming sedge *E. vaginatum* intermixed with mosses, deciduous shrubs, and evergreen shrubs. Tussocks are composed of tightly woven dead *Eriophorum* roots, and may be 10–30 cm taller than the intertussock moss mats. The soil is a Rustic Histic Aquiturbel. The average bulk density is 0.15 g/cm^3. The mineral soil is silty, overlain by an organic horizon that is made up of *Eriophorum* tussocks interspersed with moss dominated (up to 20 cm thick) intertussock spaces. The active layer is no more than 50 cm deep.

In each site (dry heath and moist tussock tundra), we established an ambient snow (control) plot and an adjacent deep snow plot. The vegetation and soils were similar between the plots. The deep snow treatment was established by constructing a snow fence. Snow fences were erected perpendicular to prevailing winds in July of 1994 to increase the depth and duration of snow cover, simulating one possible climate change scenario (Maxwell, 1992; Jones et al., 1999; Walker et al., 1999; Welker et al., 2000). Snowdrifts behind the fences typically reach a maximum depth of 3 m, and extend out for about 35 m, only diminishing to ambient snow depths 50–60 m from the fence (Jones et al., 1999; Walker et al., 1999). Snow accumulates behind the snow fence earlier than adjacent sites, and remains at least 3 weeks later in the deepest area of the drift (Fahnestock et al., 2000). In the winter of 1998/99 (when this work was done) the ground was snow covered on October 20 in the control plots of both sites, while in the snow fence plots the ground was snow covered by October 10. In the control dry heath site, snow was gone on May 15, 1999, while in the control tussock tundra site, snow was gone on May 25, 1999. Snow was gone from both snow fence treatments on June 15, 1999. Thus, the snow fence treatment extends snow cover in both fall and spring, resulting in a shortened growing season. Inorganic N in the snow is below detection level so the additional N inputs are small. Producing a 3 m deep drift may be an extreme treatment, but it was necessary to produce a large enough study zone and it should adequately represent the effects of increased winter insulation.

2.2. In situ measurements

Soil temperature data were collected in each study plot by using HOBO temperature data loggers (Onset Computer Corporation, Pocaset, MA) inserted 2 cm below the soil surface. Weekly mean soil temperatures were calculated from August through mid-July in both tundra types.

Winter CO_2 flux was estimated from the snowpack CO_2 concentration gradient, as described by Fahnestock et al. (1998, 1999). A stainless steel gas sampling probe was connected to an infrared gas analyzer (EGM-1 or 2, PP Systems, Haverhill, MA) and the CO_2 concentration at the snow-atmosphere and soil–snow interfaces were measured at 50 spots in each the control and increased snow plots in the dry heath and tussock tundra sites. Diffusional CO_2 loss from the soil to the atmosphere was then calculated using a simple derivation of Fick's law ($J_g = D_g(\mathrm{d}[g]/\mathrm{d}z)f$, where J_g is the gas flux, D_g is the diffusion coefficient, g is the measured CO_2 concentration, z is the snow depth, and f is the porosity (calculated as $[1-\rho]/\rho_{ice}$). Values were corrected for temperature, pressure, and for nonlinear diffusional flow (i.e. tortuosity) resulting from snow density (ρ) differences throughout the snow pack (Sommerfeld et al., 1993, 1996; Brooks et al., 1996, Fahnestock et al., 1998, 1999; Jones et al., 1999).

Net N mineralization over the early snow period, deep winter, thaw, and growing season was measured using an in situ soil incubation method (DiStefano and Gholz, 1986). Because of the difficulty in collecting soil samples from frozen soil, cores for all incubations were collected and installed in September 10–11, 1998. Replicate cores for each incubation period were installed in control and

increased snow depth treatments in dry heath and moist tussock tundra. Increased snow cover cores were located in an area behind the snow fence where snow depth was maximized (ca. 3 m deep). In the dry heath, cores were placed in spaces between plants in monotypic clusters of *Arctostaphylos* or *Dryas*. In moist tussock tundra, cores were placed in tussocks dominated by *E. vaginatum* and in adjacent intertussock spaces dominated by *Sphagnum* mosses. For the tussock cores, aboveground tissue was removed, the core extruded and live roots removed from the dead root mass prior to replacing in the soil. Live green moss was removed from the surface of the intertussock cores.

Six sets of triplicate cores were taken in each combination of vegetation × snow treatment × site for a total of 144 cores. The soil cores were collected by inserting 4 cm diameter PVC tubes 10 cm into the ground and then removing them intact. Cores for initial analyses were returned to the lab for analysis of soil moisture and inorganic nutrients. Cores to be incubated in situ had a mixed-bed ion exchange resin bag (20 g resin) placed at the base of the core as a leachate trap. These cores were then placed back in the soil.

Because of the logistics of recovering soil cores buried under 3 m of snow, it was necessary to cluster the sets of cores in a restricted area so that only one snow pit was dug at each harvest, reducing the impact of disturbance to the snowfence experiments. Cores in the control plots were clustered similarly. Replicate sets of cores were harvested on 15 November of 1998, and 15 March, 16 May, 15 June and 30 August of 1999.

At each harvest, cores were returned to the lab and processed within 6 h. Frozen soils (November, March, and May) were hammered into small pieces and the pieces were then homogenized as thoroughly as practical. Thawed soils were hand mixed. Subsamples were taken for analysis of moisture and inorganic N contents. Samples for nutrient analysis were extracted within 30 min of extrusion from the core. These subsamples (10 g) were extracted for 1 h with 0.5 mol/L K_2SO_4 (50 mL), filtered through prewashed glass fiber filters, and the filtrate frozen until analysis. The temperatures of the frozen soil samples ranged from -5 to -1.5 °C when placed in extractant solution. The ion exchange resins were rinsed free of soil with deionized water, extracted with 0.5 mol/L K_2SO_4 (100 mL) for 30 min, filtered and the filtrates frozen in the same manner as the soil extracts. Extract solutions were analyzed for NH_4^+ and NO_3^- by flow injection analysis (LACHAT Instruments, Mequon, WI, USA). Net N mineralization was calculated as the difference in NH_4^+ and NO_3^- between the initial harvest (soil N only) and final harvest (soil N plus leachate N) for each time period. Data were calculated on a mg N m^{-2} (to 10 cm depth) basis by multiplying the inorganic N content (per gram dry soil) by the mass of dry soil in each diameter core, adding in any nutrient extracted from the appropriate resin, and then multiplying out from a 4 cm core to a m^2 basis.

2.3. Statistical analysis

For snow depth effects on wintertime CO_2 flux, we used *t*-tests (SAS Institute, 2001) to determine whether CO_2 flux rates were higher in the deep snow than in the ambient snow plots on each sampling date. Nitrogen mineralization data were analyzed using ANOVA. Within each site, we used a three-factor ANOVA with two snow treatments (ambient and increased), two vegetation types (*Arctostaphylos* vs. *Dryas* in dry heath and tussock vs. intertussock in tussock tundra), and six sampling dates (initial and five samplings of incubated soils). We established that data were robust in terms of normality and outliers by using box plots and normal probability plots of residuals and then performed the ANOVAs using general linear models (SAS, 1998). Ammonium and NO_3^- concentrations were analyzed separately. Treatment effects that were significantly different at the $P < 0.05$ level were analyzed using a multiple range test (least significant difference). Because it was not possible to pair the cores for initial and final harvests through time, net nitrification and net N mineralization rates were calculated using the means for NO_3^- and total inorganic N from each harvest. Therefore, no statistical analyses were conducted on mineralization and nitrification rates per se. Instead, statistically significant differences in NO_3^- and total inorganic N content between harvest dates were interpreted as significant rates of nitrification or mineralization.

3. Results

3.1. Snowfence effects on the physical environment and on CO_2 fluxes

The snowfence produced a snowpack that developed 10 days earlier and was significantly deeper through the winter as described in the site description. These effects led to significantly warmer soils during the winter under the experimental snowdrifts than in adjacent sites with ambient snow depth (Fig. 1). Soils with increased snow depth never reached weekly mean temperatures colder than -7 °C in either the moist tussock or the dry heath sites. This is warm enough to sustain substantial biological activity in the soils over winter (Mikan et al., 2002; Olsson et al., 2003). In contrast, soils with ambient snow depths were extremely cold in the winter, with minimum weekly mean temperatures of -25 °C in moist tussock tundra and below -30 °C in dry heath tundra. Warming of soils behind the snowfence in the spring was delayed by the extended thaw period, resulting in prolonged near-freezing soil temperatures. However, after thaw, the soils in the snowfence warmed up to temperatures comparable to those in the control treatment.

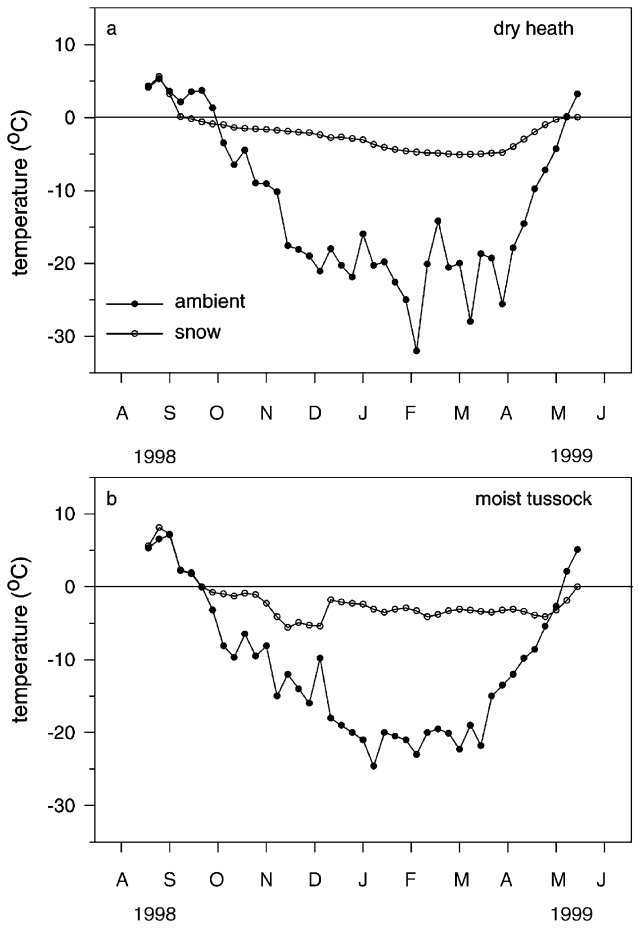

Fig. 1. Mean weekly cold season soil temperatures in ambient soils and in soils with increased snow cover. Temperatures were measured at 5 cm depth: (a) dry heath tundra and (b) moist tussock tundra.

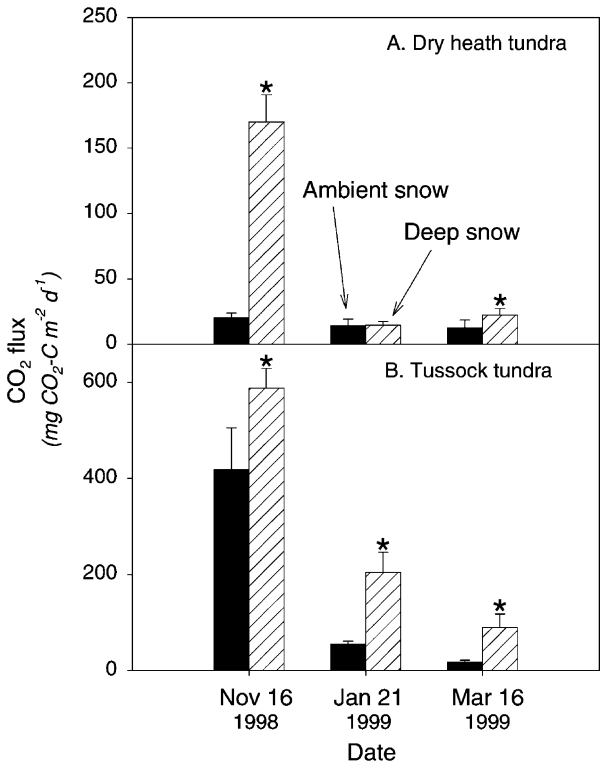

Fig. 2. The effects of increased snow cover on CO_2 fluxes in dry heath and tussock tundra. CO_2 fluxes were estimated from CO_2 concentration gradients through the snow pack. Values represent means and vertical lines are one standard error of the mean (SEM).

Wintertime CO_2 fluxes were higher in the moist tussock tundra than in the dry heath (Fig. 2), as would be expected given the higher organic matter contents in this site. In the dry heath ambient snow treatment, CO_2 fluxes were very low throughout the winter, though they were slightly higher in November than at the later dates. The deep snow treatment increased fluxes significantly in the early and late season samplings, though the increase in March was only modest. In the tussock tundra site, even in the ambient snow condition, CO_2 fluxes were quite large in the November, 'early cold' sampling (Fig. 2) but declined throughout the winter, to very low levels by the late winter when soil temperatures were extremely cold in the surface soil (Fig. 1) and would be so throughout the soil profile. The deep snow condition significantly increased CO_2 fluxes throughout the cold season, associated with the warmer soil temperatures.

3.2. Extractable soil N, nitrification, and net N mineralization rates

3.2.1. Moist tussock tundra

The concentrations of soil NH_4^+ and NO_3^- in the incubation cores were strongly affected by both snow cover treatment ($P < 0.0001$, NH_4^+ and NO_3^-) and harvest date ($P < 0.0001$, NH_4^+ and NO_3^-). The effect of snow cover varied significantly with harvest date (snow × harvest interaction $P < 0.0001$, NH_4^+ and NO_3^-, Fig. 3). While the main effect of species (tussock, intertussock) on soil NH_4^+ and NO_3^- contents was not significant ($P = 0.17$), NH_4^+ and NO_3^- contents did vary by species at some times of the year, as indicated by a significant species × harvest interaction ($P = 0.07$ and 0.055 for NH_4^+ and NO_3^-, respectively).

Mean NH_4^+ levels in tussock soils with ambient snow cover were lowest in September (47 mg N m^{-2}), increased to 412 mg N m^{-2} in November, and then declined through both the remainder of the cold season and the growing season to 38 mg N m^{-2} (Fig. 3a), despite being contained in PVC cores. In contrast, ambient intertussock soil NH_4^+ values were greatest in September (359 mg N m^{-2}), and decreased through November and March to 158 mg N m^{-2}. Intertussock soil NH_4^+ levels increased again from March to May, declining again through the growing season to 43 mg N m^{-2} (Fig. 3a). Thus, both the highest and lowest measured NH_4^+ levels were similar in tussock and intertussock soils. However, the timing of maximum NH_4^+ levels appeared to be later in the fall for tussocks than for intertussocks. Cold and growing season NO_3^- levels were low in treatments with ambient snow cover, and were not significantly different between species or

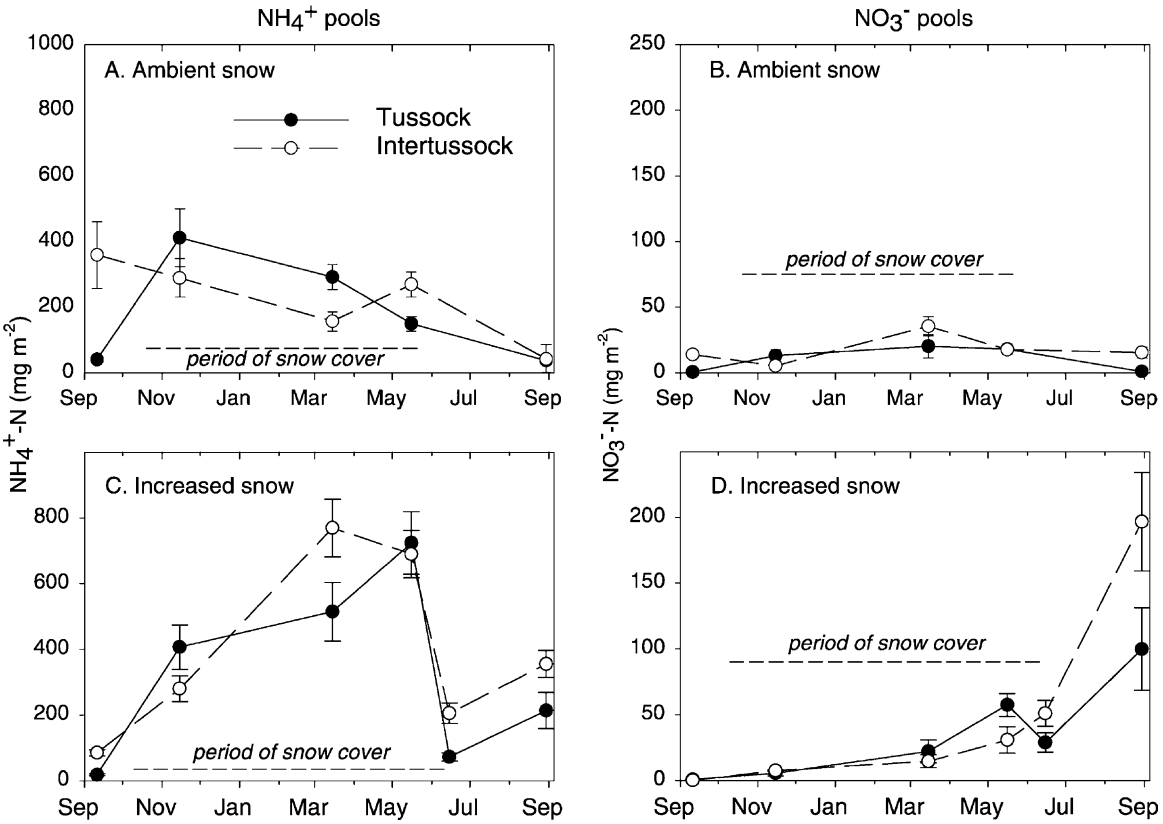

Fig. 3. The effects of increased snow cover on extractable soil NH_4^+ and NO_3^- contents in tussock and intertussock soils sampled from moist tussock tundra measured throughout an annual cycle. (a) NH_4^+, ambient snow conditions; (b) NO_3^- ambient snow conditions; (c) NH_4^+, increased snow depth; and (d) NO_3^-, increased snow depth. Values represent means and vertical lines are one standard error of the mean (SEM).

among harvests (Fig. 3b). Because NH_4^+ levels were far greater than NO_3^- levels, the temporal patterns and quantities of total inorganic N were similar to those of NH_4^+. Thus, there was a pattern of N mineralization during the early cold period in ambient moist tussock soils, while immobilization dominated later cold and growing season dynamics despite a lack of fresh C inputs in the incubated cores (Fig. 4a). High intertussock NH_4^+ and NO_3^- levels in September suggest there had been an earlier mineralization pulse in the intertussock soils. In addition, intertussock soils mineralized 94 mg N m^{-2} N in the late winter (Fig. 4b). Because NO_3^- levels were so low, nitrification rates appeared insignificant in tussock and intertussock soils with ambient snow cover (Fig. 3).

In contrast to ambient soils, NH_4^+ levels in soils incubated under deeper snow cover increased through the fall and winter to levels twice those of maximum measured values in soils with ambient snow cover (724 mg N m^{-2} tussock; 769 mg N m^{-2} intertussock; Fig. 3c). Ammonium levels declined considerably in the early spring to levels one-tenth of winter values in tussock soils and one-third of winter values in intertussock soils. These levels increased again over the growing season to 214 and 355 mg N m^{-2} in tussocks and intertussocks, respectively (Fig. 3c). Nitrate values were comparable to ambient-snow levels through the fall and winter, but increased two (tussock) to four-fold (intertussock) during the growing season (Fig. 3d). Thus, there was a pattern of mineralization throughout the winter (762 mg N m^{-2} tussock; 636 mg N m^{-2} intertussock), followed by immobilization in the late winter, and mineralization during the growing season in both tussock and intertussock soils (Fig. 4a and b). Growing season mineralization was accompanied by nitrification (71 g N m^{-2} tussocks; 146 g N m^{-2} intertussocks) (Fig. 3d). When net N mineralization rates were combined through the annual cycle, tussock soils mineralized 295 mg N m^{-2} and intertussock soils mineralized 467 g N m^{-2}. The difference in tussock and intertussock soil N mineralization was due to high immobilization during thaw in tussock soils. There was no effect of plant species composition on the pattern of extractable soil N and mineralization when snow depth was increased, and very little effect on the magnitude of response (Fig. 3c and d). Levels of NH_4^+ and NO_3^- were similar between tussocks and intertussocks through the cold season. Late winter immobilization was higher in tussocks than in intertussocks, resulting in lower levels of mineral N in tussocks in June (Figs. 3c and 4). Growing season mineralization rates were similar between tussocks and intertussocks, resulting in lower amounts of NH_4^+ in tussock than in intertussock soils at the end of the growing season (Fig. 3).

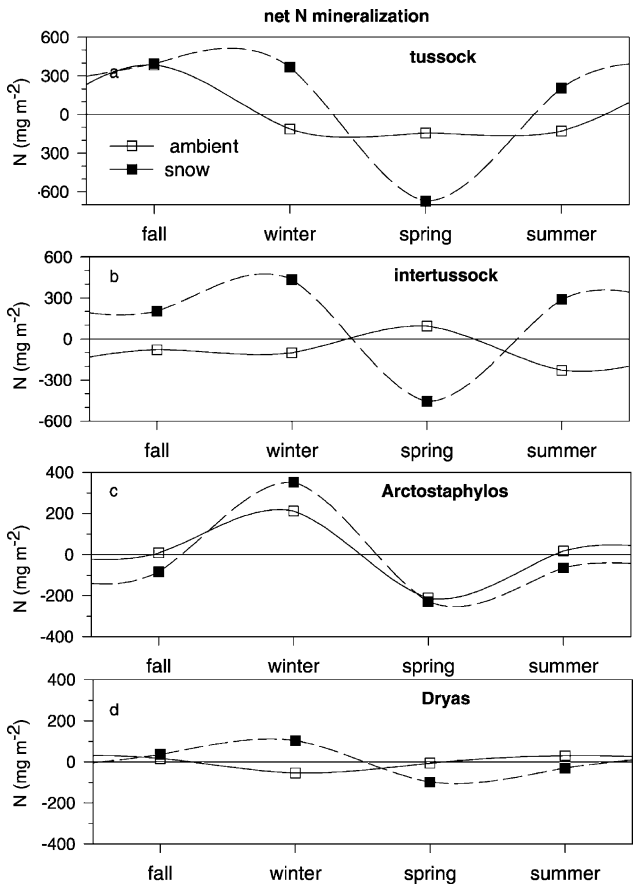

Fig. 4. The effects of increased snow cover on net N mineralization in (a) tussock, and (b) intertussocks in moist tussock tundra and (c) *Arctostaphylos*, and (d) *Dryas* soils from dry heath tundra. The intervals on the *x*-axis are: Fall—September to November; Winter—November to March in the control, November to May in the snowfence treatment; Spring (thaw)—March to May in the control, May to June in the snowfence treatment; and Summer (growing season)—May to August in the control, June to August in the snowfence treatment. Values were calculated by subtracting average soil N contents for each time period and therefore do not have an error associated with them. Note the different *y*-axis scales.

3.2.2. Dry heath tundra

The temporal patterns of soil mineral N contents in dry heath soils with ambient snow cover were affected by plant species composition during the cold season, but not during the growing season (Fig. 5). Soil NH_4^+ levels in soils incubated in situ were similar between species in early September (97 and 58 mg N m^{-2} for *Dryas* and *Arctostaphylos*, respectively), and did not change significantly from September to November (Fig. 5a). *Arctostaphylos* soil NH_4^+ levels increased four-fold in the winter to 262 mg N m^{-2}, while *Dryas* soil NH_4^+ levels decreased slightly to 71 mg N m^{-2} (Fig. 5a). During the early spring/thaw period, *Arctostaphylos* soil NH_4^+ levels decreased to the same low levels as *Dryas* soils, and NH_4^+ levels in both soil types remained low during the growing season (87 mg N m^{-2}, *Dryas* and 76 mg N m^{-2}, *Arctostaphylos*). Nitrate levels in *Arctostaphylos* soils were very low throughout the year, with detectable levels only occurring in November (16 mg N m^{-2}, Fig. 5b). Nitrate levels in *Dryas* soils were similar to *Arctostaphylos* soils in September (22 mg N m^{-2}), remained at a similar level in the winter, declined during early spring/thaw and increased in August (Fig. 5b). Thus, *Dryas* soils with ambient snow cover showed only minimal net N dynamics (Fig. 4d). In contrast, *Arctostaphylos* soils incubated in situ immobilized N in the early snow period and then shifted to mineralizing N during the deep winter. This winter mineralization was followed by immobilization during thaw (Fig. 4c). Net nitrification rates were insignificant in soils with ambient snow cover (Fig. 5b).

In contrast to moist tussock soils, the effect of increased snow depth on dry heath tundra was not apparent until late winter, when NH_4^+ levels in incubated soils increased dramatically to 387 (*Arctostaphylos*) and 231 (*Dryas*) mg N m^{-2} in May from March levels of 115 mg N m^{-2} (*Arctostaphylos*) and 47 mg N m^{-2} (*Dryas*), and were nearly four times greater than ambient soils (Fig. 5c). These levels declined in June, and were unchanged at the end of the growing season. Nitrate levels were low through the fall and winter, increasing three-fold in the late winter and early growing season to 97 (*Arctostaphylos*) and 100 (*Dryas*) mg N m^{-2}, and dropped by early autumn (Fig. 5d). The peak in NO_3^- followed the peak in NH_4^+, suggesting that the elevated NH_4^+ levels stimulated nitrification during the growing season. Total soil mineral N levels and temporal patterns were similar to those of NH_4^+, showing a marked increase in total N during the late winter. Thus, there was strong mineralization during the late cold period followed by immobilization at thaw (Fig. 4c and d). This immobilization was accompanied by an increase in NO_3^-, suggesting that some of the N lost from the NH_4^+ pool was a result of nitrification (Fig. 5d). Unlike moist tussock tundra soils, there was no evidence of growing season mineralization; in fact, immobilization continued (Fig. 4c and d).

4. Discussion

The specific effects of snow cover on soil processes have been of interest since the recognition that microbial activity does not cease during the Arctic cold season (Zimov et al., 1996; Oechel et al., 1997; Fahnestock et al., 1998). The effects on N cycling are particularly interesting as net mineralization in Arctic soils appears to be largely a cold season phenomenon (Giblin et al., 1991; Hobbie and Chapin, 1996). Lab incubation studies have also shown the intense immobilization potential of moist tussock tundra soils under growing season temperatures (Nadelhoffer et al., 1991; Weintraub and Schimel, 2003). Thus, since cold season mineralization is important in the annual tundra N cycle, it should be strongly sensitive to snow timing and depth, as that is the primary regulator of cold season soil temperatures (Olsson et al., 2003; Brooks and Williams, 1999), and microbial activity is highly temperature sensitive at sub-zero temperatures (Mikan et al., 2002).

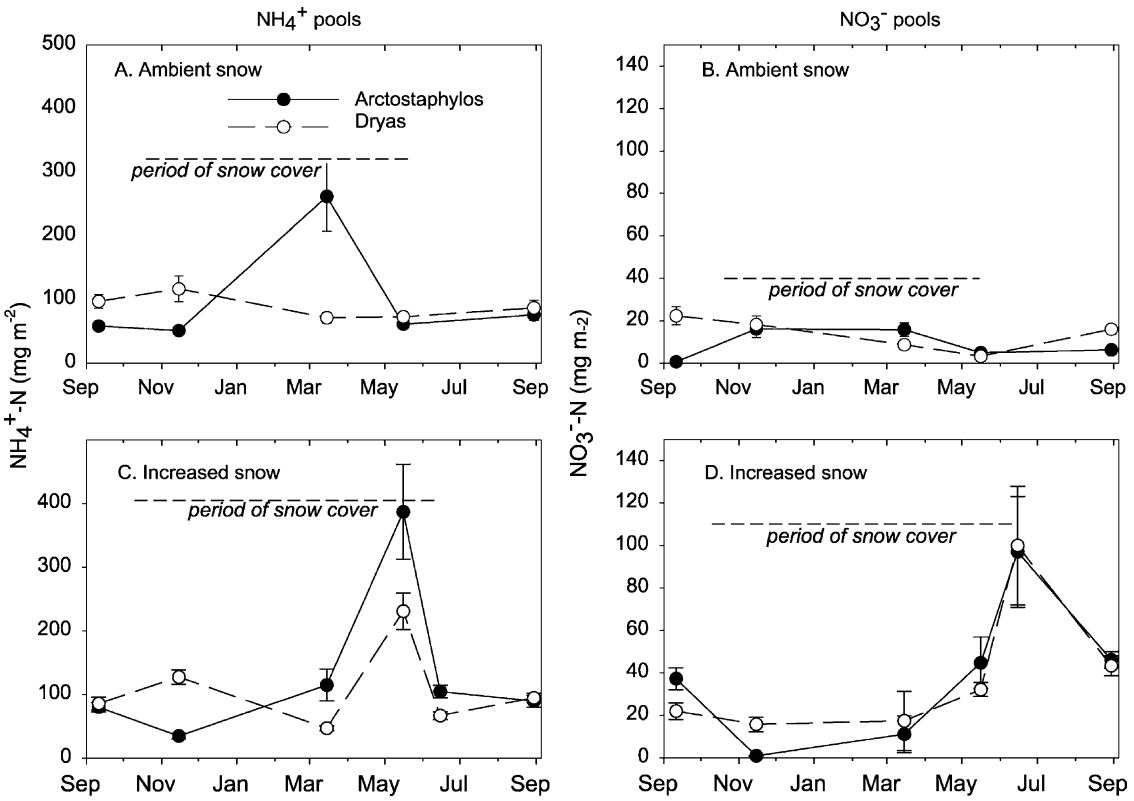

Fig. 5. The effects of increased snow cover on extractable soil NH_4^+ and NO_3^- contents in *Dryas* and *Arctostaphylos* soils sampled from dry heath tundra measured throughout an annual cycle. (a) NH_4^+, ambient snow conditions; (b) NO_3^- ambient snow conditions; (c) NH_4^+, increased snow depth; and (d) NO_3^-, increased snow depth. Values represent means and vertical lines are one standard error of the mean (SEM).

We found that increased winter snow depth and the associated warmer winter soil temperatures strongly affected soil processes in these Arctic tundra systems, as shown by both the CO_2 flux measurements (Fig. 2) and the N cycling measurements (Figs. 3–5). Associated with the increases in microbial respiration, there were striking changes in patterns of N cycling during the winter in both tundra communities. Additionally in tussock tundra, changing the winter environment for 5 years had substantial effects on growing season N dynamics (Fig. 3c,d and 4).

In the control, ambient snow plots, net N cycling was limited, though it varied somewhat with plant community and species, consistent with other studies on tundra mineralization (Giblin et al., 1991; Weintraub and Schimel, 2003). In moist tussock tundra, it appeared that in both tussock and intertussock soil, there was an increase in N levels at some point during the early snow period, a time when some plants produce overwintering roots. In intertussock soil, the increase was early enough so that NH_4^+ levels were high in September. The evidence that this reflects an increase over summer levels is twofold: first, NH_4^+ levels in situ were low the next August at the end of the growing season, and NH_4^+ levels are generally low in intertussock soil (Weintraub and Schimel, 2003). In tussocks the increase was later, with NH_4^+ peaking in November. Both tussock and intertussock soils immobilized N throughout both the winter (slowly) and the growing season, though intertussock soil showed slight mineralization at thaw in May. Thus, N was most available for plant uptake in the fall in moist tussock tundra. The amounts of N available in fall (ca. 400 mg N m^{-2}) were substantial relative to annual plant N demand (ca. 750 mg N m^{-2} for total aboveground production in tussock tundra; Chapin et al., 1988).

Dry heath tundra soils had lower levels of inorganic N than moist tussock tundra soils in both snow depth treatments. In the ambient condition, only *Arctostaphylos* showed any substantial mineralization, and that was only measured as an increase in the March sampling (Fig. 5a). It is likely that the actual mineralization occurred early in the winter, during the early cold period, when soil temperatures were warmest. The pool of inorganic N available in March was immobilized at thaw (Fig. 5a).

Cold season N cycling was generally limited under the ambient snow conditions, presumably because the extremely cold soil temperatures (ca. −30 °C) prevent any substantial microbial activity, as indicated by the extremely low CO_2 fluxes measured in mid-winter (Fig. 1). Increasing the snow depth increased soil temperatures to a point where ongoing microbial activity could be substantial (> −5 °C, Fig. 1; Coxson and Parkinson, 1987; Mikan et al., 2002). One result of warmer soil temperatures and increased microbial activity in the increased snow treatment was a stimulation of cold season N mineralization in all the soils

we studied (Fig. 4). In tussock tundra the rate of net mineralization appeared relatively constant throughout the winter and the total amount of N mineralized was large enough (roughly 700 mg N m^{-2} averaging in both tussock and intertussocks) to almost completely meet the aboveground N demand of the vegetation. In dry heath soils, net N mineralization only occurred in late winter, and the total amounts on N mineralized were lower than in the tussock tundra (120†350 mg N m^{-2} $winter^{-1}$ for dry heath soils). This amount of N, though, is still large relative to annual plant N demand.

In all soils, it appeared that the bulk of the N that had been mineralized over winter was immobilized at thaw. In the heath soils, particularly in the *Dryas* soils, it is conceivable that some of the N loss was due to denitrification, as there was NO_3^- in the soil during the thaw period when soils are saturated. It is important to note that N was immobilized at thaw even though the soil was isolated in cores and therefore inaccessible to plants. Despite the ability of soil microbes to almost completely immobilize the N mineralized over the winter, it is likely that plants would, in fact, take up some fraction of the available N if roots were present. Bilbrough et al. (2000) showed that both vascular and nonvascular plants take up N during thaw, and Schmidt et al. (1999) concluded that plants take up some of the N that is otherwise immobilized in a buried bag type incubation in tundra soils.

The finding that the N that had been mineralized during the cold season was immobilized at thaw (Fig. 4) indicates that there is a fundamental switch in the nature of microbial substrate processing between the frozen and thawed conditions. Our results suggest that the rate of the mineralizing processes increase with temperature up to approximately 0 °C, and then switch abruptly to immobilizing processes as soils thaw. The question arises: what is the nature of the change in microbial substrate processing that causes such a dramatic change in the nature of N cycling between the cold and growing seasons.

Since microbes immobilize N when they are N limited and mineralize N when they are C limited (Chapin et al., 2002), our results suggest that microbes shift their substrate use patterns from C rich material when soils are thawed to using more N rich material when they are frozen. There are two possible reasons this might occur. One would be a relative increase in the availability of N rich substrates, while the other would be a relative decrease in the availability of C rich substrates as soils freeze. There are two mechanisms that could produce an increase in N rich substrates on soil freezing: either (1) release from soil organic matter (Edwards and Cresser, 1992), or (2) release from damaged or killed roots and soil microorganisms (DeLuca et al., 1992; Brooks and Williams, 1999). However, slow freezing, as generally occurs in nature, does not appear to be particularly lethal to soil microbes (Lipson et al., 2000), and so substantial microbial death may be unlikely in situ. Additionally, generation of labile N via soil freezing would occur only in the fall at first freezing, while in the tussock deep snow treatment, net mineralization occurred continuously during the winter.

The available data suggest that the alternative mechanism, loss of access to C rich plant detritus, appears to be the more likely explanation for cold season mineralization in Arctic soils. Microbes in frozen soils appear to rely more for their organic substrates on recycling N-rich microbial biomass and small labile compounds that might remain available in water films, as hypothesized by Clein and Schimel (1995). Several lines of evidence support this argument: (1) Cold temperatures limit the ability of microbes to metabolize cellulose; there is a dramatic increase in the activation energy of endocellulase below +5 °C (Linkins et al., 1984). (2) Grogan et al. (2001) found that winter respiration is dominated by recent plant inputs in a heath ecosystem. (3) Michaelson and Ping (2003) showed that while above 0 °C, respiration correlates with total soil C, below 0 °C, respiration correlates with water soluble C. (4) The rapid immobilization of NH_4^+ at snowmelt in tussock tundra cores without fresh C inputs, suggests that microbes gain access to a C source that was not available to them while soils were frozen. (5) Using a ^{14}C labeling technique, Schimel and Mikan (unpublished resutls) showed that as soils freeze, soil microbes roughly double the proportion of C respired that comes from a small actively recycling C pool (the microbial biomass and products pool), as opposed to plant detritus. All of those results are consistent with microbes using a C rich substrate (likely plant detritus) at temperatures above 0 °C, but losing access to that material as soils freeze and being limited to more N rich material including dead microbial biomass, dissolved organic compounds, etc.

The mineralization that occurred in the tussock tundra soils during the growing season represents a major change in N cycling and may reflect multiple years of wintertime activity. Tussock soils may be incubated in the lab for as long as a year at 20 °C without mineralizing N (Weintraub and Schimel, 2003) and often show little in situ N mineralization (Giblin et al., 1991). Thus, it may take several years of increased winter activity to metabolize enough of a C-rich bioactive pool to shift microbes into C limitation and N mineralization during the growing season. The greatly increased rate of cold season respiration in the tussock tundra deep snow treatment (Fig. 1) suggests that this might have been possible. The nitrification that occurred in the deep snow plots in tussock tundra (Fig. 3) is evidence for the idea that microbes had become C limited. Nitrifying bacteria generally compete poorly for NH_4^+ against heterotrophic microbes (Chapin et al., 2002), and nitrification is uncommon in these N poor tundra soils (Giblin et al., 1991; Schimel et al., 1996, 1999). Thus the occurrence of substantial nitrification strongly suggests that microbes had become C limited and that NH_4^+ was therefore present in excess of microbial demand.

5. Conclusions

Our results suggest several important conclusions. First, under normal climate conditions, during the growing season, microbes are N limited enough to prevent substantial net N mineralization in these tundra communities. In the ambient conditions, net N mineralization only appeared to occur in tussock tundra during the early snow period and under *Arctostaphylos* plants in the winter. In most of the soils, extremely low winter soil temperatures appear to limit overall microbial activity and N mineralization during the deep winter. However, deep snow insulates the soil, increasing soil temperature, and allows microbes to remain active, as well as inducing a shift in the nature of organic matter processing; instead of immobilizing N, microbes shift to mineralizing N. The N made available during the winter would be available at thaw to plants that have either overwintering roots are able to produce a fresh cohort of roots and compete effectively with microbial uptake. Second, in tussock tundra soils, five years of increased microbial activity during the winter shifted organic matter dynamics enough so that net N mineralization occurred during the growing season. This could have long-term effects on ecosystem structure through a nutrient availability-plant community structure feedback. Increased N availability in tussock tundra causes a shift in community dominance from *E. vaginatum* to the dwarf birch, *Betula nana* (Chapin et al., 1995). *B. nana* is taller, and is able to trap more snow (Liston et al., 2002), thus helping drive a positive feedback between snow, soil temperatures, microbial activity, and plant community composition (Sturm et al., 2001).

These results indicate that in terms of year-round nitrogen dynamics, the early snow period during the fall may be the critical season of the year. Fall controls the wintertime soil microclimate. Early heavy snow insulates the soil, establishing a condition comparable to our snow fence experiment. Late snow allows the soil temperatures to drop to conditions cold enough to shut down significant winter activity (Groffman et al., 2001). The conditions during the winter then control soil nutrient availability not only during thaw, but throughout the growing season as well. While hydrologists have given extensive attention to spring conditions (e.g. Hinzman et al., 1996), very few researchers have focused on fall conditions. Fall has been seen as the end of the year. This work on cold season processes suggest that fall should rather be seen as the beginning of the year—the time that programs the functioning of the system for the rest of the year.

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