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Arctic plant ecophysiology and water source utilization in response to altered snow: isotopic (δ^{18}O and δ^2H) evidence for meltwater subsidies to deciduous shrubs

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Abstract

Warming-linked woody shrub expansion in the Arctic has critical consequences for ecosystem processes and climate feedbacks. The snow–shrub interaction model has been widely implicated in observed Arctic shrub increases, yet equivocal experimental results regarding nutrient-related components of this model have highlighted the need for a consideration of the increased meltwater predicted in expanding shrub stands. We used a 22-year snow manipulation experiment to simultaneously address the unexplored role of snow meltwater in arctic plant ecophysiology and nutrient-related components of the snow–shrub hypothesis. We coupled measurements of leaf-level gas exchange and leaf tissue chemistry (%N and δ^{13}C) with an analysis of stable isotopes (δ^{18}O and δ^2H) in soil water, precipitation, and stem water. In deeper snow areas photosynthesis, conductance, and leaf N increased and δ^{13}C values decreased in the deciduous shrubs, *Betula nana* and *Salix pulchra*, and the graminoid, *Eriophorum vaginatum*, with the strongest treatment effects observed in deciduous shrubs, consistent with predictions of the snow–shrub hypothesis. We also found that deciduous shrubs, especially *S. pulchra*, obtained much of their water from snow melt early in the growing season (40–50%), more than either *E. vaginatum* or the evergreen shrub, *Rhododendron tomentosum* (*Ledum palustre*). This result provides the basis for adding a meltwater-focused feedback loop to the snow–shrub interaction model of shrub expansion in the Arctic. Our results highlight the critical role of winter snow in the ecophysiology of Arctic plants, particularly deciduous shrubs, and underline the importance of understanding how global warming will affect the Arctic winter snowpack.

Keywords Alaska · Tundra · Ecohydrology · Water sources · δ^{18}O · Arctic precipitation · Photosynthesis · Nitrogen · δ^{13}C

Communicated by Jim Ehleringer.

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Introduction

One of the most visible vegetation changes in the Arctic over the past 60 years is the expansion of woody shrubs in response to climate warming. At Arctic sites in North America, Eurasia, and Scandinavia, shrubs have expanded their ranges as well as increased in biomass, canopy height, and cover within established stands (Sturm et al. 2001a; Myers-Smith et al. 2011; Tape et al. 2012). Shrub expansion has triggered changes in the surface energy budget (Chapin 2005; Sturm et al. 2005a, b), snow retention and distribution (Liston et al. 2002), carbon and nitrogen cycling (Weintraub and Schimel 2005), and wildlife distribution (Tape et al. 2016a, b). While the dendrochronological record (Forbes et al. 2010; Hallinger et al. 2010; Blok et al. 2011) and experimental results (Chapin et al. 1995; Bret-Harte et al. 2001; Leffler and Welker 2013; Schaeffer et al. 2013; Leffler et al. 2016) support a strong link between temperature,

precipitation, and shrub growth, uncertainty remains as to the ecophysiological mechanisms underlying recent shrub expansion.

To date, the "snow–shrub hypothesis" (Sturm et al. 2001b, 2005b), wherein deciduous shrubs indirectly increase nutrient availability under their own canopies by retaining a deeper snowpack and maintaining warmer winter soils, has been the feedback mechanism most implicated in observed shrub increases in the Arctic. Observations of deeper winter snow in shrub stands (Sturm et al. 2001b, 2005b), experimental studies linking increased microbial activity, greater nutrient availability, and higher plant leaf N contents to deeper snowpacks (Shaver and Billings 1975; Schimel et al. 2004; Welker et al. 2005; Buckeridge and Grogan 2008, 2010), and the particularly strong nutrient limitations on deciduous shrub growth relative to other tundra plants (Chapin and Shaver 1985; Chapin et al. 1995; Bret-Harte et al. 2001) support the snow–shrub hypothesis. However, ^{15}N-tracer studies have failed to document heightened N uptake by deciduous shrubs under deep snow conditions (Vankoughnett and Grogan 2014), summer cooling under the canopies of established shrub stands is of comparable magnitude to winter warming and can result in a thinner layer of seasonally thawed soil (henceforth "active layer", Blok et al. 2010; Frost et al. 2017), and herbivores maintain strong top-down control on shrub distributions in some regions (Olofsson et al. 2009; Vowles et al. 2017). Thus, while strong evidence supports a large role for nutrients in snow–shrub interactions, there is a broader need to investigate the ecophysiological mechanisms underlying shrub expansion, including the importance of snow meltwater.

The dynamics of water source utilization in arctic shrubs are among those areas of snow–shrub interactions that remain poorly understood. Prior research in arid or semi-arid systems using the stable isotopes ($^{18}O/^{16}O$ and $^2H/^1H$) in precipitation, soil, and stem water has indicated that shrubs, forbs, and grasses differ in their use of deep or shallow water sources and in their reliance on water from snow melt or rainfall (Dodd et al. 1998; Alstad et al. 1999; Welker 2000). However, the role of divergent water sources in the water and gas exchange properties of Arctic shrubs has not been investigated, especially in the context of changes in the Arctic winter snowpack that are becoming increasingly evident (Callaghan et al. 2011; Liston and Hiemstra 2011; Brown and Robinson 2011). Recently Ebbs (2016) reported that the widespread arctic shrub *Betula nana* relied on snow meltwater for 40% of its water use, but this study did not consider the codominant *Salix pulchra*, nor did it examine the isotopic composition of precipitation or soil water for a full growing season. Such a characterization of the timing and sources of water uptake by Arctic shrubs and other growth forms could deepen our understanding of competition and coexistence in Arctic plant communities, and help predict

vegetation responses to future changes in temperature and/or precipitation.

The species-specific or growth form-specific patterns commonly observed in previous ecophysiological studies of Arctic plants suggest that water source usage patterns and their sensitivity to different facets of global change may be similarly individualistic (Chapin and Shaver 1985; Pattison and Welker 2014; Cahoon et al. 2016; Leffler et al. 2016). For example, strong differences exist among deciduous shrubs, evergreen shrubs, grasses, and forbs in stomatal conductance (g_s), the seasonal timing of peak water use, and the sensitivity of water use to simulated climate change (Oberbauer and Oechel 1989; Oberbauer and Dawson 1992; Pattison and Welker 2014; Cahoon et al. 2016). Further, despite a relatively thin active layer in the Arctic, rooting depth and depth of N acquisition vary considerably across tundra plant species (Chapin and Shaver 1981; McKane et al. 2002; Iversen et al. 2015). For example, McKane et al. (2002) showed that *B. nana* acquires proportionally more of its N from deeper in the soil profile than *E. vaginatum* or *Rhododendron tomentosum*, though others have found graminoids to acquire N from deeper in the soil profile than shrubs (Zhu et al. 2016; Wang et al. 2018). These differences among growth forms and species in their seasonal water use, rooting behavior, and resource acquisition suggest that their reliance on winter precipitation (snow) versus summer precipitation (rain) may be very different, which may influence their trajectories under global change scenarios (e.g., Callaghan et al. 2011).

In this study, we explicitly link snow meltwater to the gas exchange physiology of tundra plants at Toolik Lake, Alaska. Using a 22-year-old ITEX snowfence experiment (Jones et al. 1998; Welker et al. 2000, 2005), first we revisited the question of whether winter snow depth affects the photosynthesis, water relations, or nutritional status of different tundra species or growth forms in different ways. To address this question, we paired regular measurements of leaf-level gas exchange with leaf tissue chemistry (%N and $\delta^{13}C$). Consistent with the snow–shrub feedback model, we hypothesized that the maximal rates of photosynthesis (A_{max}), g_s, and leaf N would be more responsive to snow depth in deciduous shrubs than in other growth forms and, accordingly, show greater increases under deep snow conditions or greater decreases under reduced snow conditions.

Next, we took the additional step of asking whether different plant species or growth forms utilize different water sources throughout the growing season and to what degree winter snow depth affects these patterns of water use. To address this, we analyzed the stable isotopes of oxygen (^{18}O) and hydrogen (^2H) in winter and summer precipitation, soil water, and stem water. Given their ecophysiological responsiveness to deeper snow, we hypothesized that deciduous shrubs would use more ^{18}O- and ^2H-depleted

snow meltwater from deeper in the soil profile than other growth forms, resulting in lower $\delta^{18}O$ and δ^2H values in their xylem water. We further hypothesized that deciduous shrubs would be more capable of capitalizing on additional meltwater resources where snow depth is augmented, resulting in yet lower $\delta^{18}O$ and δ^2H values, and that this would enable them to maintain more open stomata and have lower leaf $\delta^{13}C$ values. Our study is the first to link instantaneous gas exchange, leaf tissue chemistry, and water source dynamics in the Arctic. Our results offer novel insights into the ecohydrological relationships between snow and tundra plants and broaden understanding of the potential mechanisms driving shrub expansion in the Arctic.

Materials and methods

Study site and experimental design

Research took place at Toolik Field Station (68°38′N, 149°36′W, 760 m asl) in the northern foothills of the Brooks Range, Alaska, USA. The dominant features of the low Arctic climate at Toolik are long, cold, dry winters, with air temperatures averaging − 20 °C and short, cool summers with air temperatures averaging 9 °C (Environmental Data Center Team 2017). The dominant vegetation community is tussock tundra, a topographically heterogeneous mixture of raised *Eriophorum vaginatum* tussocks, dwarf shrubs (*Betula* spp., *Salix* spp., *R. tomentosum*, and *Vaccinium* spp.), lichens, and mosses. Soils are gelisols high in organic matter, with a relatively thin active layer (< 0.5 m) overlying continuous permafrost (Walker et al. 1994; Hobbie and Kling 2014).

In 1994, a 2.8 × 60 m "Wyoming"-style wood snowfence was installed perpendicular to the prevailing winter wind direction in moist tussock tundra approximately 1.5 km southwest of Toolik Field Station (Walker et al. 1999; Welker et al. 2000). Our measurements were conducted in 2016 in five 1 m² plots in "+Snow", referring to the zone 25–30 m from the snowfence, where snow typically accumulates to ca. 1.5−2 m deep, "Control", referring to an unmanipulated area adjacent to the snowfence where snow typically accumulates to ca. 0.5–1 m deep, and "−Snow", referring to the zone ca. 80 m from the fence, where snow typically accumulates to < 0.5 m deep (Tabler 1980; Walker et al. 1999; Pattison and Welker 2014).

Thaw depth and soil temperature

During the 2016 growing season, we measured thaw depth and soil temperature at approximately weekly intervals at six evenly spaced points in each of the snow zones. Thaw depth was measured from the top of the moss layer in the intertussock areas with a metal probe. Soil temperature was measured from the top of the moss layer to 10 cm depth with a handheld soil temperature probe (model HI 145, Hanna Instruments, Woonsocket, Rhode Island).

Leaf-level gas exchange and tissue chemistry

We measured leaf gas exchange [light-saturated maximum photosynthesis (A_{max}) and stomatal conductance (g_s)] during three time periods in the 2016 summer, June 19–24 ("early summer"), July 12–23 ("midsummer"), and August 11–14 ("late summer"). One fully expanded, healthy leaf per plot was used from each of the four dominant plant species, *S. pulchra* and *B. nana* (deciduous shrubs), *R. tomentosum* (evergreen shrub), and *E. vaginatum* (sedge). Measurements were made between 1200 and 1800 h with a portable gas exchange system (model LI-6400, LI-COR, Lincoln, Nebraska, USA) equipped with a 2 × 3 cm leaf chamber and red-blue LED light source. We maintained the reference CO_2 concentration at 400 μmol mol⁻¹, PAR at 1500 μmol photons m⁻² s⁻¹, chamber temperature at 15 °C, and relative humidity at 50%. We estimated leaf area using a flatbed scanner and image analysis software (WinFOLIA, Regent Instruments Inc., Quebec City, Quebec, Canada).

Leaves used in gas exchange measurements (*E. vaginatum* and *R. tomentosum* samples were supplemented with additional leaves from the same plot) were oven dried at 40 °C and ground to a fine powder with a ball mill (Mini Beadbeater-16, Biospec Products Inc., Bartlesville, Oklahoma) with 3.2 mm ball bearings. Subsamples were analyzed for N (%), C (%), and $\delta^{13}C$ with an elemental analyzer (model 4010, Costech Analytical, Valencia, CA, USA) linked to a continuous flow isotope ratio mass spectrometer (model DeltaPLUS XP, Thermo-Finnegan Scientific, Waltham, MA, USA) at the University of Alaska Anchorage. Long-term records of internal standards yield an analytical precision of 0.03% for N and 0.12‰ for $\delta^{13}C$. Carbon isotope data are expressed in the δ notation relative to the Pee Dee Belemnite standard.

Soil, stem, and precipitation water sampling

One day following each period of leaf gas exchange measurements, we collected soil water from the active layer in each plot using suction lysimeters. Samples were pulled from the full depth of the active layer in increments of 10 cm using a syringe; we included the uppermost 10 cm of the soil profile in tussocks (henceforth referred to as "tussock") and 0–10, 10–20, 20–30, 30–40, and 40–50 cm in the intertussock zone (henceforth referred to by depth). We used Rhizon Soil Moisture Samplers (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands) except for samples from greater than 40 cm depth for which we used Simpler Slim Tube Samplers (Soilmoisture Equipment Corp., Santa Barbara,

CA, USA). Samples were analyzed for $\delta^{18}O$ and $\delta^{2}H$ by cavity ring-down spectrometry (model L2130-I, Picarro Inc., Santa Clara, CA, USA) at the University of Alaska Anchorage. Long-term records of internal standards yield an analytical precision of 0.2‰ for $\delta^{18}O$ values and 2‰ for $\delta^{2}H$ values. Data are expressed in the δ notation relative to the V-SMOW standard (Dawson et al. 2002).

On the same days soil water was sampled, stems were collected for analysis of $\delta^{18}O$ and $\delta^{2}H$ of xylem water. We harvested stems of each species (culms for *E. vaginatum*) outside of each plot, removed all green leaf material, clipped them to 10 cm length, and froze them until extraction via cryogenic batch distillation (modified from Vendramini and da Sternberg 2007). Extracted stem water was analyzed for $\delta^{18}O$ and $\delta^{2}H$ with an isotope ratio mass spectrometer high temperature conversion elemental analyzer (IRMS TC/EA, Thermo Scientific, Waltham, MA, USA) at the University of Alaska Anchorage. Long-term mean and standard deviation records of a purified water QA/QC standard yield an instrumental precision of 0.63‰ for $\delta^{2}H$ and 0.06‰ for $\delta^{18}O$.

All precipitation (liquid and frozen) events from June through August were sampled and snow samples were collected in 20 cm depth increments from the drift created by the snowfence in June 2016. Samples were analyzed for $\delta^{18}O$ and $\delta^{2}H$ by cavity ring-down spectrometry.

Data analysis

We compared thaw depth, leaf gas exchange (A_{max}, g_s), tissue chemistry (%N and $\delta^{13}C$), and soil water $\delta^{18}O$ among the snow depth zones with repeated measures linear mixed models using the lme4 package in R (R Development Core Team 2018). Because differences among species for the leaf-level variables are already well-established (Welker et al. 2005; Pattison and Welker 2014), we did not make formal comparisons among species. Models contained random plot or point effects and fixed snow zone, "season", and snow zone × "season" interaction effects. For thaw depth data, a random day of year effect took the place of the "season" effect. In all cases, we examined the significance of the snow zone effect by comparing full models with a reduced model with the snow zone effect removed. We considered the overall treatment effect significant if the log-likelihood ratio test of the two models resulted in $P \leq 0.05$. We then bootstrapped parameter estimates (1000 times) from the full model and made post hoc comparisons based on median ± 95% confidence intervals derived from the bootstrapped parameter estimates. In this and subsequent mixed model analyses, data and model residuals were assessed for normality, independence, and homogeneity; no transformations were necessary with any of our datasets.

Our first goal with the stem water isotope ($\delta^{18}O$ and $\delta^{2}H$) dataset was to compare snow meltwater usage among species and treatments within each part of the growing season. Xylem water isotope data were examined using a Bayesian isotope mixing model (Parnell et al. 2010) implemented in the SIAR package in R. We ran the model (200,000 iterations, 50,000 discarded for burn-in) for each stem collection period (early summer, midsummer, late summer) using the isotopic values of the current year snow and rain as possible water sources. We did not consider meltwater from seasonally thawing ground ice or permafrost as unique sources due to isotopic overlap with snow in the samples we collected (Fig. 4); henceforth, "meltwater" refers to water from current year snow or seasonally thawing ice or permafrost. Our second goal was to compare the depth of water used among species and treatments within each part of the growing season. In this case, we ran the SIAR model for each stem collection period (early summer, midsummer, late summer) with soil waters taken in 10 cm intervals as sources. Because we found no vertical gradient in soil water $\delta^{18}O$ below 10 cm depth, we used only three depths as possible sources, "tussock", "0–10 cm", or ">10 cm."

Results

Climate and thaw depth

Mean annual air temperature in 2016 at Toolik Lake was − 6.6 °C, the warmest recorded since 1991 (Fig. 1), though the summer months were closer to normal; June was 2.2 °C cooler and July and August were 0.3 and 1.1 °C warmer, respectively, than the 26 year monthly averages (Environmental Data Center Team 2017). Compared to the previous 6 years, June 2016 at Toolik Lake was exceptionally wet (114 mm relative to 37.7 mm average), July 2016 was average (82.3 mm relative to 85.2 mm), and August 2016 was somewhat wetter than normal (66.6 mm relative to 56.2 mm).

Thaw depth was strongly influenced by winter snow depth ($\chi^2 = 15.3$, $p < 0.001$, Fig. 1). The main effects of snow depth on thaw depth were primarily derived from thaw depth increasing more rapidly in the +Snow zone (0.76 cm day^{-1}) than in the Control (0.45 cm day^{-1}) or −Snow zones (0.52 cm day^{-1}), ultimately extending ca. 50% deeper in the +Snow zone (63.7 cm) than either the Control (40.8 cm) or −Snow (44.9 cm) zones in mid-August; we did not detect any differences in thaw depth between the Control or −Snow zones on any sampling days. Snow zone did not influence growing season soil temperature at 10 cm depth ($\chi^2 = 1.4$, $p = 0.50$, Fig. 1).

Fig. 1 Mean annual 5 m air temperature data at Toolik Lake Field Station, with best-fit linear trend (**a**), monthly mean 5 m air temperature and total precipitation for 2009–2016 (**b**), and 2016 weekly mean (± 1 SE) thaw depth and 10 cm soil temperature in the three snow depth zones studied (**c**)
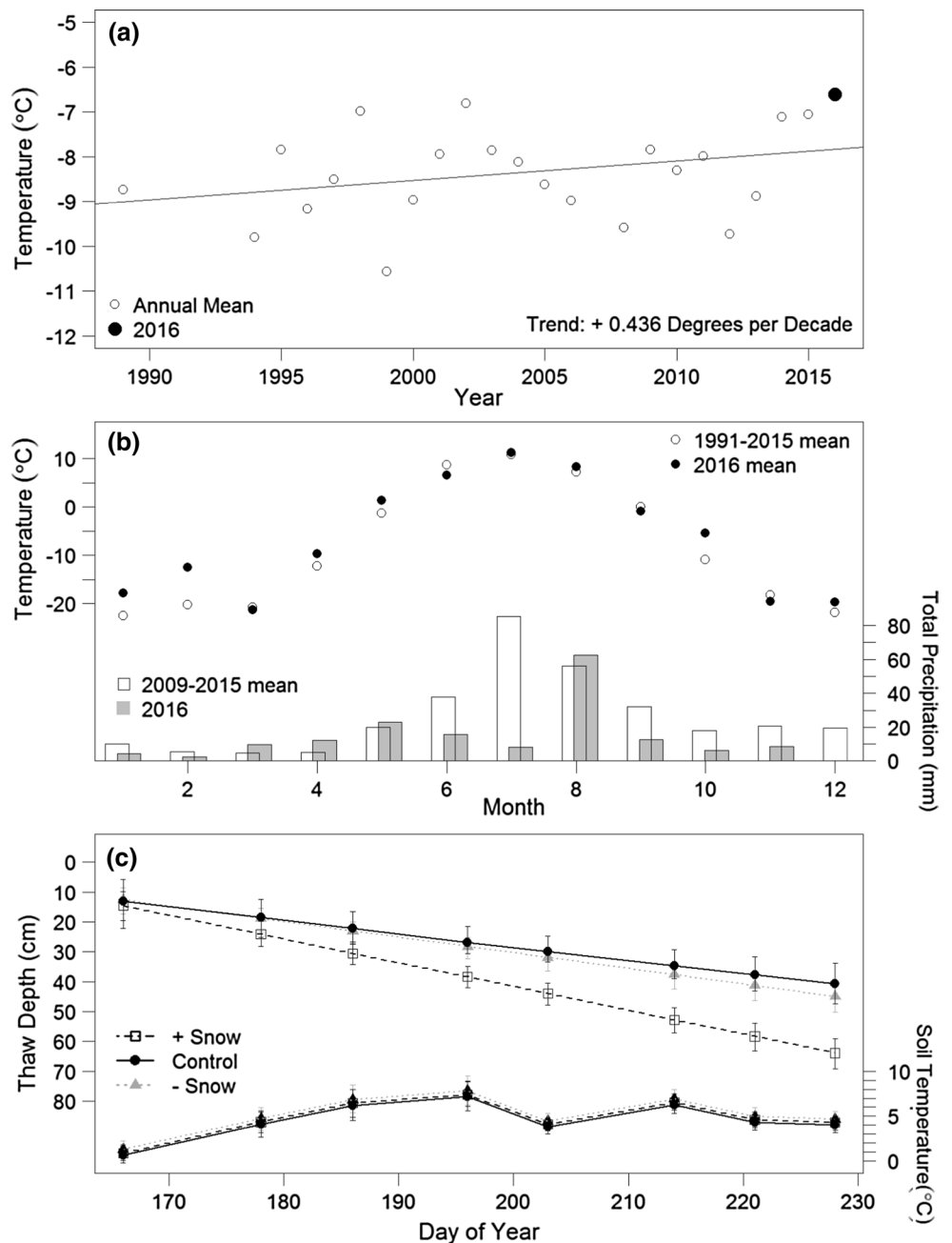
Leaf gas exchange

Winter snow depth influenced A_{max} and g_s in *B. nana*, *S. pulchra*, and *E. vaginatum*, but not *R. tomentosum* (Table 1), and treatment effects changed throughout the summer (Fig. 2). During the early summer, only *S. pulchra* from the +Snow zone was affected by winter snow depth, demonstrating ca. 60% higher A_{max} and ca. 100% greater g_s than in the other two zones. By midsummer, A_{max} and g_s in *B. nana* were > 50% higher in the +Snow zone than the −Snow zone, A_{max} and g_s in

S. pulchra were > 50% higher in the +Snow zone than either the Control or −Snow zones, and in *E. vaginatum* strong, but not statistically significant differences developed suggesting higher A_{max} and g_s in the +Snow zone relative to the −Snow zone. For most species, A_{max} and g_s were highest during the late summer sampling period, concomitant with strong snow depth treatment effects. In *B. nana* and *S. pulchra*, A_{max} and g_s were ca. 50% higher in the +Snow zone than either the Control or −Snow zones, and in *E. vaginatum* A_{max} was ca. 50% higher in the +Snow zone than either the Control

Table 1 Likelihood ratio test results of full versus reduced linear mixed models for leaf gas exchange and tissue chemistry responses to altered winter snow depth (+Snow, Control, −Snow)

Response	Treatment: snow level (+Snow, Control, −Snow)							
	Betula nana		*Salix pulchra*		*Ledum palustre*		*E. vaginatum*	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p
A_{max}	59.44	**< 0.001**	70.5	**< 0.001**	8.95	0.176	42.73	**< 0.001**
g_s	47.89	**< 0.001**	61.66	**< 0.001**	3.73	0.713	16.02	**< 0.014**
N	225.9	**< 0.001**	120.2	**< 0.001**	40.14	**< 0.001**	160.6	**< 0.001**
δ^{13}C	47.94	**< 0.001**	110.3	**< 0.001**	71.19	**< 0.001**	117.1	**< 0.001**

Models contained random plot or point effects and fixed snow zone, "season", and snow zone × "season" interaction effects. We examined the significance of the snow zone effect by comparing full models with a reduced model with the snow zone effect removed. Response variables examined included maximum light saturated photosynthesis (A_{max}), stomatal conductance (g_s), total leaf nitrogen (N), and leaf carbon (δ^{13}C isotope composition). In all cases, $df_{full} - df_{reduced} = 6$
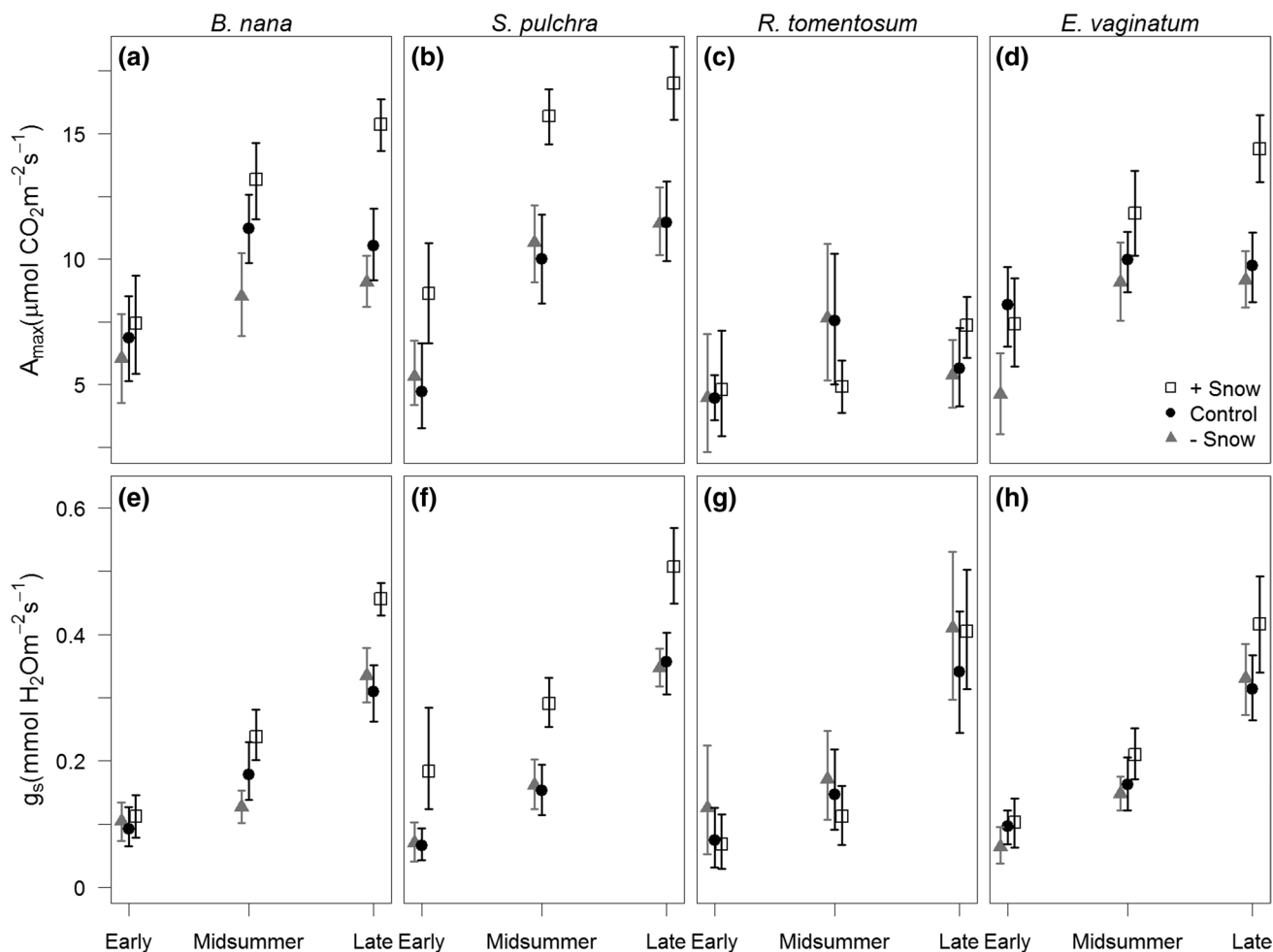

Fig. 2 Maximum light-saturated net photosynthesis (A_{max}, **a–d**) and stomatal conductance (g_s, **e–h**) in *Betula nana*, *Salix pulchra*, *Rhododendron tomentosum*, and *Eriophorum vaginatum* across three snow depth zones for the full growing season. Values are median ± 95% confidence intervals derived from bootstrapped mixed model parameter estimates

or −Snow zones. In *R. tomentosum,* A_{max} demonstrated little seasonal variability, remaining between 4.5 and 7.8 μmol CO_2 m^2 s^{-1} for all seasons and snow zones, but g_s increased throughout the summer, with late summer values > 200% higher than early and midsummer values for all snow zones.

Leaf tissue chemistry

Winter snow depth influenced leaf N and $\delta^{13}C$ in all species (Table 1), but the treatment effects differed among species and sampling periods (Fig. 3). In *B. nana*, *S. pulchra*, and *E. vaginatum* leaf N was higher in the +Snow zone than either the Control or −Snow zones throughout most of the growing season, with the largest differences observed between +Snow plants and −Snow plants in the early summer (ca. 60, 43, and 130% higher for each species, respectively). In *R. tomentosum*, leaf N was largely unresponsive to winter snow depth, though there was a slight tendency towards higher leaf N in +Snow plants during the last two sampling periods. Also, in *B. nana* and *E. vaginatum,* leaf N was 20–30% higher in the Control snow zone than the −Snow zone during the early and midsummer sampling periods, and there was a strong tendency toward higher leaf N in *S. pulchra* from the Control zone than in the −Snow zone.

We observed ca. 1–2‰ lower $\delta^{13}C$ values in the +Snow zone relative to the Control or −Snow zones during at least one sampling period in all of our species, but no differences emerged between plants from the −Snow and Control zones (Fig. 3). In *S. pulchra*, *R. tomentosum*, and *E. vaginatum*, these snow depth effects were present for the entire growing season, whereas in *B. nana*, no snow depth effect was observed until the late summer sampling period, when leaf $\delta^{13}C$ was ca. 1.5‰ lower in the +Snow zone than the Control zone.

Precipitation $\delta^{18}O$ and δ^2H

$\delta^{18}O$ and δ^2H values of the drift accumulated on the leeward side of the snowfence were lower and less variable (Fig. 4, $\delta^{18}O = - 25.2 \pm 1.7‰$, $\delta^2H = - 175.4 \pm 11.8‰$) compared to early summer snow events ($\delta^{18}O = - 21.3 \pm 5.2‰$, $\delta^2H = - 158 \pm 37.2‰$) and much lower relative to rain events ($\delta^{18}O = -16.2 \pm 3.3‰$, $\delta^2H = - 128.5 \pm 23.7‰$).
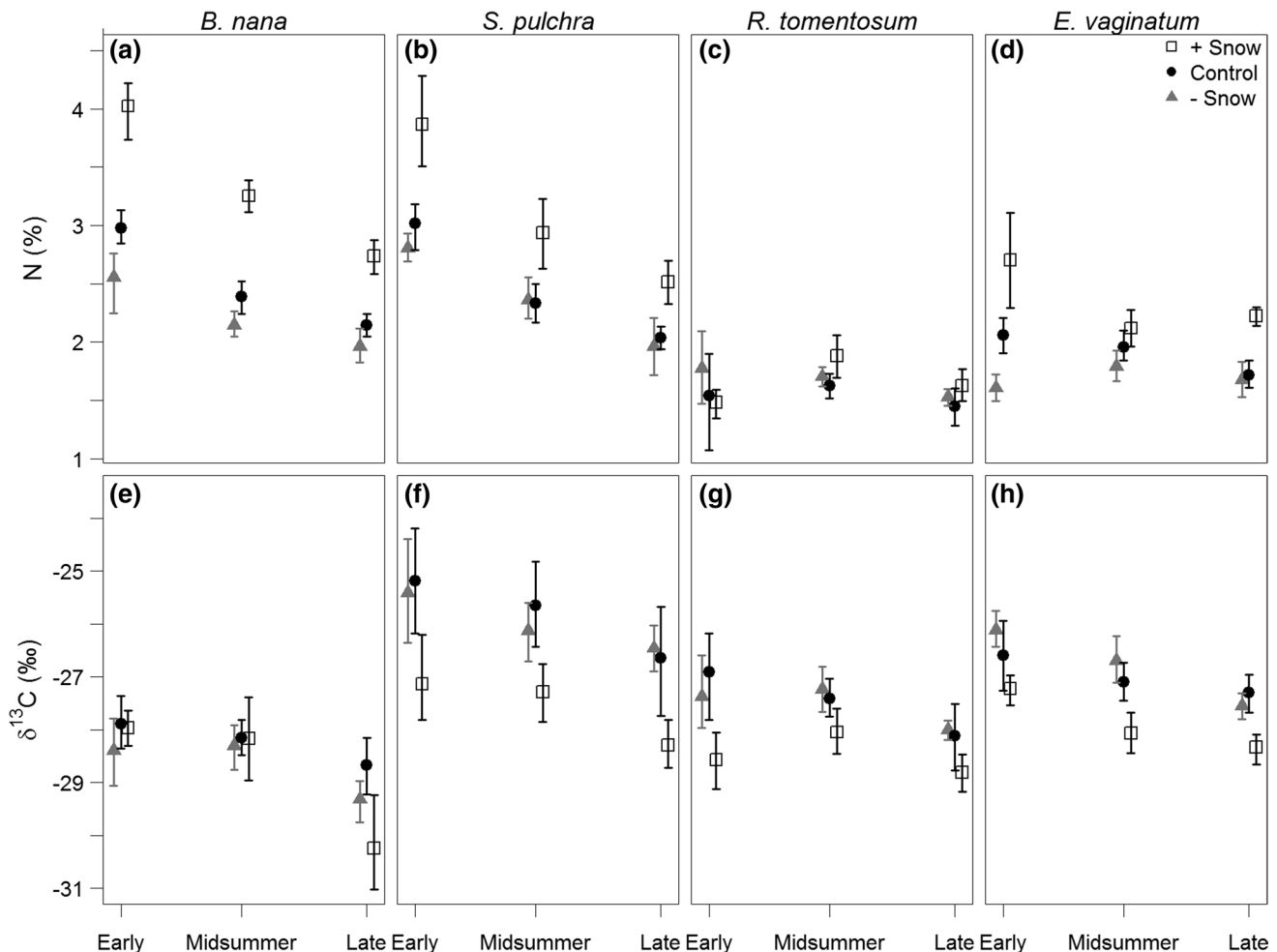

Fig. 3 Leaf tissue N (**a–d**) and $\delta^{13}C$ (**e–h**) in the four study species across three snow depth zones for the full growing season. Values are median ± 95% confidence intervals derived from bootstrapped mixed model parameter estimates

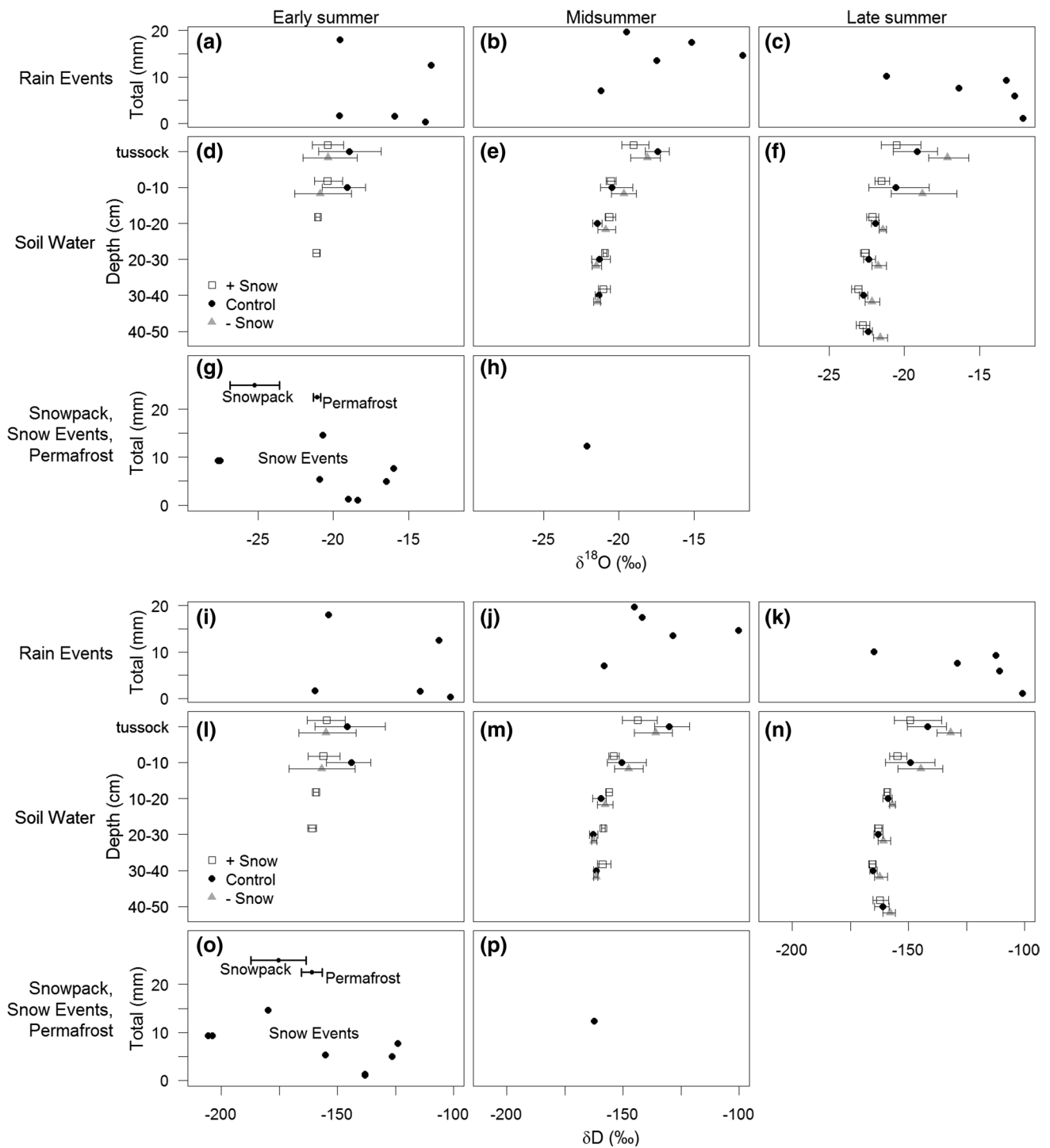Fig. 4 Precipitation totals and $\delta^{18}O$ of rain events (a–c), soil water $\delta^{18}O$ across available depths (d–f), precipitation totals and $\delta^{18}O$ for snow events (g–h), precipitation totals and δ^2H of rain events (i–k), soil water δ^2H across available depths (l–n), and precipitation totals and δ^2H for snow events through the 2016 growing season (o), (p). (g) and (o) include δ^2H values for snowpack samples taken in early June and permafrost samples taken in August (note: position for these values along the y-axis is arbitrary). Soil water values (d–f, l–n) are median ± 95% confidence intervals derived from bootstrapped mixed model parameter estimates, values for snowpack (n = 6) and permafrost (n = 3) are mean ± 1 SE, and values for precipitation events are single samples

Rain events were evenly dispersed throughout the summer months and had slightly higher $\delta^{18}O$ and δ^2H values in August ($\delta^{18}O = -15.1 \pm 3.8‰$, $\delta^2H = -123 \pm 25.2‰$) than June ($\delta^{18}O = -16.5 \pm 3.0‰$, $\delta^2H = -127.2 \pm 28‰$) or July ($\delta^{18}O = -17.0 \pm 3.7‰$, $\delta^2H = -134.8 \pm 22‰$).

Soil water $\delta^{18}O$ and δ^2H

Snow depth influenced soil water $\delta^{18}O$ and δ^2H values ($\chi^2 = 70.5$ and 54.3 for $\delta^{18}O$ and δ^2H, respectively, and $p < 0.001$ for both, Fig. 4), though the treatment effects varied throughout the growing season. During the early summer sampling period, frozen deeper soils prevented sampling from all but the shallowest soil layers (tussocks and 0–10 cm in the intertussock spaces), with the exception of the +Snow zone; $\delta^{18}O$ and δ^2H values were indistinguishable across these depths and snow zones (Fig. 4). By the midsummer sampling period, however, a vertical gradient in $\delta^{18}O$ and δ^2H had developed in the soil profile; during this and the late summer sampling period soil water $\delta^{18}O$ and δ^2H values were highest in the tussocks, followed by the intertussock

0–10 cm layer, and similarly low across the deeper depths. Soil water $\delta^{18}O$ and δ^2H values were also much more variable in the near-surface layers throughout the summer. For example, during late summer, samples from the uppermost soil layers ranged from -16 to $-21‰$ for $\delta^{18}O$ and from -135 to $-158‰$ for δ^2H, whereas samples from 10 to 40 cm depth ranged from -21 to $-23‰$ for $\delta^{18}O$ and from -155 to $-165‰$ for δ^2H. Finally, there was a slight tendency towards higher $\delta^{18}O$ and δ^2H values in surface layers in the Control zone relative to the other two zones during the early and midsummer sampling periods, but by late summer there was a broad trend towards higher $\delta^{18}O$ and δ^2H values in the −Snow zone relative to the other two snow zones across all depths and, conversely, lower $\delta^{18}O$ and δ^2H values in the +Snow zone across all depths.

Stem water isotopes

We found distinct differences among species and growth forms in their stem water $\delta^{18}O$ and δ^2H values (Fig. 5, Online Resource 3), leading to differences in our mixing

Fig. 5 Stem water, soil water, and precipitation isotopes, and source proportions for plants. Dual isotope ($\delta^{18}O$ and δ^2H) plots of xylem water samples, precipitation, soil water, and the snowpack (a–c). $N = 30$ samples species^{-1} for early and midsummer periods, and $n = 15$ samples species^{-1} for the late summer period. For stem waters, values are mean ± 1 SE, for precipitation and soil water, values are mean. The vertical order of soil water depths is the same in early and late summer as displayed in the midsummer panel. The Local Meteoric Water Line (LMWL) [$\delta^2H = -19.186‰ + 6.718(\delta^{18}O)$] is derived from 2016 summer precipitation data. The snowpack on the leeward side of the snowfence is displayed in all three panels for convenience, but was not present by the midsummer sampling period. Species symbols are the same top and bottom. Estimated proportion of extracted xylem water derived from snow meltwater for the four study species during the 2016 growing season (d). Values are median $\pm 95\%$ confidence intervals derived from the SIAR mixing model bootstrapping process
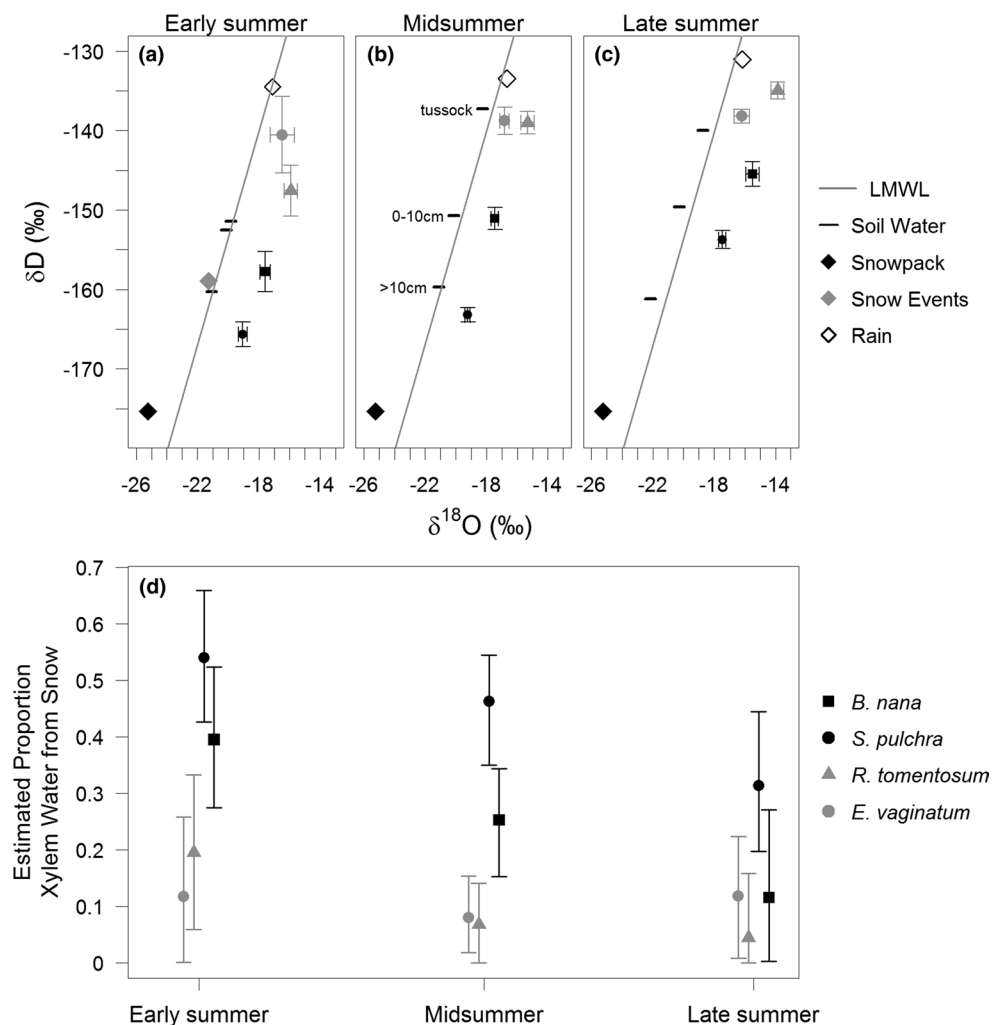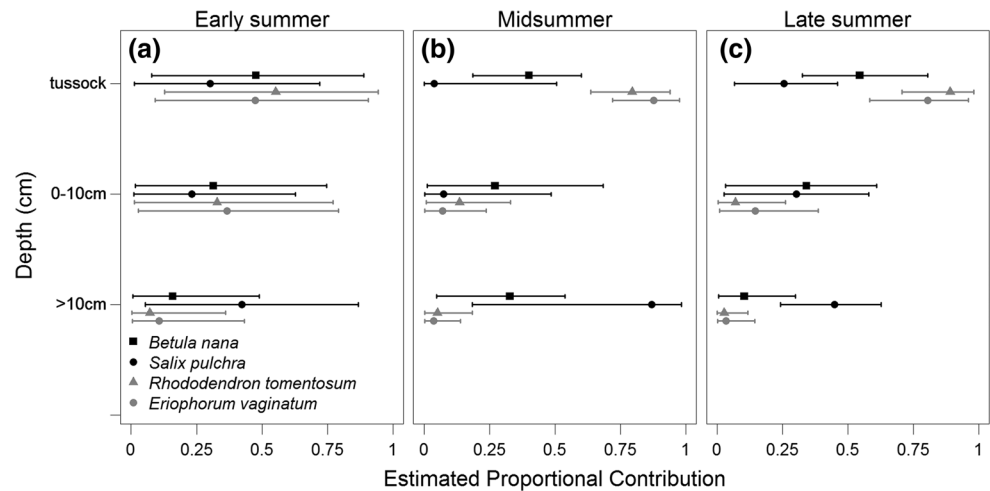
Fig. 6 Estimated proportion of extracted xylem water derived from each depth interval of the active layer for the four study species during the early (**a**), midsummer (**b**), and late summer (**c**) sampling periods. Values are median ± 95% confidence intervals derived from the SIAR mixing model bootstrapping process

model results among species and growth forms in their water sources and extraction depths (Figs. 5, 6). The two deciduous shrubs studied were particularly reliant on meltwater during the early and midsummer sampling periods. During the early summer stem water in *S. pulchra* and *B. nana* was composed of 44–66 and 26–52% meltwater, respectively, compared to 0–25% meltwater in *E. vaginatum* and 0–14% in *R. tomentosum*. At midsummer stem water in *S. pulchra* and *B. nana* was composed of 35–55 and 15–34% meltwater, respectively, whereas stem water in *E. vaginatum* was 2–15% meltwater and 0–16% meltwater in *R. tomentosum*. By the late summer sampling period, meltwater was less prevalent in *S. pulchra* (20–45%) and *B. nana* (0–27%), and remained low in *R. tomentosum* (0–16%) and *E. vaginatum* (2–23%). Winter snow depth did not influence meltwater utilization in any of our focal species during any of the sampling periods except for *E. vaginatum* during the early summer; culms in the +Snow zone contained more meltwater than culms from either of the other two zones (Online Resource 1).

Differences between the two deciduous shrubs and *R. tomentosum* and *E. vaginatum* also emerged when comparing depth of water extraction (Fig. 6, Online Resource 2). During early summer, homogeneity in soil water δ^{18}O and δ^{2}H (Fig. 4 and Online Resource 3) among the sampled depths hindered our ability to estimate depth of extraction, but for the midsummer and late summer sampling periods *R. tomentosum* and *E. vaginatum* derived 64–95 and 61–98% of their water, respectively, from the most surficial soil layers in tussocks, while *B. nana* and *S. pulchra* extracted water from the full active layer, with *S. pulchra* in particular deriving 12–98% of its water (midsummer and late summer median estimates 69.4 and 44.5%, respectively) from deeper in the soil profile (> 10 cm). Winter snow depth did not influence depth of extraction (Online Resource 2) except that due to differences in thaw rate among zones (Fig. 1), deeper water was available earlier in the +Snow zone.

Discussion

Our results offer strong evidence that Arctic deciduous shrubs capitalize on additional meltwater associated with deeper snowpacks as well as the enhanced nutrients suggested in the snow–shrub hypothesis. We found that deciduous shrubs derive a greater proportion of total water use from snowmelt than other growth forms in tussock tundra, suggesting that direct meltwater subsidies should be included as an ecophysiological mechanism in the snow–shrub interaction model (Fig. 7). Further, consistent
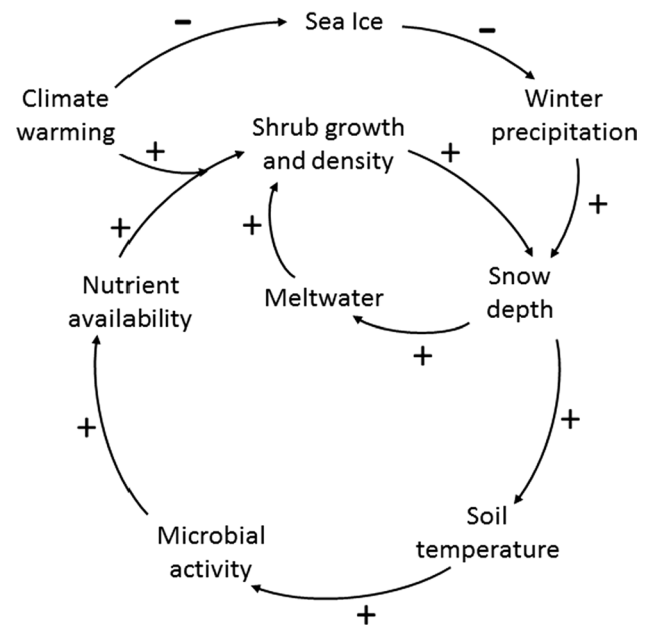

Fig. 7 A snow–shrub feedback loop, modified from Sturm et al. (2005a, b) to reflect climate impacts on winter precipitation and meltwater use by shrubs

with the nutrient-related components of the snow–shrub hypothesis, leaf-level gas exchange and tissue chemistry in deciduous shrubs were more sensitive than the other growth forms studied to long-term experimental increases and, to a lesser extent, decreases, in winter snow depth. In sum, as the Arctic climate continues to warm and deciduous shrubs expand their ranges with concomitant greater snow trapping, warmer winter soils, and increased N mineralization (Schimel et al. 2004), deciduous shrubs will be increasingly favored due to their capacity for exploiting not only the additional nutrients but also snow meltwater. Projected increases in Arctic winter precipitation (Min et al. 2008; Liston and Hiemstra 2011; Bintanja and Selten 2014) could amplify this selective feedback process, promoting more rapid shrub expansion.

We have strong isotopic evidence of asymmetric snow meltwater use by deciduous shrubs relative to other growth forms at Toolik Lake, a finding with implications for the snow–shrub hypothesis and Arctic ecohydrology. The two deciduous shrubs in our study, *B. nana* and *S. pulchra*, rely on meltwater for ca. 30–55% of their water from early through midsummer, much more than either the evergreen shrub *R. tomentosum* or the graminoid *E. vaginatum* (ca. 5–20%) studied, confirming our second hypothesis (Fig. 5). Ebbs (2016) reported a similar pattern from the 2007 and 2008 growing seasons at Toolik Lake, estimating that deciduous shrubs (*B. nana* and *Vaccinium uliginosum*) obtained 40–60% of their water from meltwater, compared to 35–40% for *R. tomentosum*. The proximate cause for this pattern appears to be deciduous shrubs extracting water from deeper in the soil profile than *E. vaginatum* or *R. tomentosum* (Fig. 6), where soil water is isotopically much closer to snow than summer rain (Fig. 4). This finding differs from several published profiles of root distribution and N uptake in other tussock tundra systems and in *E. vaginatum* in particular (Shaver and Cutler 1979; Zhu et al. 2016; Wang et al. 2018), raising the possibility of some vertical separation of water and nutrient uptake in this system, although a previous vertical profile of N acquisition at our site found patterns analogous to our findings (i.e., *B. nana* relying proportionally more on deeper N than *E. vaginatum* or *R. tomentosum* (McKane et al. 2002)). We were surprised to find that long-term snow depth manipulations have had little impact on the patterns of meltwater use or depth of water acquired (Online Resources 1 and 2), which contradicts the latter part of our second hypothesis, though Ebbs (2016) reported similarly muted effects of increased snow on meltwater use in this community. Regardless, the growth form differences we have collectively observed in meltwater usage support the addition of meltwater subsidies to the previously nutrient-focused snow–shrub feedback model (Fig. 7, Sturm et al. 2005a, b). Also, as deciduous shrubs expand in the Arctic, they may become more active in mediating the annual

pulse of meltwater to surface waters, the most important hydrologic flux in this system (Kane et al. 1989; e.g., Hinzman et al. 1991). Our stem and soil water results offer novel insights into niche differentiation and ecohydrologic function in the Arctic.

Individualistic plant ecophysiological responses to summer environmental perturbations have been a cornerstone of tundra ecological research for three decades (Karlsson 1985; Chapin and Shaver 1985; Welker et al. 2005), but our results add to the growing body of evidence in support of extending this to winter perturbations as well (Fahnestock et al. 1998; Jones et al. 1999; Welker et al. 2000; Leffler and Welker 2013). We observed enhanced A_{max} and g_s in the deeper snow areas relative to the ambient and reduced snow areas in the deciduous shrubs and *E. vaginatum*, but not *R. tomentosum*, partially consistent with our first hypothesis and the broader snow–shrub feedback model (Fig. 2). Snow depth effects on A_{max} and g_s were consistently strong in *S. pulchra* (ca. 50% or greater differences between the deeper snow area and the control or reduced snow areas), whereas in *B. nana* and *E. vaginatum* snow depth effects were smaller and confined to the latter stages of the growing season. Also, only *B. nana* and *E. vaginatum* tended to show lower A_{max} in the reduced snow area, and only *B. nana* showed any tendency toward lower g_s in the reduced snow area. These findings suggest that at the leaf level *S. pulchra* is uniquely capable of thriving with deeper winter snowpacks and also less sensitive to reductions in winter snow than some of its competitors, perhaps partially due to its ability to extract water from deeper in the active layer (Fig. 6). The positive effects we observed of deeper winter snow on leaf-level gas exchange are the strongest yet reported from Toolik, although the body of previous leaf-level ecophysiological work from this (Pattison and Welker 2014; Leffler et al. 2016) and other Arctic sites (Leffler and Welker 2013) also suggests a positive correlation between growing season leaf-level gas exchange and winter snow depth, with one recent exception (Schollert et al. 2017). The large snow depth effects we observed may be attributable to warmer growing season temperatures during 2016 relative to the measurement years of other published work from Toolik (Pattison and Welker 2014; Leffler et al. 2016). Regardless, the species-specific leaf-level ecophysiological consequences of manipulated winter precipitation at Toolik Lake suggest that continued changes to Arctic winter precipitation will influence leaf-level gas exchange of Arctic community dominants in different ways, and increased precipitation scenarios are likely to be especially significant for deciduous shrubs, in particular *S. pulchra*.

Our leaf N results offer continued support for the nutrient-related aspects of the snow–shrub hypothesis and have implications for broader ecosystem function. We found large (ca. 30%) increases in leaf N in the deciduous shrubs and

E. vaginatum in the deeper snow area, consistent with the increases in A_{max} we observed in this zone (Fig. 3). We also found slightly reduced leaf N (ca. 17%) in *B. nana* and *E. vaginatum* in the reduced snow area relative to the ambient or deeper snow areas during at least one sampling period. These findings confirm our first hypothesis and echo reports from other Arctic snowfence experiments of a positive correlation between foliar N and snow depth, particularly for deciduous shrubs (Torp et al. 2010; Leffler and Welker 2013; Semenchuk et al. 2015), most likely due to their ability to exploit expanded soil N pools associated with deeper snowpacks (Schimel et al. 2004; Buckeridge and Grogan 2008; Borner et al. 2008; Leffler and Welker 2013; Pattison and Welker 2014; Semenchuk et al. 2015), although previous work in moist tundra at Toolik has found mixed responses of leaf N to snow depth (Welker et al. 2005; Pattison and Welker 2014; Leffler et al. 2016). Given the more recent data underpinning our findings and those of Leffler et al. (2016), we must consider the confounding effect of increased litter deposition behind the snowfence enhancing the soil nutrient pool over time as a factor in the magnitude of treatment effects we observed, although previous work on this phenomenon found no relationship between litter deposition and net N mineralization (Fahnestock et al. 2000). In sum, the particularly strong positive relationship we found between winter snow depth and leaf N in the deciduous shrubs aligns with the N-cycling component of the snow–shrub hypothesis and suggests that shifts in other ecosystem components linked with leaf N, such as forage quality, may accompany increases in snow accumulation and retention, whereas reduced future snowpacks may have disparate impacts on the leaf nutrient characteristics and forage quality of shrub species, potentially forming a critical feedback into recently reported range expansions of wildlife in Arctic Alaska (Tape et al. 2016a, b).

Our δ¹³C results suggest that multiple Arctic plant species and growth forms are affected by the increased soil moisture associated with deeper winter snow, but the seasonal importance of this varies across species (Fig. 3). All the species in our study had lower (i.e., ¹³C-depleted) leaf δ¹³C values in the deeper snow area relative to the ambient or reduced snow areas during at least one sampling period, partially aligning with our second hypothesis. Together with the increased (*S. pulchra*, *B. nana*, and *E. vaginatum)* or unchanged (*R. tomentosum)* A_{max} and g_s values observed in the deeper snow area, these responses suggest that deeper winter snowpacks in this region may improve growing season water availability for most of the dominant vascular species in moist tussock tundra through a combination of deeper soil melt and direct meltwater subsidies. Previous work at this site (Pattison and Welker 2014), other arctic snowfence experiments (Morgner et al. 2010; Leffler and Welker 2013; Blok et al. 2015), and natural snow depth gradients (Sullivan and Welker 2007) has

shown similar responses in leaf δ¹³C values to deeper winter snow. Tundra vegetation is also responsive to altered summer precipitation, suggesting that broader moisture sensitivity in Arctic vegetation exists, especially in the High Arctic (Welker et al. 1993; Wookey et al. 1993, 1995; Keuper et al. 2012; Sharp et al. 2013). However, in our study no differences emerged in leaf δ¹³C between the ambient and reduced snow areas for any of the study species which, combined with the lack of differences observed between these areas in A_{max} and g_s, suggests that in this particular ecosystem partially reduced snowpacks alone may not necessarily lead to substantive changes in leaf-level gas exchange. This finding in particular differs from the only previous work in the reduced snow area at this site (Pattison and Welker 2014), highlighting the importance of repeated measurement campaigns, particularly for instantaneous gas exchange parameters. Finally, we found that δ¹³C values were more consistently low in the deeper snow area in *S. pulchra* than in *B. nana*, *R. tomentosum*, or *E. vaginatum* (Fig. 3), suggesting that *S. pulchra* is more capable of capitalizing on additional water resources throughout the full growing season to support enhanced gas exchange (Fig. 2) and that deeper future snowpacks may favor this species more than its current codominants. Chronology-based evidence of snow depth sensitivity in this and other tundra shrub species is mixed, however, with early summer temperature often found to have the strongest correlation with annual growth (Hallinger et al. 2010; Schmidt et al. 2010; Blok et al. 2011; Myers-Smith et al. 2015; Buchwal and Welker 2016; Ackerman et al. 2017).

The results of our study are valuable for several reasons. First, our results highlight the critical role of snow meltwater subsidies to tundra plants, in particular deciduous shrubs, suggesting another niche axis favoring their expansion as part of the snow–shrub feedback loop (Fig. 7) under increased Arctic precipitation projections (Min et al. 2008; Callaghan et al. 2011). Second, the strong differences we observed among snow zones in leaf-level ecophysiological traits substantiate seasonal connectivity between winter, spring, and summer ecophysiological and ecohydrological processes and reinforce the critical role of snow depth in regulating growing season ecophysiological processes in the Arctic. Finally, our results highlight the importance of refining regional climate projections for the Arctic, as high and low snow scenarios appear to have very different ecophysiological consequences for the dominant plant species.

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