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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Differential ecophysiological response of deciduous shrubs and a graminoid to long-term experimental snow reductions and additions in moist acidic tundra, Northern Alaska

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Abstract Changes in winter precipitation that include both decreases and increases in winter snow are underway across the Arctic. In this study, we used a 14-year experiment that has increased and decreased winter snow in the moist acidic tussock tundra of northern Alaska to understand impacts of variation in winter snow depth on summer leaf-level ecophysiology of two deciduous shrubs and a graminoid species, including: instantaneous rates of leaf gas exchange, and δ^{13}C, δ^{15}N, and nitrogen (N) concentrations of *Betula nana*, *Salix pulchra*, and *Eriophorum vaginatum.* Leaf-level measurements were complemented by measurements of canopy leaf area index (LAI) and depth of thaw. Reductions in snow lowered summer leaf photosynthesis, conductance, and transpiration rates by up to 40 % compared to ambient and deep snow conditions for *Eriophorum vaginatum*, and reduced *Salix pulchra* conductance and transpiration by up to 49 %. In contrast, *Betula nana* exhibited no changes in leaf gas exchange in response to lower or deeper snow. Canopy LAI increased with added snow, while reduced winter snow resulted in lower growing season soil temperatures and reduced thaw depths. Our findings indicate that the spatial and temporal variability of future snow depth will have individualistic consequences for leaf-level C fixation and water flux by tundra species, and that these responses will be manifested over the longer term by changes in canopy traits, depth of thaw, soil C and N processes, and trace gas (CO_2 and H_2O) exchanges between the tundra and the atmosphere.

Keywords Photosynthesis · Leaf area index · Thaw depth · δ^{13}C · δ^{15}N

Introduction

Global climate change has led to temperature increases in the Arctic that are nearly double those of lower latitudes, and these increases are predicted to continue (IPCC 2007; Kaufman et al. 2009; Serreze and Barry 2011). In addition, precipitation changes are also occurring, including increases in summer rainfall and regionally specific changes in the patterns of winter snow accumulation (Barber et al. 2008; Min et al. 2008; Callaghan et al. 2011; Liston and Hiemstra 2011). Snow depth appears to have increased over much of Scandinavian and Eurasian Arctic and decreased over much of the North American Arctic over the past 50 years (Callaghan et al. 2011 and references therein). However, Liston and Hiemstra (2011) document a generalized decrease in snow precipitation over the Arctic of 0.02 cm per decade from 1979 to 2009. Snow cover duration has tended to decrease throughout much of the Arctic particularly post-1980 (Callaghan et al. 2011; Liston and Hiemstra 2011). Callaghan et al. (2011) project that snow depth will increase by 0–15 % by 2050 over much of the Arctic and that snow cover duration will decrease by 10–20 %. Alaska and northern Scandinavia are projected to see decreases in snow cover duration of 30–40 % by 2050 (Callaghan et al. 2011). In addition to changes in patterns of snow accumulation, winter warming events are increasing in frequency in the Arctic (Brooks et al. 2011; Bokhorst et al. 2008).

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Increased snow cover and depth have important impacts on arctic tundra ecosystem processes leading to: (1) greater CO_2 emissions in winter (Fahnestock et al. 1998, 1999; Nobrega and Grogan 2007; Morgner et al. 2010; Rogers et al. 2011), (2) either increases or decreases in annual net ecosystem C exchange (Welker et al. 2000; Natali et al. 2012), (3) increases in winter nitrogen (N) mineralization (Schimel et al. 2004; Borner et al. 2008; Rogers et al. 2011), (4) changes in plant phenology such as delays in leaf emergence and flowering (Aerts et al. 2004; Wipf et al. 2006; Borner et al. 2008; Wipf and Rixen 2010; Cooper 2010), and (5) reductions in the number of spring-time freezing thaw and winter warming events with implications for nutrient cycling and plant damage (Grogan et al. 2004; Bokhorst et al. 2008, 2009; Nobrega and Grogan 2007; Brooks et al. 2011).

Sturm et al. (2001) originally proposed a positive feedback relationship between snow and shrubs whereby shrubs lead to a localized accumulation of snow and this in turn facilitates the continued growth of this life form. The mechanism driving this shrub-perpetuation appears to be that deeper snow leads to warmer soil temperatures in winter, higher rates of N mineralization in winter, and an additional source of N that is used by tundra plants the following summer (Bilbrough et al. 2000; Schimel et al. 2004; Welker et al. 2005b). By acquiring additional N, shrubs then grow larger and perpetuate the cycle through greater snow accumulation (Sturm et al. 2005). This feed-forward scenario is supported by increases in shrub abundance under deeper snow (Wahren et al. 2005; Mercado-Diaz 2011) and by increases in shrub abundance throughout the Arctic (Tape et al. 2006; Forbes et al. 2010). However, increases in shrubs have also been correlated to increases in summer air temperatures (Forbes et al. 2010; Blok et al. 2011). Understanding how tundra plants and ecosystems will respond to both increases and decreases in snow depth is important to predict shifts in regional vegetation traits, and exchanges of carbon (C), energy, and water at the landscape scale (McGuire et al. 2012).

While most studies to date have made comparisons between ambient and enhanced snow (Welker et al. 2005b; Larsen et al. 2007; Nobrega and Grogan 2007; Wipf and Rixen 2010 and references therein), to our knowledge, no other study has quantified how lower winter snow will affect summer-time leaf level gas exchange and mineral nutrition and the plant canopies of Arctic tundra ecosystems. Understanding how reduced winter snow depths affects tundra plant processes and ecosystems traits in the summer is important to understand how declines in snow cover such as those seen over the North American Arctic (Callaghan et al. 2011) may lead to changes in soil thermal regimes, N supplies for plants, shifts in the role of snow melt water as a plant water source (Welker et al. 2005a), and the cascading consequences for the timing and magnitudes of forage quality and quantify used by herbivores (Walsh et al. 1997). Insights into decreased snow impacts on tundra communities will also lead to a greater understanding of the impacts of inter-annual and spatial variations in snow fall. Understanding the consequences of reduced snow also provides an important means by which to fully evaluate our aforementioned snow–shrub hypothesis that has been developed principally on studies of deeper snow (Sturm et al. 2005). If deeper snow leads to greater N availability and increases in shrub productivity, then decreases in snow cover should lead to reduced N availability and less productive shrubs (i.e. lower rates of photosynthesis) and a possible change in C dynamics of tundra under shrubbier conditions (Welker et al. 2000; Anderson-Smith 2013). In addition, as increased snow leads to increases in winter-time respiratory carbon loss (Nobrega and Grogan 2007; Natali et al. 2012), decreases could have the opposite effect.

In this study, we used long-term (14 years) experimental manipulations of snow to evaluate the response of leaf gas exchange, leaf $\delta^{13}C$, $\delta^{15}N$, and leaf N concentrations of three dominant species in the moist acidic tussock tundra of northern Alaska to increases and decreases in snow depth and the associated changes in snow cover duration. Measures of leaf $\delta^{13}C$, and N were made to provide integrated insights into levels of leaf gas exchange (Evans et al. 1986; Farquhar et al. 1989), while measures of $\delta^{15}N$ were made to provide insights into N availability (Craine et al. 2009). At the ecosystem scale, we made measurements of leaf area index (LAI) and canopy height in response to these manipulations to assess potential changes in canopy structure and vegetation productivity that may be a result of our species leaf-level responses. We tested the following hypotheses regarding snow depth:

1. Decreased snow depth results in decreased summer-time soil temperature, N availability, and thaw depth.
2. Decreases in snow depth lead to decreases in summer-time leaf-level photosynthesis, transpiration, conductance, leaf N concentrations, and leaf $\delta^{15}N$, and increases in summer-time $\delta^{13}C$ of two deciduous shrubs and a graminoid.
3. Decreases in snow depth lead to reductions in summer-time LAI and canopy height.

Materials and methods

Site and treatment descriptions

This study took place at the Toolik Lake Long Term Ecological Research Site (68°38′N, 149°34′W, elevation 760 m asl) in the northern foothills of the Brooks Range, Alaska, USA. The tundra type where the treatments took place is moist acidic tussock dwarf shrub. The sedge *Eriophorum vaginatum* forms tussocks that are a dominant component of the community, as are deciduous (*Betula nana* and *Salix pulchra*) and evergreen shrubs and mosses (Walhen 2002). In the summer of 1994, a wooden snow fence, 2.8 × 60 m, was constructed to increase snow depth. Snow drifts behind the fence typically reached a maximum depth of 3 m adjacent to the fence. Peak snow depth in the drift zone where we worked was ~2 m deep at a distance of 25 m from the fence. Snow accumulates behind the fence earlier, and in the deepest part of the drift remains at least 3 weeks later during the spring (Fahnestock et al. 2000). In addition to generating a snow drift, a decreased snow treatment is generated 80 m in the lee of the fence. This area was documented early in the study (Walker et al. 1999), but our focus on this treatment did not begin until May 2008. The location of the decreased snow zone used in this study (85 m) is approximately 13 m closer than the suggested use of snow fences for preventing snow drifts on roads (SHRP 1991), but is generally consistent with studies of patterns of snow accumulation behind snow fences (SHRP 1991). The decreased snow and drift treatments have been in place since the initiation of the experiment in 1994. Unlike other studies that increased snow depth while maintaining consistent snow cover duration (Natali et al. 2012), our manipulations of snow led to changes in both snow depth as well snow cover duration.

In 2008, we took measurements in six 1-m^2 plots in an area of ambient snow located adjacent to the fence, six 1-m^2 plots in the deeper snow area located 25 m from the fence, and six 1-m^2 plots in the decreased snow zone (85 m from the fence). Plot selection occurred by randomly selecting the first plot of each zone and spacing the remaining five at 9-m intervals.

Leaf gas exchange, leaf N and isotope measurements

Leaf level gas exchange measurements were made in the early (June 19–24), mid- (Aug 1–5) and late growing season (Aug 15–17) of 2008. Leaf gas exchange was measured on the youngest fully expanded leaves of each species in each plot at the time of measurement with a LI-6400 portable gas exchange system (LI-COR, Lincoln, NE, USA). Reference CO_2 concentration was maintained at 400 μmol mol^{-1}. Incoming PAR was maintained at 1,500 μmol photons m^{-2} s^{-1}. Measurements were made between 1000 and 1700 hours. Leaf area in the cuvette was determined from marking leaves and measuring the area with a LI-3100 leaf area meter (LI-COR). Gas exchange measurements were adjusted for leaf areas. Leaves used in gas exchange measurements were dried at 60 °C in convection ovens, then ground to a fine powder in a ball mill, and analyzed for N and C concentrations and δ^{13}C and δ^{15}N on a Costech Elemental 4010 elemental analyzer (Costech Analytical, Valencia, CA, USA) interfaced with a Thermo-Finnigan Delta Plus XP continuous-flow stable isotope ratio mass spectrometer (Thermo Electron, Waltham, MA, USA) at the University of Alaska Anchorage.

Canopy measurements

Canopy leaf area was measured in each of the plots in the three snow zones on August 6 and 7, 2008 using an ACCU-PAR linear PAR ceptometer (Decagon, Pullman, WA, USA). The greatest distance from the top of the canopy to the moss surface of the inter-tussocks below along a 1-m east–west transect centered on the middle of each plot was measured in each plot in each treatment.

Microclimate measurements

Soil temperature measurements at 10 cm depth from the top of the moss layer were made during gas exchange measurements with a 10-cm temperature probe (Model 82021-156; VWR International, West Chester, PA, USA).

Thaw depth during the 2008 growing season was measured from the top of the moss layer using a graduated metal probe placed in the inter-tussock areas of each of the plots ($n = 6$) in the ambient, drift, and decreased snow zones. Measurements were made at approximately weekly intervals during the 2008 growing season.

Soil nitrogen availability was assessed using ion exchange membranes (PRS Probes; Western Ag Innovations, Saskatoon, Saskatchewan, Canada). Two cation and two anion exchange probes were installed in five inter-tussock areas and five tussocks in the ambient and drift zones but not the decreased snow zone. Probes were installed on 24 June 2008 and collected on 10 August 2008. Probes were washed thoroughly with distilled water soon after collection and were eluted as replicates (2 cation and 2 anion probes) for 1 h by the manufacturer using 0.5 mol l^{-1} HCL. The eluate was analyzed for NO_3^- and NH_4^+ concentrations by automated colorimetry.

Surface temperature during the winter months was measured using iButton sensors (Maxim, Sunnyvale, CA, USA) which recorded the average temperature over 4 h. The data used in this study were summarized into daily averages. iButton sensors were placed in the field, 2 cm under the moss layer, on September 23, 2008 and removed on June 14, 2009. Sensors were placed in the ambient ($n = 4$), drift ($n = 5$), and decreased snow zones ($n = 5$).

Snow depth was measured in 20 locations in each of the ambient, drift, and decreased snow zones on 10 January

2009, and the ambient and decreased snow zones on 19 March 2009. All snow depths were measured with a graduated probe.

Statistical analyses

Statistical analyses were carried out with SAS 9.2 (SAS Institute, Cary, NC, USA) and SigmaPlot 12 (Systat Software, Chicago, IL, USA). In all ANOVA analyses, the data were tested for normality (Shapiro–Wilk) and homogeneity of variance (Levene's). If data failed these tests, attempts were made to transform data to meet these conditions. All post hoc analyses of significant effects beyond the main effects were carried out using Tukey's Honest Significant Difference (Tukey ($P < 0.05$) unless otherwise noted. Five covariance structures were tested for all repeated measures mixed model ANOVA analyses (Proc MIXED; SAS) and the one with the lowest Akaike's Information Criterion was chosen (Littell et al. 2006). In all repeated measures analyses, snow zone (decreased, ambient, and drift) and date (e.g., early, mid- or late season) were considered fixed effects. Data in one-way ANOVA analyses that failed normality or homogeneity of variance were analyzed with Kruskal–Wallis tests for differences between treatments unless otherwise noted.

Potential differences between decreased, ambient and drift snow depth in January 2009 were analyzed with a one-way ANOVA (Proc GLM; SAS). The lack of multiple measurements in the drift zone in March 2009 excluded these data from a repeated measures analysis. Difference between low and ambient snow in March failed homogeneity of variance and were compared with a Mann–Whitney *U* test using SigmaPlot 12. Over-winter soil surface temperature data failed normality; as a result, we compared differences in the average daily temperatures from September 26, 2008 to April 20, 2009 between the three snow zones (decreased, ambient, and drift) with a Kruskal–Wallis test, and all pairwise multiple comparison procedures (Dunn's) to test for significant differences using SigmaPlot 12. Soil temperature at 10 cm depth in each of the three snow zones and growing season dates were analyzed with a repeated measures mixed model ANOVA with snow zones and season considered as fixed effects (Proc MIXED). Growing season thaw depth data were analyzed with a two-way repeated measures mixed model ANOVA (Proc MIXED) with treatment and date as main effects and all pairwise comparisons based on the coefficient vectors defining the snow and date least-squares means for a given date. There was no difference in the tussock and inter-tussock total soil N levels ($F_{1,34} = 0.128$, $P = 0.724$), so tussock and inter-tussock results were pooled for a sample size of $n = 10$ per treatment. Probes were only placed in the ambient and drift zones and not the decreased snow. Differences between ambient and drift total soil N, NO_3^-, and NH_4^+ were measured with independent samples *t* tests (SAS). Unbalanced repeated measures mixed model ANOVA analysis (Proc MIXED) was used to test for significant differences in the six leaf-level variables: photosynthetic capacity (A_{max}), stomatal conductance (g_s), leaf transpiration (T_l), N, $\delta^{13}C$, and $\delta^{15}N$ within a species across the three treatments and three dates (early, mid- and late season). Differences in LAI and canopy height between treatments were tested for using a one-way ANOVA (Proc GLM).

Results

There was a significant effect of snow zones ($F_{2,57} = 263.5$, $P < 0.0001$) on snow depth in January. Mean snow depths in the decreased, ambient and drift snow zones on January 19, 2009 were 40 cm (±2), 65 cm (±1), and 109 cm (±2), respectively, and were all significantly ($P < 0.05$) different from each other. Snow depths in the decreased and ambient snow zones on March 19, 2009 were 32 cm (±1) and 64 cm (±3), respectively, and were significantly different from each other ($U = 1.5$, $P < 0.001$).

The average daily temperature at 2 cm depth from September 26, 2008 to April 20, 2009 was −7.1 °C (±0.1) for decreased snow, −4.7 °C (±0.2) for ambient snow, and −2.9 °C (±0.2) for the drift snow (Fig. 1). There was a significant effect ($P < 0.001$) of snow zone on the average daily temperatures across these dates with post hoc tests revealing differences between the drift and decreased snow zones. A one-way ANOVA testing for differences in daily temperatures between the three snow zones on March 24, 2009, the date with the lowest daily temperature,

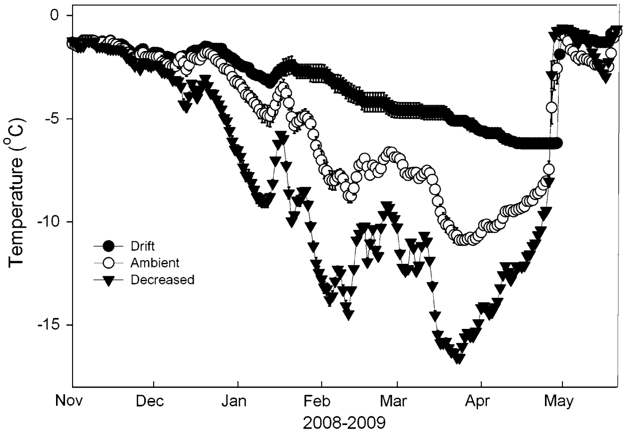

Fig. 1 Average daily temperatures 2 cm below bryophyte surface in the intertussock area of three snow regimes; ambient, drift near a snow fence; and a decreased snow area (80 m) from the fence. Values are the means of sensors, and *error bars* are ±1SE of the mean. Error bars are graphed but *symbols* are often larger than error bars

revealed an effect of snow zone ($P < 0.001$) with differences between all snow zones. Daily temperature in the drift (−5.1 ± 0.3 °C) was highest followed by temperature in the ambient snow (−10.9 ± 0.3 °C) and decreased snow (−16.5 ± 0.1 °C).

Analysis of soil temperatures at 10 cm depth made during 1–2 days in the early, mid- and late growing seasons revealed that there was an effect of snow zone ($P < 0.0001$) and season ($P = 0.0002$) but not a snow zone by season interaction ($P = 0.5432$). Post hoc analyses of the main effects of snow zone revealed that temperatures in the drift (2.0–3.2 °C) were 60 and 97 % warmer than in ambient (1.5–2.0 °C) ($P < 0.0001$) or decreased snow (0.9–1.6 °C) ($P < 0.0001$), respectively, but there was only a marginally significant difference between ambient and decreased snow zone temperatures ($P = 0.0996$). Soil temperatures in the late season were 56–62 % greater than in either the early ($P < 0.0001$) or mid- ($P = 0.0005$) season but there was no difference between early and mid- ($P = 0.8003$) season soil temperatures. Analyses within dates revealed that temperatures in the drift were warmer than the decreased snow throughout the growing season and warmer than the ambient snow only in the late season. Temperatures in the decreased and ambient snow zone did not differ for any dates.

There were effects of snow zone ($P = 0.0093$), season ($P < 0.001$), and a snow zone by season interaction ($P = 0.0207$) on thaw depth. Tests for simple effects within dates revealed that thaw depths in the decreased snow zone were up to 42 % shallower than in the ambient snow zone for three of the measurement dates (Fig. 2). At the end of the growing season, thaw depth in the decreased snow zone was 26 % lower than in the drift but not lower than the ambient.

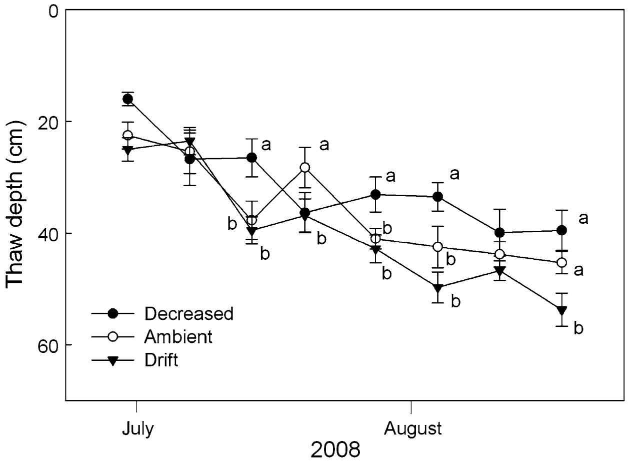

Fig. 2 Depth to permafrost in three different areas of snow accumulation: ambient snow; a snow drift behind a snow fence; and an area of decreased snow accumulation created by the same snow fence. *Symbols* are the means, and *error bars* represent ±1SE of the mean

Mean total N availability (μg cm^{-2} $47^{-\mathrm{days}}$) in the drift (66.9 ± 7.5) was 67 % greater ($P = 0.0030$) than in the ambient snow (40.1 ± 4.8). There was no difference between ambient (2.56 ± 0.34) and drift (1.72 ± 0.50) snow zone values of $\mathrm{NO_3}^-$ concentrations ($P = 0.1270$). The values of $\mathrm{NH_4}^+$ in the drift (65.22 ± 7.57) were 74 % greater than those in the ambient snow (37.52 ± 4.68) ($P = 0.0024$).

Snow zone had an effect on the maximum photosynthetic capacity (A_{max}) of *E. vaginatum* but did not affect A_{max} values of either *S. pulchra* or *B. nana* (Table 1; Fig. 3). Post hoc analyses of this main effect revealed that values of A_{max} in the decreased snow were lower than ambient ($P = 0.0015$) and drift ($P = 0.0004$) snow, but that there were no differences ($P = 0.5785$) between ambient and drift values. Analyses within seasons demonstrated that early season A_{max} of *E. vaginatum* in the decreased snow was 43 % lower than in the ambient ($P = 0.0024$) and 34 % lower than in the drift snow ($P = 0.0296$), with no difference between ambient and drift snow ($P = 0.2815$). Mid-season A_{max} of *E. vaginatum* in the decreased snow was 36 % lower than in drift snow ($P = 0.0361$), but was not different from values in the ambient snow ($P = 0.2364$) (Fig. 4), and nor was there a difference between ambient and drift snow ($P = 0.3369$) A_{max} values at this date. There were no differences between A_{max} values of *E. vaginatum* in the late season for any of the snow zones.

There was a significant effect of snow zone on the rates of stomatal conductance (g_s) for both *E. vaginatum* and *S. pulchra* but not for *B. nana* (Table 1). Analysis of the main effect of snow zone on *E. vaginatum* g_s values revealed that g_s was lower in the decreased snow than ambient ($P = 0.0453$) or drift ($P = 0.0115$) snow but that there was no difference between ambient and drift values ($P = 0.3931$) (Fig. 3). A similar trend was found for g_s of *S. pulchra* where decreased snow g_s values were lower than ambient ($P = 0.0025$) or drift ($P = 0.0131$) but there were no differences between ambient and drift snow g_s values ($P = 0.4329$). Analyses of snow zone effects within dates found that g_s of *E. vaginatum* did not differ between snow zones for early or late season measurements but that mid-season g_s values in the decreased snow were 39 % lower than those in the drift ($P = 0.0449$) and tended to be 35 % lower than those in the ambient ($P = 0.0910$). There was no difference between the ambient and drift zone values of g_s ($P = 0.7080$) of *E. vaginatum* at this date. For *S. pulchra* in the early season, the values of g_s in the decreased snow were 47–52 % lower than those in the ambient ($P = 0.0045$) or drift ($P = 0.0270$) but there were no differences ($P = 0.5821$) between ambient and drift values. In the mid-season, the values of g_s for *S. pulchra* in the decreased snow were 35 % lower than those in the ambient ($P = 0.0411$) with no other differences between snow

Table 1 Results of repeated measures mixed model ANOVA (Proc MIXED, SAS) of the effects of snow (*Sn*) and time of growing season (*Sea*) for each of three common moist acidic tundra species in 2008 on the following leaf variables

	B. nana			*S. pulchra*			*E. vaginatum*		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
A_{max}									
Sn	2	0.20	0.8188	2	2.81	0.0933	2	9.14	**0.0025**
Sea	2	4.92	**0.0145**	2	1.62	0.2148	2	20.99	**<0.0001**
Sn × Sea	4	0.80	0.5349	4	2.39	0.0741	4	1.74	0.1697
g_s									
Sn	2	1.44	0.2686	2	7.61	**0.0060**	2	4.12	**0.0384**
Sea	2	3.50	0.0624	2	0.59	0.5608	2	6.56	**0.0098**
Sn × Sea	4	0.75	0.5666	4	0.56	0.6935	4	1.19	0.3543
T_l									
Sn	2	0.99	0.3898	2	9.10	**0.0031**	2	9.30	**0.0022**
Sea	2	9.92	**0.0006**	2	1.86	0.1953	2	8.95	**0.0030**
Sn × Sea	4	0.96	0.4448	4	0.96	0.4557	4	2.97	0.0527
N									
Sn	2	1.78	0.2029	2	1.50	0.2558	2	0.72	0.5064
Sea	2	216.0	**<0.0001**	2	99.11	**<0.0001**	2	6.08	**<0.0001**
Sn × Sea	4	1.76	0.1896	4	0.85	0.5140	4	0.30	0.8755
$\delta^{13}C$									
Sn	2	0.31	0.7384	2	6.21	**0.0067**	2	13.26	**0.0007**
Sea	2	4.2	**0.0253**	2	1.12	0.3403	2	3.98	**0.0472**
Sn × Sea	4	0.29	0.8790	4	0.87	0.4947	4	1.5	0.2571
$\delta^{15}N$									
Sn	2	19.49	**<0.0001**	2	4.19	**0.0325**	2	6.45	**0.0080**
Sea	2	1.03	0.3727	2	5.98	**0.0065**	2	3.18	0.0585
Sn × Sea	4	0.26	0.8996	4	2.37	0.0742	4	0.05	0.9957

Photosynthetic capacity [A_{max} (μmol CO_2 m^{-2}/s^{-1})], stomatal conductance [g_s (mmol H_2O m^{-2} s^{-1})], transpiration [T_l (mmol H_2O m^{-2} s^{-1})], N concentration (mg g^{-1}), $\delta^{13}C$ (‰), and $\delta^{15}N$ (‰). Concentration of N for *B. nana* leaves did not meet the conditions of ANOVA and data were not analyzed. See Figs. 3 and 4 for means and SE

Significant values in bold ($P < 0.05$)

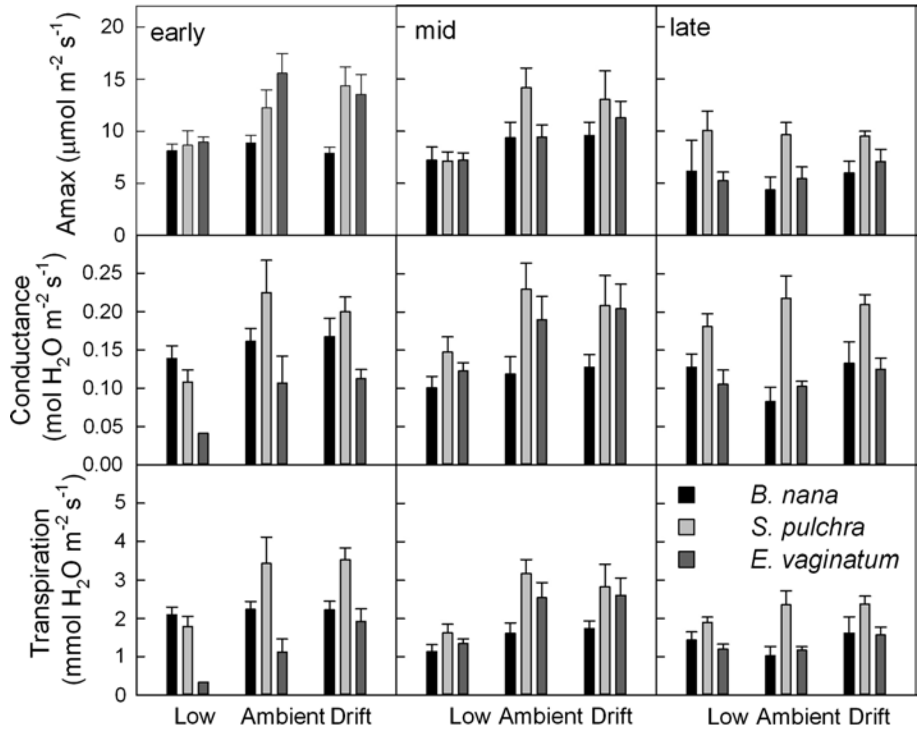

Fig. 3 The leaf level gas exchange responses of three common moist acidic tundra species, *Betula nana*, *Salix pulchra*, and *Eriophorum vaginatum*, to long-term snow and temperature manipulations. Data were collected in early, mid-, and late growing season. *Symbols* are the means and *error bars* represent ±1SE of the mean

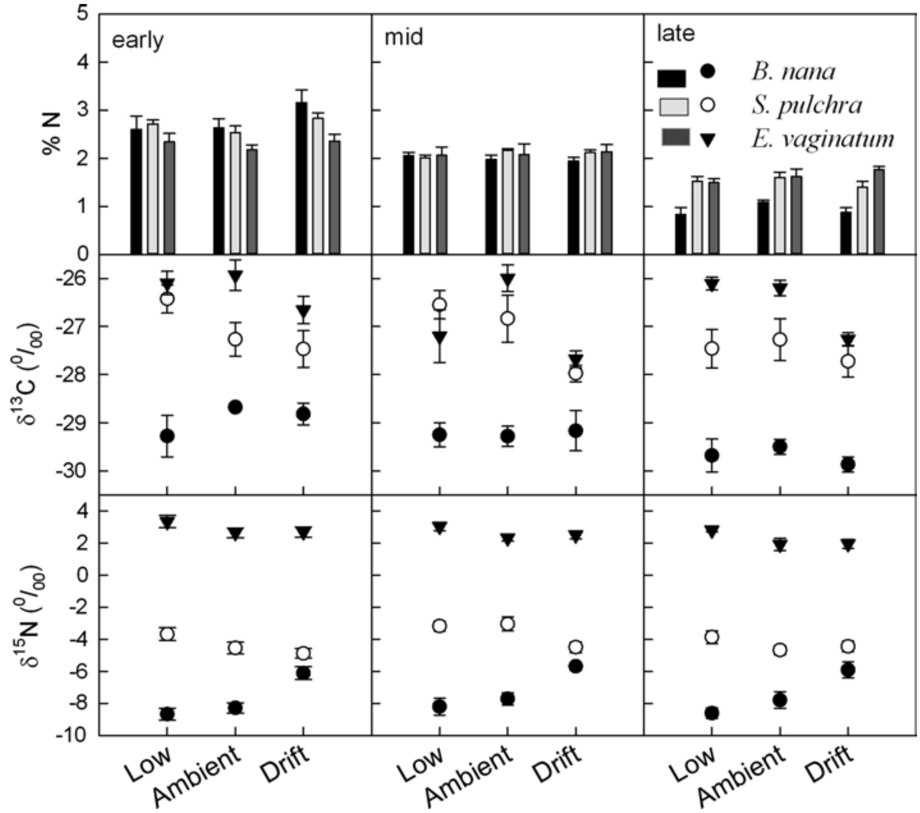

Fig. 4 The leaf level responses of three common moist acidic tundra species, *Betula nana*, *Salix pulchra*, and *Eriophorum vaginatum*, to long-term snow and temperature manipulations. Data were collected in early, mid-, and late growing season. *Symbols* are the means and *error bars* represent ±1SE of the mean

zones. The late season values of g_s for *S. pulchra* did not differ between snow zones.

Snow zone affected the rates of leaf transpiration (T_l) of *E. vaginatum* and *S. pulchra* but not *B. nana*. Analysis of the main effect of snow zone on T_l for *E. vaginatum* revealed that T_l was lower in decreased snow than in either ambient ($P = 0.0175$) or drift ($P = 0.0005$) snow and that there were marginally significant lower values in the ambient than drift ($P = 0.0575$) snow (Fig. 3). Similarly, the values of T_l for *S. pulchra* in the decreased snow were lower than ambient ($P = 0.0021$) or drift ($P = 0.0034$) snow but there were no differences between ambient and drift values ($P = 0.8390$). Within season analyses revealed that early season T_l values of *E. vaginatum* in the decreased snow were 83 % lower than in the drift ($P = 0.0237$), with no other difference in T_l between snow zones at this date. Mid-season values of T_l for *E. vaginatum* were 47–48 % lower in the decreased snow than in the ambient ($P = 0.0304$) or drift ($P = 0.\ 0240$). Late season values of T_l for *E. vaginatum* tended ($P = 0.0870$) to be 25 % lower in the decreased than ambient snow but there were no other differences between snow zones at this date. Rates of T_l of *S. pulchra* in the decreased snow in the early season were 47–49 % lower than in the ambient ($P = 0.0213$) or drift ($P = 0.0177$) snow with no differences between ambient and drift ($P = 0.8625$). Mid-season rates of T_l for *S. pulchra* in the decreased snow were 43–49 % lower than those in the ambient snow ($P = 0.0208$) and were marginally significantly lower than the drift snow ($P = 0.0627$). There were no differences in the late season T_l values of *S. pulchra* between snow zones.

Snow zones did not affect leaf N of any of the species (Table 1).

Snow zones affected the δ^{13}C values of both *E. vaginatum* and *S. pulchra* but not *B. nana* (Table 1). Analysis of the main effects of snow zones revealed that the values of δ^{13}C for *E. vaginatum* in the decreased ($P = 0.0081$) and ambient ($P = 0.0002$) snow were enriched (less negative) relative to the drift snow but were not different ($P = 0.0853$) from each other (Fig. 4). The δ^{13}C values for *S. pulchra* in the decreased snow were also enriched relative to those in the drift ($P = 0.0050$) but there were no other differences between snow zones for this species.

The values of δ^{15}N for *E. vaginatum* in the decreased snow were enriched relative to ambient ($P = 0.0032$) and drift ($P = 0.0144$) snow areas with no difference between ambient and drift snow zones ($P = 0.4796$) (Table 1). *Salix pulchra* δ^{15}N values in the drift were enriched relative to decreased snow ($P = 0.0099$) with no other differences between snow zones. The values of δ^{15}N for *B. nana* in the drift were enriched relative to ambient ($P = 0.0008$) and decreased snow ($P < 0.0001$) but there was no difference between ambient and decreased snow zone values ($P = 0.6829$) (Fig. 4).

Snow zone had a significant effect on LAI ($P = 0.0348$) and canopy height ($P = 0.0009$). The values of LAI in the drift (mean = 1.42, SE = 0.21) were 52 % greater than in the decreased snow zone while there were no other differences in the LAI values between snow zones. Canopy height in the drift (mean = 59 cm, SE = 6) was 40–47 % higher ($P < 0.05$) than in the ambient and decreased snow zones. There were no differences in canopy height between ambient and decreased snow zones.

Discussion

Long-term experimental reductions in snow depth lead to 42 % lower rates of photosynthesis and transpiration for the dominant graminoid *E. vaginatum* and 49 % lower rates of transpiration in the deciduous shrub *S. pulchra* relative to rates in ambient snow depths. In contrast, leaf level physiology of the deciduous shrub *B. nana* was not impacted by reduced snow. The reductions in leaf level gas exchange seen in *E. vaginatum* in particular are consistent with colder soils and reduced thaw depth effects on water flux across root membranes and reduced gas exchange rates of tundra plants (Dawson and Bliss 1989; Sullivan and Welker 2007). These differences in the rates of leaf level gas exchange across decreased, ambient and deeper snow highlight the complexity of snow effects on the processes that regulate leaf photosynthesis, transpiration, and conductance (Fig. 3), and set the stage for developing more comprehensive understanding of the role of winter in controlling important feedback processes of C and water cycling. For example, increased snow depth has led to increases of winter time C flux in other tundra systems with the potential to change these ecosystems from net annual sinks of C to annual sources (Nobrega and Grogan 2007; Natali et al. 2012). While ecosystem level C flux was not measured in this study, the heretofore unstudied experimental reductions in winter time snow depth in Arctic tundra systems suggest that reductions in snow depth could have important impacts on ecosystem annual net carbon exchange.

Changes in snow depth also resulted in the alteration of the snow free date for these areas which can have impacts on plant phenology such as delaying or increasing the timing of flowering and leaf development (Aerts et al. 2004; Wipf et al. 2006; Borner et al. 2008; Wipf 2010; Cooper 2010). Typically, the ambient snow zone becomes snow free in the first week of June and is approximately 1 week to 10 days earlier than melt out in the drift zone of this study (Borner et al. 2008). Early season observations from 2008 and 2009 indicate that the decreased snow zone was free of snow 1–2 weeks prior to the ambient snow zone (Pattison, personal observation). Borner et al. (2008) working at the same snow fence found that *B. nana* and *S. pulchra* leafed out within 4 days of release of snow cover and that snow cover did not have an effect on the length of time needed for *E. vaginatum* to flower. These trends suggest that leaf age and developmental status likely varied between the snow zones used in this study. However, Starr et al. (2008), who worked in the same tundra community type at the same field site, reported that leaf gas exchange properties of these and other species were largely unaffected by potential differences in leaf age brought about by early season snow removal.

Snow melt water can be a source of water for tundra plants during the growing season and may be a secondary consequence of different snow depths in winter (Welker et al. 2005a, b). The extent to which increased water availability influenced the physiology of these species is, however, limited for the following reasons: (1) no differences in soil water content between the ambient and deep snow zones were found throughout the growing season in another study (Borner et al. 2008); (2) many of the differences in leaf gas exchange properties seen between snow zones in our study occurred in the early or mid-seasons not later in the season when water limitations would be more likely; and (3) early season δ^{13}C values of our tundra plants were not significantly depleted, typical of water limitation alleviations due to additional water resources (Welker et al. 1993).

Reduction in stomatal conductance in response to colder soil temperatures appears to be the mechanism underlying the reductions in gas exchange where snow depth is low in the prior winter. Reduced soil temperatures lowered A_{max} and g_s of *E. vaginatum* and another common tundra graminoid, *Carex bigellowii* (Starr et al. 2004), and g_s in the tundra shrub *Salix arctica* (Dawson and Bliss 1989). In our study, both *S. pulchra* and *E. vaginatum* had the lowest g_s values in decreased snow zones where soil temperatures tended to be lowest. There were, however, no significant relationships ($P < 0.05$) between soil temperature and g_s for any species.

Leaf δ^{13}C values can provide integrated insights into g_s. Enriched (less negative) δ^{13}C values can be the consequence of decreased g_s and/or increased A_{max} (Evans et al. 1986; Farquhar et al. 1989). The values of δ^{13}C for *E. vaginatum* were more enriched in the ambient and decreased snow zones than in the drift zone. At the same time, the A_{max} for *E. vaginatum* was lower in the decreased snow than the drift snow zone. A similar pattern was found in the values of δ^{13}C for *S. pulchra* where values in the decreased snow zone were enriched relative to those in the drift snow (Fig. 4). The A_{max} values of *S. pulchra* were not significantly higher in the decreased snow zone. These patterns of enriched δ^{13}C without significantly higher A_{max} suggest that g_s values were consistently lower in the decreased snow zone than in the drift snow for *E. vaginaturm* and *S.*

pulchra. These reductions in g_s under decreased snow suggest that reduced snow could lower the carbon assimilation capacity of these ecosystems (Oechel et al. 2000).

Increases in available N where snow was deep in the prior winter did not result in increased rates of A_{max}. This result is consistent with fertilization studies in arctic tundra which have resulted in little to no stimulation of leaf level photosynthesis (Bigger and Oechel 1982; Bret-Harte et al. 2001). However, Chapin and Shaver (1996) found that NPK fertilization led to increases in leaf level photosynthesis of *B. nana*. Other studies in the region show that increased growing season lengths and warmed soils did not increase photosynthetic capacity of graminoids, forbs, and shrubs in tussock tundra (Starr et al. 2008). The primary response of tundra species to fertilization and warming appears to be through increases in leaf area rather than increases in leaf level gas exchange (Bowman et al. 1995). Our results are consistent with these studies in that there were no differences in leaf gas exchange rates by plants from the drift and ambient snow areas, but canopy LAI was greater in the drift snow zone compared to the ambient snow zone. These results suggest that snow addition and the associated soil warming in winter and increases in available N lead to increases in canopy cover, while reductions in snow lead to reductions in soil temperature which drives decreases in g_s and results in decreases in overall leaf level gas exchange.

Our measurements of LAI did not differentiate by species composition; however, the increased LAI in the drift snow area was likely due in large part to increases in *B. nana* which has shown a 200 % increase in cover based on community composition analysis every 5 years since 1994 (Mercado-Diaz 2011). This finding is in agreement with earlier community composition studies that found that shrubs accounted for most of the increases in cover in the area referred to as the drift snow area in this study (Wahren et al. 2005). These increases in canopy leaf area are of particular importance, as they may explain in part the increases in NDVI depicted for the North Slope of Alaska and a greening of the Arctic (Jia and Epstein 2003). Greater shrub leaf area may lead to increases in sensible heat flux and reduced albedo, further warming the boundary layer (Chapin et al. 2005), while greater shrub density can also lead to higher rates of ecosystem C sequestration (Anderson-Smith 2013) and reductions in permafrost thaw depths (Blok et al. 2010).

Several lines of evidence from our study suggest that there were increases in available N in the drift snow; these include the following: (1) total available N measured with ion exchange resins (placed only in the ambient and drift zones) was 67 % greater in the drift zone compared to the ambient snow zone; (2) the enriched values of foliar δ^{15}N for *B. nana* and *S. pulchra* in the drift snow zone relative to the decreased snow zone are consistent with increased inorganic N availability (Craine et al. 2009); however, in contrast, the enriched values of δ^{15}N for *E. vaginatum* under decreased snow may be attributed to changes in the relative proportions of N sources (ammonium, nitrate, amino acids) (Craine et al. 2009); (3) the increase in LAI in the drift snow zone without concurrent declines in leaf N (Fig. 4) suggests that there was greater available N under the drift snow zone (Natali et al. 2012); and (4) increased thaw depth during the growing season (Fig. 2) is consistent with increased total soil N pools (Schimel et al. 2004). The ultimate causes of the increases in available N in the drift snow are likely to be the increased winter N mineralization and or increases in soil N pool via greater thaw depth (Schimel et al. 2004; Sturm et al. 2005; Brooks et al. 2011). However, differences in total available N measured with ion exchange resins and foliar δ^{15}N values may be more directly associated with potential increases in litter inputs and soil organic matter under a denser canopy (Sturm et al. 2005; Buckeridge et al. 2010).

Increased winter snow depth can lead to increased growing season thaw depths (Borner et al. 2008; Natali et al. 2012) that can alter tundra ecosystem productivity. Deeper snow with a late spring snow removal in another tundra ecosystem led to a 10 % increase in thaw depth and 20 % increases in above-ground biomass and annual net primary productivity (Natali et al. 2012). In our study, thaw depths in the decreased snow tended to be shallower than those in either ambient (19–29 % shallower) or drift (39–42 % shallower) snow, but thaw depth was not consistently deeper in the drift snow zone compared to the ambient snow zone (Fig. 2). Borner et al. (2008), working at the same experimental site, found that thaw depths in the ambient snow zone were initially deeper than mid-drift or deep drift snow areas, but that by the end of the growing season deeper snow areas had deeper thaw depths. Increased thaw depth in the early season in decreased snow is consistent with earlier snow melt leading to increased early season radiative inputs that drive greater thaw depths (Woo et al. 2007). However, these trends were not apparent in our study. Our results suggest that reductions in snow depth may have greater effects on tundra ecosystem summer soil properties and, subsequently, productivity than potential increases in snow; a non-linear property and an example of biocomplexity in the Arctic (Walker et al. 2008).

Decreases in thaw depth associated with decreased snow depth suggest that reductions in snow depth may partially offset deepening thaw depths induced by climate warming (Osterkamp and Romanovsky 1999; Brooks et al. 2011). Another important factor influencing thaw depths is canopy structure (Blok et al. 2010). Cover of *B. nana* was inversely correlated with thaw depth in another arctic tundra ecosystem (Blok et al. 2010), suggesting that the higher LAI found in our drift zone potentially insulates (keeps colder) the understory soils during the growing season (Blok et al. 2010), and serves as a negative feedback to the effects of winter warming under deeper snow on active layer thaw. Similarly, the reduced LAI under the decreased snow relative to the drift snow may allow greater radiative inputs both early in the season when there is a lack of snow cover (Woo et al. 2007) and throughout the growing season.

Decreases in snow depth resulted in greater variability of soil surface temperatures during the winter (Fig. 1). As winter warming events are projected to increase in frequency in the Arctic (Bonsal et al. 2001), with potentially negative impacts on the phenology and productivity of tundra plants (Bokhorst et al. 2008, 2009), reductions in snow depth may have important impacts on tundra ecosystems. Reductions in snow cover are also likely to increase the occurrence and number of spring time freeze–thaw events (Nobrega and Grogan 2007) with potential impacts on nutrient cycling and tundra productivity (Grogan et al. 2004).

The results of this work highlight the importance of snow and winter-time processes in general to Arctic tundra ecosystems (Cooper 2010). Experimental manipulations of this nature can provide a more complete understanding of spatial heterogeneity in tundra structure and composition associated with snow accumulation patterns across the landscape, and insights into inter-annual variability in tundra function and into the impacts of long term changes in snow accumulation (Callaghan et al. 2011; Liston and Hiemstra 2011) on tundra ecosystems.

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