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Effects of Simulated Climate Change on Plant Phenology and Nitrogen Mineralization in Alaskan Arctic Tundra

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Abstract

This study was part of the International Tundra Experiment (ITEX) and examined the effects of increased winter snow depth and decreased growing season length on the phenology of four arctic plant species (*Betula nana*, *Salix pulchra*, *Eriophorum vaginatum*, and *Vaccinium vitis-idaea*) and seasonal nitrogen availability in arctic snowbed communities. Increased snow depth had a large effect on the temporal pattern of first date snow-free in spring, bud break, and flowering, but did not affect the rate of plant development. By contrast, snow depth had a large qualitative effect on N mineralization in deep snow zones, causing a shift in the timing and amount of N mineralized compared to ambient snow zones. Nitrogen mineralization in deep snow zones occurred mainly overwinter, whereas N mineralization in ambient snow zones occurred mainly in spring. Concentrations of soil dissolved organic nitrogen (DON) were approximately 5 times greater than concentrations of inorganic nitrogen (DIN) and did not vary significantly over the season. Projected increases in the depth and duration of snow cover in arctic plant communities will likely have minor effects on the rate of plant phenological development, but potentially large effects on patterns of N cycling.

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Introduction

Landscape-scale distribution of snow is one of the most important variables controlling biological systems in the Arctic (Billings and Bliss, 1959; Canaday and Fonda, 1974; Bell and Bliss, 1979; Walker et al., 1993; Walker et al., 2001), affecting soil temperatures, plant phenology, plant species distribution, growing season length, active layer depths, and nutrient availability. The intensification of hydrological processes predicted by models of the arctic climate includes increases in the winter snowpack (Maxwell, 1992; Hinzman et al., 2005), which has important consequences for both arctic vegetation and animals. Length of growing season strongly influences plant species distributions through indirect effects on rates of resource supply (Stanton et al., 1994) and quality of plant litter inputs (Hobbie, 1996). One of the greatest uncertainties with global change in the Arctic is how changes in growing season length will affect nutrient uptake and production (Kielland and Chapin, 1992). Previous studies have shown that moist tussock tundra, a dominant arctic plant community, may be the most sensitive to increases in temperature in terms of nutrient dynamics (Giblin et al., 1991; Nadelhoffer et al., 1992; Chapin et al., 1995; Jonasson et al., 1999; Bret-Harte et al., 2001; Shaver et al., 2001) because of its large carbon stores in the form of frozen peat and relatively shallow thaw depths. Any increase in thaw depth in the moist tussock tundra ecosystems could potentially cause an increase in organic matter decomposition, soil respiration, and plant nutrient availability (Fahnestock et al., 1998, 1999; Hobbie et al., 2000; Weintraub and Schimel, 2003; Schimel et al., 2004). In addition, winter temperatures may be warmer under the increased snowpack due to the insulating properties of snow (Sturm et al., 2005).

An increase in snow accumulation is likely to have several indirect impacts on plant species distributions through changes in nutrient availability, soil organic matter chemistry, and soil moisture. As was evidenced by toposequence studies (Giblin et al., 1991), vegetation and physical characteristics (soil moisture, thaw depth, soil temperature, carbon content, etc.) of a site play a large role in dictating the seasonal availability of nutrients in arctic ecosystems. Nadelhoffer et al. (1991) showed that rates of nitrogen mineralization potentials varied more between different ecosystem types than under varying temperatures between 3 and 9°C (natural temperature range currently experienced by these soils), suggesting that quality of organic matter is more important in determining nitrogen mineralization than small changes in summer temperature. Nitrogen availability may be largely influenced by the species that are able to tolerate certain snow depth regimes and by the feedbacks these species have on the ecosystem biogeochemical cycles (Giblin et al., 1991; Hobbie, 1996).

This research focused on plant phenology and seasonal nutrient availability under experimentally manipulated snow depth, using a snowfence to augment snow, and two natural snowbed sites that had similar snow depth gradients. Our overarching research questions were (1) how may increased snow cover/depth affect plant phenological development, and (2) how will snow depth with the accompanying increased soil temperatures affect patterns of nitrogen mineralization?

We hypothesized that as snow depth increased, plant development would be accelerated to compensate for a shorter growing season and, further, that nitrogen (N) mineralization would increase because of higher fall and winter soil temperatures. We also expected that total dissolved inorganic nitrogen pools (DIN) and total dissolved organic nitrogen pools (DON) would decrease through the summer because these two pools would be heavily utilized during the peak growing season. By comparing experimental snow additions to natural snowbeds, we sought to juxtapose short-term versus long-term effects of increased snow on arctic plant communities.

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Study Site and Experimental Design

The study was conducted at the University of Alaska, Toolik Field Station located in the northern foothills of the Brooks Range, Alaska (68°37′N, 149°32′W, approx. 700 m a.s.l.), as part of the International Tundra Experiment (ITEX) (Molau and Mølgaard, 1996; Henry and Molau, 1997). We used the Toolik snowfence plots and grid that were established in the summer of 1994. The snowfence was located in moist acidic tundra (MAT), where *Eriophorum* tussock tundra was the predominant vegetation (Walker et al., 1994). The snowfence was 60 m long and 3 m tall and was aligned on an east-west axis because the prevailing winter winds came from the Brooks Range to the south. Permanent plots (1 m^2) were established within the snowfence grids under the influence of increased snow (experimental plots) as well as in areas outside the influence of the snowfence (control plots; Walker et al., 1999). There were six rows, each containing three plots, along the snow depth gradient behind the snowfence, and one set of plots as a control placed upslope and outside the influence of the snowfence. Each row of plots was considered a different snow depth "zone." For the purposes of this experiment, only data from the deep, mid, and ambient (control) zones were considered.

In addition, two natural snowbed sites were established on the southwest side of Toolik Lake in the summer of 1999. The sites for the natural snowbeds were chosen because they had similar alignment to winter winds, similar winter and spring snow depths in the deep and mid snow depth zones, similar aspect and drainage, and similar vegetation in the ambient and mid snow depth zones as compared to the experimental snowfence site. Three rows of 1-m^2 plots were established corresponding to deep, mid, and ambient snow depth zones. At one of the natural snowbed sites there were four plots in each zone (natural snowbed 1 or NS1) and at the second, smaller site (natural snowbed 2 or NS2) there were three plots in each zone.

Snow depth in the deep areas of both the snowfence site and at natural snowbeds was about 3 m and the snow depth in the ambient areas was about 50 cm or less. Since there is a slight slope to the site and the soil is still frozen when the snow drift is melting, there is a considerable amount of overland flow of water away from the plots during meltout.

Vegetation was distinctly different in the three snow depth zones (ambient, mid, and deep) of the natural snowbed sites. Vegetation in the ambient snow areas was most similar to the moist tussock tundra vegetation of the snowfence site, dominated by *Eriophorum vaginatum* tussocks, low-statured *Salix pulchra*, *Betula nana*, and *Vaccinium vitis-idaea* and is classified as moist graminoid dwarf-shrub tundra. The mid snow depth zones at the natural snowbeds were characterized by larger shrubs, less *Eriophorum,* and fewer understory species. The deep snow areas at the natural snowbed sites contained virtually no *Eriophorum*, had smaller shrubs and more snow-tolerant species such as *Cassiope tetragona* and *Salix reticulata*, and had a thinner organic layer than the ambient snow zones.

Methods

PLANT PHENOLOGY

Phenological events of four species (*Betula nana, Salix pulchra, Eriophorum vaginatum,* and *Vaccinium vitis-idaea;* Hultén, 1968) were monitored according to the standardized protocols of the ITEX experiment (Molau and Mølgaard, 1996). The snow-free date of each plot was recorded when the plot was two-thirds melted out, and is the same for each species within the same plot. The phenological events monitored for the deciduous shrub species *Betula nana* and *Salix pulchra* were (1) first green leaf (green-up or budburst) and (2) first color change (the onset of senescence). Phenological events monitored for the graminoid *Eriophorum vaginatum* were (1) first flower open (first pollen visible) and (2) seed dispersal. For the evergreen shrub *Vaccinium vitis-idaea* the events monitored were (1) first flower open and (2) last corolla drop (end of flowering). Phenology was monitored every other day throughout the growing season, starting from the time plots became snow free until the very end of August or beginning of September. The Julian date recorded for each phenological event, for each species, is the first date that event was seen to occur in that plot. The number of plots monitored for each phenological event in each snow depth zone was six ($n = 6$) in the deep snow zone and three ($n = 3$) each in the mid and ambient snow zones at the experimental snowfence (SF) site, four ($n = 4$) in each zone at the natural snowbed 1 (NS1) site, and three ($n = 3$) in each zone at the natural snowbed 2 (NS2) site.

SOILS DATA

Active Layer Depth

At the snowfence site, active layer measurements were taken weekly throughout the season starting from the time each plot became snow free. Measurements were taken by pushing a 1-m-long stainless steel probe into the ground until the probe hit permafrost. In each plot, three tussock and three intertussock measurements were taken in plots designated for thaw depth and other intrusive measurements.

Soil Sampling

Four 7.5-cm-diameter soil cores were collected to approximately 18 cm depth in each snow depth zone at each site, approximately every 2 wk throughout the summer. After collection, soil cores were transported to the lab for immediate processing. Care was taken to keep collected soil cores at approximate field temperature by placing them in a 4°C refrigerator until processing. Large woody roots and stems were removed from the soil cores and the soil of each core was homogenized. Subsamples (15 g fresh weight) were taken from each core for determining gravimetric soil moisture, soil carbon concentration, and inorganic and organic nitrogen concentrations.

Soil Carbon Concentration and Soil Moisture

Total C concentrations were measured using the LECO CNS-2000 (LECO Corporation, St. Joseph, MI, U.S.A.) analyzer following the Dumas dry combustion procedure (Sollins et al., 1999). Gravimetric soil moisture was determined on oven dried (65°C) samples and calculated as the difference between the 15 g wet mass and the dry mass of the oven-dried soil as g H_2O g^{-1} dry soil.

Net Nitrogen Mineralization

Net nitrogen mineralization was measured using the *in situ* buried bag technique (Robertson et al., 1999). The first N mineralization assay was initiated in the end of June 2000 when the soil was thawed in all three snow depth zones. A new incubation was initiated every 12 to 14 d throughout the summer until the beginning of September, at which time an overwinter incubation was started. Four intact intertussock replicate cores were placed into individually sealed, gas-permeable polyethylene

bags and placed back into the soil to be incubated *in situ* for the 12- to 14-d incubation period.

Fresh weight subsample (15 g) of each core was extracted with 75 mL 0.5 M K_2SO_4. A separate sample was taken from each core for determination of water content. Root removal and extraction procedures were completed for all 36 cores the same day that they were collected. Soil extracts were placed in 50 mL centrifuge tubes and immediately frozen until further analysis for ammonium and nitrate was possible.

Immediately prior to chemical analysis all samples were quickly thawed using a warm water bath. All samples were analyzed for ammonium and nitrate (+ nitrite) simultaneously using a Technicon autoanalyzer following the indophenol blue (ammonium) and Cd reduction (nitrate + nitrite) Gries-Ilosvay methods (Mulvaney, 1996). Net N mineralization was calculated as the difference in initial and final concentration of ammonium and nitrate. Cumulative N mineralization over summer was calculated by summing net N mineralization values (both positive and negative) for each of the four sampling periods for each plot, whereas cumulative N mineralization over winter was calculated as the difference between September and June values.

Total Dissolved Organic Nitrogen

Total dissolved organic nitrogen was determined by oxidation of soil extracts from all the initial soil cores collected throughout the summer using the alkaline persulfate reaction (Koroleff, 1983; Cabrera and Beare, 1993; Sollins et al., 1999). To perform digestions, 5 mL aliquots of both sample and oxidizing reagent were added to a 15 mL glass tube and immediately sealed with Teflon-lined screw caps. Tubes were then autoclaved at 120°C for 30 min. A set of NH_4Cl standards was also digested with each batch of autoclaving to verify the digestion efficiency. Each sample that lost volume during autoclaving was rerun. Nitrate concentrations were determined using the same Gries-Ilosvay Cd reduction procedure described above. Total DON concentration was calculated by subtracting the total DIN value measured in the initial core from the amount of nitrate measured after digestion.

STATISTICAL ANALYSES

Two MANOVAs were performed for each species, one using development rate data and the other using timing data. Development rate data are the number of days it takes a phenological event to occur relative to a previous event. For *Betula* and *Salix* the rates used in the analysis were "time to green-up" (Julian date of first leaf evident – Julian date of snow-free) and "leaf green period" (Julian date of first color change – Julian date of first leaf evident). For *Eriophorum* the rates used were "time to flowering" (Julian date of first flower open – Julian date of snow-free) and "seed development time" (Julian date of seed dispersal – Julian date of first flower open). For *Vaccinium* the rates used in the analysis were "time to flowering" (same as *Eriophorum*) and "flowering duration" (Julian date of last corolla drop – Julian date of first flower open). The timing analysis was performed using the Julian date of each phenological event in order to determine differences in the relative timing of phenological events in the different snow depth zones. Separate two-way ANOVAs were performed for each independent variable when a significant result was obtained for any of the main effects in the MANOVA and Tukey's multiple comparison test was used when a significant result was obtained from an ANOVA. Because there was no *E. vaginatum* in the deep snow zones at the natural snowbed sites, and MANOVA requires a complete data set, the analysis of this species was split up. MANOVAs were performed on rate and timing data using only data from mid and ambient snow depth zones at all three sites (SF, NS1, and NS2). And one-way ANOVAs were performed on rate and timing data from all three snow depth zones at the experimental snowfence only.

Average total soil carbon concentration was obtained by pooling data from the five summer sampling dates (initial soil cores) and obtaining a mean for each snow depth zone at all sites. Statistical analysis was performed using ANOVA, followed by Tukey's multiple comparison test when a significant result was obtained. Nitrogen mineralization data were analyzed using ANOVA for each site (SF, NS1, and NS2), and time period (summer, summer cumulative N mineralization, and overwinter mineralization) grouped separately, followed by Tukey's multiple comparison tests when a significant result was obtained from an ANOVA. Total soil DON and DIN pool concentrations were analyzed using ANOVA for each site (SF, NS1, and NS2) separately, followed by Tukey's multiple comparison tests when a significant result was obtained from an ANOVA. All statistical analyses were performed using SAS version 8 (SAS Institute Inc., Cary, NC, USA).

Results

PLANT PHENOLOGY

Snow had a large effect on the onset of the growing season for plants in the different snow depth zones ($P<0.0001$). The ambient snow depth zones melted out in the beginning of June, approximately two weeks before the plants in the deep snow depth zones ($P<0.0001$) and approximately one week before the plants in the mid snow depth zones ($P<0.0001$) at all three sites (Fig. 1a, 2a, 3a, 4a).

Betula nana *phenology*

Betula nana leafed out approximately 2 to 4 d after being released from snow cover (Fig. 1b). Snow depth did not have an effect on time needed for leaf out as exhibited by the similar slopes for the period snow free date to first leaf evident ($P = 0.2391$, Fig. 1a, b). There was a significant difference between the three snow depth zones with respect to the timing of "first leaf evident" ($P<0.0001$, Fig. 1a). However, senescence occurred at roughly the same time in all snow depth zones ($P = 0.9476$, Fig. 1a). There was a trend toward decreased leaf green period in the deep snow zones, although no statistical difference was detected between snow depth zones within sites (Fig. 1c).

Salix pulchra *phenology*

Salix pulchra leafed out within 4 d of release from snow cover (Fig. 2a, b). As with *B. nana*, snow did not have an effect on time needed for leaf-out in *S. pulchra* ($P = 0.2239$, Fig. 2a, b), and therefore the timing of green-up was significantly different in the different snow depth zones ($P<0.0001$, Fig. 2a). Similarly to *B. nana*, there was no significant difference in the onset of senescence at the end of the growing season between snow depth zones ($P = 0.2659$, Fig. 2a), and although there was a trend toward decreased leaf green period in the deep snow depth zones, we detected no statistical difference between snow depth zones (Fig. 2c).

Eriophorum vaginatum *phenology*

Eriophorum vaginatum occurred at all three of the study sites but was uncommon or absent in the deep snow zones (Fig. 3a). It

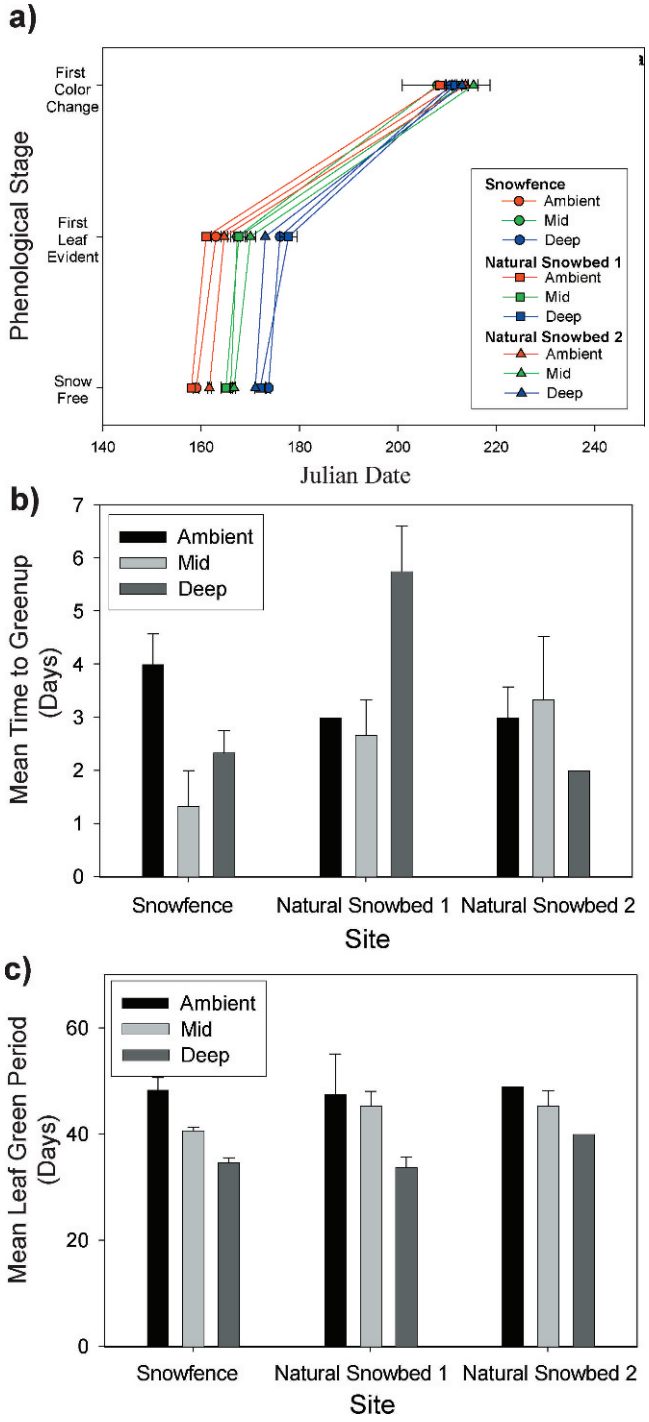

FIGURE 1. Relative timing of phenological events for *Betula nana* at all three sites and snow depth zones (a). Development rates for mean "time to green-up" (b) and mean "leaf green period" (c) for *Betula nana* at all three sites and snow depth zones. Values are means and SE ($n = 6$ in the deep zone and $n = 3$ in mid and ambient zones at snowfence site; $n = 4$ in each zone at natural snowbed 1 site; and $n = 3$ in each zone at natural snowbed 2 site).

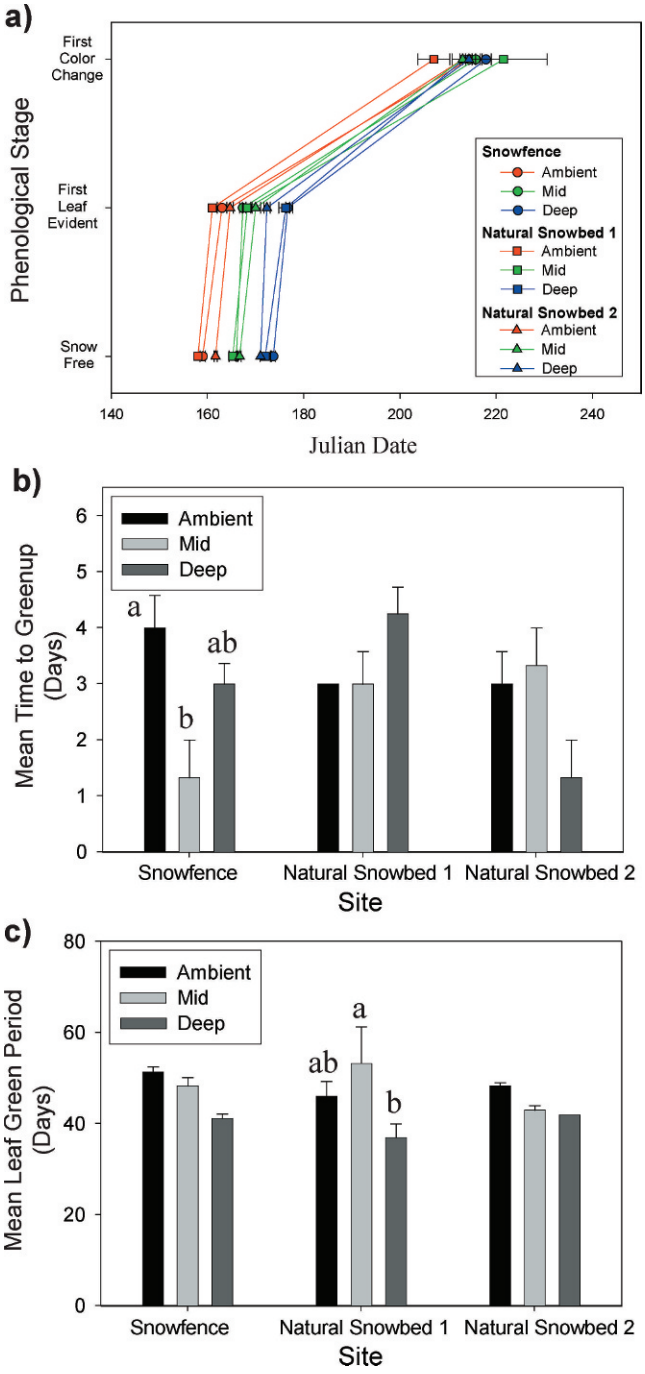

FIGURE 2. Relative timing of phenological events for *Salix pulchra* at all three sites and snow depth zones (a). Development rates for mean 'time to green-up' (b) and mean 'leaf green period' (c) for *Salix pulchra* at all three sites and snow depth zones. Values are means and SE ($n = 6$ in the deep zone and $n = 3$ in mid and ambient zones at snowfence site; $n = 4$ in each zone at natural snowbed 1 site; and $n = 3$ in each zone at natural snowbed 2 site). Within each site, bars marked with different letters are significantly different from one another (two-way ANOVAs followed by Tukey's multiple comparison test).

occurred rarely in the deep zone of the NS2 site, not at all in the deep zone of the NS1 site, and was dying off in the deep zone of the experimental snowfence site. In an analysis conducted on only data from the snowfence site, increased snow did not have an effect on the length of time needed for flowers to open in *E. vaginatum* ($P = 0.4014$) although there was a trend toward increased time to flowering in the deep snow zone (Fig. 3b). Using the combined data set from the ambient and mid snow depth zones of all three sites, snow only had a marginal effect on flower development at the NS1 site where flowering occurred marginally faster in the mid snow depth zone than in the ambient zone ($P = 0.0694$). Snow did not have an effect on flower development rate at the SF and NS2 sites. Across all three sites, using data from the

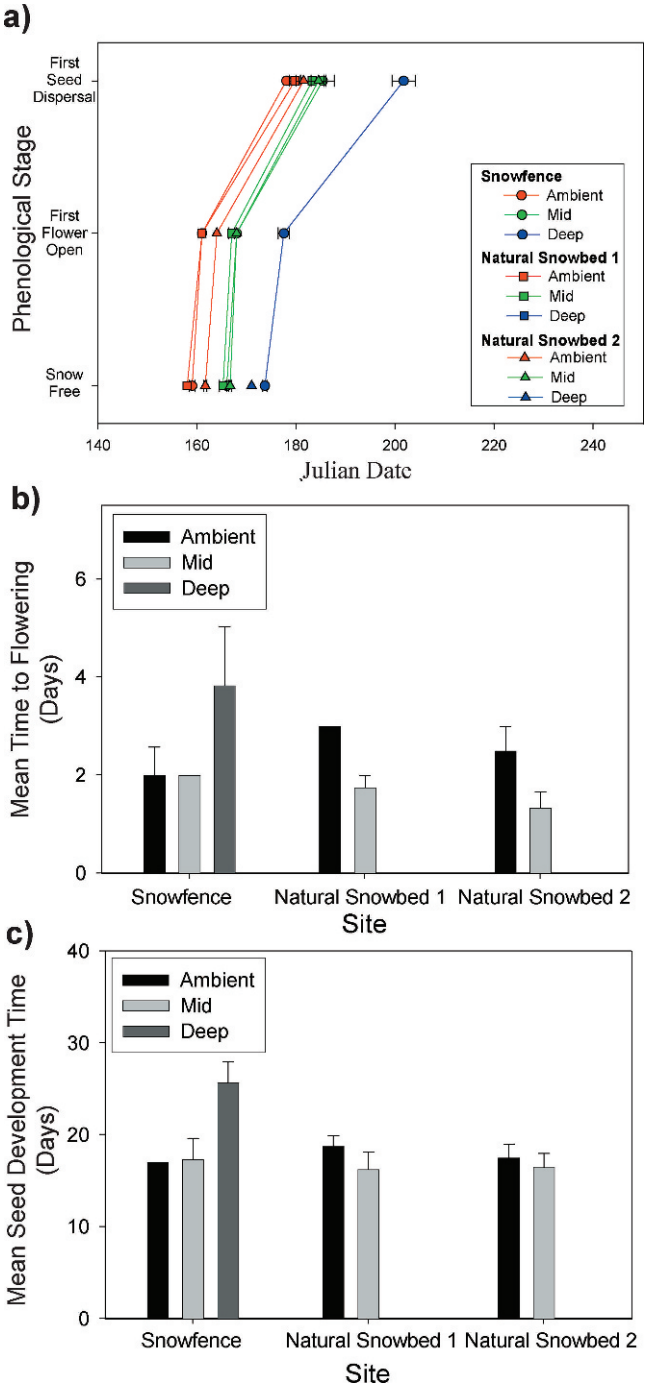

FIGURE 3. Relative timing of phenological events for *Eriophorum vaginatum* at all three sites and snow depth zones (a). Development rates for mean "time to flowering" (b) and mean "seed development time" (c) for *Eriophorum vaginatum* at all three sites and snow depth zones. Values are means and SE ($n = 6$ in the deep zone and $n = 3$ in mid and ambient zones at snowfence site; $n = 4$ in each zone at natural snowbed 1 site; and $n = 3$ in each zone at natural snowbed 2 site). Within each site, bars marked with different letters are significantly different from one another (one-way ANOVA followed by Tukey's multiple comparison test on snowfence data only).

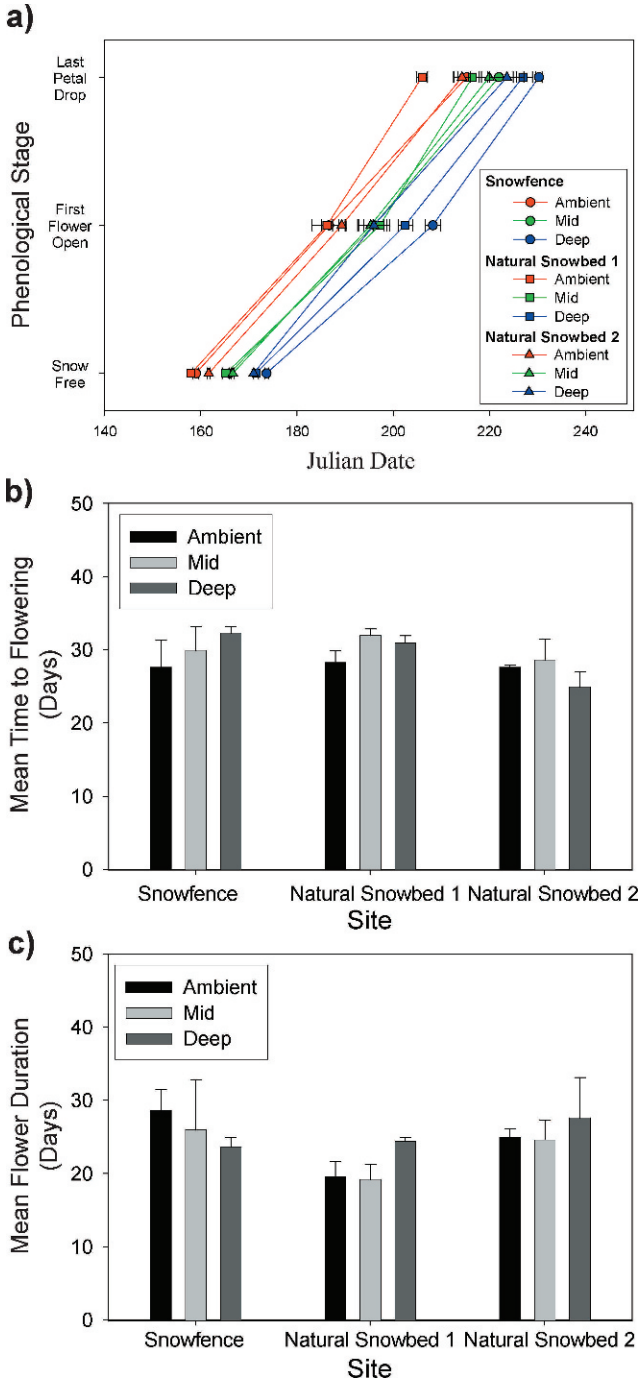

FIGURE 4. Relative timing of phenological events for *Vaccinium vitis-idaea* at all three sites and snow depth zones (a). Development rates for mean "time to flowering" (b) and mean "flower duration" (c) for *Vaccinium vitis-idaea* at all three sites and snow depth zones. Values are means and SE ($n = 6$ in the deep zone and $n = 3$ in mid and ambient zones at snowfence site; $n = 4$ in each zone at natural snowbed 1 site; and $n = 3$ in each zone at natural snowbed 2 site).

ambient and mid snow depth zones, the time needed for seed development was not affected by snow ($P = 0.4772$, Fig. 3c). However, data from all three snow depth zones at the snowfence site showed that ambient and mid zones developed faster than the deep zone ($P = 0.0417$ and $P = 0.0485$, respectively, multiple comparisons of snow depth zones from one-way ANOVA on SF data only).

Vaccinium vitis-idaea *phenology*

Vaccinium vitis-idaea did not begin flowering until three to four weeks after snow-free date in all snow depth zones (Fig. 4a). Overall, snow depth had a large effect on the timing of flowering and last petal drop for *V. vitis-idaea*, with deep snow zones

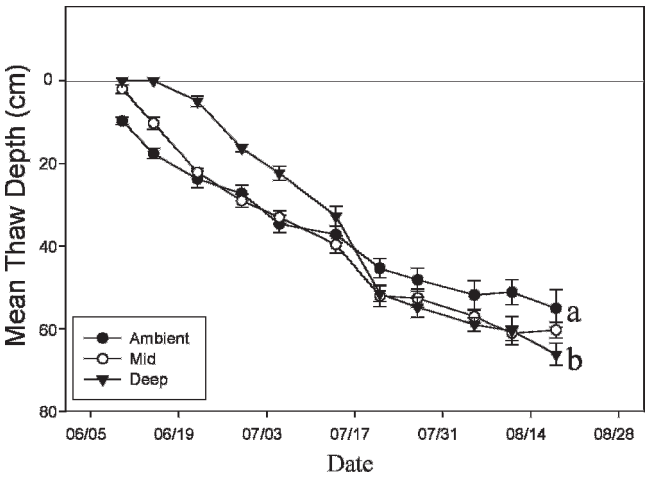

FIGURE 5. Thaw depth in the ambient, mid, and deep snow depth zones at the snowfence during the summer of 2000. Values are means and SE ($n = 9$ for each data point). Symbols marked with different letters are significantly different from one another ($P = 0.0498$, t-test).

flowering and ending flowering later than ambient zones ($P<0.0001$, Fig. 4a). However, snow depth did not have an effect on the rate of flower development ($P = 0.4153$, Fig. 4b) or duration of flowering ($P = 0.7891$, Fig. 4c), as evidenced by similar slopes between snow-free date to flowering, and flowering to last petal drop (Fig. 4a). All three snow depth zones were statistically distinct from one another for first flower open date ($P<0.0001$) and last petal drop date ($P<0.0001$, Fig. 4a).

SOILS DATA

Active Layer Depth

Although ambient and mid snow depth zones melted out earlier than the deep snow zones, thaw depth of the deep zone was similar to the thaw in the mid and ambient zones by the middle of the growing season. However, at the end of the growing season, the deep zone had the deepest thaw depth (Fig. 5, $P = 0.0498$, t-test between ambient and deep on last sampling date). The thaw depth was approximately 17% deeper in the deep snow zone than in the ambient snow zone. At the natural snowbed site the deep snow zone also melted out 15 to 20 d after the ambient snow zones, and exhibited a similar degree of increased thaw depth as the snowfence site.

Soil Moisture

At the snowfence site, soil moisture content did not vary among the three snow depth zones (Fig. 6a). This was probably due to the fact that this site had only been under snow manipulation for six winters at the time of sampling, a period of time that was too short to allow any significant changes in soil quality and drainage. At the NS1 site, the ambient zones had higher moisture content than the deep zones (Fig. 6b). Here, the ambient zone had more soil, a thicker organic mat, and more vegetation cover, whereas, the deep snow zone had less soil, more cobbles in the soil, and thus better drainage. At the NS2 site, soil moisture did not significantly vary between the snow depth zones (Fig. 6c).

Soil Carbon Concentration

Overall, snow had a significant effect on total soil carbon concentration ($P<0.0001$). At the experimental snowfence site, soil carbon concentration did not vary among the three snow

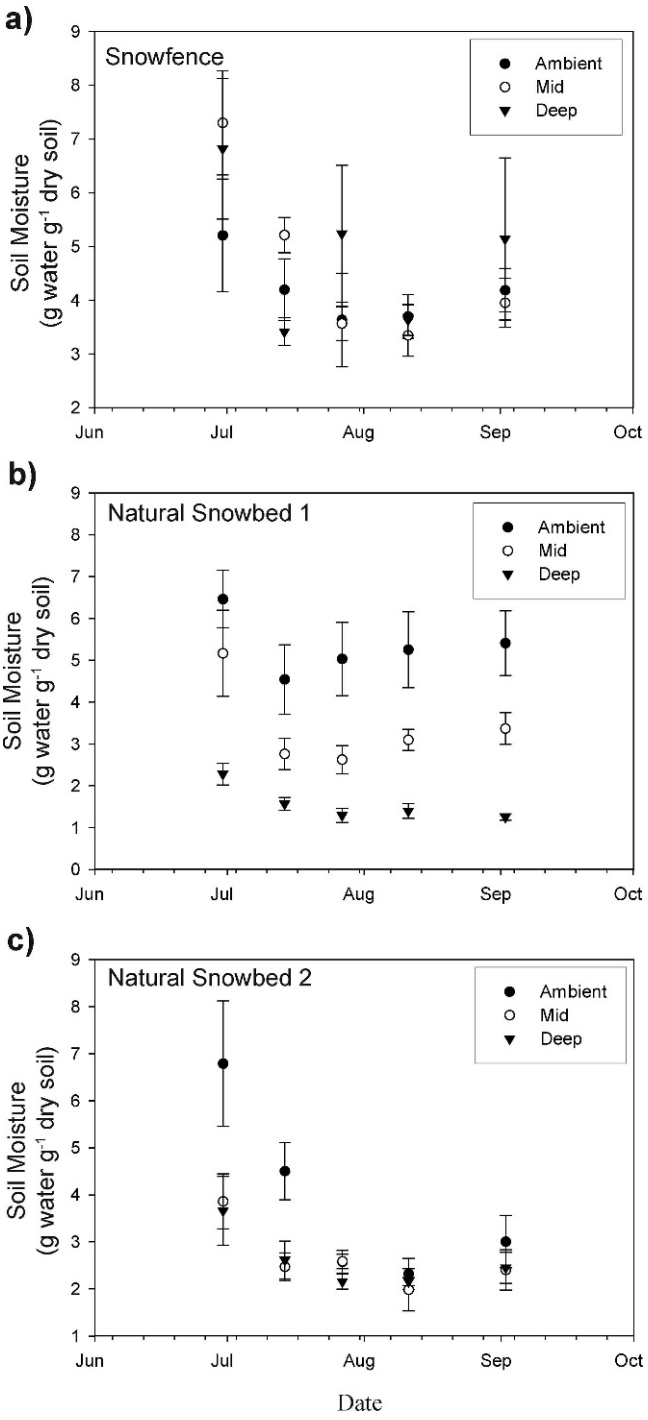

FIGURE 6. Gravimetric soil moisture for (a) snowfence site, (b) natural snowbed 1 site, and (c) natural snowbed 2 site during the summer of 2000. Values are means and SE ($n = 4$ for each data point).

depth zones (Fig. 7). In contrast, at the natural snowbed 1 site, carbon concentration in the three snow depth zones decreased with increasing snow (Fig. 7). At the natural snowbed 2 site, the mid and deep snow depth zones did not differ from each other in total C concentration but had lower carbon concentration than the ambient snow zone (Fig. 7).

Net Nitrogen Mineralization

Increased depth of snow did not have a significant effect on the rate of net N mineralization during the summer at either the

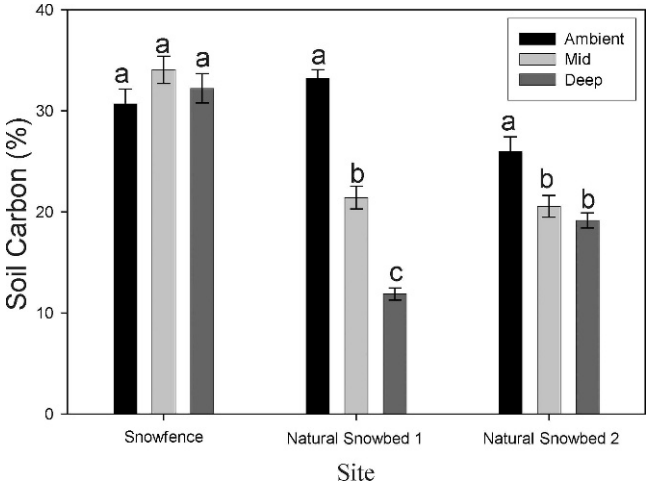

FIGURE 7. Soil carbon concentration (%) at experimental snowfence site and natural snowbeds. Values are means and SE (n = 20 for each snow depth zone at each site). Within each site, bars marked with different letters are significantly different from one another (two-way ANOVA followed by Tukey's multiple comparison test).

experimental site or the natural snowbeds (Fig. 8). However there was a general trend toward increased immobilization as the summer progressed, with all sites strongly immobilizing N at the end of the growing season (Fig. 8). By contrast, there were several differences between the ambient and deep snow depth zones at the snowfence site (P = 0.0383) with respect to cumulative N mineralized during the growing season, where ambient zones had approximately no net N mineralization, but large N immobilization occurred in the deep snow zone (Fig. 9a). Increased snow had a large effect on overwinter net N mineralization processes at the snowfence site (P = 0.0107), particularly between the ambient snow zone, in which net N immobilization occurred, and the deep zone where large net N mineralization occurred (P = 0.0092, Fig. 9b).

The two natural snowbed sites showed similar trends in net N mineralization. Snow depth had no effect on net N mineralization throughout summer (Fig. 8b, c) or on summer cumulative net N mineralization rates (Fig. 9a). However, as with the snowfence site, there was a trend toward increased net N immobilization with increasing snow cover (Fig. 9a).

The effect of snow depth on overwinter net N mineralization at the natural snowbed sites was variable. At the natural snowbed 1 site, snow depth had no effect, but there was a trend toward increased overwinter N mineralization in the mid and deep snow zones, similar to the snowfence site (Fig. 9b). At the natural snowbed 2 site, net N mineralization in the mid snow depth zone was significantly higher than in the ambient snow zone (P = 0.0261, Fig. 9b).

Overall, snow did not have a significant effect on summer net N mineralization at any of the three sites. During summer, N immobilization appeared to be the dominant process, particularly in deep snow zones (Fig. 9a). Snow had a significant effect on fall and winter net N mineralization rates, as evidenced by observations of high net N mineralization in mid and deep snow depth zones at both the experimental snowfence site and the two natural snowbeds in overwinter incubations (Fig. 9b). Snow depth did not have a significant effect on either DON or DIN pool sizes throughout the season (Figs. 10, 11). DON pool sizes were approximately 5 to 6 times larger than DIN pool sizes throughout the season (Figs. 10, 11). In addition, DON and DIN pool sizes

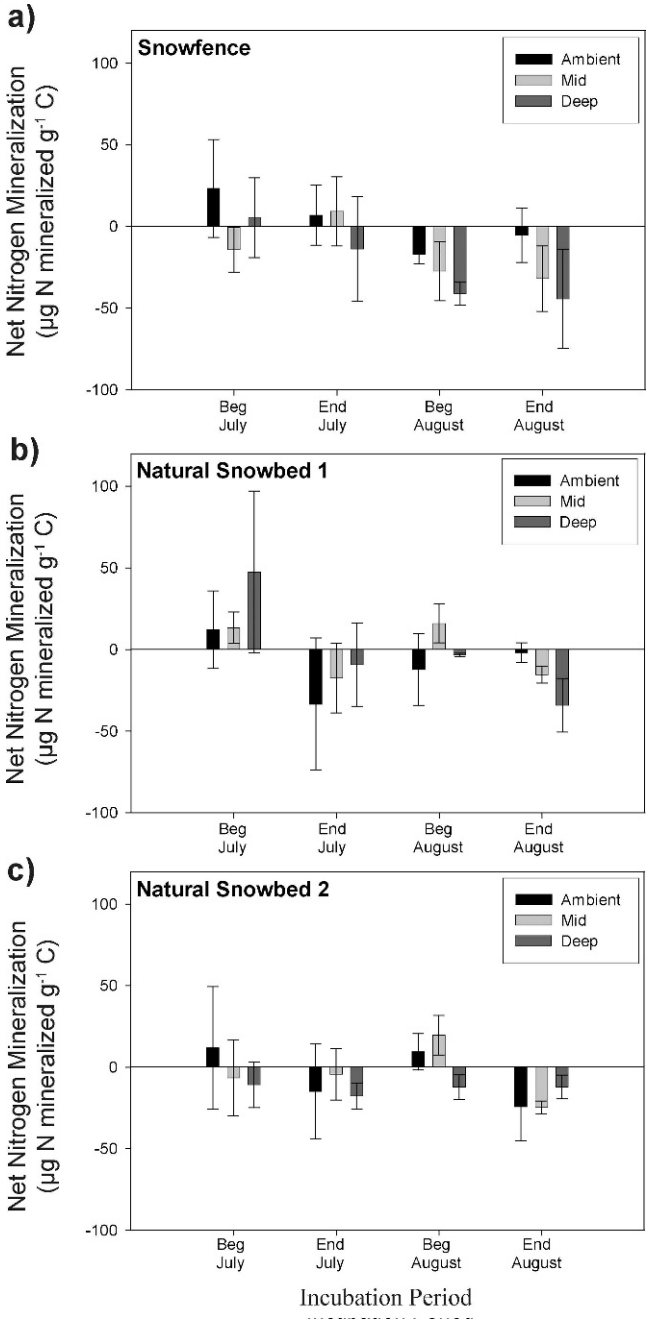

FIGURE 8. Net nitrogen mineralization through the summer for all four buried bag incubations for all three snow depths at the (a) snowfence site, (b) natural snowbed 1 site, and (c) natural snowbed 2 site. Values are means and SE (n = 4 for each snow depth zone on each date).

did not fluctuate significantly seasonally, with only the DON pool sizes of the last three sampling dates at the NS2 site being significantly lower than the first two sampling dates of the season (P<0.0001, Fig. 10a, b, c).

Discussion

PLANT PHENOLOGY

Although increased snow decreased the effective growing season length, it did not have a significant effect on the rate of phenological development. Of the species studied here, the deciduous shrubs *Betula nana* and *Salix pulchra* had similar rates

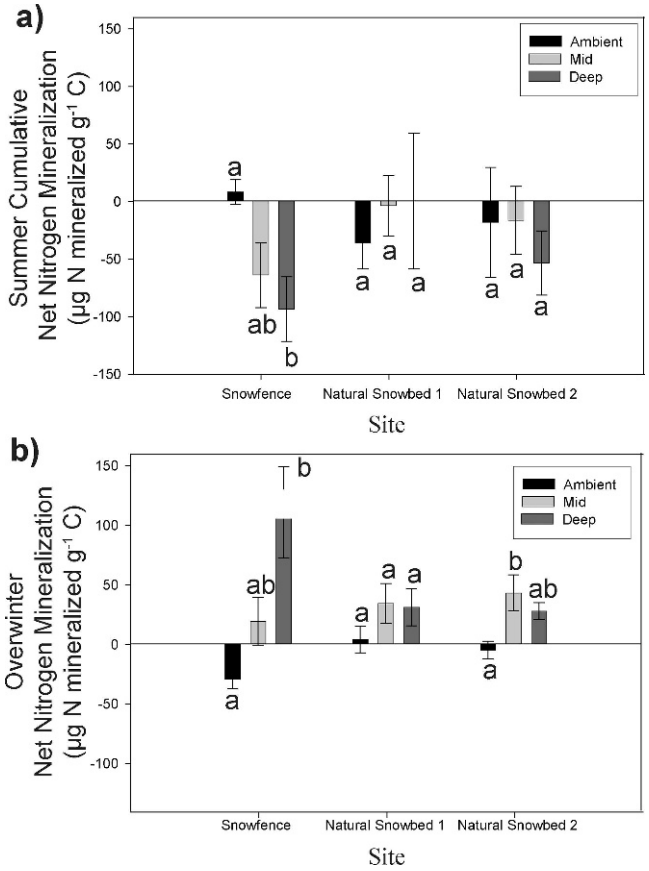

FIGURE 9. Summer cumulative net nitrogen mineralization from the end of June to the end of August 2000 for all three sites and snow depth zones (a). Overwinter net nitrogen mineralization, measured in cores incubated from September 2000 to Spring 2001 for all three sites and snow depth zones (b). Values are means and SE ($n = 4$ for each snow depth zone at each site). Within each site, bars marked with different letters are significantly different from one another (one-way ANOVA followed by Tukey's multiple comparison test).

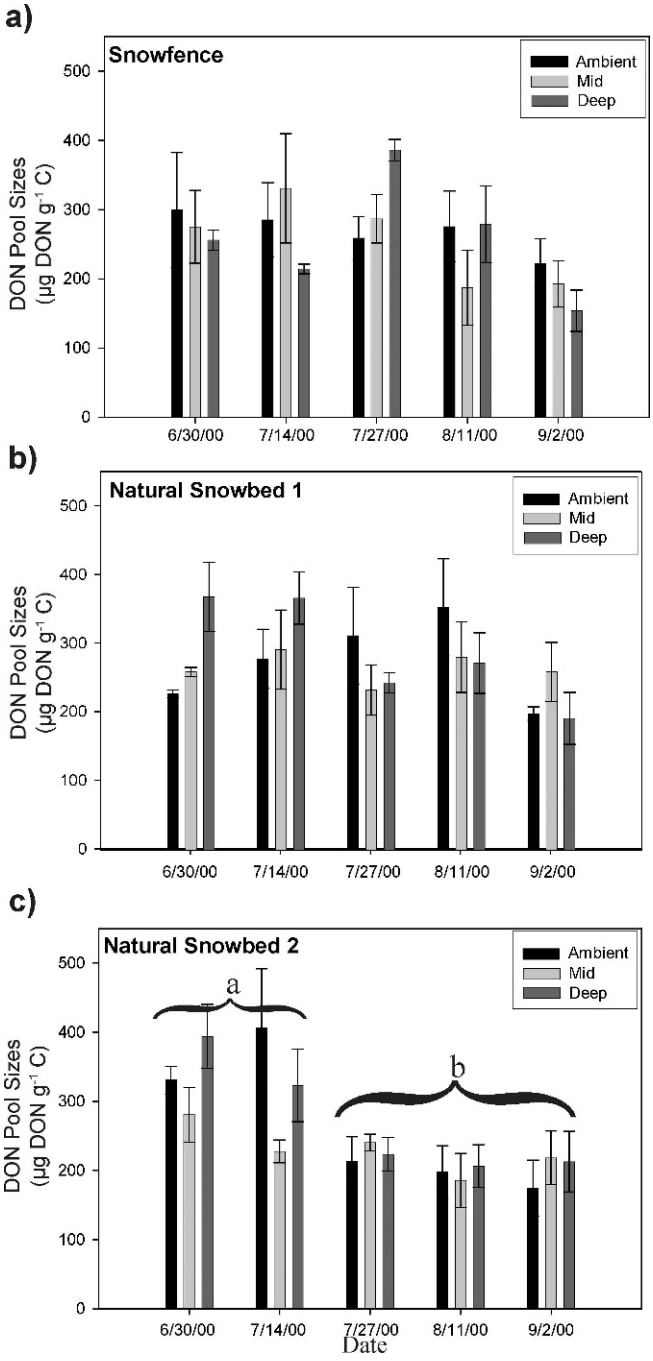

FIGURE 10. Total dissolved organic nitrogen (DON) pool sizes for all three snow depth zones at the (a) snowfence site, (b) natural snowbed 1 site, and (c) natural snowbed 2 site. Values are means and SE ($n = 4$ for each snow depth zone on each date). Dates marked with different letters are significantly different from one another (two-way ANOVA followed by Tukey's multiple comparison test).

of green-up in all snow depth zones, and *Eriophorum vaginatum* and *Vaccinium vitis-idaea* had similar flower development times and flowering duration in all snow depth zones. Our observations suggest that these phenological processes are under strong genetic control and that the species were not able to adjust development times in consort with environmental changes. For the deciduous shrubs, senescence occurred at approximately the same time in all snow depth zones at the end of the season, suggesting that timing of senescence was influenced primarily by an environmental factor, such as declining photoperiod or air temperature. However, the delay in both green-up of deciduous shrubs and flower emergence in *Eriophorum vaginatum* brought about by increased snow cover illustrates how climate may have significant effects on the local fauna, such as caribou. Because caribou calve during the first week of June, availability of high-quality forage is critical. In particular, reduced availability of *Eriophorum* inflorescences, which may constitute nearly 80% of caribou diet during calving (Thompson and McCourt, 1981), could have important consequences for milk production, calf growth, and ultimately population dynamics of caribou.

In an 8-yr study of the same vegetation plots at the snowfence site, Wahren et al. (2005) found that snow addition had a much larger effect on vegetation than warming by open top chambers. Results from that study showed that *Betula nana*, *Salix pulchra*, and *Eriophorum vaginatum* accounted for over 45% of the overall difference in mean cover between 1994 and 2002 and that the largest increase in shrub cover and height occurred in the mid snow depth zone (Wahren et al., 2005). From the results of that study, due to the point framing method used, it is unclear as to which shrub species are declining in the deep snow zone. Only the top (canopy) and bottom plant hits were recorded, so if snow-intolerant plants such as *Ledum decumbens* and *Vaccinium vitis-idaea* are declining, more hits of the dominant canopy species, *Betula nana*, *Eriophorum vaginatum*, and *Salix pulchra,* may be recorded even though they may be declining as well in the deep

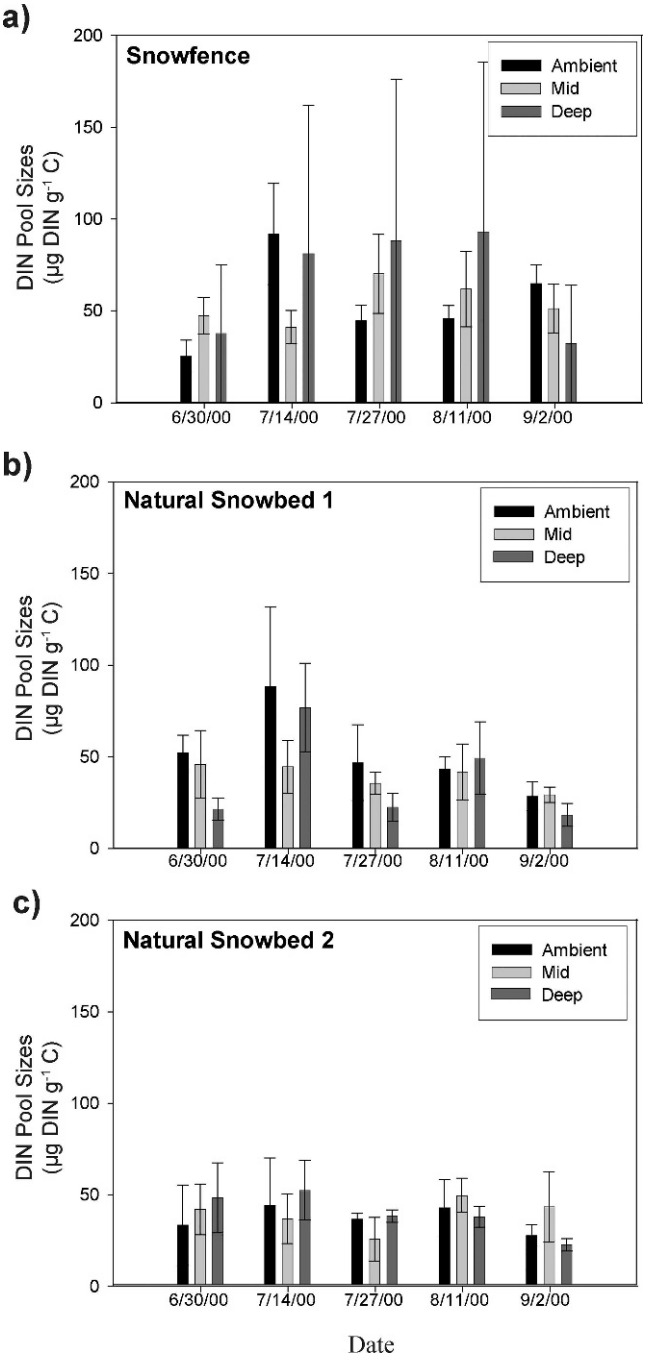

FIGURE 11. Total dissolved inorganic nitrogen (DIN) pool sizes for all three snow depth zones at the (a) snowfence site, (b) natural snowbed 1 site, and (c) natural snowbed 2 site. All values are means and SE ($n = 4$ for each snow depth zone on each date).

snow areas. Wahren et al. (2005) found that live overlapping vegetation cover (a measure of how dense the vegetation cover is) in the mid and ambient snow zones increased over 8 yr of snow addition, mainly due to an increase in *E. vaginatum*, while in the deep snow zone live vegetation cover decreased, mainly due to a loss of shrub cover, which supports our field observation that *E. vaginatum* and *B. nana* are declining in the deepest parts of the snow drift. This is further evidence that snow is having an effect on tundra vegetation that is not readily visible from observing phenology data directly.

At the experimental snowfence site, we observed that *Eriophorum vaginatum* had drastically reduced flowering success and was dying off in the deep snow zone. *Eriophorum vaginatum* is a species known to preform flower buds and each tiller dies after it flowers. The observed die-off in the deep zone of the experimental snowfence site may be due to a combination of a lack of time to accumulate resources needed to initiate new structures for upcoming years and a change in species abundance which alters interspecific competition. In this analysis, the deep zone plots were the same six plots that were used by Wahren et al. (2005). The row closest to the fence received snow accumulation earliest in the season, and the time needed to flower was approximately three times as long (about 6 d vs. about 2 d) as needed in the second deep row, and the mid and ambient snow depth zones. In addition, *E. vaginatum* did not produce seeds at all in the row closest to the fence (deepest snow). Other studies have found plant reproduction (flowering and seed production) to be drastically reduced as a result of increased snow and shortened growing season (Galen and Stanton, 1995; Huelber et al., 2006). This evidence, combined with the facts that *E. vaginatum* occurred in very low abundance but did not flower at the deep zone in the NS2 site and did not occur at all in the deep snow zone at the NS1 site, suggests that *E. vaginatum* may be at the edge of its growing season tolerance or may be outcompeted for resources by other species better able to tolerate deep snow. The increased snow depth earlier in the fall in the row of plots closest to the snowfence provided increased insulation to the soil, which potentially allowed the plants to maintain higher rates of respiration later into the fall and winter (Fahnestock et al., 1999; Starr and Oberbauer, 2003; Schimel et al., 2004), while the mid and ambient plots were still exposed and froze earlier and to a lower temperature. This potential for continued high plant respiration in the deep snow zone may have caused *E. vaginatum* to consume carbohydrate reserves and thereby decreased its potential for survival and reproductive output for the next growing season.

Following the same trend, rates of flower development and duration were not affected by snow in *Vaccinium vitis-idaea*. A decrease in cover of evergreen shrubs (Wahren et al., 2005) was possibly due to shading and increased competition caused by the increase in deciduous shrubs. The increases in deciduous shrubs and decreases in evergreen shrubs seen at the experimental snowfence site (Wahren et al., 2005) have also been documented in warming and fertilization experiments (Shaver and Chapin, 1980; Chapin et al., 1995).

Depth of snow, through effects on growing season length, dictates which plant functional types will be dominant with varying snow depth. Different plant species and functional types have different litter qualities, therefore changes in vegetation and litter inputs to the soil will have feedbacks on soil nutrient dynamics (Nadelhoffer et al., 1991; Hobbie, 1996), with potentially important feedbacks on community composition and net primary production. The apparent increase in shrubs under moderate increases in snow cover, but significant decrease in shrub abundance with further increases in snow depth exemplify the potential nonlinear behavior of vegetation response to changes in climate.

NITROGEN MINERALIZATION

Effects of snow became most apparent when comparing summer vs. winter processes in the deep and ambient snow zones. The ambient snow zone at the snowfence site exhibited cumulative net N mineralization during summer, with mineralization occurring during the first half of the summer and net immobilization occurring in the second half of the summer. Similar temporal patterns of microbial N immobilization have been observed in

alpine ecosystems (Jaeger et al., 1999). However, in the deep snow zone of the snowfence site, N immobilization was the dominant process during summer. During the winter, these processes were reversed, with the ambient zone undergoing N immobilization and the deep snow zone undergoing large net N mineralization. Thus, the greatest extent of snow increase changed the soil from a net consumer of DIN in the summer to a net producer of DIN during winter.

The switch in timing of N mineralization in the deep snow areas might be explained by a combination of several interacting factors. Deep snow zones of the snowfence site received a covering of snow earlier in the winter than the ambient snow zone, thereby creating an insulating layer, causing delayed soil freezing and warmer soil temperatures later into the fall and winter (Sturm et al., 2005). In addition, the dying (*E. vaginatum* in particular) and senescing plants in the deep snow zones may have supplied a large amount of labile carbon to the soil (retranslocated sugars, root exudates, dying roots, and fresh leaf litter) that soil microbes could utilize in the fall and early winter. Soil temperatures in the deep snow zone of the snowfence site have been measured to reach their minimum of between -5°C and -7°C at 5 cm soil depth during late winter (Walker et al., 1999; Schimel et al., 2004), and soil microbes have been shown to remain active at such temperatures (Clein and Schimel, 1995; Mikan et al., 2002; Michaelson and Ping, 2003; Schimel et al., 2004). However, in the absence of plant carbon flow during winter, soil microbes could be more energy limited and therefore may be mineralizing N for much of the winter. Soil temperature in ambient snow areas typically go down to -20°C, effectively halting microbial processes and N mineralization.

We found that winter was the dominant season in which N mineralization occurred in the mid and deep snow depth zones at all three sites. Furthermore, it has been found that shrub cover has increased in the mid snow depth zone at the snowfence site (Wahren et al., 2005), and that the largest shrubs at the natural snowbed sites occur in the mid snow depth zones (pers. obs.), corresponding to the zone of greatest winter N mineralization. The observed increase in shrub abundance in the Arctic (Sturm et al., 2001a) suggests a possible snow-shrub-soil-microbe feedback loop (Sturm et al., 2001b, 2005), whereby shrubs trap snow (acting as small snowfences), insulating the soil and increasing soil temperatures, microbial activity, and N mineralization during the fall and winter (Sturm et al., 2005; Weintraub and Schimel, 2005a). This increased nutrient availability causes a positive feedback loop, promoting the spread of shrubs that accumulate more snow. Moderate increases in winter snow cover and moderate decreases in growing season length could lead to an increase in shrub cover. However, there seems to be a limit to this feedback loop; with drastic increases in snow, fewer shrubs may be present.

Overwinter N mineralization measured in the deep snow zone of the snowfence site was approximately 2 to 3 times greater than in the mid or deep snow zones of the two natural snowbed sites. This stimulation of N mineralization may be partially explained by the deeper thaw depth at the end of the summer in the deep snow zone of the snowfence site (approximately 17% deeper thaw in deep than ambient snow zones at the snowfence site). These patterns are likely occurring because late-lying snowbeds provide a thermal blanketing effect for the underlying tundra, thereby creating permafrost temperatures closer to 0°C (Zhang, 1996). Permafrost temperatures closer to 0°C may allow deep snow areas to "catch up" and even exceed thaw depths of ambient snow areas. As explained by Sturm et al. (2005), cryoturbation in the Arctic is the slow convective overturning of the active layer which mixes organic material from near the surface layer into subsurface layers (Michaelson and Ping, 1996). These subsurface layers have higher silt content, and therefore contain more numerous and larger unfrozen water films than soils higher in the soil column (Romanovsky and Osterkamp, 2000). A combination of the early snow cover for insulation, warmer winter soil temperatures, deeper thaw depths, and possible influence of cryoturbation in the deep snow zone of the snowfence site create an environment in which microbes can mineralize N long into the winter.

In this study DON concentrations were approximately 5 times higher than concentrations of DIN, and were not affected by either snow depth or season. Little is known about the seasonality of soil DON pool sizes in the Arctic, but concentrations measured in this study are consistent with past measurements at Toolik Lake, Alaska (Kielland, 2001; Weintraub and Schimel, 2005b). Weintraub and Schimel (2005c) measured DON concentrations between 5 times and 2 orders of magnitude higher than salt-extractable NH_4^+ concentrations. They observed DON concentrations to decrease during the end of July, which corresponded to an increase in proteolysis. Furthermore, they found that DON was poorly or negatively correlated with amino acids and DIN, suggesting that DON may be utilized during the production of more labile forms of N. They suggested that during this time of peak plant and root growth and N uptake, microbes become N limited and are increasing protease production to take advantage of the larger molecules that make up DON (Weintraub and Schimel, 2005b, 2005c). Winter DON concentrations and processes are virtually unknown in the Arctic, but because the winter occupies such a large part of the year, organic nitrogen processes play a potentially large role in arctic N cycling.

Conclusions

Increased snow depth exerts a considerable influence on tundra plant communities. Increased snow has a large effect on the temporal pattern of the onset of the growing season, green-up, and flowering, by delaying snowmelt by approximately 2 wk in the deep snow zones. However, the plant species studied did not compensate for the shorter growing season by speeding up their development rates in deep snow zones. In deep snow zones, *Eriophorum vaginatum* actually took twice to three times as long to flower than in ambient snow areas, which could be an indication that this species is at the edge of its growing season tolerance. Increased snow depth had both strong qualitative and quantitative effects on N mineralization in deep snow zones, causing a switch in both the timing and amount of mineralization compared to ambient snow zones. Nitrogen mineralization occurred mainly overwinter in deep snow zones, whereas N mineralization occurred mainly in the spring in ambient snow zones. There was a qualitative shift from deep snow zones being net nitrogen consumers during the summer to being net nitrogen producers overwinter. A moderate increase in snow depth could lead to an increase in deciduous shrubs and overwinter nitrogen mineralization. However, a drastic increase in snow depth, resulting in a reduced growing season, would limit the time available for net primary productivity, would reduce or eliminate certain key species (such as *E. vaginatum* and deciduous shrubs), and would result in a qualitative change in N availability. The net effect of these changes would alter plant community composition and distribution with possible feedbacks to regional climate.

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