PLANT PHENOLOGY AND SEASONAL NITROGEN AVAILABILITY

IN ARCTIC SNOWBED COMMUNITIES

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A

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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 plant phenology, but potentially large effects on patterns of N cycling.

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Introduction

Average temperatures in the Arctic are predicted to rise between 2° and 5°C as a result of the increase in atmospheric CO_2 concentration (Maxwell, 1992, 1997). Global warming is expected to produce the largest effects at high latitudes. In fact, warming in the Arctic has already been documented over the past 25 years (Serreze et al., 2000; Walther et al., 2002). Global circulation models project great variability for arctic climate in the future, but hydrologic processes may be intensified, with increased winter snowpack (Maxwell, 1992; Hinzman et al., 2005). Increased winter snowpack will have large effects on winter and summer soil temperatures, permafrost temperatures, nutrient cycling dynamics, and growing season length (Sturm et al., 2005).

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 growing season length, plant phenology, plant species distribution, soil temperatures, active layer depths, and nutrient availability. Snow depth, rate of snowmelt, and snowfree date in the spring dictate the time available for resource assimilation during the growing season (Inouye and McGuire, 1991; Galen and Stanton, 1993, 1995) and will affect different plant species in proportion to their capacity to respond to changes in growing season length. Plant species which are unable to adjust to changes in growing season length may not survive or have reduced fitness (Inouye and McGuire, 1991; Galen and Stanton, 1991, 1995; Walker et al., 1994a). It has been shown that shifts in snowfall patterns and growing season lengths can have significant impacts on vegetation composition, abundance, and productivity (Holway and Ward, 1963; Miller, 1982; Walker et al., 1994b; Stanton et al., 1994; Sturm et al., 2001a, 2001b, 2005; Wahren et al., 2005); therefore, the study of plant phenology can provide important insight into how increased snow might affect species differentially.

Length of growing season also 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). Data from the International Tundra Experiment (ITEX) (Molau and Mølgaard, 1996) at Toolik Lake, Alaska showed that the minimum temperatures under the deepest parts of the experimental snow drift do not go below about -7°C at 5cm soil depth (Walker et al., 1999; Schimel et al., 2004). Due to the warmer temperatures under the snowpack, plant respiration may be taking place during much of the winter (Shaver and Kummerow, 1992). Prolonged snow cover in the spring could therefore reduce growth in some species even further by causing respiratory depletion of carbohydrate reserves.

Previously, it has been thought that environmental site factors such as snow depth, growing season length, soil moisture, and thaw depth were the main factors controlling plant community composition, but other studies have found that nitrogen availability is also important (Shaver and Chapin, 1980; Miller et al., 1982, 1984; Robertson et al., 1988; McKane et al., 2002). It is likely that interactions among these environmental site characteristics contribute to plant community composition. An increase in snow accumulation will have 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; Nadelhoffer et al., 1992), 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). Previous studies of toposequences have looked only at inorganic nitrogen availability (ammonium and nitrate); however, there appears to be a discrepancy between soil N mineralization and plant N requirements in many arctic ecosystems (Shaver and Chapin, 1991). Moreover, recent work has shown that arctic plants may be able to directly take up organic forms of nitrogen as free amino acids, and may provide the remaining nitrogen not accounted for by net nitrogen mineralization (Chapin et al., 1993; Kielland, 1994, 1995, 1997; Schimel and Chapin, 1996; Raab et al., 1999; Lipson and Näsholm, 2001; Weintraub and Schimel, 2005a). Studying the dynamics of both organic and inorganic forms of nitrogen will be an important part of understanding the nutrient mechanisms of arctic ecosystems.

Mesotopographic gradients (Billings, 1973) across arctic landscapes may provide an understanding of the direct and indirect effects snow distribution has on plant species distribution. Assuming that plant communities along the topographic gradient all had the same or similar histories and that the major environmental conditions have been similar over long time periods along this gradient (i.e. no major disturbances affecting only some of the plant communities along the gradient), we can evaluate what effects different snow depth regimes will have on the development of different plant communities.

This research focused on conducting a species comparison of plant phenology and seasonal nutrient availability between an experimentally manipulated snow depth site, using a snowfence to augment snow, and two natural snowbed sites that had similar snow depth gradients. Such an approach may provide insights into the following questions:

- How does snow depth affect the phenology of different plant species along the snow gradient?
- How does snow depth affect inorganic nitrogen pool sizes and mineralization rates along the snow gradient?
- How does snow depth affect total organic nitrogen along the snow gradient?
- Does having information on plant phenology, soil moisture, soil organic matter content, and soil nutrient availability move us toward a better understanding of plant community distribution in the Arctic?

I 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. Lastly, I hypothesized 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.

At the experimental snowfence site I investigated the effects of increased snow on the tundra vegetation and biogeochemical cycles. Because of the lag time involved, I saw only the direct effects of increased snow (decreased growing season and increased winter soil temperatures) on the plant community. However, natural snowbeds have been under the influence of increased snow for much longer than the snowfence plots, and, as a result, these snowbeds can be used to understand the changes we could expect to see at the snowfence site as the treatment continues to influence the vegetation over the long-term. By comparing plant phenology and nitrogen dynamics at the snowfence site and natural snowbeds, the direct effects of increased snow can be teased apart from the indirect mechanisms such as feedbacks from litter quality and organic matter content of the soil. Understanding the extent to which snow depth directly and indirectly affects plant species distributions and plant community dynamics will allow us to predict the long-term effects of increased snow on tundra vegetation.

Study Site and Experimental Design

This 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.). This project was part of the International Tundra Experiment (ITEX) (Molau and Mølgaard, 1996; Henry and Molau, 1997) and used the Toolik snowfence plots and grid that were established in the summer of 1994. The snowfence used in this project was located in moist acidic tundra (MAT), where *Eriophorum* tussock tundra was the predominant vegetation (Walker et al., 1994b). 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 (Figs. 1 and 2a,b,c,d). 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 (Figs. 1 and 2e,f). 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 1m^2 plots were established corresponding to deep, mid and ambient snow depth zones. In the case of the natural snowbeds, the ambient plots were located down slope of the deep and mid 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.

Natural snowbeds occur due to topographical features in the landscape that accumulate wind-driven snow. At the two natural snowbeds in this study, snow

accumulated due to an approximately 5 m drop in elevation in the tundra. The elevation drops roughly from south to north and the topographical feature is aligned roughly west to east, which is very similar to the orientation of the experimental snowfence (Fig. 1). Snow accumulates at the natural snowbed sites in much the same way as at the experimental snowfence site, because the catabatic winds blow out of the south for much of the winter. The deepest parts of the drift form at the base of the hill, where the slope eases to an even gradient through all three snow depth zones similar to the snowfence plots. 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. These differences in vegetation patterns at the natural snowbed sites were likely caused by species' season length requirements, moisture requirements, and feedbacks to the system through the quality of litter input from the plants that were able to survive in different areas along the gradient.

Methods

PLANT PHENOLOGY

Phenological events of four ITEX species were monitored at the snowfence and natural snowbed sites within the established $1 m^2$ plots. Measurements were made

according to the standardized protocols of the ITEX experiment (Molau and Mølgaard, 1996) and follow earlier work monitoring natural variation in phenology (Walker et al, 1994a, 1995; Arft et al. 1999). The species monitored at the snowfence and natural snowbed sites were *Betula nana, Salix pulchra, Eriophorum vaginatum,* and *Vaccinium vitis-idaea* (Hultén, 1968). The snowfree 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: first green leaf (green-up or budburst) and first color change (the onset of senescence). Phenological events monitored for the graminoid *Eriophorum vaginatum* were: first flower open (first pollen visible) and seed dispersal. For the evergreen shrub *Vaccinium vitis-idaea* the events monitored were: first flower open and last corolla drop (end of flowering). Phenology was monitored every other day (three times per week) 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) at the natural snowbed 1 (NS1) site, and three (n=3) at the natural snowbed 2 (NS2) site (Fig. 1). Each plot was visually scanned for the next phenological event for each species every other day throughout the season.

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 from the organic layer in each snow depth zone at each site, approximately every two weeks 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. Multiple 15 g subsamples 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

A 15 g fresh weight subsample was placed in an aluminum soil tin and oven-dried (65°C). Total C concentrations were measured using the LECO CNS-2000 (LECO Corporation, St. Joseph, MI, USA) analyzer following the Dumas dry combustion procedure (Sollins et al., 1999). Gravimetric soil moisture was calculated for each sample as the difference between the 15 g wet mass and the dry mass of the oven-dried soil, and reported 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 (initial and buried bag cores) was initiated in the end of June 2000 when the soil was thawed in all three snow depth zones. A new incubation was initiated (initials and buried bags) every 12 – 14 days throughout the summer until the beginning of September, at which time an overwinter incubation was started. Four intertussock soil cores were collected from each snow depth zone at each of the three sites for use as the initial cores. At the same time, 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 12-14 day incubation period.

A 15 g fresh weight subsample 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 (see above). The 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 by comparing the 0.5 M K_2SO_4 extractable ammonium and nitrate from the buried bag cores to that of the initial cores taken at the beginning of each incubation period. Positive values represent net N mineralization and negative numbers represent net N immobilization. Summer cumulative N mineralization was calculated by summing net N mineralization values (both positive and negative) for each of the four sampling periods for each plot.

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). The oxidizing reagent was prepared by first combining 30 g H_3BO_4 and 15 g NaOH, and bringing the volume close to 1L with deionized water. After placing the mixture on a stir table and allowing it to dissolve and cool, 50 g low-N $K_2S_2O_8$ was added and the solution was diluted to 1 L. The oxidizing reagent was prepared in this order because dissolving NaOH is an exothermic reaction and heat increases the degradation and oxidizing rate of

$K_2S_2O_8$. Therefore, adding the $K_2S_2O_8$ to this hot solution would have decreased its potential of oxidizing the entire DON in the samples to nitrate.

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 minutes. 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 greenup" (Julian date of first leaf evident – Julian date of snowfree) 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 snowfree) 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.

Mean 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. 3a, 4a, 5a, 6a).

Betula nana phenology

Betula nana leafed out approximately 2 to 4 days after being released from snow cover (Fig. 3b). 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. 3a, b, Table 1). There was a significant difference between the three snow depth zones with respect to the timing of 'first leaf evident' (p<0.0001, Table 1, Fig. 3a). However, senescence occurred at the same time in all snow depth zones (p=0.9476, Table 1, Fig. 3a). 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. 3c).

Salix pulchra phenology

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

Eriophorum vaginatum phenology

Eriophorum vaginatum occurred at all three of the study sites but was uncommon or absent in the deep snow zones (Fig. 5a). It 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, Table 3a) although there was a trend toward increased time to flowering in the deep snow zone (Fig. 5b). 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, Table 3b). Snow did not have an effect on flower development rate at the SF and NS2 sites (Table 3b). Across all three

sites, using data from the ambient and mid snow depth zones, the time needed for seed development was not affected by snow (p=0.4772, Fig. 5c, Table 3). 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, Table 3a, 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 snowfree date in all snow depth zones (Fig. 6a). Overall, snow depth had a large effect on the timing of flowering and last petal drop for *V. vitis-idaea*, with deep snow zones flowering and ending flowering later than ambient zones ($p<0.0001$, Table 4, Fig. 6a). However, snow depth did not have an effect on the rate of flower development (p=0.4153, Fig. 6b, Table 4) or duration of flowering (p=0.7891, Fig. 6c, Table 4), as evidenced by similar slopes between snowfree date to flowering, and flowering to last petal drop (Figure 6a). All three snow depth zones were statistically distinct from one another for first flower open date ($p<0.0001$, Table 4) and last petal drop date ($p<0.0001$, Table 4, Fig. 6a).

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. 7, 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 15-20 days after the ambient snow zones, and exhibited a similar degree of increased thaw depth as the snowfence site.

Gravimetric Soil Moisture

At the snowfence site, soil moisture content did not vary among the three snow depth zones (Fig. 8a). This was probably due to the fact that this site had only been under snow manipulation for 6 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. 8b). 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. 8c).

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 depth zones (Fig. 9). In contrast, at the natural snowbed 1 site, carbon concentration in the three snow depth zones decreased with increasing snow (Fig. 9). 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. 9).

Net Nitrogen Mineralization

At the snowfence site, snow did not have a significant effect on the rate of net N mineralization throughout the summer, although there was a general trend toward increased immobilization as the summer progressed (Fig. 10a). However, there was a difference 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 immobilization occurred in the deep snow zone (Fig. 11a). 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 immobilization occurred, and the deep zone where large net mineralization occurred ($p=0.0092$, Fig. 11b).

The two natural snowbed sites showed similar trends in net N mineralization. Snow depth had no effect on net N mineralization throughout summer (Fig. 10b and c) or on summer cumulative net N mineralization rates (Fig. 11a). However, like the snowfence site, there was a trend toward increased net immobilization with increasing snow cover (Fig. 11a).

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. 11b). 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. 11b).

Overall, snow did not have an effect on summer net N mineralization at any of the three sites. When looking at summer cumulative net N mineralization data, immobilization appeared to be the dominant process, particularly in deep snow zones (Fig. 11a). 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 over-winter incubations (Fig. 11b). Snow depth did not have a significant effect on either DON or DIN pool sizes throughout the season (Figs. 12 and 13). DON pool sizes were approximately 5 to 6 times larger than DIN pool sizes throughout the season (Figs. 12 and 13). In addition, DON and DIN pool sizes 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. 12a, 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 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. These observations suggest that these phenological processes are under strong genetic control and that these 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. This suggests that the timing of senescence was influenced primarily by an environmental factor, such as declining photoperiod or air temperature, toward the end of the growing season rather than genetic control.

In an 8-year study of the same vegetation plots at the snowfence site, Wahren et al. (2005) found that the snow addition treatment 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 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 eight years 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 my 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, I 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 during previous growing seasons 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). These six plots were from the first two rows of plots directly behind the snowfence. 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 days vs. about 2 days) as needed in the second deep row, and the mid and ambient snow depth zones. In addition, *E. vaginatum* did not produce seed at all in the row closest to the fence in the 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 Oberbaurer, 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*. According to Wahren et al. (2005), mean cover and height decreased for evergreen shrubs in deep snow zones. This decrease 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 been documented in warming and fertilization experiments (Chapin et al, 1995) as well as predicted in models (Epstein et al., 2000) of arctic vegetation change.

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). As illustrated by Giblin et al. (1991) and Nadelhoffer et al. (1991), the higher the quality of the organic matter, the greater nitrogen mineralization rates will be. This available nitrogen, produced by mineralization, has a large effect on plant community composition and net primary production.

NITROGEN MINERALIZATION

At the experimental snowfence site, snow depth affected both the timing and rate of net N 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 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. 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. Similar patterns, though subtle, were observed in the two natural snowbed sites.

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). Furthermore, soil microbes have been shown to remain active at temperatures below freezing (Clein and Schimel, 1995; Mikan et al., 2002; Michaelson and Ping, 2003; Schimel et al., 2004), and therefore may be mineralizing N for much of the fall and early winter. Soils in ambient snow areas freeze earlier in the fall halting microbial processes and N mineralization.

My study 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 (personal observation), corresponding to the zone of greatest winter N mineralization. Researchers have observed increasing shrub abundance in the Arctic (Sturm et al., 2001a), and have suggested a snow-shrub-soil-microbe feedback loop (Sturm et al., 2001b; Sturm et al., 2005). They suggest that the shrubs trap snow (acting as small snowfences), thereby insulating the soil and increasing soil temperatures, microbial activity, and N mineralization during the fall and winter (Sturm et al., 2005; Weintraub and Schimel, 2005c). 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.

In this experiment, the 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 et al., 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, 2005a). Weintraub and Schimel (2005b) 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, 2005a, 2005b). 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 two weeks 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.

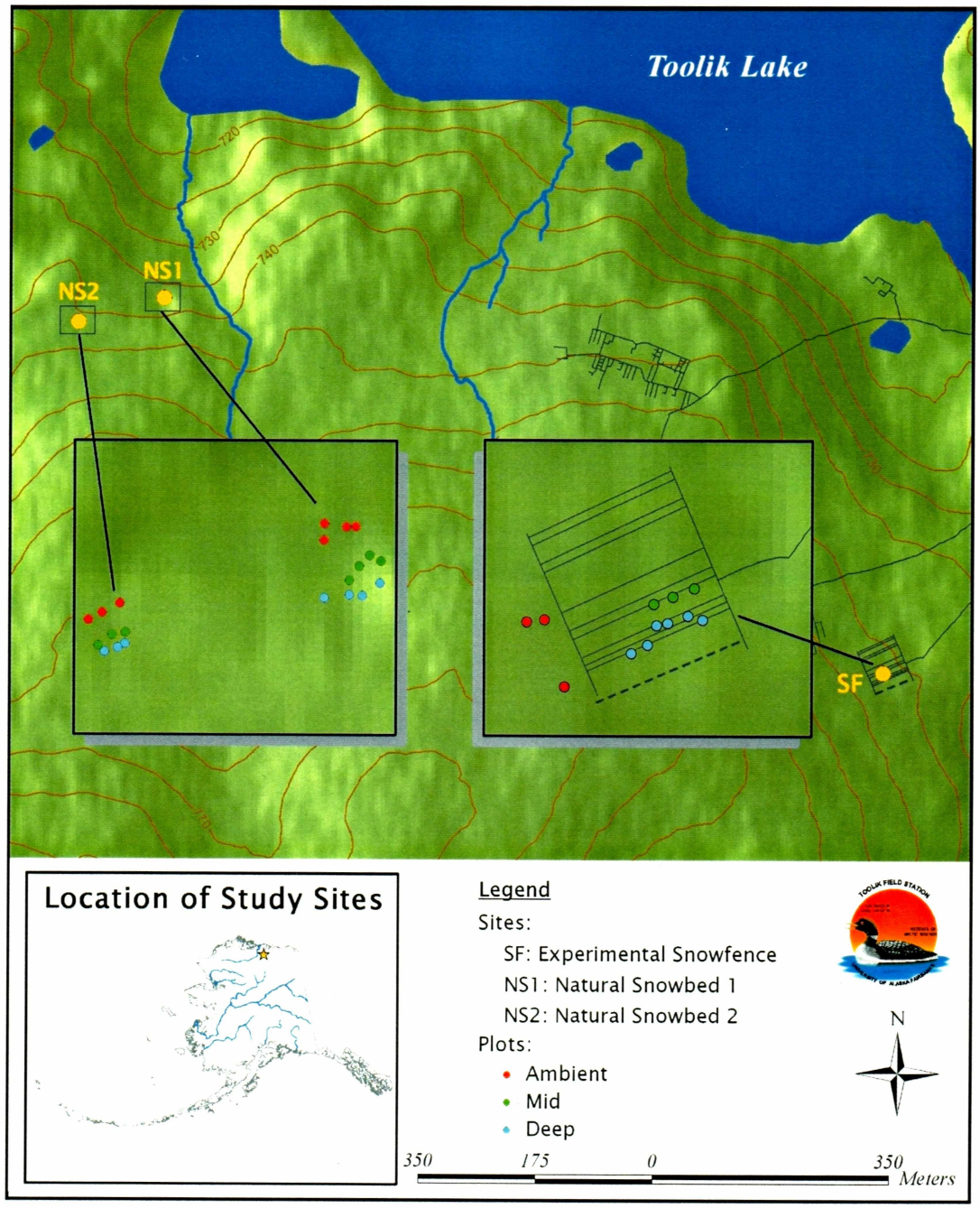

Figure 1. Map of Study Area. Map of study area at Toolik Field Station, in the northern foothills of the Brooks Range, Alaska, depicting relative location of experimental snow-fence site and two natural snowbed sites. Insets depict relative location of individual plots in all three snow depth zones (points representing plots are not to scale).

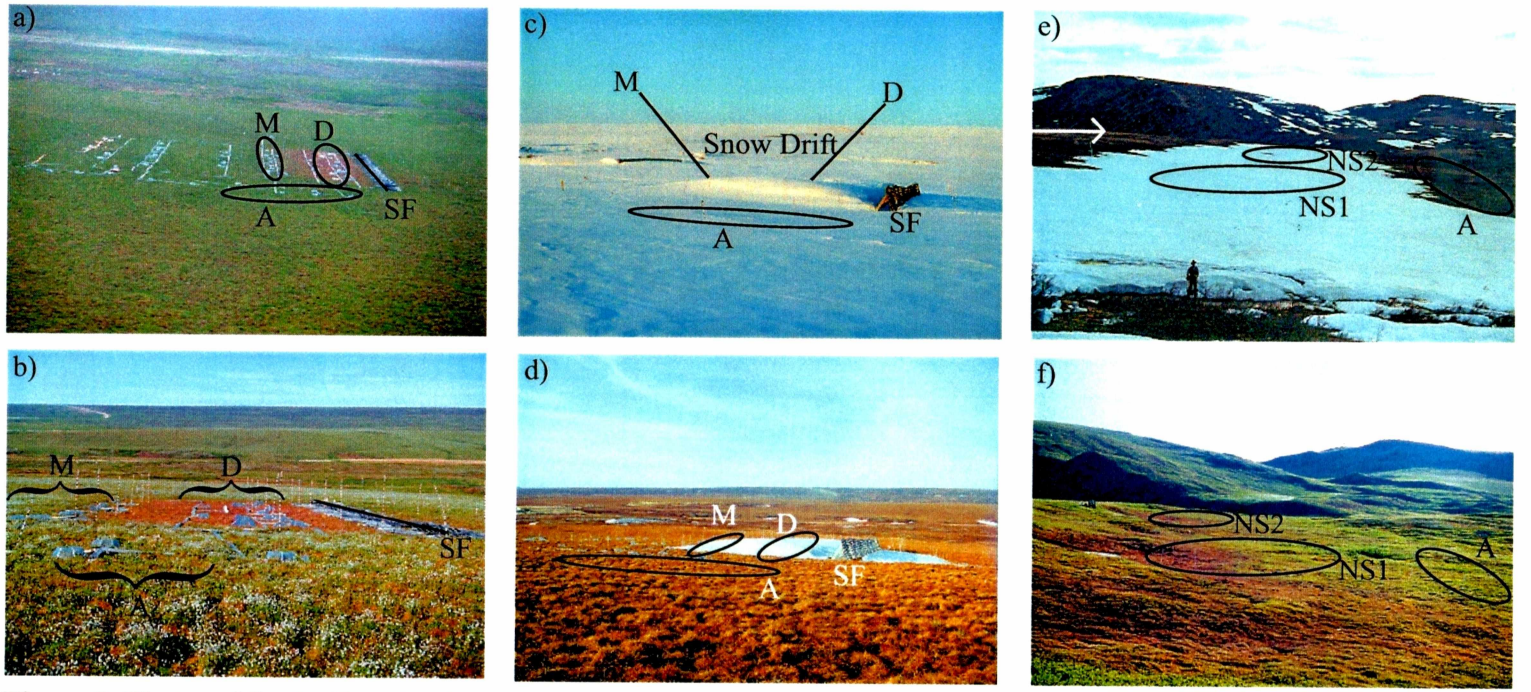

Figure 2. Photos of Study Sites. D=deep zone, M=mid zone, A=ambient zone, SF=snowfence, NS1=natural snowbed 1, NS2=natural snowbed 2 (a) Aerial photo of the experimental snowfence site in moist tussock tundra. The snowfence (laid down) is located on the right side. (b) Close-up view of the snowfence site in late June with the snowfence laid down on the right side of the photo. Photo depicts the delay of green-up, flowering, and die-off of *Eriophorum vaginatum* in the deep snow zone. (c) Photo of the snowfence site in early spring at maximum snow depth. The snowfence (3m tall x 60m long) is on the right side of the photo and the snowdrift extends to the left of the snowfence. The snow drift is 3m deep in the deep zone and extends approximately 35m beyond the fence. The snow is approximately 1.5m deep in the mid zone and 30-50cm deep in the ambient zone. (d) Photo of the snowfence in early June. Snow depth in the deep zone is approximately 2.5m while the snow has melted completely in the ambient zone. (e) Photo of the natural snowbeds in early June. Both snowbeds are located in moist graminoid, dwarf-shrub tundra. The prevailing winds (indicated by white arrow) come from the south and deposit snow in drifts that reach a maximum snow depth of approximately 3m. (f) Photo of the natural snowbeds in mid to late June.

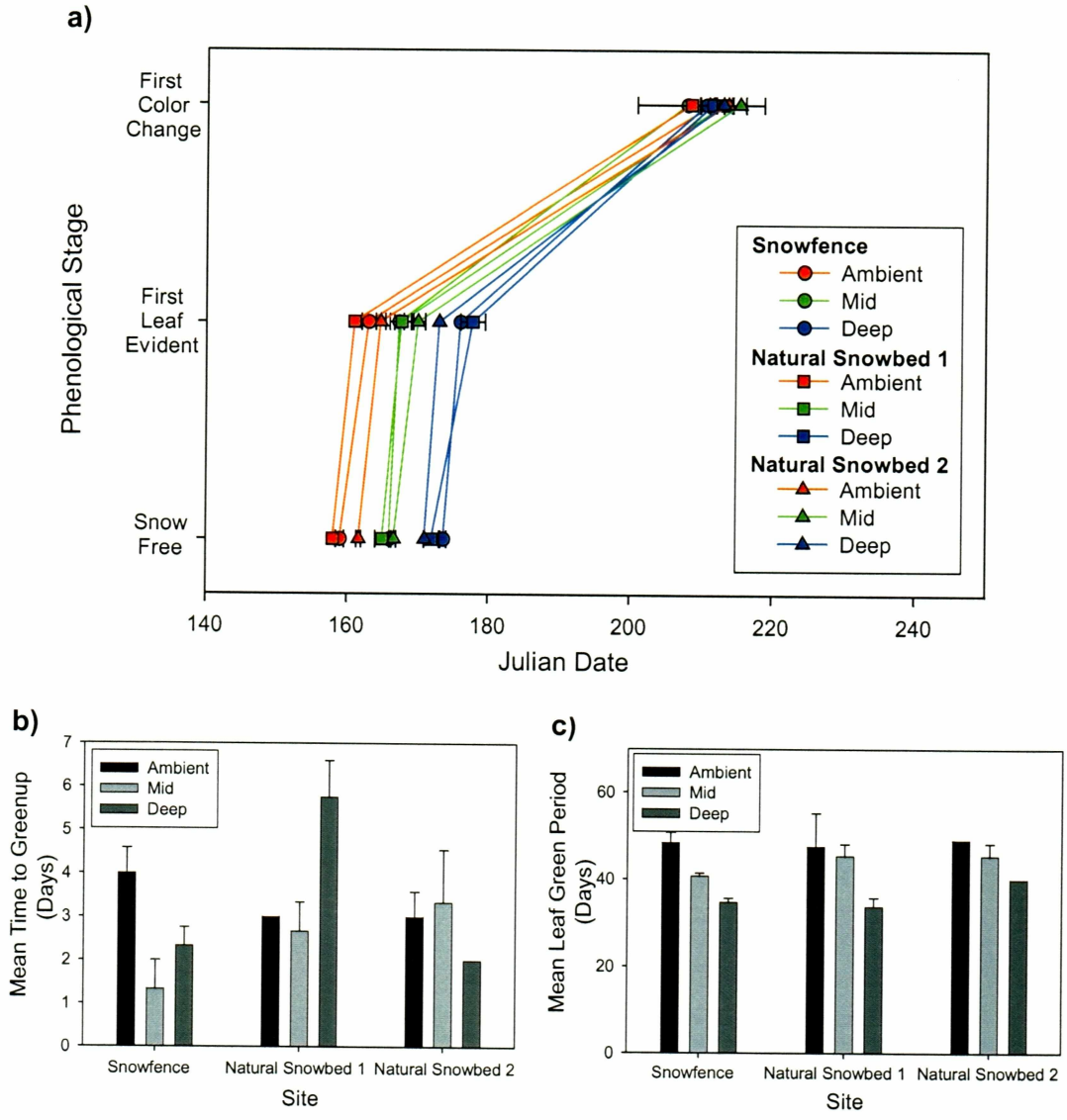

FIGURE 3. Phenological Development of *Betula nana*. (a) Relative timing of mean snowfree date, mean 'bud break' date, and mean 'first color change' (senescence) date for all three sites and snow depth zones. (b) Mean 'time to green-up' for all three sites and snow depth zones. (c) Mean 'leaf green period' for all three sites and snow depth zones. All values are means and SE (n=6 in the deep zone, 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. Some sample sizes were smaller due to variability in species distribution).

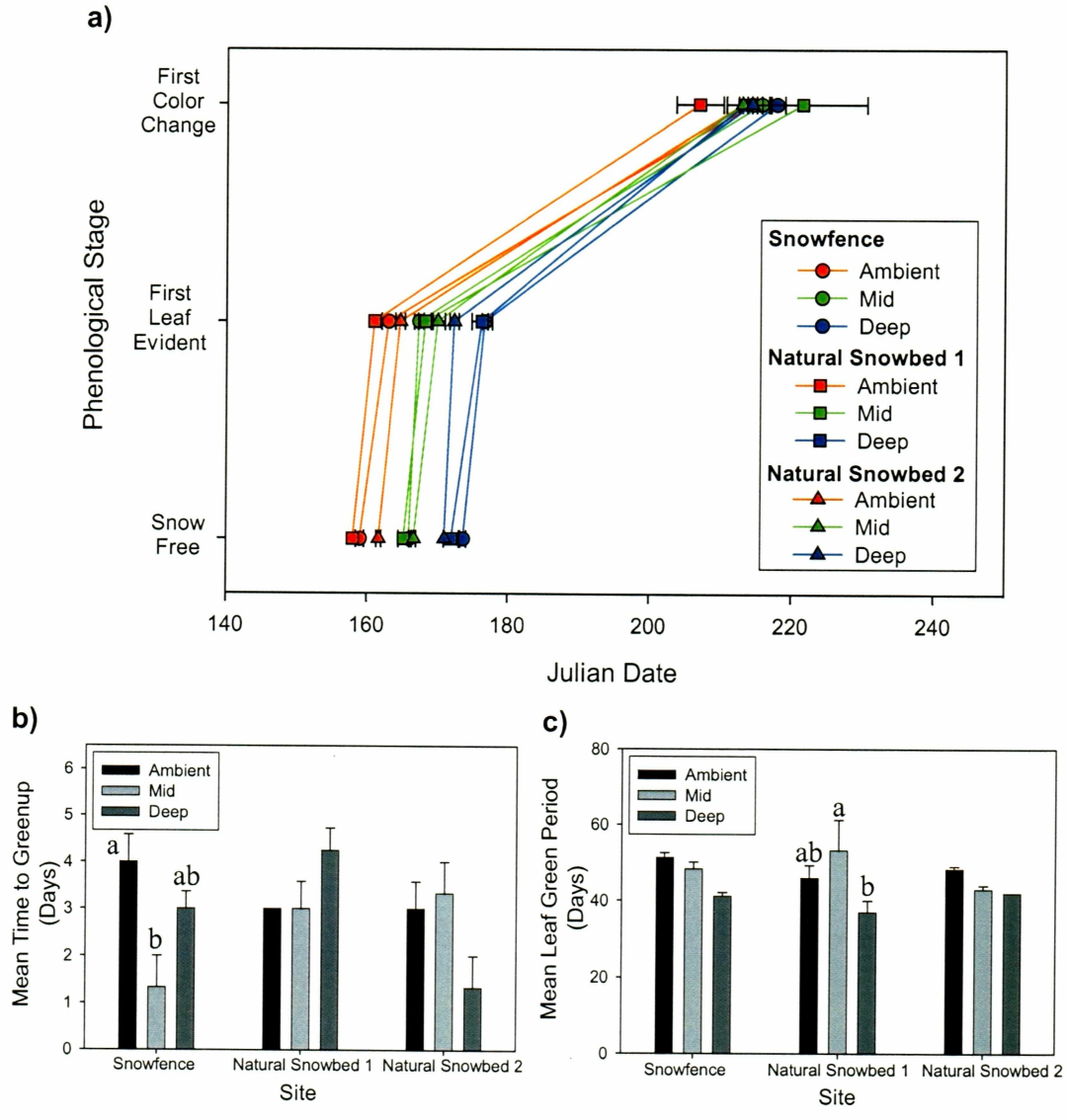

FIGURE 4. Phenological Development of *Salix pulchra*. (a) Relative timing of mean snowfree date, mean 'bud break' date, and mean 'first color change' (senescence) date for all three sites and snow depth zones. (b) Mean 'time to green-up' for all three sites and snow depth zones. (c) Mean 'leaf green period' for all three sites and snow depth zones. All values are means and SE (n=6 in the deep zone, 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. Some sample sizes were smaller due to variability in species distribution). Within each site, bars marked with different letters are significantly different from one another (two-way ANOVAs followed by Tukey's multiple comparison test).

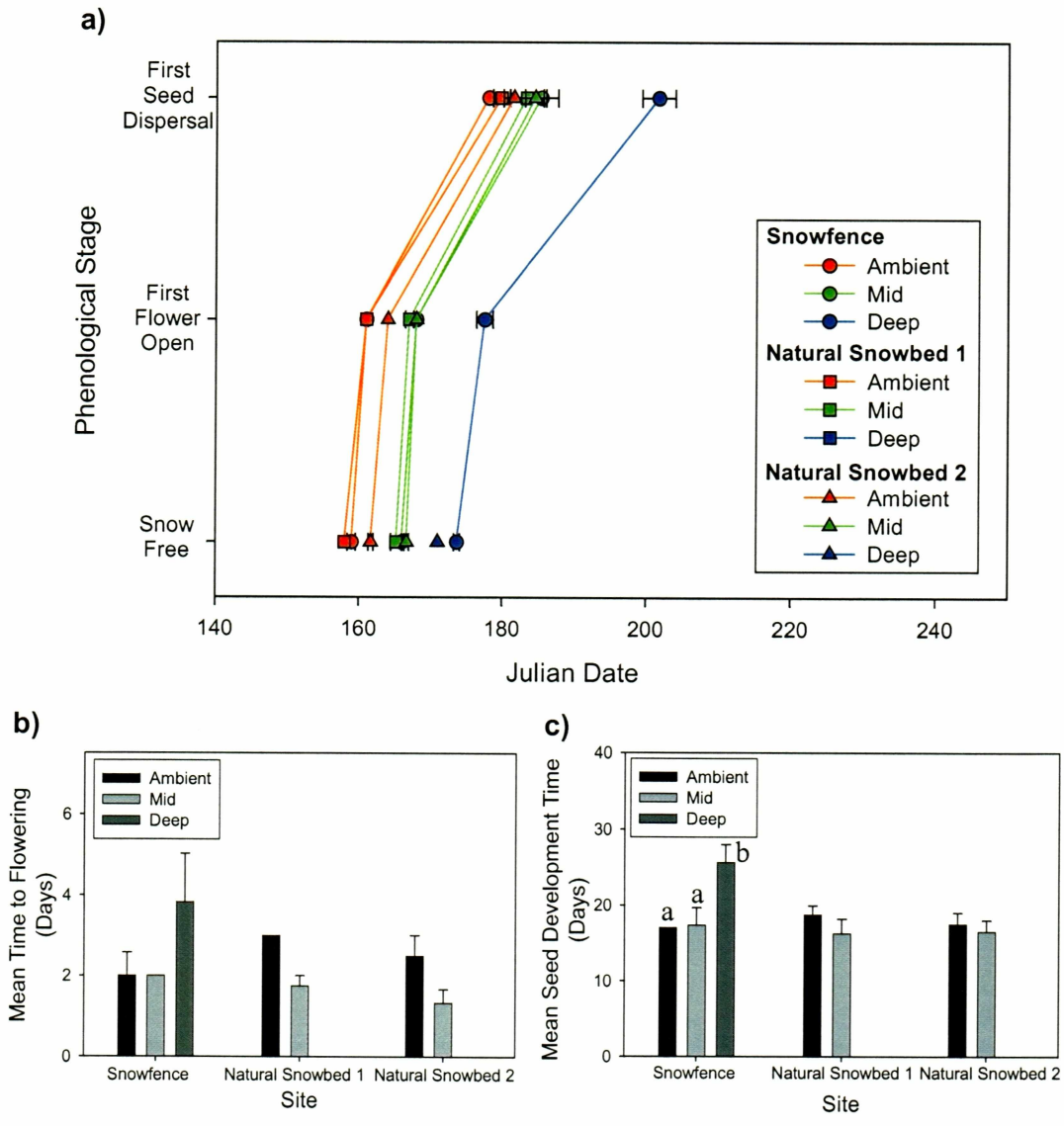

FIGURE 5. Phenological Development of *Eriophorum vaginatum*. (a) Relative timing of mean snowfree date, mean 'first flower open' date, and mean 'first seed dispersal' date for all three sites and snow depth zones. (b) Mean 'time to flowering' for all three sites and snow depth zones. (c) Mean 'seed development time' for all three sites and snow depth zones. All values are means and SE (n=6 in the deep zone, 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. Some sample sizes were smaller due to variability in species distribution). 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).

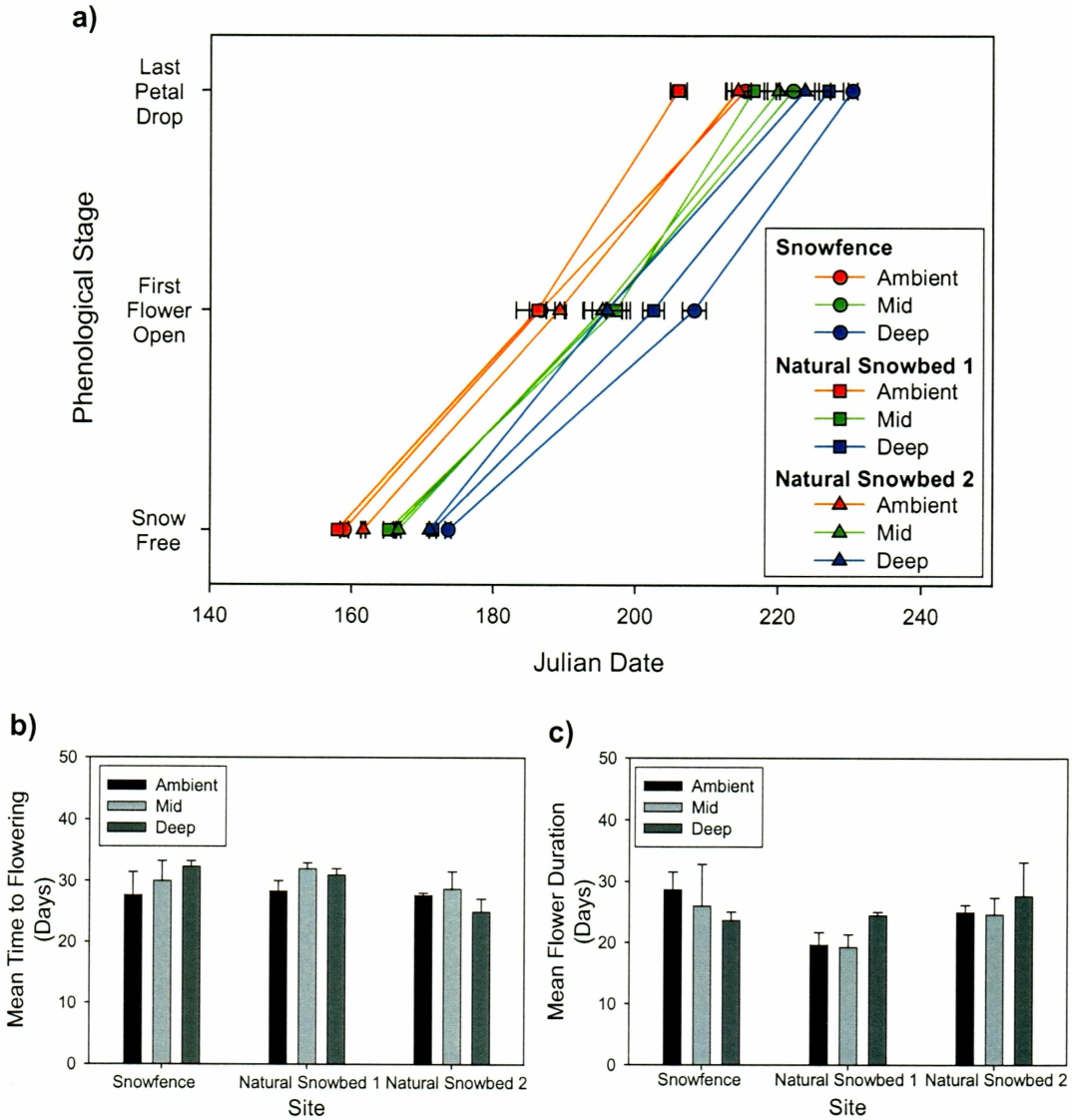

FIGURE 6. Phenological Development of *Vaccinium vitis-idaea*. (a) Relative timing of mean snowfree date, mean 'first flower open' date, and mean 'last petal drop' date for all three sites and snow depth zones. (b) Mean 'time to flowering' for all three sites and snow depth zones. (c) Mean 'flower duration' for all three sites and snow depth zones. All values are means and SE (n=6 in the deep zone, 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. Some sample sizes were smaller due to variability in species distribution).

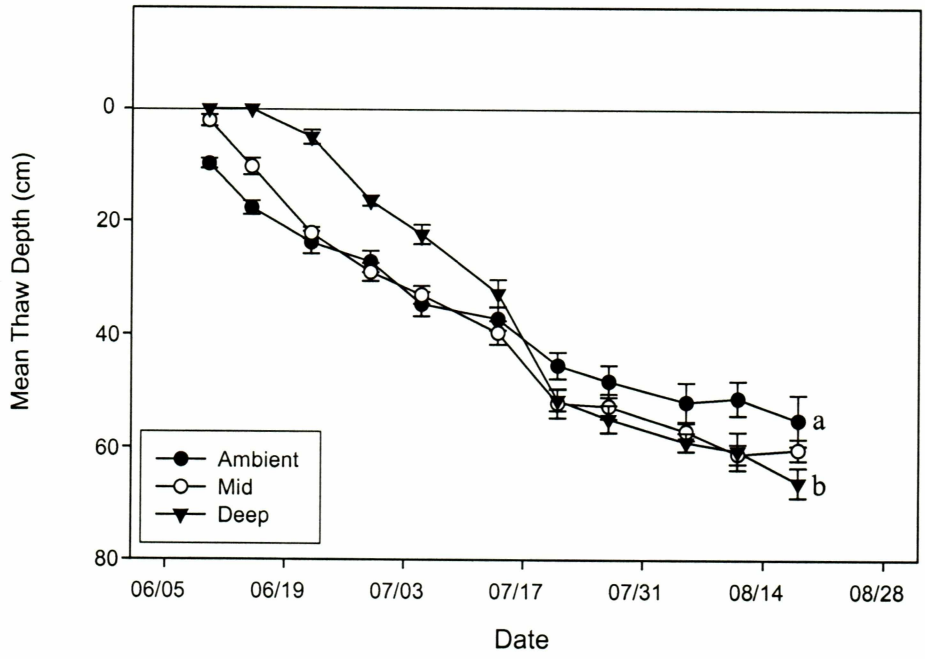

FIGURE 7. Snowfence Thaw Depth. Thaw Depth in the ambient, mid, and deep snow depth zones at the snowfence during the summer of 2000. All values are means and SE (n=9 for each data point). Symbols marked with different letters are significantly different from one another (p=0.0498, t-test).

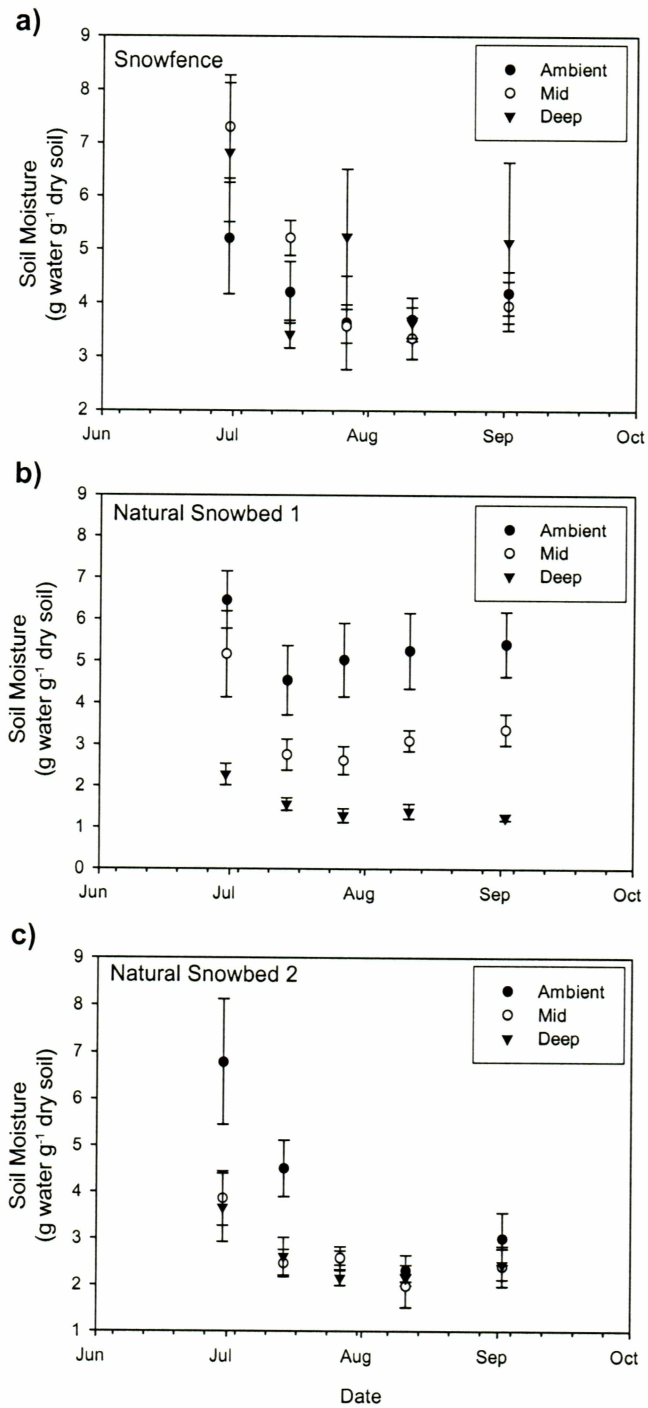

FIGURE 8. Gravimetric Soil Moisture. Gravimetric soil moisture measurements for (a) snowfence site, (b) natural snowbed 1 site, and (c) natural snowbed 2 site during the summer of 2000. All values are means and SE (n=4 for each data point).

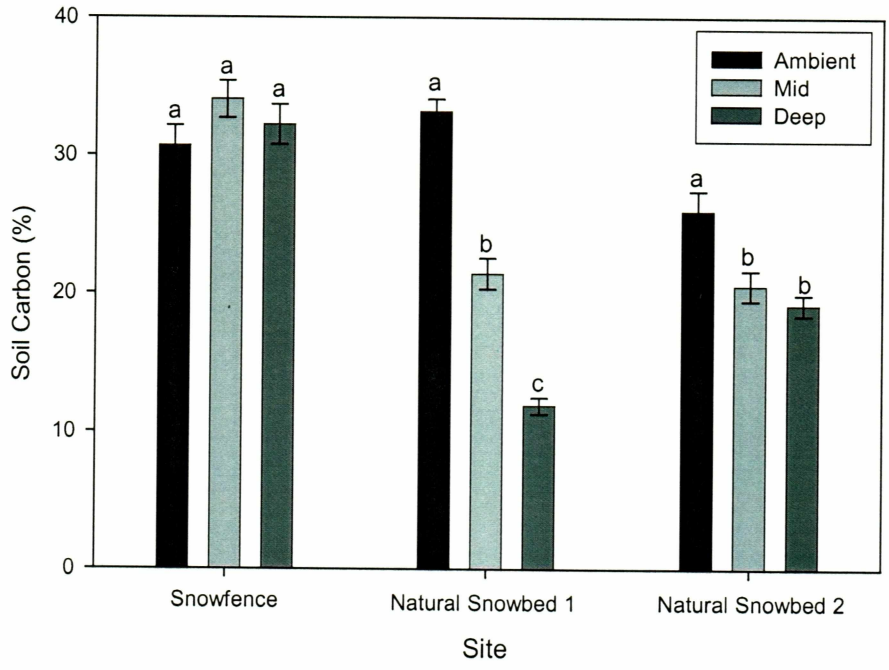

FIGURE 9. Soil Carbon Concentration. Soil carbon concentration (%) measured for all three sites and snow depth zones using the LECO CNS-2000 instrument. All values are means and SE (n=20 for each snow depth zone at each site). Within each site, bars marked with different letters are significantly different from one another (two-way ANOVA followed by Tukey's multiple comparison test).

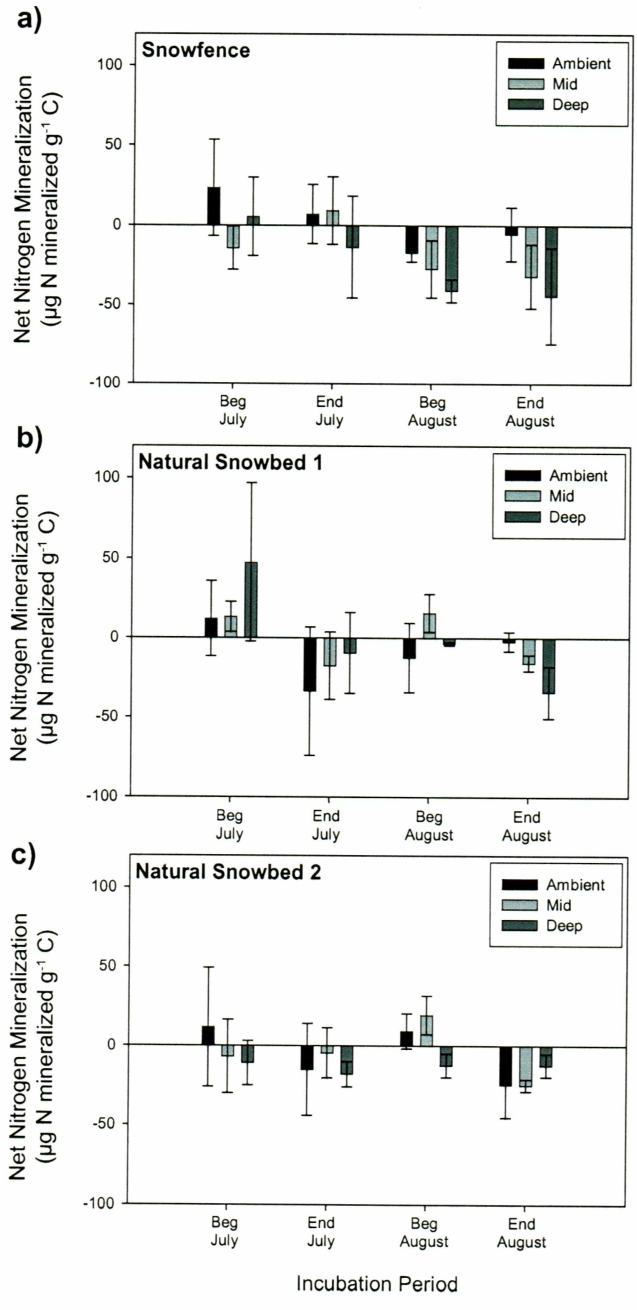

FIGURE 10. Net Nitrogen Mineralization. Net nitrogen mineralization through the summer for all four buried bag incubations for all three snow depths at the (a) snowfence site, (b) natural snowbed 1 site, and (c) natural snowbed 2 site. All values are means and SE (n=4 for each snow depth zone on each date).

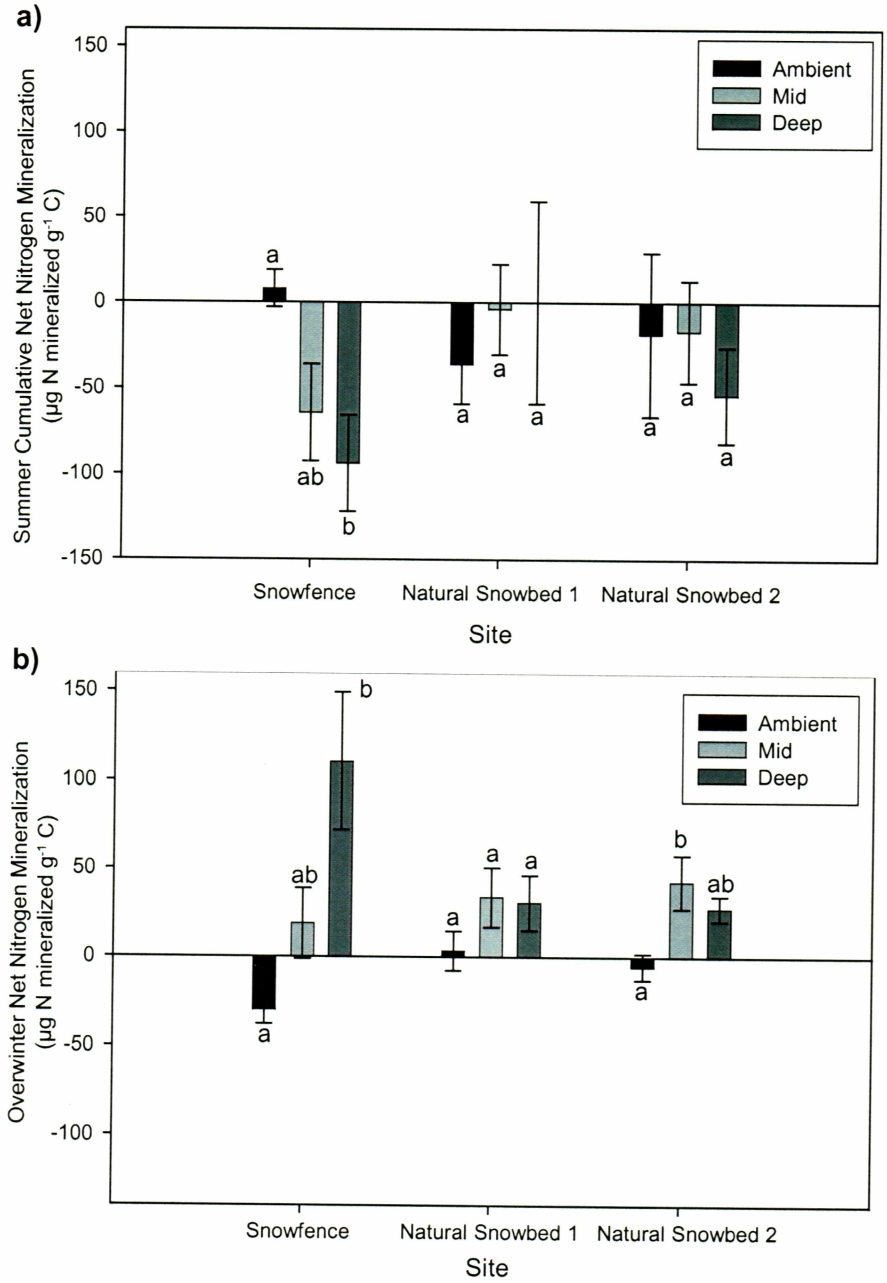

FIGURE 11. Summer and Overwinter Net Nitrogen Mineralization. (a) Summer cumulative net nitrogen mineralization from the end of June to the end of August 2000 for all three sites and snow depth zones. (b) Overwinter net nitrogen mineralization, measured in cores incubated from September 2000 to Spring 2001 for all three sites and snow depth zones. All 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).

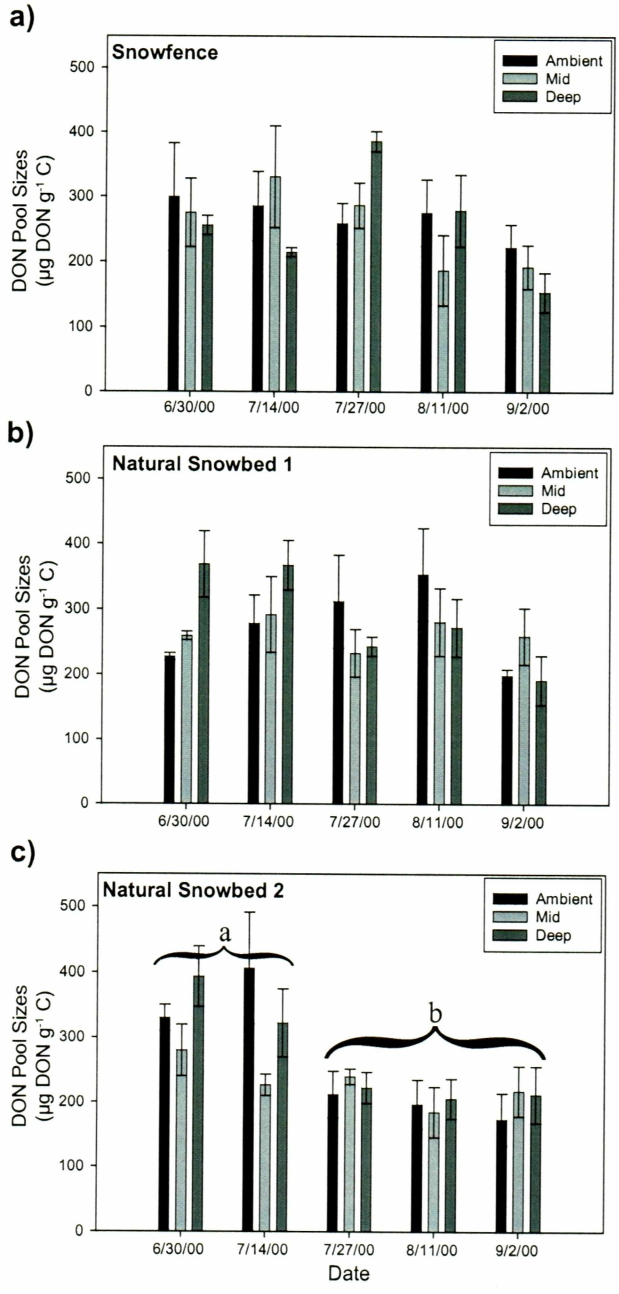

FIGURE 12. Pool Sizes of Total Dissolved Organic Nitrogen. Total dissolved organic nitrogen (DON) pool sizes for all three snow depth zones at the (a) snowfence site, (b) natural snowbed 1 site, and (c) natural snowbed 2 site. All values are means and SE (n=4 for each snow depth zone on each date). Dates marked with different letters are significantly different from one another (two-way ANOVA followed by Tukey's multiple comparison test).

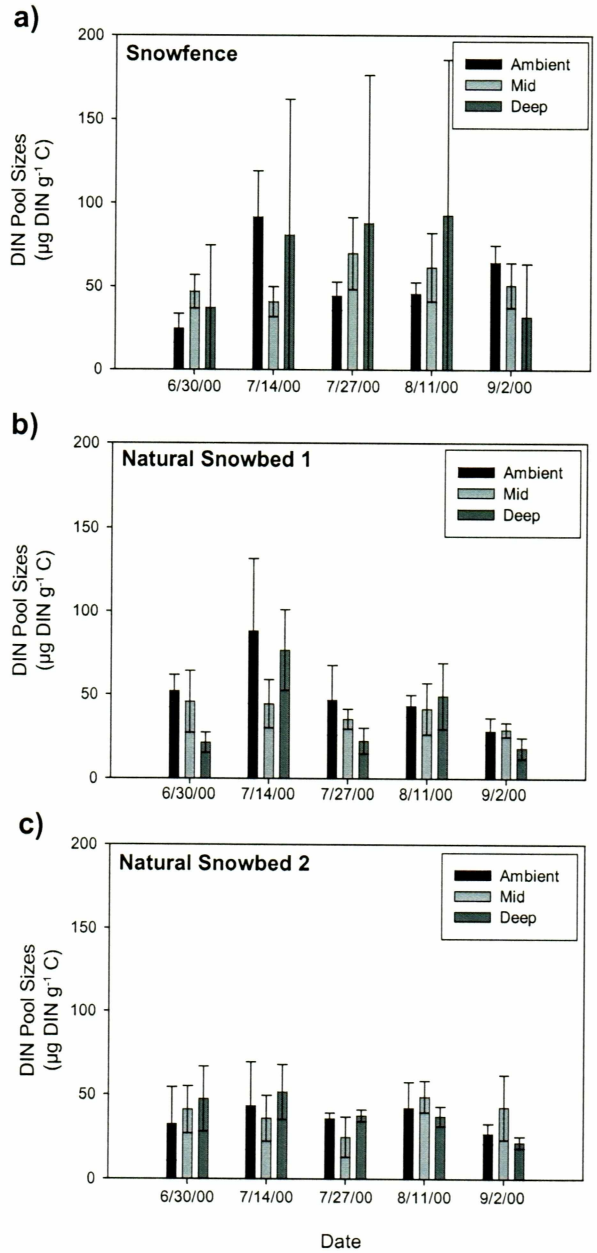

FIGURE 13. Pool Sizes of Total Dissolved Inorganic Nitrogen. Total dissolved inorganic nitrogen (DIN) pool sizes for all three snow depth zones at the (a) snowfence site, (b) natural snowbed 1 site, and (c) natural snowbed 2 site. All values are means and SE (n=4 for each snow depth zone on each date).

Table 1. *Betula nana* results: MANOVA and ANOVA analyses on rate and timing data

ns=no snow effects apparent

		Rate	Timing
MANOVA Wilks Lambda	Site	$F_{4,40}$=1.67 P=0.1754	$F_{4,40}$=0.41 P=0.8036
	Snow	$F_{4,40}$=3.74 P=0.0112	$F_{4,40}$=21.37 P<0.0001
	Site x Snow	$F_{8,40}$=1.94 P=0.0797	$F_{8,40}$=1.57 P=0.1644
Snow Effects on Individual Phenophases		Time to Greenup (FL_SF)	Timing of Greenup (FL)
ANOVA	Model	F=3.71 P=0.0075	F=38.90 P<0.0001
	Site	F=2.99 P=0.0720	F=0.12 P=0.8880
	Snow	F=1.53 P=0.2391	F=92.43 P<0.0001
	Site x Snow	F=4.33 P=0.0104	F=3.30 P=0.0301
	Snowfence	ns	P<0.0001 Ambient<Deep P<0.0001 Mid<Deep Ambient, Mid<Deep
	Natural Snowbed 1	marginal P=0.0718 Mid<Deep P=0.0909 Ambient<Deep	P<0.0001 Ambient<Deep P=0.0028 Ambient<Mid P<0.0001 Mid<Deep Ambient<Mid<Deep
	Natural Snowbed 2	ns	P=0.0176 Ambient<Deep P=0.393 Ambient<Mid Ambient<Mid,Deep
		Duration of Green Leaves (LGP)	Timing of Senescence (FC)
ANOVA	Model	F=3.08 P=0.0183	F=0.46 P=0.8724
	Site	F=0.53 P=0.5944	F=0.74 P=0.4883
	Snow	F=6.62 P=0.0059	F=0.05 P=0.9476
	Site x Snow	F=0.27 P=0.8937	F=0.35 P=0.8437
			Overall, model not significant. Therefore, there is no significant difference in senescence data between sites or snow depths.
	Snowfence	ns	ns
	Natural Snowbed 1	ns	ns
	Natural Snowbed 2	ns	ns

Table 2. *Salix pulchra* results: MANOVA and ANOVA analyses on rate and timing data

ns=no snow effects apparent

		Rate	Timing
MANOVA Wilks Lambda	Site	$F_{4,46}$=1.25 P=0.3036	$F_{4,46}$=0.34 P=0.8483
	Snow	$F_{4,46}$=3.39 P=0.0164	$F_{4,46}$=35.86 P<0.0001
	Site x Snow	$F_{8,46}$=3.05 P=0.0078	$F_{8,46}$=3.77 P=0.0018
Snow Effects on Individual Phenophases		Time to Greenup (FL_SF)	Timing of Greenup (FL)
ANOVA	Model	F=3.46 P=0.0087	F=48.77 P<0.0001
	Site	F=2.29 P=0.1234	F=0.36 P=0.7036
	Snow	F=1.59 P=0.2239	F=154.83 P<0.0001
	Site x Snow	F=5.16 P=0.0038	F=6.82 P=0.0008
	Snowfence	P=0.0550 Mid<Ambient margina	P<0.0001 Ambient<Deep P=0.0644 Ambient<Mid Ambient, Mid<Deep P<0.0001 Mid<Deep
	Natural Snowbed 1	ns	P<0.0001 Ambient<Deep P<0.0001 Ambient<Mid Ambient<Mid<Deep P<0.0001 Mid<Deep
	Natural Snowbed 2	ns	P=0.0002 Ambient<Deep Ambient<Mid,Deep P=0.0118 Ambient<Mid
		Duration of Green Leaves (LGP)	Timing of Senescence (FC)
ANOVA	Model	F=2.36 P=0.0498	F=1.23 P=0.3233
	Site	F=0.36 P=0.7047	F=0.35 P=0.7057 Overall, model not significant. Therefore, there is no significant
	Snow	F=5.76 P=0.0091	F=1.40 P=0.2659 difference in senescence data between sites or snow depths.
	Site x Snow	F=1.41 P=0.2617	F=1.22 P=0.3300
	Snowfence	ns	ns
	Natural Snowbed 1	P=0.0465 Deep<Mid marginal	ns
	Natural Snowbed 2	ns	ns

Table 3. *Eriophorum vaginatum* results: MANOVA and ANOVA analyses on rate and timing data. (a) ANOVA results reported for snowfence data only. (b) MANOVA and ANOVA results excluding deep zone data. ns=no snow effects apparent.

a)

		Rate		Timing		
Snow Effects on Individual Phenophases		Time to Flowering (FO_SF)		Timing of Flowering (FO)		
ANOVA	Snow	F=1.01		F=66.13	Ambient<Deep	P<0.0001
		P=0.4014		P<0.0001	Ambient<Mid	P=0.0069
					Mid<Deep	P=0.0003
					Ambient<Mid<Deep	
		Seed Development Time (SDT)		Timing of Seed Dispersal (SD)		
ANOVA	Snow	F=6.64	Ambient<Deep	F=40.44	Ambient< Deep	P=0.0003
		P=0.0301	Mid<Deep	P=0.0003	Ambient<Mid	P=0.0770
			Ambient,Mid<Deep		Mid<Deep	P=0.0022
					Ambient≤Mid<Deep	

b)

		Rate		Timing	
MANOVA	Site	$F_{4,22}$=0.66		$F_{4,22}$=6.18	
Wilks Lambda		P=0.6254		P=0.0017	
	Snow	$F_{2,11}$=5.60		$F_{2,11}$=235.92	
		P=0.0210		P<0.0001	
	Site x Snow	$F_{4,22}$=1.71		$F_{4,22}$=3.67	
		P=0.1826		P=0.0196	
Snow Effects on Individual Phenophases		Time to Flowering (FO_SF)		Timing of Flowering (FO)	
ANOVA	Model	F=3.04		F=103.37	
		P=0.0532		P<0.0001	
	Site	F=1.00		F=16.17	
		P=0.3966		P=0.0004	
	Snow	F=7.48		F=400.15	
		P=0.0181		P<0.0001	
	Site x Snow	F=2.24		F=8.17	
		P=0.1486		P=0.0058	
	Snowfence	ns		P<0.0001	Ambient<Mid
	Natural Snowbed 1	P=0.0694	Mid<Ambient	P=0.0002	Ambient<Mid
	Natural Snowbed 2	ns		P<0.0001	Ambient<Mid
		Seed Development Time (SDT)		Timing of Seed Dispersal (SD)	
ANOVA	Model	F=0.34		F=2.31	
		P=0.8815		P=0.1087	
	Site	F=0.05		F=0.31	
		P=0.9559		P=0.7399	
	Snow	F=0.54		F=8.47	
		P=0.4772		P=0.0131	
	Site x Snow	F=0.40		F=0.77	
		P=0.6765		P=0.4825	
	Snowfence	ns		ns	
	Natural Snowbed 1	ns		ns	
	Natural Snowbed 2	ns		ns	

Table 4. *Vaccinium vitis-idaea* results: MANOVA and ANOVA analyses on rate and timing data

ns=no snow effects apparent.

		Rate	Timing
MANOVA Wilks Lambda	Site	$F_{4,34}$=2.36 P=0.0728	$F_{4,34}$=2.53 P=0.0586
	Snow	$F_{4,34}$=0.84 P=0.5094	$F_{4,34}$=15.18 P<0.0001
	Site x Snow	$F_{8,34}$=0.81 P=0.5974	$F_{8,34}$=1.78 P=0.1160
Snow Effects on Individual Phenophases		Time to Flowering (FO_SF)	Timing of Flowering (FO)
ANOVA	Model	F=1.23 P=0.3385	F=9.37 P<0.0001
	Site	F=2.04 P=0.1592	F=1.33 P=0.2885
	Snow	F=0.92 P=0.4153	F=30.48 P<0.0001
	Site x Snow	F=0.89 P=0.4898	F=2.74 P=0.0613
	Snowfence	ns	P=0.0001 Ambient<Deep P=0.0559 Mid<Deep — Ambient, Mid<Deep
	Natural Snowbed 1	ns	P=0.0046 Ambient<Deep P=0.0294 Ambient<Mid — Ambient<Mid,Deep
	Natural Snowbed 2	ns	ns
		Duration of Flowering (FD)	Timing of End of Flowering (LP)
ANOVA	Model	F=0.94 P=0.5121	F=8.11 P=0.0001
	Site	F=1.83 P=0.1884	F=4.14 P=0.0332
	Snow	F=0.24 P=0.7891	F=24.76 P<0.0001
	Site x Snow	F=0.56 P=0.6952	F=1.23 P=0.3318
	Snowfence	ns	P=0.0125 Ambient<Deep
	Natural Snowbed 1	ns	P=0.0014 Ambient<Deep
	Natural Snowbed 2	ns	ns

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Appendix 1. Natural Snowbed Plot Location Information. Coordinates for natural snowbed sites (projection: geographic, units: decimal degrees, datum: WGS84). The phenology plots are marked with wooden stakes at each of the four corners of the $1m^2$ plots. Soils were sampled near the plots.

	x-coord (N)	y-coord (W)
Natural Snowbed 1		
Ambient	68.625854	149.628479
	68.625854	149.628357
	68.625877	149.628754
	68.625801	149.628769
Mid	68.625687	149.628067
	68.625717	149.628204
	68.625671	149.628342
	68.62561	149.628479
Deep	68.625534	149.628815
	68.625542	149.628494
	68.625534	149.628326
	68.625587	149.628098
Natural Snowbed 2		
Ambient	68.625572	149.631378
	68.625534	149.631607
	68.625504	149.63179
Mid	68.625381	149.631683
	68.625427	149.6315
	68.625435	149.631332
Deep	68.625381	149.631348
	68.625366	149.631439
	68.625351	149.631607

Appendix 2. Snowfence Plot Numbers. Plots are labeled with metal tags located on a corner stake of each plot. Plots are also numbered on the boardwalks running along each of the snow depth zones. A map of the snowfence site can be found in Walker et al. (1999).

Ambient	155 CTL
	163 CTL
	165 CTL
Mid	119 CTL
	122 CTL
	123 CTL
Deep	101 CTL
	108 CTL
	111 CTL
	116 CTL
	115 CTL
	113 CTL