Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra

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Abstract:

Three 60 m long, 2·8 m high snowfences have been erected to study long-term effects of changing winter snow conditions on arctic and alpine tundra. This paper describes the experimental design and short-term effects. Open-top fiberglass warming chambers are placed along the experimental snow gradients and in controls areas outside the fences; each warming plot is paired with an unwarmed plot. The purpose of the experiment is to examine short- and long-term changes to the integrated physical-biological systems under simultaneous changes of winter snow regime and summer temperature, as part of the Long-Term Ecological Research network and the International Tundra Experiment. The sites were at Niwot Ridge, Colorado, a temperate high altitude site in the Colorado Rockies, and Toolik Lake, Alaska, a high-latitude site. Initial results indicate that although experimental designs are essentially identical at the arctic and alpine sites, experimental effects are different. The drift at Niwot Ridge lasts much longer than do the Toolik Lake drifts, so that the Niwot Ridge fence affects both summer and winter conditions, whereas the Toolik Lake fence affects primarily winter conditions. The temperature experiment also differs in effect between the sites. Although the average temperature increase at the two sites is similar (daily increase 1·5 °C at Toolik and 1·9 °C at Niwot Ridge), at Toolik Lake there is only minor diurnal variation, whereas at Niwot Ridge the daytime increases are extreme on sunny days (as much as 7–10 °C), and minimum nighttime temperatures in the chambers are often slightly cooler than ambient (by about 1 °C). The experimental drifts resulted in wintertime increases in temperature and CO_2 flux. Temperatures under the deep drifts were much more consistent and warmer than in control areas, and at Niwot Ridge remained very close to 0 °C all winter. These increased temperatures were likely responsible for observed increases in system carbon loss. Initial changes to the aboveground biotic system included an increase in growth in response to both snow and warming, despite a reduced growing season. This is expected to be a transient response that will eventually be replaced by reduced growth. At least one species, *Kobresia myosuroides*, had almost completely died at Niwot Ridge three years after fence construction, whereas other species were increasing. We expect in both the short- and long-term to see the strongest effects of snow at the Niwot Ridge site, and stronger effects of temperature at Toolik Lake. Copyright © 1999 John Wiley & Sons, Ltd.

KEY WORDS   snow; arctic; alpine tundra; climate warming; ecosystems

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INTRODUCTION

Predicting the effects of complex changes in summer and winter climate on ecosystems represents a challenge from both scientific and practical standpoints. The problems are particularly acute in ecosystems where winter climate exerts a strong control on overall system function. Arctic and alpine landscapes in particular require integrated studies of physical and biological systems because of strong feedbacks and controls (Oechel *et al.*, 1997). We present an integrated experimental study of the effects of increased winter snow and increased summer temperature at one alpine and two arctic sites.

The landscape-scale distribution of snow is perhaps the single most important mesoscale variable controlling biological systems in arctic and alpine ecosystems (Walker *et al.*, 1993). Although global circulation models show great variability in potential climate in arctic and alpine systems in coming decades, it is clear that warming will be enhanced at high latitudes, and that hydrologic processes may be intensified in all systems (Houghton *et al.*, 1996; Maxwell, 1992, 1997). Arctic and alpine systems are useful for comparative study because they share a dominance of winter processes, cold summer temperatures, and have similar species and vegetation. Snow is a major control of many patterns and processes in both systems. Yet they also have important differences that should strongly influence their responses, most of them driven by differences in solar radiation patterns and topography. Arctic ecosystems are strongly linked to temperature, particularly in their biology and patterns of species distribution and diversity. Thus, they may respond most strongly to changes in temperature. Although snow is an important control over species and community distribution, the influences of snow in arctic ecosystems may be tied most closely to winter processes, because the melt patterns are such that there is no more than a few weeks difference between early and late-melting sites. Alpine ecosystems, on the other hand, are likely to be very sensitive to changes in snow regime. The snowmelt period extends throughout the summer in these systems, and in certain topographic locations snow may be permanent in some years. The influence of alpine tundra to regional biogeochemical and hydrologic extends far beyond its limited area. The temperate alpine and subalpine region of North America supplies most western water and much of that used in the plains region as well. The North American continental climate is strongly influenced by this region (Greenland and Swift, 1990; Manabe and Broccoli, 1990).

We are using large snow fences and small portable open-top chambers to examine the effects of altered snow regimes and air temperatures in arctic and alpine tundra. In this paper, we describe the experimental design and short-term changes to physical and biological components of the system in response to the experiment. The experiment is intended to last for a much longer time period than the standard three to five year ecology experiment (Walker *et al.*, 1993). The long term of the experiment is essential, because tundra vegetation communities do not equilibrate quickly. Changes to below ground resources and substrate require long adjustment periods, and a series of transient plant communities without apparent natural equilibrium analogues may occur in the interim. The experiment is part of the NSF-sponsored Long-Term Ecology Research (LTER) project on Niwot Ridge, CO, and the International Tundra Experiment (ITEX) at Toolik Lake, AK. The Toolik Lake site is also part of the LTER site network. Previous studies have examined tundra response to increased snowpack over a similar time period (e.g. Webber *et al.*, 1976), but this is the first experiment to combine the ITEX warming simultaneously with a snow increase. The study integrates processes within the physical system (soil and air temperature, season length, snow chemistry and composition), the below ground biotic system (decomposition, trace gas fluxes), and the above ground biotic system (phenology, growth, greenness, and community composition).

METHODS

Study areas and experimental design

In the summers of 1993 and 1994, we erected three snowfences at Niwot Ridge, Colorado, and Toolik Lake, Alaska for the purpose of manipulating snowpack (Figures 1 and 2). The Niwot Ridge site (40°03′N, 105°36′W) is a broad tundra upland ridge at 4085 m a.s.l. elevation. Toolik Lake (68°37′N, 149°32′W), in the
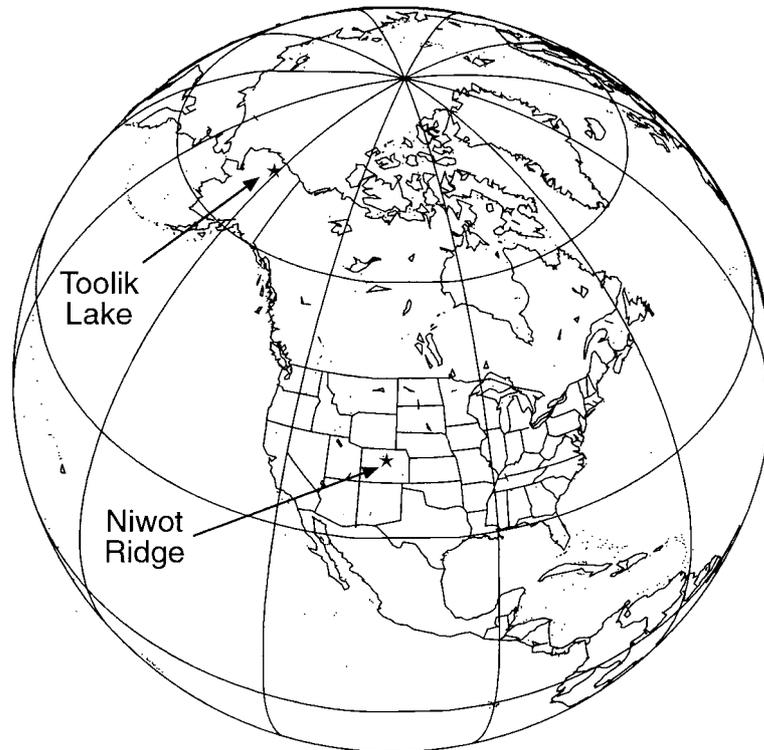
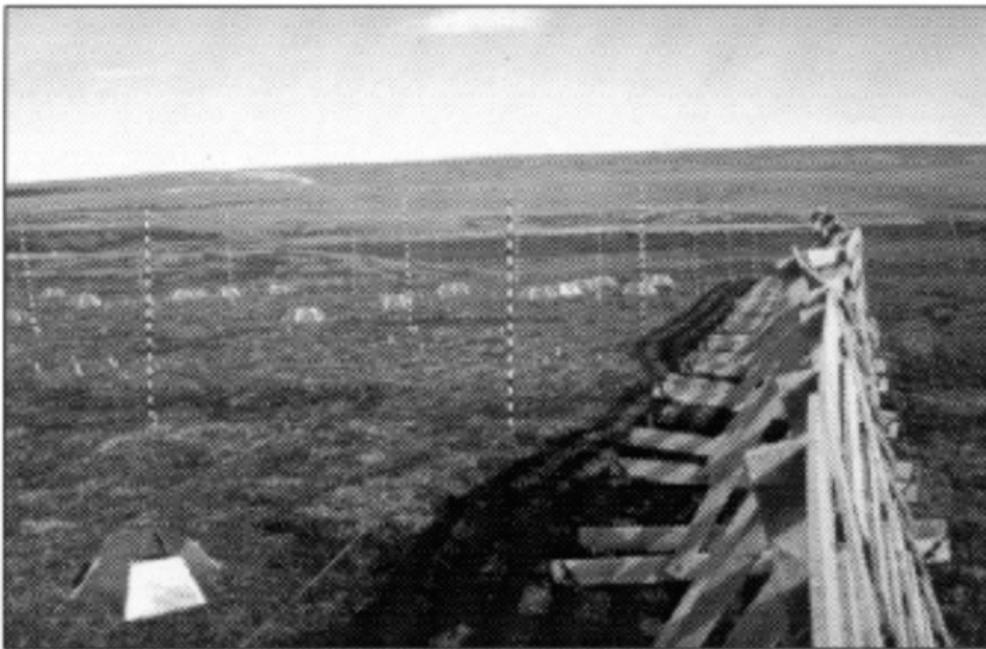Figure 1. Locations of Niwot Ridge and Toolik Lake snow-warming experiments

Figure 2. The Toolik Lake dry-site snow fence and open-topped chambers (OTCs). OTCs are 40 cm high, 1 m across, and are constructed of translucent fiberglass. They raise summer air temperatures about 2 to 5 °C (Marion *et al.*, 1997). OTCs are placed over experimental plots as soon as 50% of the plot becomes snow-free; they are removed in late August or early September
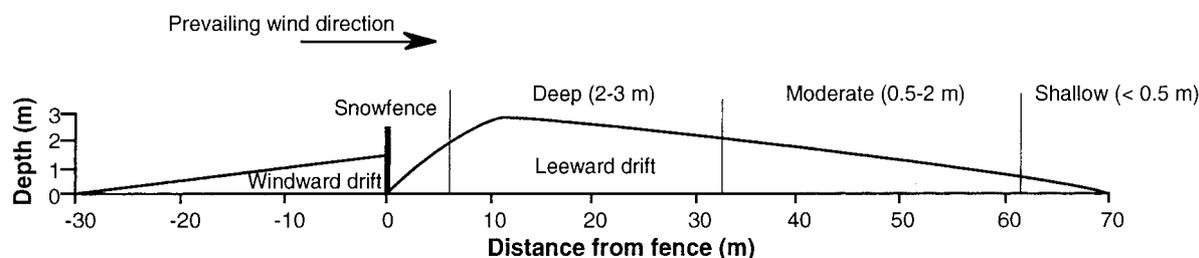
Figure 3. Experimental drift profile. The shape and depth profile of the actual experimental drifts varies somewhat from this theoretical profile, particularly early in the season. Once the drift has filled, however, the shape and depth are quite similar to what is shown here

northern foothills of the Brooks Range at about 700 m a.s.l. elevation, is a gently rolling site with predominantly tussock tundra vegetation (Walker *et al.*, 1994a). The fences are all 2·8 m tall and 60 m long and create leeward drifts approximately 60 m long (Figure 3). Areas further than 60 m from the fence receive less than ambient amounts of snow. At Niwot, we placed one fence in an ecotone separating a moist meadow from a dry meadow. At Toolik Lake, we located one fence in a dry tundra site and the other in a moist tussock-tundra site. Fences are either removed or laid down during the summer so as not to affect ambient summer wind regimes. The Niwot Ridge fence is on a north-south axis, because predominant winds are from the west, and the Toolik Lake fences are on east-west axes, because the predominant winter winds and storms are from the Brooks Range to the south.

The experimental design is factorial. Plots are subjected to increased winter snow (+S), increased summer temperature (+T), and both simultaneously (+S+T); full controls (ambient snow and temperature) are designated as +0. Summer air temperatures are elevated using small greenhouses, 1 m² open top chambers (OTCs) that passively warm the tundra (Marion *et al.*, 1993, 1997) (Figure 2). The OTCs are also used at 24 circumpolar and alpine sites in replicated experiments and are of the standard International Tundra Experiment (ITEX) design (Henry and Molau, 1997). Control plots are located in areas adjacent to the fences.

Permanent plots were established within the snow fence grids and in locations outside of the influence of the snow fences (Figure 4). Several types of plots were established, including: (1) undisturbed OTC and non-OTC plots along the snow gradient for examining tundra plant phenology, growth, and community composition, (2) OTC and non-OTC plots along the snow gradient for disruptive or destructive sampling (soil chemistry, mineralization and decomposition, soil and leaf moisture, temperature), (3) CO_2 and CH_4 flux plots along the snow gradient only, and (4) normalized difference vegetation index (NDVI[1]) plots along the snow gradient only. Vegetation maps were prepared at all the fences to portray the pre-experiment vegetation patterns (Figure 5). The total experimental design includes the response of species along the gradient of snow regimes, including decreased snow at distances beyond about 60 m.

Because our primary purpose here is to present the experimental design, details of methods are presented in the figure captions. Measurements of the physical system include depth, extent, and density of snowpack, soil and air temperature, and snow chemistry and composition. Snow measurements are made at a grid behind the experimental fences and at fixed landscape points outside the experimental areas. Site-scale climate monitoring is provided by the Niwot Ridge and Arctic LTER programs operating at each of the sites.

Soil measurements include rates of decomposition and of CO_2 flux. Baseline measurements of major soil properties — organic matter, pH, texture, water-holding capacity, bulk density, depth of O and A horizons — were taken in order to be compared with data much later in the experiment. Because we do not expect major physical soil properties to change noticeably in the first few years of the experiment, they are not addressed here.

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[1] NDVI = (NIR − R)/(NIR + R), where NIR is the spectral reflectance in the near-infrared, where light scattering from the canopy dominates, and R is the reflectance in the red, chlorophyll-absorbing portion of the spectrum.
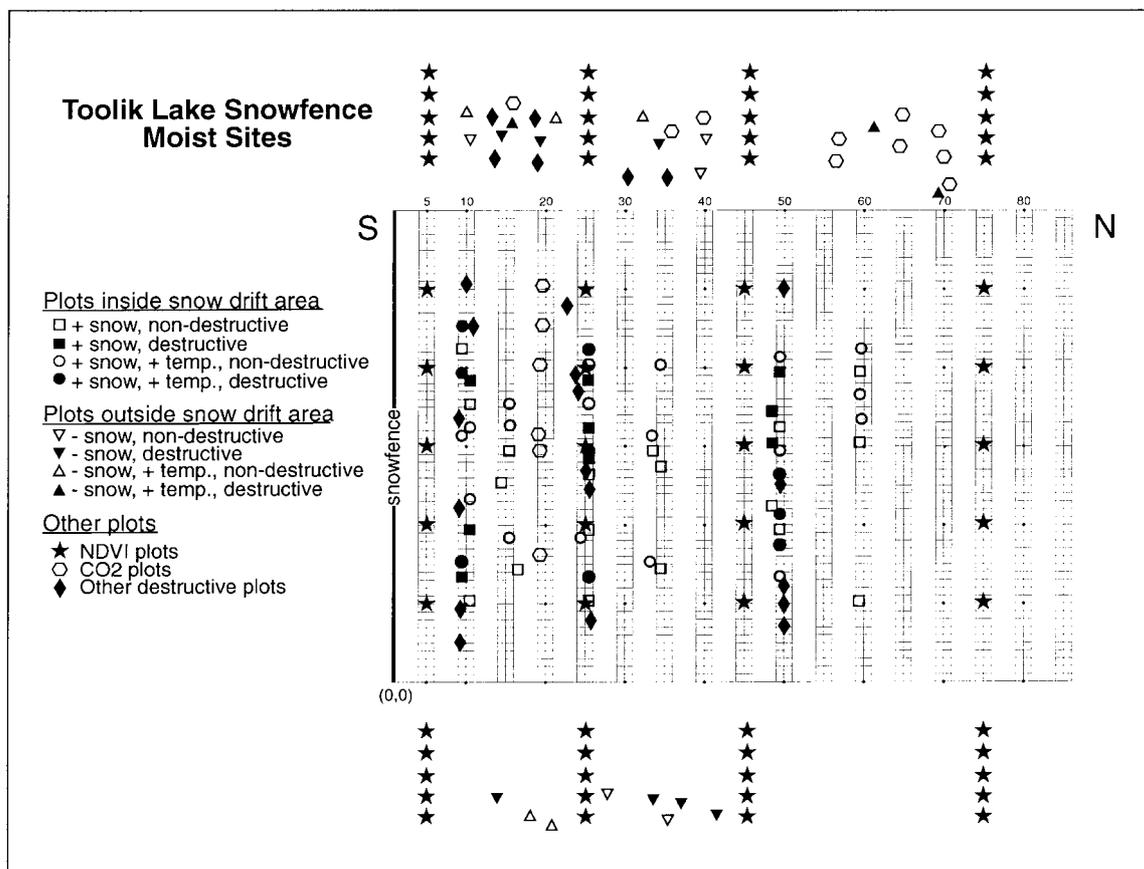
Figure 4. Experimental plot layout at the Toolik moist site. The snow gradient is used to divide the drift up into a series of sections of different depths. Each warmed plot is paired with an unwarmed plot at the different fence distances (snow regimes). Destructive sampling is kept separated from long-term permanent vegetation plots. NDVI is measured on snow treatments only because there is no way to get accurate readings on chambered plots due to reflection from markers and tags

Like the soils, measurements of the vegetation system include both short- and long-term components, and we focus here on the short-term components. Measurements for which we expect to see short-term responses include a series of variables that can be categorized as either phenology or growth variables. Phenologic measurements capture timing of critical biological events, and growth measurements are analogues for biomass and allocation. These measurements follow earlier work on natural variation in phenology and growth in response to interannual climatic variability (Walker et al., 1994b, 1995b). Measurements are standardized according to ITEX guidelines (Molau and Mølgaard, 1996). Unfortunately, there are no species abundant enough at both sites to provide a direct comparison, but nonetheless we can look at and compare overall patterns for the three fences. The phenology and growth data from both sites have also been used in a meta-analysis of 17 ITEX sites worldwide (Arft et al., 1999).

We are also using measurements of NDVI to supplement the direct measures of phenology and growth and to serve as a non-destructive measure of green biomass. It is useful for examining phenological development, and serves as an analogue for leaf area index and biomass of tundra landscapes (Shippert et al., 1995; Walker et al., 1995a).

We expect the short-term variations in phenology and biomass to ultimately result in significant shifts in community composition. To document these changes, we are also taking extensive long-term
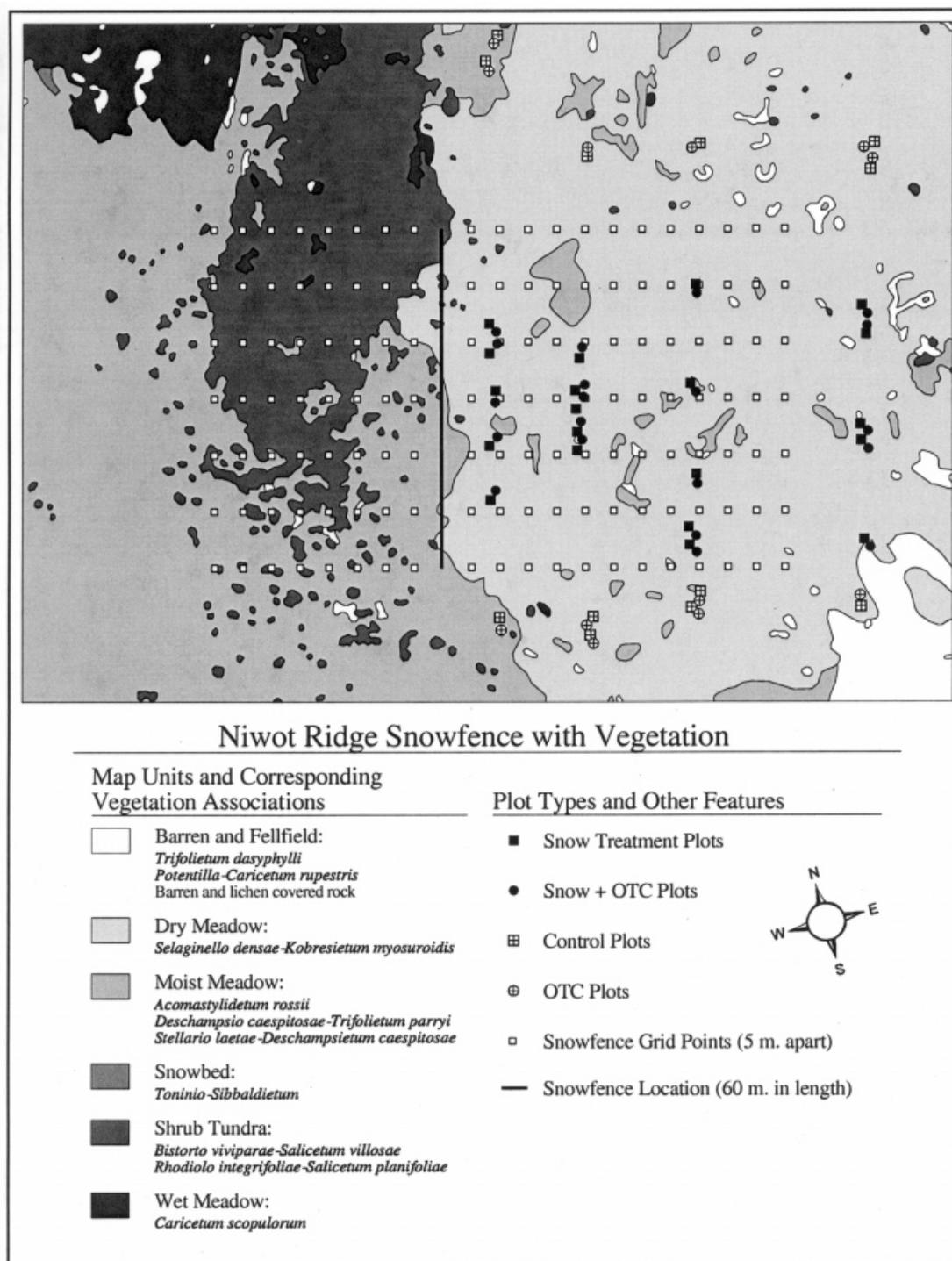
Figure 5. Vegetation map of the Niwot Ridge snow fence site. Associations are according to Komárková (1979) as mapped by Walker (Walker *et al.*, 1993). Scale is provided by the fence, which is 60 m in length. Note the ecotone between dry and mesic tundra along the fence. The increased snow cover provided by the fence should cause a shift in conditions more similar to those currently found on the windward side

community-scale measurements of vegetation as well as measurements of community biomass. These data will be used to look at longer-term changes over five to ten year time periods and thus are not presented here.

RESULTS

Physical system

There were two main effects of snow on soil temperature: (1) higher average temperatures, and (2) more spatially and temporally consistent temperatures. Deep snow accumulation behind the fences causes large increases in winter soil temperature at all sites. Soil surface temperatures in the deepest part of the drifts at Toolik Lake and Niwot Ridge are about 15 °C warmer on average than adjacent controls (Figure 6). Although shallow snow areas have occasional warming periods related to periodic storms, they are short lived. Temperatures under the deep part of the Toolik Lake drift remained near freezing in 1994, declining to a minimum of about −7 °C in early May. At Niwot Ridge, soil temperatures at −15 cm under deep snow did not decline below freezing all winter, in contrast to the pre-fence conditions where mid-winter temperatures were in the −10 to −12 °C range (Figure 7). The presence of snow led to a much more consistent set of conditions through the winter, so that the pattern of temperatures prior to the fence was largely influenced by time (of year), and after the fence by spatial position relative to the fence.

The OTCs had somewhat different effects at the two sites, which has also been recognized in other studies of their effects across a broad spectrum of sites (Marion *et al.*, 1997). Mid-day summer air temperatures in the OTCs are more strongly elevated at Niwot Ridge than at Toolik Lake, probably due to much higher mid-day solar radiation at the lower latitude site (Figure 8). The mean daily increase at Niwot Ridge is 1·9 °C, compared to 1·5 °C at Toolik Lake. Diurnal fluctuations are also greater at Niwot Ridge, with cooler nighttime temperatures and warmer daytime temperatures. Soil temperatures are not elevated at the arctic
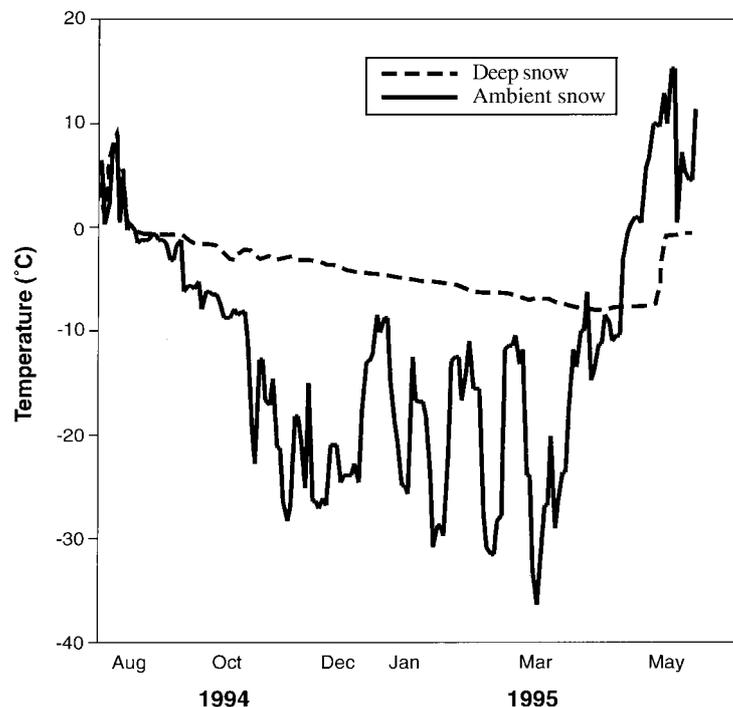

Figure 6. Soil surface temperatures beneath the Toolik Late dry-site fence and control plots, winter 1994–1995. Temperatures were recorded every 48 minutes using Hobo temperature logging devices (Onset Computer Corporation, Pocasset, MA). A very similar pattern was found at Niwot Ridge
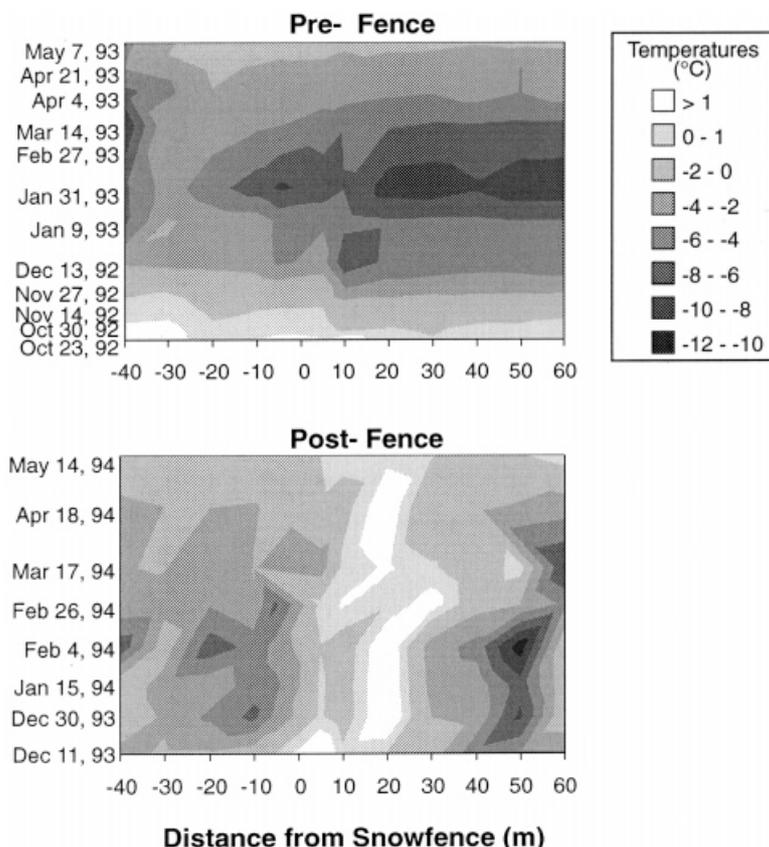
Figure 7. Niwot Ridge −15 cm soil temperatures before (1992–93) and after (1993–94) fence construction. Temperatures were measured approximately every three weeks on a 10 m grid on both leeward and windward sides of the fence

site, but are elevated about 1–2 °C on average at the alpine site. These differences in mean increase and in diurnal distribution of change mean that the chambers have a potentially greater effect at Niwot Ridge. Toolik Lake is more subject to long periods of cloudy weather, which will also tend to dampen the chamber effect.

Organic and mineral inputs from the snowpack potentially influence the nutrient availability in these sites, but in different ways. Snow composition varies markedly between Toolik Lake and Niwot Ridge (Figure 9). Most notable are the large differences in sediment and organic matter inputs; the Niwot Ridge snow contained very little organic material, and mineral inputs at Toolik Lake were nearly twice that at Niwot Ridge. The very high organic matter accumulation in the Toolik Lake snow occurs primarily in early winter, before substantial snowfall covers the region. It represents a large input of leaves and organic debris stripped from nearby snowfree areas in early winter and deposited in the artificial drift. The much deeper alpine snowpack and relative scarcity of deciduous shrubs results in less organic matter in the alpine snow drift. Snow pH at Toolik Lake is higher than at Niwot Ridge due to carbonate-rich loess blown from nearby river systems.

The high concentrations of mineral and organic debris found directly behind the fences also occur in natural tundra snowbeds, although at somewhat lower concentrations (personal observation). The densities of the snow fence drifts were comparable to the snow outside of the drift areas. This suggests that the best areas for examining the ecosystem effects of enhanced snow cover are in the areas farther downwind from the
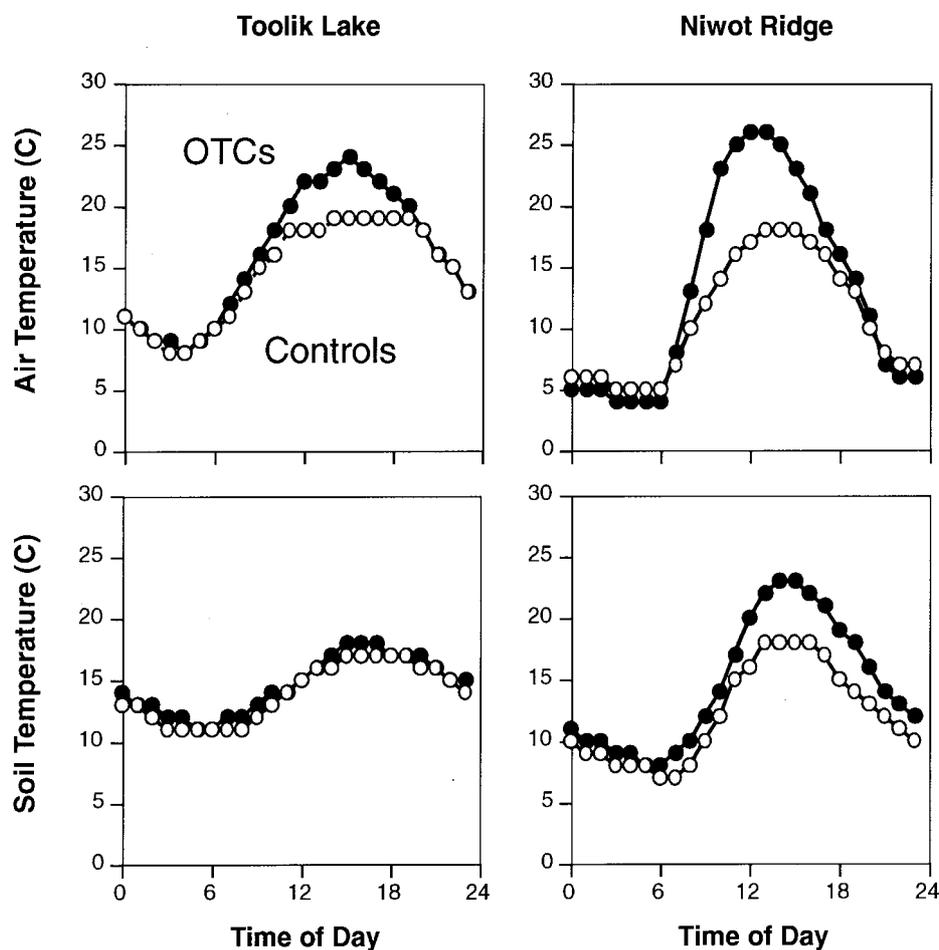
Figure 8. Diurnal variation in air (15 cm) and soil (0 cm) temperatures inside and outside OTCs at Toolik Lake and Niwot Ridge. Data are integrated values for a few midsummer days at both sites. Actual measurements were taken at five minute intervals using a Campbell data recorder

early-winter drift formation (beyond 25 m from the fences). In these regions snow cover is enhanced, but based on our observations there is no artificial increase in organic material.

Belowground biotic system

Decomposition patterns at the two sites varied significantly in their response to snow. Placement of litterbags with respect to the experimental snow gradient had a very significant effect on decay after two years in the field at Niwot Ridge but absolutely no detectable effect at Toolik Lake (Figure 10). These results are somewhat difficult to reconcile with other soil measurements. Our interpretation is that the change in microclimatic conditions in the alpine resulting from enhanced snow appears biologically much more significant at Niwot Ridge than at Toolik Lake. Presumably, the observed differences relate to the length of time the substrates remain non-frozen and available as a resource for microbes and invertebrates. Temperature effects on decomposition have not yet been assessed.

The differences in rate of decay between the sites can be attributed to substrate-quality differences. *Acomastylis rossii* contains large quantities of polyphenols, which are lost during the early stages of decomposition (Dearing, 1997), and this species therefore has a relatively rapid decomposition rate during the first
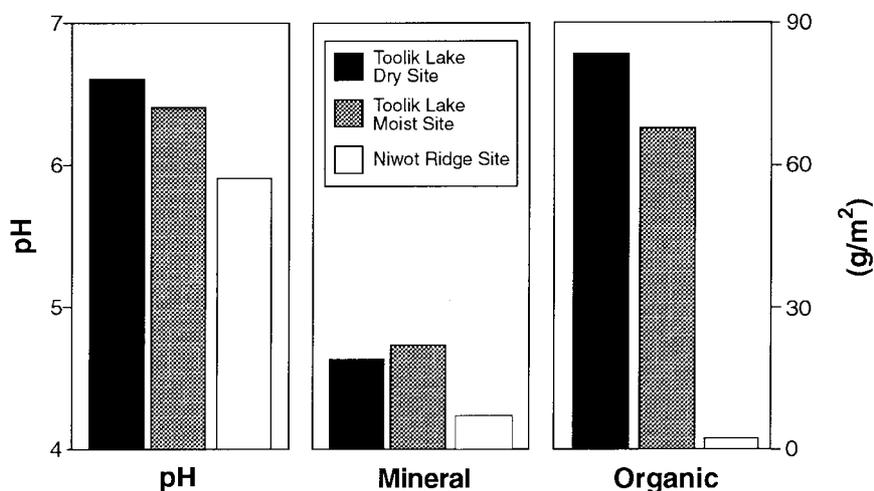
Figure 9. Snow pH, mineral sediment, and organic matter in the deepest part of the three drifts. Snow samples were collected in spring at maximum and annual depths. Samples represent a complete snow column
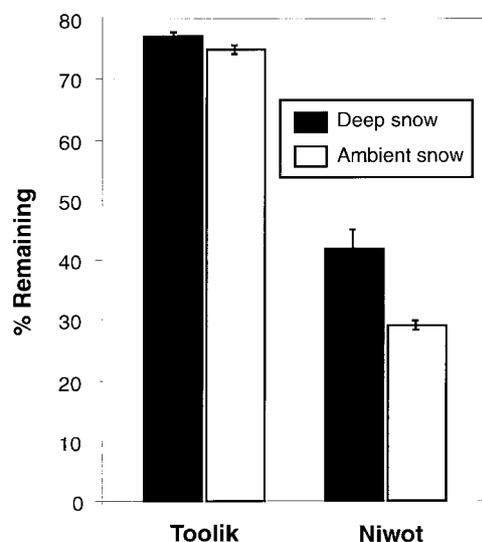

Figure 10. Mean and standard error of percent of initial mass remaining after two years of decay at the Toolik Lake moist site and at Niwot Ridge, in the deepest part of the drift and under ambient snow conditions. Litterbags containing senescent foliage were placed in deep and ambient snow conditions at the two sites. Alpine avens (*Acomastylis rossii*) foliage litter was used at Niwot Ridge, and foliage litter of dwarf birch (*Betula nana*) was used at the Toolik Lake most site. Both species are dominants at their respective sites. Decay rates of both of these species have been studied in their respective environments (Hobbie, 1996; O'Lear and Seastedt, 1994), so we have a baseline for comparison. Procedures used in the litterbag experiments are detailed in O'Lear and Seastedt (1994)

year of decay. *Betula nana* has a smaller percentage of labile compounds and therefore exhibits a substantially lower rate of decomposition. Although this difference explains the overall greater rate of decay at Niwot Ridge, it does not explain the lack of a snow effect at Toolik Lake.

The snowfences cause an increase in winter CO_2 flux on a scale similar to that found in natural snowdrifts (Figure 11a). At Niwot Ridge, CO_2 fluxes were measured before and after the installation of the snow fence and integrated over the full season in 1993 and 1994. Increases were detected under the deeper snow in the snow-fence drift as compared to pre-fence measures. Fluxes under the enhanced snowpack fit into the
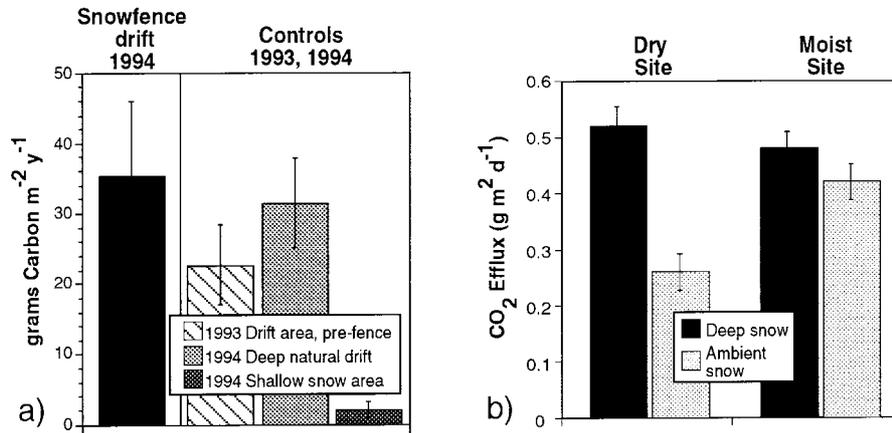
Figure 11. Winter CO_2 efflux at the Niwot Ridge (a) and Toolik Lake (b) sites. At Niwot Ridge, the flux of C is significantly less in the naturally shallow snow area than in the experimental and natural drifts and the pre-fence drift. Although the mean flux increased in the drift area following fence construction, differences are not significant. There were no pre-fence measurements of flux at Toolik Lake, where both fences increased CO_2 efflux, but only at the dry site was the increase statistically significant. Measurements at Niwot Ridge were taken over a full year before (1993) and after (1994) fence construction, and are therefore presented on an annual basis. At Toolik Lake, CO_2 fluxes were measured in base traps which were placed before snow fall in 1994 and collected as soon as the traps became snow-free the following spring. Measurements are integrated into a daily average for that period

observed variation found in a natural drift of similar magnitude. The difference between the 1993 pre-fence site and the 1994 low-snow control site demonstrates the natural variation in similar sites between years with different snowfall (Brooks *et al.*, 1996).

At Toolik Lake, the dry site showed a two-fold difference between deep snow and controls, whereas there was little difference at the moist site (Figure 11b). Winter CO_2 flux in natural communities is strongly controlled by depth of the winter snowpack (Fahnestock *et al.*, 1998), and during spring, as the subnivian soils warm, the fluxes increase several fold.

Aboveground biotic system

There were immediate responses of the phenology and growth of vegetation to the experiment; temperature and snow had predictably different effects. The main short-term effect of increased snow cover is a shortened growing season. The growing season in the deepest part of the drift at Niwot Ridge was reduced to 51 days, or about 50% of the pre-fence growing season (Figure 12). Snowmelt in the Arctic was much faster and resulted in only about a two to three week delay in season start. The large difference between the two sites is due primarily to the much lower nighttime temperatures at the temperate alpine site compared to 24 hours of daylight in the Arctic.
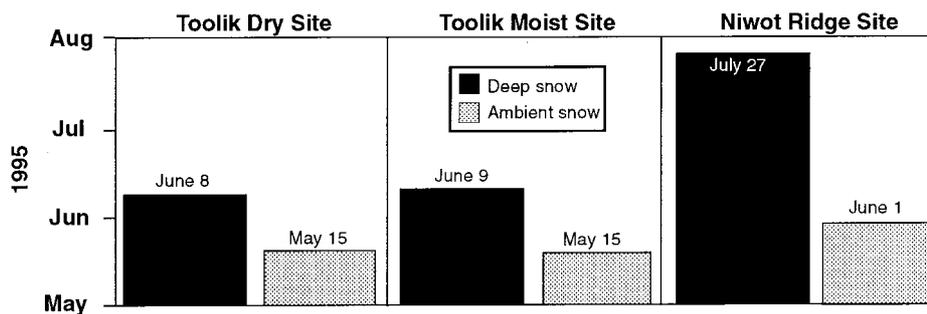

Figure 12. Meltout dates for the three fences in 1995. These are the dates on which all experimental plots were free of snow
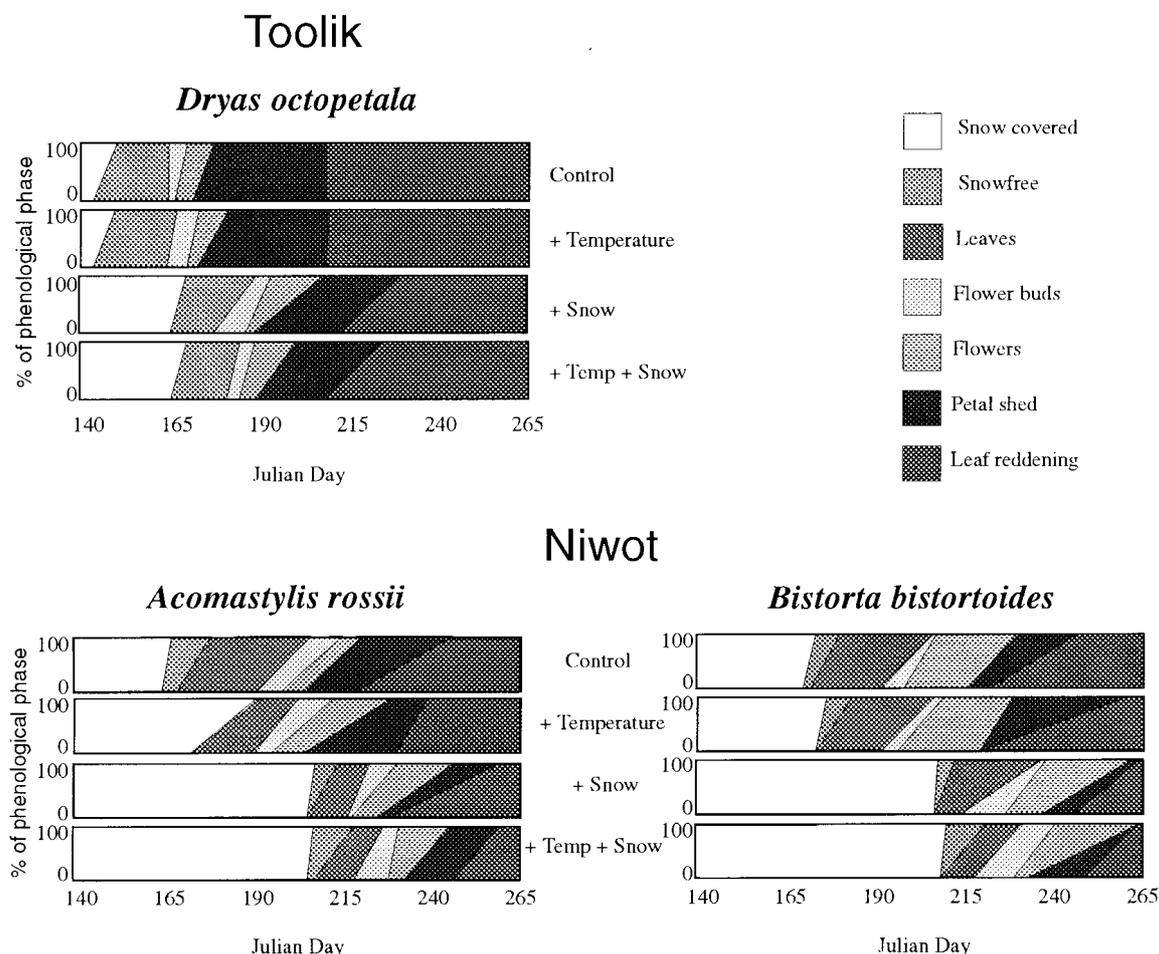
Figure 13. Phenology of *Dryas octopetala* in experimental manipulations and controls at the Toolik Lake dry site and of *Acomastylis rossii* and *Bistorta bistortoides* on Niwot Ridge. Note the compressed phenology in the snow treatment plots. Phenological diagrams were constructed from data which recorded the first and last occurrence of major phenological events within the study plots: release from snow, appearance of leaves (which in these species is the first appearance of the plants), flowering buds, opening of buds, anthesis, seed dispersal, and leaf senescence, which signals the end of the season

Phenological diagrams for *Acomastylis rossii* and *Bistorta bistortoides* at Niwot Ridge and for *Dryas octopetala* at Toolik Lake indicate that, at least in this early period of the experiment, plants respond to increased snow with a compressed growing season (Figure 13). These two species are able to complete a full growth and reproductive cycle under these conditions, they just do it in a shorter span of time. By the end of the season there were as few as nine days separating the phenology of plants in the deep part of the drift from those in the control area. Temperature had a somewhat complementary effect of snow by lengthening the growth season on the autumn end. Both of these effects will likely have important influences on species composition and community function in the long-term. Although most arctic and alpine plants should be able to survive the rare shortened year, a series of short years will result in a depletion of belowground reserves.

The effects of changing growth season length are already evident at Niwot Ridge for *Kobresia myosuroides*, the dominant plant there prior to fence construction. After three years, most of it has been killed in the deep drift areas, most likely because it cannot translocate sufficient amounts of carbohydrates to belowground reserves before the end of the growing season (Willard and Marr, 1970; Bell and Bliss, 1979). Compression in
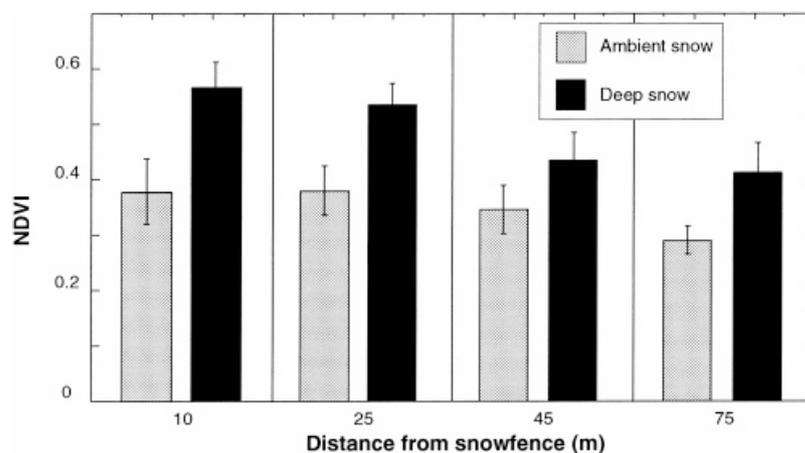
Figure 14. End of season NDVI (normalized difference vegetation index) at four distances from the Niwot Ridge fence and controls at the same distance outside the drift area. The trend in lower NDVI for the controls indicates a natural gradient of drier conditions at greater distances from the fence. NDVI was measured using a PS 2 hand-held spectrometer. The increases are statistically significant at the 95% confidence level for the 10 m, 25 m, and 75 m distances. Measurements were taken in the middle three hours of a cloudless early September day

the early season might therefore lead to reduced growth in a particular year, and extension in the late season can lead to failure to properly harden and store nutrients and carbohydrates before winter. Several other changes in species composition have been noted in the alpine site, but so far none have been noted in the arctic site. The site differences are likely due primarily to the phenological differences related to snow melt date.

NDVI measurements at Niwot Ridge corroborate the end-of-season lengthening seen in the individual species. In September 1994, NDVI in the snow-fence area was considerably higher than control areas on either side of the fence, indicating a much greener area behind the fence with delayed senescence (Figure 14). Similar measurements of NDVI at Toolik Lane showed no differences in greenness at the end of the season, although some differences are evident early on due to the delayed season start.

Both *Acomastylis rossii* and *Bistorta bistortoides* on Niwot Ridge responded to the experiment with increased growth (Figure 15), but specific responses varied with species and variables measured. Maximum height and maximum leaf length of *B. bistortoides* in the +S+T treatment were higher than in other treatments, and plant height in particular was increased. *A. rossii* responded most strongly to the +T treatment; its growth was less in the +S+T treatment, possibly due to the much later growing season start. Examining the overall pattern of response, both species generally respond positively to temperature, and in some cases there is a synergistic effect of temperature and snow, but in no case did the snow-only treatment lead to a significant increase in growth.

DISCUSSION AND CONCLUSIONS

Because snow and temperature together define much of the landscape-scale pattern of arctic and alpine ecosystems, changes in these regimes should have major influences on these ecosystems. Our results indicate that interactions between snow and temperature are important to account for and may affect ecosystems in somewhat surprising ways.

The snowfences had very different influences on the growing season in the arctic vs. the alpine. Despite identical drift size and nearly identical snow water equivalent, the arctic drift melted out over 1·5 months before the alpine drift, a consequence of the different solar insolation regimes in the two regions. In a growing season of only about 90–100 days, this is a major difference indicating that increased snowfall could have

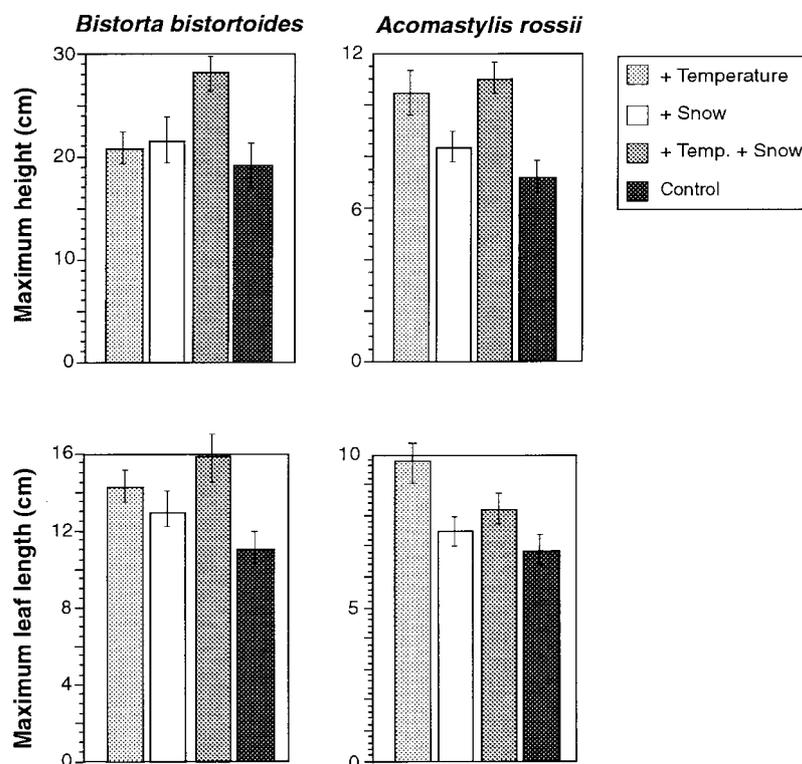**Bistorta bistortoides**   **Acomastylis rossii**

Figure 15. First-year leaf length and height of *Acomastylis rossii* and *Bistorta bistortoides* in experimental manipulations on Niwot Ridge. *A. rossii* plants were significantly taller than controls in both +T and +S+T manipulations, whereas *B. bistortoides* plants were significantly taller only when both temperature and snow were increased. *B. bistortoides* leaves were significantly longer than controls in the +T and the +S+T treatments, and *A. rossii* leaves were significantly longer than controls only in the +T treatments. Measurements were taken weekly throughout the growing season on permanently marked individual plants; bars represent standard errors for the entire treatment. The same individuals are followed through the years of the experiment to the extent possible. Other measured quantitative variables included number of leaves, number of inflorescences, seed number, total seed weight, and average seed weight. Seed germinability will be assessed on a small subset of species

more significant ecosystem consequences in the alpine than in the Arctic. The growth and phenology responses, including the death of the dominant species *Kobresia myosuroides* at the Niwot Ridge site, support this. Webber *et al.* (1976) also noted a fairly rapid decline and demise of *K. myosuroides* in their study of experimentally increased snowpack in the San Juan Mountains of southwestern Colorado. The measurement of NDVI at both sites also suggests that changes to phenology have been most noticeable in the alpine.

On the other hand, the Arctic generally has less snowfall than alpine areas, and small changes in arctic winter snowpack could have greater impacts on arctic soil temperatures than in the alpine. Increased winter soil temperature in both areas will have major impacts to a wide variety of ecosystem functions including winter plant activity, decomposition, flux of trace gases, and subnivian animal activity (Walker *et al.*, 1999). Furthermore, arctic winter soil temperatures are critical to permafrost temperatures (Zhang, 1993), and enhanced winter snow cover could lead eventually to a melting of the permafrost particularly in areas with permafrost temperatures near 0 °C. At regional scales, snow may interact with other variables to change the entire system state, affecting vegetation, soil chemistry and nutrients, permafrost depth, and trace gas flux (Walker *et al.*, 1998, 1999).

Effects on decomposition and carbon flux show the strong importance of snow in particular on these processes. The addition of snow causes an immediate increase in CO_2 loss, which is indicative of complex

changes in the soil microbial system. Williams *et al.* (1998) found that increasing snow in alpine ecosystems will also result in increased N mineralization, increase in N_2O flux, and increase in net nitrification. Our data indicate the importance of snow in trapping mineral and organic debris, leading to a major redistribution of these materials on the landscape, and therefore having a key role in soil development and landscape-scale soil patterns (Burns and Tonkin, 1982).

The results presented here are short-term responses in an experiment meant to last at least for decades. Many of the transient responses related to increased rates of nutrient cycling and loss and plant growth will not likely be sustained, but the rates at which each will change to a new quasi-equilibrium are unknown (e.g. Webber *et al.*, 1976). The phenology and growth data serve as a surrogate for demonstrating the complexity of interaction between the physical and biological components of this experiment and the switch between short and long-term processes. Growth of most measured species increased with both temperature and snow, even though snow caused a greatly shortened growing season. Although this result seems at first contradictory, Walker *et al.* (1995a) noted the same response in natural populations following an El Niño year with deep snowpack and delayed melt. They speculated that the increase was due to two things: (1) additional snow leads to additional growth season moisture, an important limiting factor in the alpine tundra late in the growing season, and (2) the delayed melt causes the growth to be pushed into a warmer period. This can only be a short-term response, however. These alpine species depend primarily on stored resources from the previous year for growth in the current year (Mooney and Billings, 1960; Walker *et al.*, 1994b, 1995b). They then use these resources to fix more carbon and take up more nitrogen, which is again stored over the winter. Species' ability to adapt to changing phenological conditions in the long term will depend greatly upon their relative use of stored versus currently available nutrients.

One of the key things that we will be able to accomplish with this long-term experiment will be to understand the different rates at which certain processes and species switch from transient to long-term. Initial changes in nutrient cycling, for example, will likely not be maintained as the nutrient and microbial pools gradually adjust to the changing conditions. The ability of the system to maintain 'extra' carbon made available through a pulse of mineralization will depend upon the specific capacities of the plant species and microbes, or in their ability to quickly increase biomass and therefore conserve system nutrients. Interspecific competition for nutrients will lead to changing composition of both plant and microbial communities. Over the longer-term, these will feed back into changes in soil organic matter pools, causing more profound changes to the overall ecosystem state.

This is the first long-term, large-scale manipulation of snow and temperature simultaneously, and by working in both arctic and alpine ecosystems we gain a much broader understanding of the complex system functions involved. With this integrated, experimental approach, we hope to gain a much better understanding of how these ecosystems are likely to change in the coming decades to centuries.

REFERENCES

Arft AM, Walker MD, Gurevitch JM, Alatalo JM, Bret-Harte MS, Dale M, Diemer M, Gugerli F, Henry GHR, Jones MH, Hollister R, Jónsdóttir IS, Laine K, Lévesque E, Marion GM, Molau U, Mølgaard P, Nordenhäll U, Raszhivin V, Robinson CH, Starr G, Stenström A, Stenström M, Totland O, Turner L, Walker L, Webber P, Welker JM, Wookey PA. 1999. Response patterns of tundra plant species to experimental warming: a meta-analysis of the International Tundra Experiment. *Ecological Monographs*, in press.
Bell KL, Bliss LC. 1979. Autoecology of *Kobresia bellardii*. Why winter snow accumulation limits local distribution. *Ecological Monographs* **49**: 377–402.

Brooks PD, Williams MW, Schmidt SK. 1996. Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. *Biogeochemistry* **32**: 93–113.

Burns SJ, Tonkin PJ. 1982. Soil-geomorphic models and the spatial distribution and development of alpine soils. In *Space and time in geomorphology*. Thorn CE (ed.) Allen and Unwin: London: pp. 25–43.

Dearing MD. 1997. The manipulation of plant toxins by a food hoarding herbivore, the North American pika, *Ochotona princeps*. *Ecology* **78**: 774–781.

Fahnestock JT, Jones MH, Brooks PD, Walker DA, Welker JM. 1998. Winter and early spring CO_2 efflux from tundra communities of northern Alaska. *Journal of Geophysical Research* **103**: 29023–29027.

Greenland D, Swift LW Jr. (eds). 1990. *Climate Variability and Ecosystem Response: Proceedings of a Long-term Ecological Research Workshop, Niwot Ridge/Green Lakes Valley LTER Site, Mountain Research Station, University of Colorado, Boulder, Colorado, August 21–23, 1998*. General Technical Report SE; 65, Southeastern Forest Experiment Station: Asheville, 90 pp.

Henry GHR, Molau U. 1997. Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global Change Biology* **3**: 1–9.

Hobbie SE. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs* **66**: 503–522.

Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (eds). 1996. *Climate Change 1995: The Science of Climate Change*. Cambridge University Press: Cambridge: 572 pp.

Komárková V. 1979. *Alpine Vegetation of the Indian Peaks Area, Front Range, Colorado Rocky Mountains*. J. Cramer: Vaduz: 591 pp.

Manabe S, Broccoli AJ. 1990. Mountains and arid climates of middle latitudes. *Science* **247**: 192–194.

Marion GM, Henry GHR, Molgaard P, Oechel WC, Jones H, Vourlitis GL. 1993. Open-top devices for manipulating field temperatures in tundra ecosystems. In *Fourth International Symposium on Thermal Engineering and Science for Cold Regions*, Lunardini VJ, Bowen SL (eds) CRREL Special Report 93-22, US Army Corps of Engineers: Hanover: pp. 205–210.

Marion GM, Henry GHR, Freckman D, Johnstone J, Jones G, Jones MH, Lévesque E, Molau U, Mølgaard P, Parsons AN, Svoboda J, Virginia RA. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology* **3**: 20–32.

Maxwell B. 1992. Arctic climate: potential for change under global warming. In *Arctic Ecosystems in a Changing Climate*, Chapin FS III, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J (eds) Academic Press: San Diego: pp. 11–34.

Maxwell B. 1997. Recent climate patterns in the Arctic. In *Global Change and Arctic Terrestrial Ecosystems*, Oechel WC, Callaghan, T, Gilmanov T, Holten JI, Maxwell B, Molau U, Sveinbjörnsson B (eds) Ecological Studies vol. 124: Springer: New York: pp. 21–46.

Molau U, Mølgaard PE (eds). 1996. *ITEX Manual*. Danish Polar Center: Copenhagen, Denmark: 51 pp.

Mooney HA, Billings WD. 1960. The annual carbohydrate cycle of alpine plants as related to growth. *American Journal of Botany* **47**: 594–598.

O'Lear HA, Seastedt TR. 1994. Landscape patterns of litter decomposition in alpine tundra. *Oecologia* **99**: 95–101.

Oechel WC, Callaghan T, Gilmanov T, Holten JI, Maxwell B, Molau U, Sveinbjörnsson B (eds). 1997. *Global Change and Arctic Terrestrial Ecosystems*, Ecological Studies vol. 124, Springer: New York: 493 pp.

Shippert MM, Walker DA, Auerbach NA, Lewis BE. 1995. Biomass and leaf-area index maps derived from SPOT images for Toolik Lake and Imnavait Creek areas, Alaska. *Polar Record* **31**: 147–154.

Walker DA, Halfpenny JC, Walker MD, Wessman C. 1993. Long-term studies of snow-vegetation interactions. *BioScience* **43**: 287–301.

Walker MD, Walker DA, Auerbach NA. 1994a. Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. *Journal of Vegetation Science* **5**: 843–866.

Walker MD, Webber PJ, Arnold EH, Ebert-May D. 1994b. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. *Ecology* **75**: 393–408.

Walker DA, Auerbach NA, Shippert MM. 1995a. NDVI, biomass, and landscape evolution of glaciated terrain in northern Alaska. *Polar Record* **31**: 169–178.

Walker MD, Ingersoll RC, Webber PJ. 1995b. Effects of interannual climate variation on phenology and growth of two alpine forbs. *Ecology* **76**: 1067–1083.

Walker DA, Auerbach NA, Bockheim JG, Chapin FS III, Eugster W, King JY, McFadden JP, Michaelson GJ, Nelson FE, Oechel WC, Ping CL, Reeburg WS, Regli S, Shiklomanov NI, Vourlitis GL. 1998. Energy and trace-gas fluxes across a soil pH boundary in the Arctic. *Nature* **394**: 469–472.

Walker DA, Bockheim JG, Chapin FS III, Eugster W, Nelson FE, Ping CL. 1999. Calcium-rich tundra, wildlife, and the 'Mammoth Steppe'. *Quaternary Science Review*, in press.

Webber PJ, Emerick JC, Ebert-May DC, Komárková V. 1976. The impact of increased snowfall on alpine vegetation. In *Ecological Impacts of Snowpack Augmentation in the San Juan Mountains, Colorado*, Steinhoff HW, Ives JD (eds) US Dept. of the Interior, Bureau of Reclamation: Denver: pp. 201–258.

Willard BE, Marr JW. 1970. Effects of human activities on alpine tundra ecosystems in Rocky Mountain National Park, Colorado. *Biological Conservation* **2**: 257–265.

Williams MW, Brooks PD, Seastedt T. 1998. Nitrogen and carbon soil dynamics in response to climate change in a high-elevation ecosystem in the Rocky Mountains, USA. *Arctic and Alpine Research* **30**: 26–30.

Zhang T. 1993. *Climate, Seasonal Snow Cover and Permafrost Temperatures in Alaska North of the Brooks Range*. Ph.D. Thesis, University of Alaska Fairbanks: Fairbanks: 232 pp.