

Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment

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Abstract

We used snow fences and small (1 m²) open-topped fiberglass chambers (OTCs) to study the effects of changes in winter snow cover and summer air temperatures on arctic tundra. In 1994, two 60 m long, 2.8 m high snow fences, one in moist and the other in dry tundra, were erected at Toolik Lake, Alaska. OTCs paired with unwarmed plots, were placed along each experimental snow gradient and in control areas adjacent to the snowdrifts. After 8 years, the vegetation of the two sites, including that in control plots, had changed significantly. At both sites, the cover of shrubs, live vegetation, and litter, together with canopy height, had all increased, while lichen cover and diversity had decreased. At the moist site, bryophytes decreased in cover, while an increase in graminoids was almost entirely because of the response of the sedge *Eriophorum vaginatum*. These community changes were consistent with results found in studies of responses to warming and increased nutrient availability in the Arctic. However, during the time period of the experiment, summer temperature did not increase, but summer precipitation increased by 28%. The snow addition treatment affected species abundance, canopy height, and diversity, whereas the summer warming treatment had few measurable effects on vegetation. The interannual temperature fluctuation was considerably larger than the temperature increases within OTCs (< 2 °C), however. Snow addition also had a greater effect on microclimate by insulating vegetation from winter wind and temperature extremes, modifying winter soil temperatures, and increasing spring run-off. Most increases in shrub cover and canopy height occurred in the medium snow-depth zone (0.5–2 m) of the moist site, and the medium to deep snow-depth zone (2–3 m) of the dry site. At the moist tundra site, deciduous shrubs, particularly *Betula nana*, increased in cover, while evergreen shrubs decreased. These differential responses were likely because of the larger production to biomass ratio in deciduous shrubs, combined with their more flexible growth response under changing environmental conditions. At the dry site, where deciduous shrubs were a minor part of the vegetation, evergreen shrubs increased in both cover and canopy height. These changes in abundance of functional groups are expected to affect most ecological processes, particularly the rate of litter decomposition, nutrient cycling, and both soil carbon and nitrogen pools. Also, changes in canopy structure, associated with increases in shrub abundance, are expected to alter the summer energy balance by increasing net radiation and evapotranspiration, thus altering soil moisture regimes.

Keywords: climate change, ITEX, passive warming, snow addition

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Introduction

Arctic landscapes are covered with snow for two-thirds of the year, and are characterized by low temperatures during the growing season; thus, ecological processes and vegetation patterns are strongly affected by both temperature and snow (Walker *et al.*, 1993, 1994, 2001). Temperature directly affects almost all ecosystem processes, from photosynthesis and soil nutrient mineralization to the rate that litter decomposes (Nadelhoffer *et al.*, 1991; Hobbie, 1996; Shaver *et al.*, 2000), while the distribution and persistence of snow directly or indirectly affects processes such as soil temperatures and nutrient regimes, vegetation microclimate, and spring run-off (Pomeroy & Brun, 2001; Walker *et al.*, 2001). Recent evidence indicates that the Arctic has become warmer, particularly since the mid-20th century, and that precipitation has increased during autumn and winter (Dai *et al.*, 1997; Serreze *et al.*, 2000). The snow-covered area, however, generally decreased in the Northern Hemisphere during the 20th century, mostly during spring (Serreze *et al.*, 2000). Such a decrease in snow-covered area does not mean that snow depth has decreased or will decrease in all regions, because the distribution of snow in the Arctic is controlled as much by wind, especially during winter, as by spatial variation in precipitation (Sturm *et al.*, 2001a, b).

Predicted vegetation changes in arctic tundra because of climate change have therefore been based on a warmer climate that is either drier or wetter than at present. Both scenarios predict an increase in shrub abundance and, because of a more flexible growth response, mainly in deciduous shrubs (Chapin *et al.*, 1995b; Hobbie, 1995; Bret-Harte *et al.*, 2001). A drier climate is also expected to favor forbs and reduce the abundance of evergreen shrubs, graminoids, and mosses, whereas, a wetter climate should favor mosses and hygrophilous graminoids (Hobbie, 1995). Some of these predicted vegetation changes already seem to be occurring in the Arctic, such as an increase in shrub cover (Sturm *et al.*, 2001c; Stow *et al.*, 2004), overall increase in vegetation leaf area because of earlier snow melt (Myneni *et al.*, 1997; Silapaswan *et al.*, 2001; Jia *et al.*, 2003), and northward migration of treeline (Serreze *et al.*, 2000; but see Lloyd & Fastie, 2002).

Nevertheless, observed changes in climate and vegetation reveal little detail about how the two interact. Yet, establishing strong causal links between climate and vegetation change is essential to increase our understanding of how ecosystems function and, perhaps more importantly, to predict with some degree of confidence how the Arctic tundra is likely to respond to current and future environmental changes. Develop-

ing such predictions and elucidating the interconnections between climate and ecosystem responses have proven challenging, because they require not only knowledge of how and which ecosystem processes are affected by climate, but also how these processes affect vegetation (Shaver *et al.*, 2000). Difficulties arise because the effects of climate warming extend beyond the direct effects of increased CO₂ to, on the one hand, the direct and indirect effects of temperature and, on the other, the often nonadditive (or nonlinear) interactions among ecosystem components and processes directly affected by environmental change. Further, ecological processes are often linked; operate at different spatial and temporal scales; and at different rates. Thus, teasing out this web of interconnections requires a variety of studies, especially long-term, manipulative and integrative experiments at different spatial scales (Shaver *et al.*, 2001). Such studies provide almost the only way of distinguishing between short-term fluctuations and long-term trends (Baron, 2001).

In the Arctic, such studies have focused at various levels of organization, from species (e.g. Shaver & Laundre, 1997; Stenström & Jonsdottir, 1997; Molau, 2001; Saavedra *et al.*, 2003) to ecosystems (Molau & Alatalo, 1998; Shaver *et al.*, 2001), and on various ecological processes, from litter decomposition (Hobbie, 1996) to nutrient cycling (Chapin *et al.*, 1988; Nadelhoffer *et al.*, 1991; Broll *et al.*, 1999; Shaw & Harte, 2001b). These processes have also been studied experimentally, using a combination of treatments that reproduce expected environmental changes, such as increased air or soil temperatures, greater nutrient availability, and shading (e.g. Chapin & Shaver, 1985; Jonasson, 1992; Chapin *et al.*, 1995b; Shaver & Laundre, 1997; Press *et al.*, 1998; Bret-Harte *et al.*, 2001; Graglia *et al.*, 2001a; Shaver *et al.*, 2001). The International Tundra Experiment (ITEX), a collaborative experiment that commenced in 1990, is part of this growing body of research (Henry & Molau, 1997). At present, ITEX consists of 30 sites in 13 countries (Henry & Molau, 1997; Molau, 2001), with sites distributed from alpine to the high Arctic, mostly in the Northern Hemisphere (Henry & Molau, 1997). The experiment is based on a common warming treatment using small (1–2 m diameter), open-topped greenhouses that raise summer ambient temperatures inside chambers by 1–3 °C (Marion *et al.*, 1997). Research to date has focused on phenological responses of species (e.g. Mølgaard & Christensen, 1997; Stenström *et al.*, 1997; Molau, 2001) and major growth forms (Arft *et al.*, 1999). Short-term (<5 years) results have shown that major vegetative and reproductive events, such as leaf bud burst and flowering, occur early in the warming treatment, and that responses change from a vegetative response in the

first 3 years to a greater reproductive response (Arft *et al.*, 1999).

The study, presented in this paper, is part of the ITEX program, and extends this research by using open-topped chambers (OTCs) combined with large snow fences to assess both the short- and longer-term effects on arctic tundra vegetation of increased summer air temperatures and modified winter snow regimes. We wished to separate the effects of increased winter snow and its indirect effects on summer processes from the direct effects of summer warming. We hypothesized that increased winter snow cover would improve summer growth of vegetation more than summer warming by itself, because plant production in arctic tundra is strongly nutrient limited (Shaver & Chapin, 1980, 1986; Chapin & Shaver, 1985; Chapin *et al.*, 1995b; Shaver *et al.*, 2001), and because increased winter snow cover in this experiment, by insulating the soil, maintained higher soil temperatures and promoted nitrogen (N) mineralization and CO₂ efflux over winter (Schimel *et al.*, 2004). Although increased snow cover also reduces the length of the growing season, we expected that the negative effect of a shorter growing season on plant growth would be more than offset by positive effects on plant growth of the snow-mediated increase in N mineralization.

Arctic plant communities do not adjust rapidly to environmental change, and transient responses in vegetation are expected, while biotic and abiotic systems adjust to the new environmental conditions (Walker *et al.*, 1999; Shaver *et al.*, 2000). Here, we report on how the vegetation of two tundra sites has responded 8 years into the experiment, focusing on species composition, relative abundance, diversity, and canopy height. We chose to manipulate snow cover and temperature in two contrasting ecosystem types, a dry tundra mostly dominated by evergreen shrubs, and a moist tussock tundra site characterized by co-dominance of evergreen shrubs, deciduous shrubs, graminoids, and nonvascular plants, because we thought that the characteristics of the plant species already present in a community would affect community response to perturbations. We interpret our results in light of current knowledge and predicted vegetation changes, thus adding to a growing body of knowledge about the Arctic and how tundra vegetation may respond to increases in temperature and snow cover.

Methods

Study sites, experimental design, and vegetation sampling

In the summer of 1994, we erected two snow fences at Toolik Lake (68°38'N, 149°34'W), in the northern foot-

hills of the Brooks Range at 760 m a.s.l. One snow fence was established in moist tussock tundra and the other in dry tundra vegetation (Walker *et al.*, 1994), referred to as the moist and dry sites, respectively. The snow fences were 2.8 m high, 60 m long, and created leeward snowdrifts about 60 m long, and 3 m at their deepest each year (Walker *et al.*, 1999). Areas beyond 60 m received slightly less than ambient amounts of snow. The snowdrifts delayed the start of the growing season by about 2–3 weeks. To avoid affecting summer wind regimes and shading the vegetation, both snow fences were laid flat during summer. Each snowdrift was divided into three snow-depth zones: deep (2–3 m), medium (0.5–2 m), and ambient (0.5 m). The leeward distances of each zone from the snow fences were approximately 10–30 m (deep), 30–60 m (medium), and >60 m (ambient). Ambient snow depths also occurred adjacent to each snow fence on the sides.

The experimental design was factorial, with plots subjected to snow addition (+S), increased summer temperature (+W), and both simultaneously (+S+W). Ambient summer temperature and snow are designated –W and –S, respectively; full controls are therefore –S–W. We set up 42 permanent plots per site, distributed among the three snow-depth zones as follows: 12 in the deep zone, consisting of six (+S+W) and six (+S–W); 18 in the medium zone, nine (+S+W) and nine (+S–W); and 12 control plots (half of which were adjacent to the snow fence, and half in the ambient zone >60 m), six (–S+W) and six (–S–W). There were more plots in the medium zone than in the deep zone because it was 10 m longer. The warming treatment used 1 m² clear fiberglass OTCs, approximately 0.4 m high, that passively increased summer air temperatures within chambers at our sites by a mean daily average of 1.5 °C (Walker *et al.*, 1999). OTCs were of the standard ITEX design (Marion *et al.*, 1997). Each spring, OTCs were installed as soon as 50% of the ground area of a given plot was free of snow, and remained until the last measurements were made, usually at the end of August or early September. Thus, OTCs were installed later in the deeper snow zones than in the ambient zones, although they were removed at the same time. In addition to increasing summer air temperature, OTCs reduced wind within the chambers, but did not affect light intensity or rainfall (Marion *et al.*, 1997).

The cover and canopy height of vegetation, within our treatments, was assessed using a 75 cm × 75 cm square point-frame that provided data from 100 points (Kent & Coker, 1992), spaced 7.5 cm apart. The data recorded at each point followed standard ITEX guidelines (Walker, 1996), and consisted of the identity, height, and state (live or dead) of the canopy (top) and

surface (bottom) layer species. At points without a bottom layer, the surface condition was identified as litter, bare soil, rock, or animal scat. These point-frame data provided cover estimates for all species and surface conditions by plot. Diversity was also calculated from the point-frame data. Canopy height of each species and functional type within a plot was based on data from at least two points. Here, we report on these vegetation measurements from 1994, 1996, 1998, 2000, and 2002.

Our plots were not instrumented to record soil or air temperatures through all the years of the experiment. However, wind speed and direction, air temperature, soil temperatures, relative humidity, and light intensity are measured by the Arctic LTER approximately 600 m from our plots, and are available at <http://ecosystems.mbl.edu/arc/home.htm>

Analysis of vegetation cover and canopy height

The cover data were explored by site and treatment through ordination analysis, using detrended correspondence analysis (DCA) and nonmetric multidimensional scaling (NMDS) (ter Braak, 1995; Kent & Coker, 1992; Legendre & Legendre, 1998). We used both methods because there is currently no consensus on the most appropriate indirect ordination method (Kent & Coker, 1992; ter Braak, 1995); DCA assumes a unimodal species response curve, whereas NMDS makes no such assumption, deriving configuration scores only from the rank order of the dissimilarities between samples or species (Faith *et al.*, 1987); and where both methods produced similar results, we felt more confident that the patterns represented an inherent structure in the data. Where DCA uses a χ^2 distance measure, for NMDS we used the Czekanowski dissimilarity coefficient (Kent & Coker, 1992). Ordinations were based on cover data of three types: untransformed, downweighted by rare species (DCA only), and presence/absence. Where downweighting by rare species was used, only species rarer than $F_{\max}/5$ (F_{\max} : frequency of most common species) were downweighted in proportion to their frequency. In almost all cases the two ordination techniques produced similar configurations, the main difference being an apparent compression of sample points in DCA configurations. This may have been because of the arch effect, more common in ordinations based on correspondence analysis (ter Braak, 1995). Because no compression was evident in any NMDS configurations, presented ordinations are based on NMDS. Goodness-of-fit, or how well distances in an NMDS configuration represents the rank order of dissimilarity scores, is assessed by the loss or stress function (Legendre & Legendre,

1998). This function was less than 0.18 for all three-dimensional solutions, which was lower than the generally accepted maximum stress value of 0.2 (Minchin, 1987; Clarke, 1993). We therefore used the three-dimensional solutions, but because the third axis added little or no additional information, figures show only the first two axes. Ordinations were generated using PC-Ord (McCune & Mefford, 1999) and DECO-DA (Minchin, 1989).

Differences between and among groups (year and treatments) of the ordinations were tested using the Anosim routine (Clarke, 1993; Chapman & Underwood, 1999) and the multiresponse permutation procedure (MRPP, Biondini *et al.*, 1988). Both Anosim and MRPP are nonparametric randomization procedures that test for differences between and among *a priori* groups (Clarke, 1993; Chapman & Underwood, 1999). In Anosim, the diagnostic statistic, R , can range from -1 to 1 , where $R = 1$ indicates that all samples within groups are more similar to each other than those between groups and $R = -1$ indicates the reverse. In MRPP we used within-group homogeneity or effect size (A). The maximum value of the A statistic is 1 and occurs if all samples within groups are identical, whereas $A = 0$ indicates that within-group heterogeneity equals that expected by chance, and $A < 0$ that within-group heterogeneity is less than expected by chance.

Cover and canopy height data conformed to a normal distribution, with little difference among variances. Because the data were correlated over time, we used univariate repeated-measures ANOVA (von Ende, 2001). Subsequent to each analysis, residuals were explored by plotting them against estimated values for a normal distribution, which showed that assumptions of normality were met in all cases. To reduce the chance of a Type I error because of analyses of multiple-dependent variables (species and growth forms), probability values were adjusted using the sequential Bonferroni's procedure (Holm, 1979; Legendre & Legendre, 1998). SYSTAT 10.0 (SPSS, 2000) was used for all statistical analyses.

Species composition

Species composition within and among sample groups (year and treatments) of the ordinations was analyzed using the Simper routine (Clarke, 1993), which uses the dissimilarity indices between all pairs of samples to identify species that characterize groups and discriminate between groups. Thus, given a dissimilarity index D for a sample pair, the level of contribution of the i th species to D is D_i . These values are then used to calculate the mean dissimilarity among samples (\bar{D})

within and between groups, and the mean contribution of each species (\bar{D}_i) to \bar{D} . How consistently the i th species contributes to \bar{D}_i is represented by the standard deviation of all D_i values ($SD(\bar{D}_i)$) within or between groups. A useful species in discriminating between two groups would therefore have a low $SD(\bar{D}_i)$ and high $\bar{D}_i/SD(\bar{D}_i)$ (Clarke, 1993).

Diversity

For each plot, three diversity indices were calculated: richness, Shannon–Wiener index, and Pielou’s evenness index (Magurran, 1988). Both the Shannon–Wiener and Pielou’s evenness index met assumptions of ANOVA and were analyzed by repeated-measures ANOVA. Richness was count data and analyzed by the nonparametric Friedman’s test (Sokal & Rohlf, 1995).

Results

Moist tundra site

Ordination diagrams for the moist tundra site suggest major changes in vegetation composition over the 8-year sampling period (Fig. 1). This interpretation was supported by single factor ANOSIM, which produced a significant difference among years ($R: 0.542, P < 0.001$). Pairwise comparisons were also significant ($P < 0.001$), and contrasts with the 1994 data showed that the R -statistic increased from 0.201 (1994 vs. 1996) to 0.675 (1994 vs. 2002), indicating that changes became more apparent over time. Ordinations by treatment suggested that most change occurred in the ambient snow zone (Fig. 2). There was a significant difference among years ($P < 0.001$), although the R -statistic was relatively low ($R < 0.270$) for all except the 1994 vs. 2002 deep snow-zone comparison ($R = 0.569$). Assessing treatment groups by MRPP showed that the effect size (within-group agreement) of the snow addition treatment increased over time, whereas that of the warming treatment remained almost unchanged (Fig. 3).

The main species differentiating plant community composition in 1994 and 2002 at the moist site are listed in Table 1 in order of their contribution to the mean dissimilarity among plots. Results show that most vegetation change over the sampling period can be attributed to an increase in cover of three species, which accounted for over 45% of the overall difference between 1994 and 2002: the sedge *Eriophorum vaginatum* and two deciduous shrubs, *Betula nana* and *Salix pulchra* (Table 1). Other species whose changes in cover over time contributed strongly to the observed changes in community composition included the evergreen shrub *Ledum decumbens*, the moss *Aulacomnium turgidum*, and

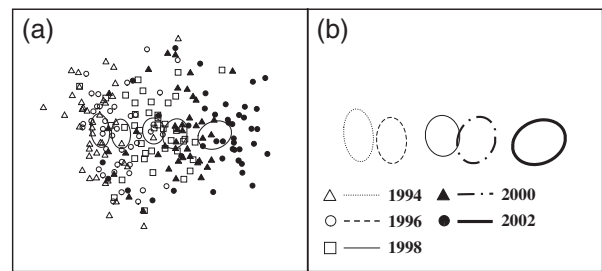


Fig. 1 Nonmetric multidimensional scaling ordination of samples from the moist site, 1994–2002. (a) Configuration of plots with 95% confidence ellipses; (b) confidence ellipses only, enlarged for clarity.

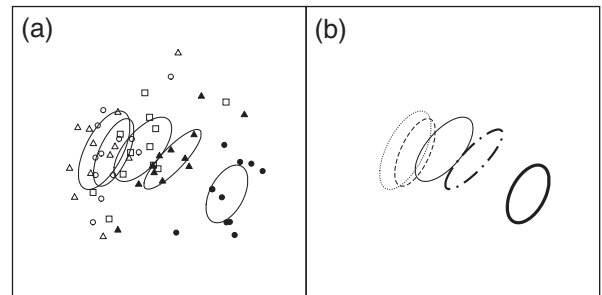


Fig. 2 Nonmetric multidimensional scaling ordination of samples from the ambient snow zone of the moist site, 1994–2002. (a) Configuration of plots with 95% confidence ellipses; (b) confidence ellipses only.

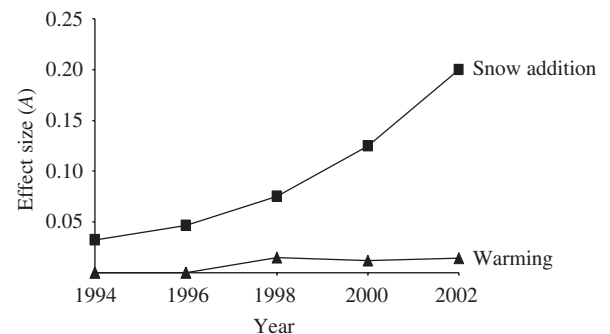


Fig. 3 Changes in effect size (A) from multiresponse permutation procedure analysis of the moist site data, assessing the snow addition and warming treatment, 1994–2002.

two lichens, *Flavocetraria cucullata* and *Cladonia amaurocraea*, species that all decreased in cover by $>1\%$ over the sampling period, and did so consistently among plots (i.e. the ratio $\bar{D}_i/SD(\bar{D}_i)$ was higher than for other species) (Table 1). Thus, despite the sedge *Carex bigelowii* decreasing in cover by about 7%, this was not a useful species in differentiating between sample years.

Table 1 Mean cover (%) of diagnostic species at the moist site, 1994 and 2002

Species	1994	2002	\bar{D}_i	$\bar{D}_i/SD(\bar{D}_i)$	Cum%
<i>Eriophorum vaginatum</i>	11.9	76.6	21.0	1.97	33.4
<i>Betula nana</i>	15.6	26.9	5.5	1.26	42.1
<i>Salix pulchra</i>	2.8	10.6	3.0	1.01	46.9
<i>Hylocomium splendens</i>	9.2	8.9	2.8	1.09	51.4
<i>Carex bigelowii</i>	2.8	10.2	2.8	0.84	55.9
<i>Aulacomnium turgidum</i>	10.2	5.6	2.7	1.18	60.2
<i>Ledum decumbens</i>	10.3	7.0	2.7	1.43	64.5
<i>Vaccinium vitis-idaea</i>	10.2	9.6	2.4	1.38	68.3
<i>Sphagnum rubellum</i>	6.2	2.5	2.2	0.95	71.9
<i>Sphagnum. angustifolium</i>	6.0	1.9	2.2	0.72	75.4
<i>Vaccinium. uliginosum</i>	4.2	4.8	1.9	1.05	78.4
<i>Dicranum sp.</i>	3.2	2.6	1.3	0.95	83.1
<i>Flavocetraria cucullata</i>	3.9	0.9	1.2	1.22	85.1
<i>Cladonia amaurocraea</i>	3.0	0.6	1.0	1.02	86.6
<i>Peltigera aphthosa</i>	2.1	1.5	0.8	0.87	87.9
<i>Cladina. arbuscula</i>	1.9	0.5	0.7	0.75	89.0
<i>Cladina. rangiferina</i>	1.4	1.0	0.6	0.81	90.0

\bar{D}_i , mean contribution of the *i*th species to the mean dissimilarity among samples (\bar{D}); $SD(\bar{D}_i)$, standard deviation of each species' contribution to \bar{D} ; Cum%, cumulative percentage contribution to \bar{D} ; \bar{D} (1994 vs. 2002), 63%.

These interpretations were further supported by results from repeated-measures ANOVA of the cover data, which suggest a community change over time, with few significant main effects of warming and some effect of the snow addition treatment (Table 2). Shrub cover increased significantly overall, but only in the medium and ambient snow zones (about 7% in these zone), while in the deep zone shrub cover decreased by 5%. Trends in cover differed between shrub type, with deciduous shrubs increasing significantly and evergreen shrubs decreasing significantly. The trend in deciduous shrub cover was mainly because of *B. nana*, which increased by 12%, 7%, and 14% in the deep, medium, and ambient snow zones, respectively. The decrease in cover of evergreen shrubs was mainly because of *L. decumbens*, which decreased by about 5% in each of the snow zones (Tables 1 and 2). In graminoids, the significant main effect of snow addition was entirely because of *E. vaginatum*, whose mean cover increased by 67% (15–82%) in the ambient zone, 75% (11–86%) in the medium zone, and by only 25% (11–36%) in the deep zone. Hence, for this species both the time and time by snow addition interaction were significant (Table 2). Bryophytes decreased significantly

Table 2 Probability values from univariate repeated-measures ANOVA of the moist site cover and diversity data

Variable	Source of variation						
	Between groups			Within groups			
	S	W	S × W	T	T × S	T × W	T × S × W
<i>Growth forms, vegetation, and litter</i>							
Shrubs	ns	ns	ns	0.015	ns	ns	ns
Deciduous shrubs	ns	ns	ns	<0.001	ns	<0.001	ns
Evergreen shrubs	ns	ns	ns	<0.001	0.022	ns	ns
Forbs	ns	ns	ns	ns	ns	ns	ns
Graminoids	<0.001	ns	ns	<0.001	<0.001	ns	ns
<i>Sphagnum</i>	ns	ns	ns	ns	ns	ns	ns
Bryophytes	ns	0.036	ns	<0.001	<0.001	ns	ns
Bryophytes minus <i>Sphagnum</i>	<0.001	ns	ns	<0.001	<0.001	ns	ns
Lichens	ns	ns	ns	<0.001	<0.001	ns	ns
Live vegetation	<0.001	ns	ns	<0.001	<0.001	ns	ns
Litter	<0.001	0.019	ns	<0.001	ns	0.017	ns
<i>Five most common species in 1994</i>							
<i>Betula nana</i>	ns	ns	ns	<0.001	ns	<0.001	ns
<i>Eriophorum vaginatum</i>	<0.001	ns	ns	<0.001	<0.001	ns	ns
<i>Vaccinium vitis-idaea</i>	ns	ns	ns	<0.001	<0.001	ns	ns
<i>Aulacomnium turgidum</i>	0.011	ns	ns	<0.001	ns	ns	ns
<i>Ledum decumbens</i>	ns	ns	ns	<0.001	ns	ns	ns
<i>Diversity</i>							
Evenness	<0.001	ns	ns	<0.001	<0.001	ns	ns
Shannon	<0.001	ns	ns	<0.001	<0.001	ns	ns

Significant values are shown in bold.

S, snow addition; W, warming treatment; T, time; ns, nonsignificant.

in cover, from 38% in 1994 to 32% in 2002, but, similarly to the changes in shrub cover, this trend differed among treatments, with bryophytes decreasing by about 15% in both the ambient and medium zones, while increasing by about 10% in the deep zone. Further, bryophyte cover decreased most in OTCs of the medium zone (20%), and increased most in control plots (15%). Thus, warming, time, and the time by snow addition interaction were all significant (Table 2). Removing *Sphagnum* spp. from analyses of bryophytes resulted in a significant main effect of snow addition, while the warming treatment was nonsignificant (Tables 1 and 2). Similar to bryophytes, lichen cover decreased significantly over the sampling period, by 9% in the ambient zone and by about 14% in the medium and deep zones. Both the time and time by snow addition interaction were, therefore, significant. Comparing the proportion of total cover provided by each functional group showed that, over the 8-year sampling period, the amount contributed by graminoids, essentially *E. vaginatum*, increased markedly, while that of evergreen shrubs, lichens, and bryophytes all decreased (Fig. 4). Even though deciduous shrubs increased significantly in cover, their relative contribution to total cover changed little over time.

Mean live vegetation cover remained at 100% throughout the 8-year sampling period, but live overlapping vegetation cover increased significantly (Table 2). Hence, the number of points intercepting both a canopy and surface-layer species increased over time. The largest change occurred in the medium and ambient snow zones, where overlapping cover increased from about 115% in 1994 to 142% in 2002. Most of this increase was because of *E. vaginatum*. In

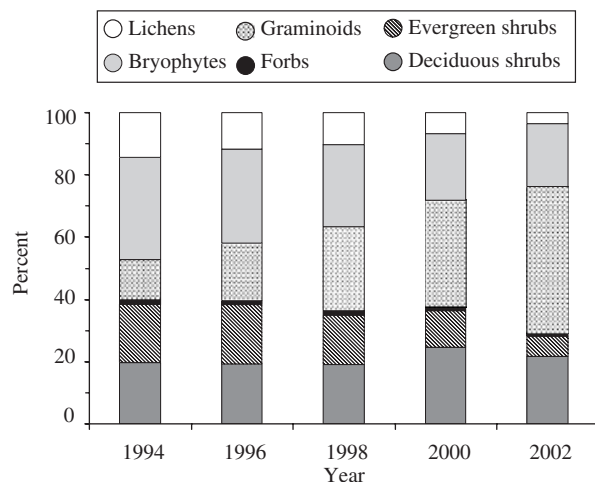


Fig. 4 Proportional abundance of the main functional groups at the moist tundra site, 1994–2002.

contrast to the ambient and medium zones, in the deep zone live vegetation decreased from 114% to 108%, most decrease being because of overall shrub cover. Hence, the main effects of snow addition, time and the time by snow addition interaction were all significant (Table 2). Litter cover increased in all snow zones over the sampling period, although by a greater amount in the deep (18–30%) than the other zones (approximately 16–24%). Also, most increase in litter occurred in OTCs, so the main effects of snow addition and warming, together with time and the time by warming interaction, were significant (Table 2).

Diversity, measured as Pielou's evenness and the Shannon index, decreased significantly over the 8 years (Table 2). Most changes in these indices occurred in the medium and ambient snow zones, resulting in a significant effect of snow addition, time, and time by snow addition interaction. The effect of the warming treatment was nonsignificant. Richness remained at about 19 species/plot in the deep zone, while in the medium and ambient zones richness decreased from 18 to 15 and 17 to 15, respectively. Overall, the number of species at the moist site remained at 49, indicating that vegetation changes were due mainly to changes in relative abundance of species rather than a loss of species. These findings were supported by ordinations based on presence/absence data, where configurations showed little difference among sampling times, and by relative abundance distributions (Fig. 5), showing increased dominance of a few resident species. For example, between 1994 and 2002 the number of species with a relative abundance of 40% or more decreased from 9 to 1 among control plots and from 6 to 2 among OTCs (Fig. 5).

Mean canopy height of the vegetation increased significantly at the moist tundra site, from 6 cm in 1994 to 12 cm in 2002 (Table 3). The increase in shrub canopy height was mainly because of *B. nana* (7–15 cm) and *S. pulchra* (9–14 cm). These canopy-height changes occurred in all zones, but mostly in the medium and ambient zones, especially within OTCs. Thus, main effects of snow addition and warming, and both the time by snow addition and time by warming interactions were all significant (Table 3). In contrast to deciduous shrubs, mean canopy height of evergreen shrubs decreased significantly, particularly in the deep zone. In the ambient zone, however, the mean canopy height of evergreen shrubs increased most in control plots. These contrasting trends in evergreen shrub height contributed to the nonsignificant time by snow addition and time by warming interactions (Table 3). The increase in mean canopy height of graminoids was because of *E. vaginatum* (4–7 cm), and occurred mainly in the medium and ambient zones.

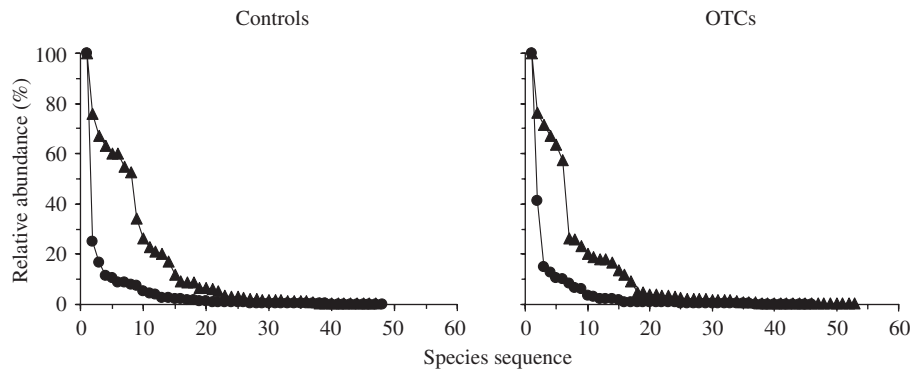


Fig. 5 Relative abundance distributions of the control and open-topped chamber (OTC) plot data from the moist site, 1994 (▲) and 2002 (●).

Table 3 Probability values from univariate repeated-measures ANOVA of the moist site canopy height data

Variable	Source of variation						
	Between groups			Within groups			
	S	W	S × W	T	T × S	T × W	T × S × W
Overall canopy height	<0.001	<0.001	ns	<0.001	<0.001	<0.001	ns
Shrubs	<0.001	0.004	ns	<0.001	<0.001	<0.001	ns
Deciduous shrubs	<0.001	<0.001	ns	<0.001	<0.001	<0.001	ns
Evergreen shrubs	<0.001	ns	ns	<0.001	ns	ns	ns
Graminoids	<0.001	0.004	ns	<0.001	<0.001	ns	ns

Significant values are shown in bold.

S, snow addition; W, warming treatment; T, time; ns, nonsignificant.

Dry tundra site

Similar to the moist site, ordinations indicated clear vegetation change over the sampling period at the dry site (Fig. 6). There was a significant difference among years ($R = 0.192$, $P < 0.001$), and the largest pairwise difference was between 1994 and 2002 ($R = 0.394$, $P < 0.001$). Nevertheless, the R statistics were considerably lower than for the moist site, suggesting that at the dry site vegetation changes were less pronounced (Figs 1 and 6). Most changes at the dry site occurred in the deep snow zone, for which ANOSIM results were similar to that using the whole dataset. Analysis using MRPP found no significant effect of the warming treatment and no change in effect size. By comparison, the effect size of snow addition was significant ($P < 0.001$) and, although increasing over time, remained low (< 0.1) over the entire sampling period.

The main species contributing to the vegetation differences between 1994 and 2002 are listed in Table 4, which shows that changes were largely because of an increase in cover of four shrubs: *Loiseleuria procumbens*, *Dryas octopetala*, *Arctostaphylos alpina*, and *Vaccinium*

vitis-idaea. The remaining change can be attributed mainly to lichens, most of which decreased in cover over the sampling period, such as *Sphaerophorus globosus*, *Alectoria ochroleuca*, and *F. nivalis* (Table 4). The lichen *Ochrolechia frigidida*, increased from $< 1\%$ in 1994 to 3% in 2002, and usefully differentiated sample years because of its relatively large $\bar{D}_i/SD(\bar{D}_i)$ ratio.

Analysis of the cover data showed that most vegetation changes occurred independently of any treatment effects (Table 5). The warming treatment was nonsignificant for all analyses, whereas the main effect of snow addition was significant only for lichens, *L. procumbens*, *A. ochroleuca*, and litter. Lichens decreased in cover within the deep snow zone, from a mean of 45% in 1994 to 21% in 2002, while in the ambient and medium snow zones lichen cover remained at approximately 44%. Despite lichen cover in the deep zone decreasing by 12% more in OTCs compared with control plots, this was nonsignificant. These trends were reflected in most lichen species, although for *S. globosus* the snow addition treatment was nonsignificant. Shrub cover increased significantly over time and, in contrast to the moist site, was because of an increase

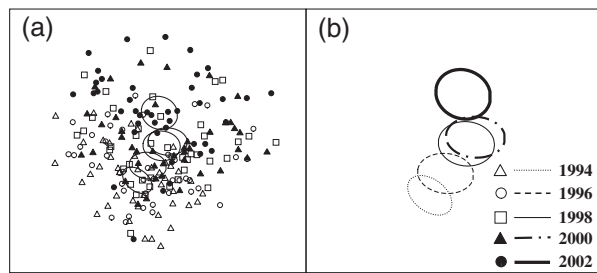


Fig. 6 Nonmetric multidimensional scaling ordination of samples from the dry site, 1994–2002. (a) Configuration of plots with 95% confidence ellipses; (b) confidence ellipses only, enlarged for clarity.

Table 4 Mean cover (%) of diagnostic species at the dry site, 1994 and 2002

Species	1994	2002	\bar{D}_i	$\overline{SD}(\bar{D}_i)$	Cum%
<i>Dryas octopetala</i>	6.3	19.1	9.2	1.19	15.6
<i>Loiseleuria procumbens</i>	5.0	9.8	5.4	1.07	24.8
<i>Arctostaphylos alpina</i>	3.4	8.0	5.0	0.94	33.4
Unknown lichens	6.6	4.8	3.0	1.29	38.6
<i>Polytrichum piliferum</i>	4.6	5.2	2.9	1.05	43.5
<i>Vaccinium vitis-idaea</i>	2.9	5.4	2.6	1.13	47.9
<i>Sphaerophorus globosus</i>	5.6	2.8	2.6	1.29	52.3
<i>Alectoria ochroleuca</i>	4.6	3.0	2.4	1.15	56.3
<i>Bryocaulon divergens</i>	3.1	3.8	2.0	1.30	59.8
<i>Ochrolechia frigida</i>	0.0	3.0	1.9	1.26	63.0
Unknown crustose lichen	3.4	0.9	1.7	1.39	66.0
<i>Flavocetraria nivalis</i>	3.4	2.5	1.6	1.23	68.7
<i>Cladonia arbuscula</i>	1.2	2.6	1.4	1.19	71.0
<i>Flarocetraria cucullata</i>	2.1	2.0	1.2	1.23	73.1
<i>Thamnolia subuliformis</i>	2.4	1.7	1.1	1.19	75.0
<i>Cetraria islandica</i>	1.8	0.3	1.1	0.97	76.9
<i>Asahinea chrysantha</i>	1.7	1.0	1.1	0.98	78.8
<i>Alectoria nigricans</i>	1.4	0.4	0.9	0.89	80.3
<i>Salix phlebophylla</i>	0.7	1.1	0.9	0.83	81.8
<i>Diapensia lapponica</i>	0.7	1.0	0.8	0.78	83.2
<i>Cladonia</i> sp.	1.2	0.0	0.8	0.59	84.6
<i>Cetraria nigricans</i>	0.1	1.1	0.7	0.97	85.9
<i>Hypogymnia</i> sp.	0.6	0.7	0.7	0.75	87.0
<i>V. uliginosum</i>	0.6	0.5	0.7	0.54	88.1
<i>Cladonia pyxidata</i>	0.3	1.0	0.6	0.98	89.2
<i>Cladonia amaurocraea</i>	0.4	0.8	0.6	0.60	90.2

\bar{D}_i , mean contribution of the i th species to the mean dissimilarity among samples (\bar{D}); $\overline{SD}(\bar{D}_i)$, standard deviation of each species' contribution to \bar{D} ; Cum%, cumulative percentage contribution to \bar{D} ; \bar{D} (1994 vs. 2002), 59%.

in cover of both deciduous and evergreen shrubs. Despite mean shrub cover increasing more in the deep and medium snow zones, the snow addition treatment was significant only for the evergreen shrub *L. procumbens*. The cover of this species increased in all zones, but remained highest in the deep snow zone

over the entire sampling period. Consequently, the main effect of snow addition was significant, whereas the time by snow addition interaction was nonsignificant (Table 5).

Live vegetation cover increased significantly over time, from 68% in 1994 to 72% by 2002. Trends differed significantly among snow addition treatments, with live vegetation cover increasing most in the ambient to medium snow zone, while decreasing in the deep zone from 72% in 1994 to 62% in 2002. Litter cover had little overall trend, remaining at about 15% over the sampling period. The time by snow addition interaction was significant, however, reflecting contrasting trends among snow zones (Table 5). Litter increased from 11% to 30% in the deep snow zone, while decreasing by 6% (19–13%) and 3% (13–10%) in the medium and ambient zones, respectively. Although litter increased by 6% more in OTCs than in control plots, the time by warming interaction was nonsignificant.

Diversity decreased significantly over the sampling period, but, as at the moist tundra site, this was mainly because of changes in relative abundance of functional groups rather than loss of species (Fig. 7). Richness remained at about 19/plot (55 species at the site). Despite a greater decrease in diversity within the deep compared with other snow zones, this difference was nonsignificant (Table 5). Similar to the moist site, the main reasons for these changes in diversity were an increase in the cover of a few dominant species and a decrease in the abundance of minor species. Canopy height increased significantly, from a mean of 1 cm in 1994 to 2 cm by 2002 (Table 6). This was due only to shrubs and was not significantly affected by either the summer warming or snow addition treatments.

Changes in the environment

Although the Arctic has experienced a regional warming over the last 30 years (Serreze *et al.*, 2000), the Arctic LTER climate data do not provide evidence for regional summer warming near our site during the time period of this experiment. Regressions of mean summer air temperatures (June, July, and August) against time showed a slight, marginally significant, decrease from 1988 to 2002 ($R^2 = 0.239$, $F_{1,13} = 4.08$; $P = 0.064$), while mean winter air temperatures did not change ($R^2 = 0.036$, $F_{1,12} = 0.412$, $P = 0.539$). There was no significant change in degree-day accumulations (sum of mean daily temperatures $>0^\circ\text{C}$) during the summer months. By contrast, summer precipitation significantly increased from 1988 to 2002 ($R^2 = 0.403$, $F_{1,13} = 8.789$, $P = 0.011$). There was a 28% increase in regional summer precipitation during the experiment (1994–2000), calculated from the regression relationship (Fig. 8).

Table 5 Probability values from univariate repeated-measures ANOVA of the dry site cover and diversity data

Variable	Source of variation						
	Between groups			Within groups			
	S	W	S × W	T	T × S	T × W	T × S × W
<i>Growth forms, vegetation, and litter</i>							
Shrubs	ns	ns	ns	<0.001	ns	ns	ns
Deciduous shrubs	ns	ns	ns	<0.001	<0.001	ns	ns
Evergreen shrubs	ns	ns	ns	<0.001	ns	ns	ns
Forbs	ns	ns	ns	ns	ns	ns	ns
Graminoids	ns	ns	ns	ns	ns	ns	ns
Lichens	<0.001	ns	ns	<0.001	<0.001	ns	ns
Live vegetation	ns	ns	ns	0.024	<0.001	ns	ns
Litter	<0.001	ns	ns	0.024	<0.001	ns	ns
<i>Five most common species in 1994</i>							
<i>Dryas octopetala</i>	ns	ns	ns	<0.001	ns	ns	ns
<i>Sphaerophorus globosus</i>	ns	ns	ns	<0.001	<0.001	ns	ns
<i>Polytrichum piliferum</i>	ns	ns	ns	0.024	ns	ns	ns
<i>Loiseleuria procumbens</i>	<0.001	ns	ns	<0.001	ns	ns	ns
<i>Alectoria ochroleuca</i>	0.030	ns	ns	0.012	ns	ns	ns
<i>Diversity</i>							
Evenness	ns	ns	ns	<0.001	ns	ns	ns
Shannon	ns	ns	ns	<0.001	ns	ns	ns

Significant values are shown in bold.

S, snow addition; W, warming treatment; T, time; ns, nonsignificant.

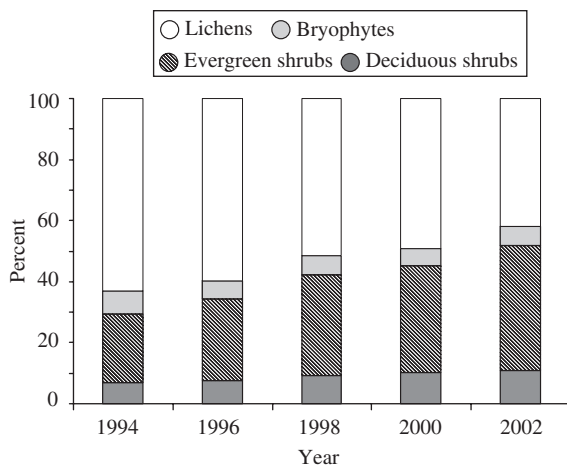


Fig. 7 Proportional abundance of the main functional groups at the dry tundra site, 1994–2002.

Discussion

Perhaps the most striking finding of this study is that over the 8-year sampling period the vegetation changed within control plots of both sites. Canopy height and the cover of shrubs, live vegetation, and litter all increased at the two sites, while lichen cover and diversity decreased. At the moist site, bryophytes decreased in cover, and an increase in graminoids

was almost entirely because of the sedge *E. vaginatum*. These changes in the control plots are qualitatively similar to those obtained in nutrient addition and warming experiments in the Arctic (e.g. Chapin & Shaver, 1985; Jonasson, 1992; Chapin *et al.*, 1995b; Press *et al.*, 1998; Robinson *et al.*, 1998; Shaver *et al.*, 1998; Arft *et al.*, 1999; Graglia *et al.*, 2001a; Molau, 2001; Shaver *et al.*, 2001), which have generally found an increase in vascular plant cover, especially deciduous shrubs, and a decrease in the abundance of lichens and mosses. Changes observed in unmanipulated vegetation over time (Chapin *et al.*, 1995b; Myneni *et al.*, 1997; Sturm *et al.*, 2001c; Lloyd & Fastie, 2002; Kudo & Suzuki, 2003) are also consistent with our results and those from the nutrient addition and warming experiments mentioned above. Also, observed changes closely match both expected (e.g. Chapin *et al.*, 1995b; Molau, 2001) and modeled (Epstein *et al.*, 2000) responses of arctic tundra vegetation to climate change. Soil and litter studies have shown a strong link between these changes in vegetation and faster carbon (C) and N cycling in the soil (Nadelhoffer *et al.*, 1991; Robinson *et al.*, 1995; Hobbie, 1996, 2000). This agreement with other studies increases our confidence in predictions based on small-scale studies like that reported here (Shaver & Jonasson, 1999). Because there is no evidence of recent disturbances at our study sites (Chapin *et al.*, 1995b), such as

Table 6 Probability values from univariate repeated-measures ANOVA of the dry site canopy height data

Variable	Source of variation						
	Between groups			Within groups			
	S	W	S × W	T	T × S	T × W	T × S × W
Overall canopy height	ns	ns	ns	0.006	ns	ns	ns
Shrubs	ns	ns	ns	<0.001	ns	ns	ns
Deciduous shrubs	ns	ns	ns	<0.001	ns	ns	ns
Evergreen shrubs	ns	ns	ns	0.012	ns	ns	ns

Significant values are shown in bold.

S, snow addition; W, warming treatment; T, time; ns, nonsignificant.

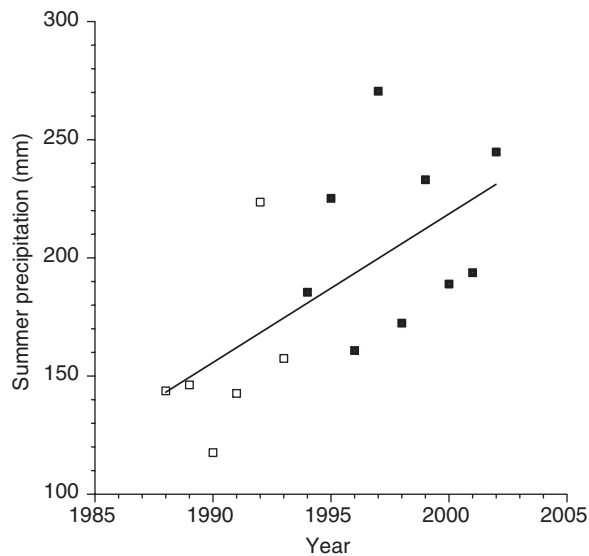


Fig. 8 Annual summer precipitation (June, July, August) recorded by the Arctic LTER approximately 600 m from our site, immediately prior to (open squares) and during (filled squares) our experiment.

from fire or significant herbivore outbreaks, we attribute the community changes measured within our control plots to regional climatic change. However, the most prominent change in climate detected at our site during the time period of our experiment was increased summer precipitation, not increased temperature. It is conceivable that this increased precipitation deepened the active layer and led to greater N availability in the soil, and thus to the community changes we observed. Experimentally increased summer precipitation enhanced plant growth, root and soil respiration, and the N fixation potential of arctic cryptogams (Phoenix *et al.*, 2001; Solheim *et al.*, 2002; Illeris *et al.*, 2003), although most of these studies were carried out in high arctic sites that are drier than ours.

Our snow addition treatment affected species abundance, canopy height, and diversity, whereas the

warming treatment had few measurable effects on vegetation. In addition, over the 8-year sampling period the effects of the snow treatment became more pronounced at the two sites. Based on short-term phenological responses that have been reported from these and other sites (e.g. Arft *et al.*, 1999; Walker *et al.*, 1999; Molau, 2001), the lack of a warming response at our two tundra sites was surprising. Conversely, the distribution and persistence of snow have long been recognized as major influences controlling ecological processes and vegetation patterns in arctic landscapes (Walker *et al.*, 1993, 2001). Although temperature has important direct and indirect effects on arctic plants (Chapin, 1983; Walker *et al.*, 1999; Shaver *et al.*, 2000), the interannual temperature fluctuation at our and other study sites has been considerably larger than the temperature increases within OTCs (Stenström *et al.*, 1997; Walker *et al.*, 1999; Molau, 2001). Also, the difference in soil temperature (2 cm depth) between deep and ambient snow zones during winter is about 15 °C (Walker *et al.*, 1999; Schimel *et al.*, 2004), considerably greater than the 1.5 °C difference between OTCs and control plots during summer.

The main community changes at the two sites were because of increases in cover of species dominant at the beginning of the study, particularly shrubs. This trend of increased shrub cover in response to climatic change supports predicted shifts in the herbaceous-woody balance of arctic tundra toward woody species (Chapin *et al.*, 1995b). We suggest that this response is largely an indirect effect of greater nutrient availability that may have resulted from increased summer precipitation deepening the active layer (Kane *et al.*, 1992) and/or increased winter soil temperatures in the snow addition treatments leading to greater overwinter mineralization (Schimel *et al.*, 2004), and associated increases in the rate of decomposition (Nadelhoffer *et al.*, 1991; Jonasson *et al.*, 1999). Several studies have shown the sensitivity of arctic and sub-arctic vegetation to altered nutrient regimes (e.g. Jonasson, 1992; Chapin *et al.*, 1995b;

Shaver & Chapin, 1995; Jonasson *et al.*, 1999; Graglia *et al.*, 2001a) and demonstrated the predominance of nutrient limitation, particularly with respect to N and P.

The differential trends exhibited by deciduous and evergreen shrubs at the moist tundra site also match anticipated responses (Chapin *et al.*, 1995b), and can be attributed to a greater production to biomass ratio of deciduous shrubs (Chapin, 1980; Shaver & Chapin, 1991), probable differences in timing and efficiency of N uptake (McKane *et al.*, 2002), combined with a greater physiological and morphological plasticity under altered environmental conditions (Chapin & Shaver, 1996). *B. nana* is particularly flexible in its development, and, with an increase in nutrients, will adjust how resources are allocated, thereby increasing the number of branches and rate that new apical meristems are produced (Bret-Harte *et al.*, 2001, 2002). By also altering the long to short-shoot ratio toward long shoots, *B. nana* is capable of significantly increasing both canopy density and height, which can effectively displace species intolerant to shading (Chapin *et al.*, 1995b; Bret-Harte *et al.*, 2001; Shaver *et al.*, 2001). At the moist site, *B. nana* and another common deciduous shrub, *S. pulchra*, increased in canopy height and cover by about the same amount, but it remains unclear whether the decrease in evergreen shrub cover reflected a decline in abundance caused because of shading by deciduous shrubs, or simply a decrease in the proportion of the canopy in which evergreen shrubs were the uppermost component, with no decline in abundance. At the dry site, where deciduous shrubs were a minor component of the vegetation, evergreen shrub cover increased.

The snow addition treatment had a significant effect on community changes at the two sites, particularly shrub abundance. Most increases in shrub cover and canopy height occurred in the medium snow zone of the moist site and the deep to medium zones of the dry site. Although snow addition reduced the growing season, this was only by about 2 weeks (Walker *et al.*, 1999), which therefore allowed plants to begin growing during a warmer period than would occur otherwise. Also, snow is an effective insulator and will protect vegetation from exposure to both wind and temperature extremes (Pomeroy & Brun, 2001; Walker *et al.*, 2001). Consequently, soil temperatures are generally higher in snow-covered than snow-free areas, an effect that increases with snow depth (Pomeroy & Brun, 2001). In winter, soil surface temperatures in the deep zone of the moist site remained about 15 °C warmer than in the ambient zone and minimum temperatures stayed above about -7 °C (Walker *et al.*, 1999; Schimel *et al.*, 2004). Such comparatively warm soil temperatures below snowpack can potentially raise microbial activity (Clein & Schimel, 1995; Williams *et al.*, 1998;

Brooks & Williams, 1999; Walker *et al.*, 2001), which may increase the rate that soil organic matter decomposes, thus raising nutrient availability during the spring thaw. Increased overwinter N mineralization and CO₂ flux were observed at both sites after 5 years (Schimel *et al.*, 2004), although there was no significant difference in the amount of decomposition in buried bags between deep and ambient snow zones after 2 years (Walker *et al.*, 1999). Increased shrub growth in the medium to deep zones might also have been promoted by either greater summer water availability or reduced exposure. Protection from wind and low temperatures may also help explain the increase in cover and canopy height of *E. vaginatum* at the moist site. Despite the sustained increase in *E. vaginatum* in our control plots, in control plots of a nearby site *E. vaginatum* biomass decreased significantly from 1982 to 1995, but increased between 1989 and 1995 (Shaver *et al.*, 2001). Thus, changes in abundance of this and other species at the two sites require cautious interpretations because they may represent either sustained trends or more short-term fluctuations, both of which require long-term data to differentiate.

Trends in lichen and bryophyte cover at the two sites suggest a negative effect associated with greater snow depth and increases in abundance of vascular plants. For example, bryophytes in the deep snow zone of the moist site increased in cover while overall vegetative cover, especially shrubs, decreased; this trend was reversed in the two other zones. Several studies in arctic tundra have found a negative relationship between bryophyte abundance and increases in vascular plant cover (e.g. Chapin *et al.*, 1995b; Jonasson *et al.*, 1999; also Cornelissen *et al.*, 2001 and references therein), while altered snow regimes have been shown to reduce lichen abundance (Benedict, 1990, 1991). Similar patterns occur in natural moist sedge tundra and have been interpreted as mainly because of shading (Jonasson, 1992; Tenhunen *et al.*, 1992). The accumulation of litter at our sites could have contributed to the decrease in lichen abundance (Chapin *et al.*, 1995b), especially within the deep zone where snow samples collected in 1994 contained more than 60 g m⁻² of organic matter in wind-blown litter (Walker *et al.*, 1999). Since then litter cover has continued to increase.

Most of the litter deposited on the leeward side of the snow fences arrives in early winter, coming from nearby snow-free areas and accumulating in the deep part of the two snowdrifts (Walker *et al.*, 1999). Because litter plays a fundamental role in biogeochemical processes (Hobbie, 1995), such an influx of litter may have significant effects on nutrient cycling, contributing to soil C and N pools (Hobbie, 1996; Bryant *et al.*, 1998; Fahnestock *et al.*, 2000; Shaw & Harte, 2001a). Yet, to

what extent accumulation of litter at the two sites might have caused an increase in soil nutrients remains unknown. Fahnestock *et al.* (2000) found that litter accumulation reduced soil surface temperature. Litter quality and temperature mainly control the rate of litter decomposition (Hobbie, 1996). Decomposition rate decreases with increasing concentrations of lignin and phenolic compounds, as well as colder temperatures (<25 °C, Nadelhoffer *et al.*, 1991; Clein & Schimel, 1995). Moss litter is the slowest to decompose, then litter from shrub stems and roots, followed by evergreen leaves, deciduous leaves, and graminoid tissue (Hobbie, 1995, 1996). Thus, changes in species abundance, particularly the growth of deciduous shrubs at the moist site, may already be affecting C and N cycling, and subsequently modifying nutrient pools. The increased density and canopy height of *B. nana*, for example, should promote C storage and slow the turnover of C and N in litter, while the diminishing bryophyte to graminoid ratio should increase the rates of both litter decomposition and nutrient mineralization (Hobbie, 1996; Shaver & Jonasson, 1999).

The reduction in apparent diversity at our sites, which was mainly because of increases in the cover of species most abundant at the beginning of the experiment, is consistent with findings from other manipulation experiments in the Arctic (Press *et al.*, 1998; Jonasson *et al.*, 1999; Shaver & Jonasson, 1999; Graglia *et al.*, 2001b; Shaver *et al.*, 2001). Broadly, these studies have shown an increase in growth of vascular plants, particularly shrubs, is accompanied by a decrease in abundance mainly of bryophytes and lichens, and sometimes loss of species. After 9 years of a fertilizer and warming experiment in moist tundra, Chapin *et al.* (1995b) reported a decrease in species richness of 30–50%, mostly because of loss of minor forb species. Such a decrease in diversity associated with climate warming is likely to have significant and long-term consequences for arctic landscapes (Chapin *et al.*, 1997). For instance, a decrease in the abundance and diversity of bryophytes may change soil–water and soil–temperature regimes, increase the depth of the active layer, and affect biogeochemical processes through altered litter composition (Chapin *et al.*, 1995b; Walker *et al.*, 1999; Shaver *et al.*, 2000; Graglia *et al.*, 2001a). Because a decrease in abundance or loss of a functional group, such as bryophytes, can have major effects on ecosystems, a decrease in species diversity within a group may reduce the ability of the functional group, and therefore, the entire system, to respond to environmental change (Chapin *et al.*, 1995a, 2000, but see Naeem, 2002; Pfisterer & Schmid, 2002).

In coming years, what community changes are likely at our two tundra sites and, based on the vegetation

changes described, what general predictions can we make for arctic tundra? The most conspicuous change at the sites will probably be a continuing increase in shrub cover, especially deciduous shrubs in moist tundra. This was a clear trend in the control plots and appears to be a more widespread phenomenon in the Alaskan Arctic (Sturm *et al.*, 2001c). Because shrubs act like small, natural snow fences, such an increase in shrub abundance may already be affecting the distribution and persistence of snow. Predictions suggest that the expected increase in shrub cover could raise snow depths by 10–25%, with a subsequent increase in spring run-off from such shrub-rich sites (Sturm *et al.*, 2001b; Liston *et al.*, 2002). The greater snow depth among shrubs raises winter soil temperatures and, compared with adjacent areas having few or no shrubs, may promote higher rates of litter decomposition and an increase in nutrient availability. Such positive feedback may already be occurring within control plots of the moist tundra site and would encourage further shrub growth. Increases in shrub cover will also change canopy structure, which is expected to alter the summer energy balance by increasing the absorption of solar radiation and evapotranspiration (Shaver *et al.*, 2000; Sturm *et al.*, 2001b), thus, raising soil moisture in some areas, while decreasing it in others. In moist tundra, where vegetation cover is usually complete, an expanding shrub canopy will adversely affect shade intolerant forbs, bryophytes, and lichens. In dry tundra, where the canopy is more open, lichens may be less affected, at least in the short term (<10 years), while the vegetation remains free of taller plants and unvegetated areas are colonized by prostrate evergreen shrubs.

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