

Plant production and nitrogen accumulation above- and belowground in low and tall birch tundra communities: the influence of snow and litter

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Abstract

Background and Aim A vegetation transition to taller and denser deciduous shrub tundra is currently occurring in many locations across the low Arctic, and is associated with climate change. Here, we investigated if deeper snow is a mechanism for enhanced shrub growth.

Methods To determine if a moderate and climatically realistic increase in snow depth can enhance shrub productivity, we compared growth responses between ambient and experimentally deepened snow plots in low birch hummock tundra. To determine the potential influence of factors other than deepened snow that are associated with taller, denser shrubs, we also compared shrub growth between low birch hummock and tall birch-dominated tundra.

Results Neither deciduous shrub above- nor belowground production nor nitrogen accumulation was enhanced by deepened snow. However, deciduous birch shrub new shoot production was 23× larger and total

vascular shoot to belowground biomass ratios were higher in the tall birch tundra than the birch hummock (~0.7 and ~0.4, respectively), indicating that the combination of deeper snow together with other internal feedbacks greatly enhanced birch growth.

Conclusions Together, our results strongly suggest that the much larger litter production in tall birch ecosystems is an important internal feedback that may or may not interact with deeper snow to promote birch growth in tall shrub tundra.

Keywords Arctic · *Betula* · Increased snow · Plant production · Shrub expansion · Snow-shrub feedback hypothesis

Introduction

The Arctic has experienced substantial climate warming in recent decades (Overpeck 1997; ACIA 2004), which has coincided with increased plant productivity and leaf phytomass in the vegetation across the Arctic (Goetz et al. 2005; Forbes et al. 2010; Beck and Goetz 2011; Xu et al. 2013). Observational and experimental data indicate that this increased plant productivity and leaf phytomass is at least partially caused by increased growth of deciduous shrubs, such as willow (*Salix* spp.), alder (*Alnus* spp.), and birch (*Betula* spp.) (Sturm et al. 2001; Tape et al. 2006; Myers-Smith et al. 2011; Elmendorf et al. 2012a, 2012b). A transition from low stature tundra vegetation to tall deciduous shrubs is expected to reduce albedo (Sturm et al. 2005a; Chapin

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et al. 2005; Loranty et al. 2011), alter drainage and erosion patterns (Tape et al. 2011), as well as increase permafrost destabilization provided that rising temperatures overwhelm the cooling effect caused by shrub cover soil shading (Bonfils et al. 2012). In addition, denser deciduous shrub cover may create either a positive or negative feedback to atmospheric carbon dioxide concentrations depending on whether increased litter production or other tall shrub features enhance carbon release from soil organic matter decomposition more than the carbon uptake associated with their enhanced plant productivity (Shaver et al. 1992; Mack et al. 2004). In that context, although aboveground biomass and production in the principal arctic vegetation-types have been well characterized (Jonasson et al. 1999; Elmendorf et al. 2012b; Sistla et al. 2013; Zamin et al. 2014), very few studies have comprehensively investigated species root components even though estimates from the literature suggest that the majority of tundra plant biomass in these ecosystems is belowground (Shaver and Chapin 1991). Therefore, careful quantification of the belowground plant biomass components, especially for deciduous shrubs, is a critical and urgently needed baseline dataset to allow determination of the future potential climate warming impacts on plant carbon accumulation, and hence arctic ecosystem net carbon balance.

Plant primary production in the Arctic is nutrient-limited (Shaver and Chapin 1980), and deciduous shrubs are often the most responsive to nutrient additions (Chapin et al. 1995; Jonasson et al. 1999; Bret-Harte et al. 2002a, 2002b; Zamin and Grogan 2012; Zamin et al. 2014), as well as to warming experiments (Zamin and Grogan 2012; Elmendorf et al. 2012a), that have presumably increased soil nutrient availability (Nadelhoffer et al. 1991). Together, these studies indicate that shrub growth and expansion across the Arctic is linked to mechanisms that increase nutrient availability. Thus, characterization of mechanisms contributing to enhanced nutrient availability is critical to understanding future expansion of deciduous shrubs across the Arctic, and therefore potential feedbacks to climate.

The Snow-Shrub Feedback Hypothesis is one proposed mechanism to explain the recent enhanced deciduous shrub growth. This hypothesis predicts that shrubs promote their own growth through a snow-shrub interaction where relatively tall shrubs accumulate deeper snow cover, increasing winter soil temperature minima. The resulting higher soil temperature enhances over

winter microbial activity, leading to increased availability of nutrients during the spring which are then taken up by shrubs (Sturm et al. 2001, 2005b). Many components of the Snow-Shrub Feedback Hypothesis have been supported by recent studies. Relatively tall shrubs do accumulate deeper snow than low stature plants (Sturm et al. 2005b), and deeper snow increases soil temperature minima (Nobrega and Grogan 2007), enhancing microbial activity (Schimel et al. 2004; Nobrega and Grogan 2007; Grogan 2012), that leads to a large nutrient pulse in late spring (Buckeridge and Grogan 2010). Nevertheless, despite this large soil nutrient pulse, an isotopic nitrogen study in those same plots found that deepened snow alone did not enhance deciduous shrub nitrogen uptake or production within two years (Vankoughnett and Grogan 2014). In a comparable Alaskan study, deciduous shrub aboveground net primary production was unaffected by two years of deepened snow alone (Natali et al. 2012). In another, there were >40 % increases in *Betula nana* and *Salix pulchra* shrub cover after eight years of deepened snow treatment (Wahren et al. 2005), but the snowfences were 2.8 m high (6× ambient levels) and therefore demonstrate the potential for change but perhaps not the likely change at least within current climate projections for arctic snow accumulation (ACIA 2004). Consequently, the final component of the Snow-Shrub Feedback Hypothesis, whether moderately deepened snow can enhance deciduous shrub species production is not yet fully resolved.

Few studies have specifically compared species production rates between low and tall shrub tundra ecosystems, and therefore the mechanistic basis for determining the potential for a vegetation transition from low to taller and denser birch vegetation is limited. Apart from the direct effects that deeper snow cover provides to winter processes, areas of tall dense deciduous shrubs have greater winter and summer nitrogen mineralization due to the relatively greater quantity and possibly higher chemical quality of leaf litter and soil organic matter that permits faster decomposition (Buckeridge et al. 2009; Chu and Grogan 2010; DeMarco et al. 2011). Under these more fertile conditions, deciduous shrubs can out-compete other species for nitrogen (Vankoughnett and Grogan 2014), but how this affects shrub and other species production in these ecosystems remains unclear. Furthermore, species-level studies comparing the communities in low and tall birch ecosystems are urgently required to evaluate and interpret recent patterns of not

just deciduous but also evergreen shrub change (Elmendorf et al. 2012b), as well as to predict future change (Myers-Smith et al. 2011).

For this study, we investigated the impact of deepened snow on above- and belowground plant production of all species in low birch hummock tundra over four years in the Canadian sub-Arctic. In addition, to determine if factors other than deepened snow alone such as the quantity and quality of litterfall that are associated with the increased shrub stature and density in tall birch tundra also influence deciduous shrub production, we compared species growth responses between low birch hummock and tall birch-dominated tundra ecosystems. We used our data to test the following hypotheses:

- I. Deepened snow in low birch hummock tundra significantly enhances birch shrub growth.
- II. Birch shrub above- and belowground biomass and growth are greater in tall birch than in low birch hummock tundra ecosystems.
- III. Tall birch ecosystems may promote higher production and faster nitrogen cycling than in low birch ecosystems by producing larger quantities of litter.

Methods

Site description

The study was conducted at the Tundra Ecological Research Station (TERS) at Daring Lake (64° 52' N, 111° 35' W) that is located in the Coppermine River watershed, ~300 km northeast of Yellowknife, NWT. Local climate records (Bob Reid, Indian and Northern Affairs Canada, unpublished data, 1996–2011) indicate average annual mean diel temperatures as low as -30 °C in winter and as high as 14 °C in summer, with a mean annual air temperature of -9 °C. Mean annual rainfall is 160 mm, with snowfall accumulation generally occurring for ~200 days of the year, starting in mid-October, reaching a depth of 10 cm by early November, peaking at ~35 cm in April, and persisting until mid-June (Buckeridge and Grogan 2008). Our research area is located along a gently sloping valley bordered by an esker to the north and Canadian Shield bedrock outcrops to the south. The region is underlain by continuous permafrost (>160 m depth), with an active layer that varies by vegetation type from 0.3 to 1.2 m depth at

maximum (Dredge et al. 1999; Lafleur and Humphreys 2008). Many different types of circumpolar vegetation inhabit the area. The vegetation community-types along toposequences range from exposed ridges where dry heath is common down to mesic low birch hummock and ultimately wet sedge at the base of the valley. Tall birch patches are scattered across the landscape in areas close to obvious seasonal surface water flow, but also in apparently mesic locations including relatively high elevation areas protected from the prevailing wind where snow preferentially accumulates (Obst 2008).

The experiment was conducted in a mesic low birch hummock and tall birch tundra ecosystems. The mesic low birch hummock vegetation is part of the erect dwarf shrub category of arctic vegetation types (CAVM 2003) where birch hummocks are 30 cm high and consist of 20–30 cm tall deciduous dwarf birch (*Betula glandulosa* (Michx.)) shrubs. Our mesic low birch hummock tundra study site is dominated by evergreen shrubs, mountain cranberry (*Vaccinium vitis-idaea* L.) and labrador tea (*Rhododendron subarcticum*), bog rosemary (*Andromeda polifolia* L.), constituting ~48 % of the aboveground biomass, with mosses and lichens (predominantly *Cetraria* spp. and *Cladonia* spp.) constituting ~20 and 25 % respectively, and dwarf birch shrub shoots comprising 7 % (Zamin et al. 2014). Bog blueberry (*Vaccinium uliginosum* L.), cloudberry (*Rubus chamaemorus* L.), and graminoids (mainly *Carex* spp.) are also present but less frequent (Nobrega and Grogan 2007). An experimentally deepened snow treatment was established in replicate patches of low birch hummock tundra in summer 2004 using snowfences in a staggered formation ~30–60 m apart from one another down a gentle slope, and control plots ($n = 5$) were generally located alongside (20–40 m away, not paired) in nearby patches of similar vegetation composition and topography (Nobrega and Grogan 2007). Plots (40 cm × 40 cm) centered around a single dwarf birch shrub were randomly located in each of the control and snowfence birch hummock sites, resulting in five plots per treatment (App. Fig. 1).

Tall birch ecosystems are dominated by *B. glandulosa* shrubs ~80 cm high, with species composition in this ecosystem that was almost identical to the birch hummock vegetation, except that *A. polifolia* was absent, and occasional tall willow shrubs (*Salix* spp.) were present (App. Fig. 1). Five plots (80 cm × 80 cm) were randomly located along a down-slope transect within a large patch (~40 m × 130 m) of tall birch tundra located on a gentle slope in the same

valley as the low birch hummock sites (Buckeridge et al. 2009). This patch of tall birch was chosen as our study site because, unlike all other nearby tall birch patches in the landscape, it was not located in an area of obvious surface water flow (although springtime surface flow seems to be prevalent there), or in an area protected from the prevailing wind where snow preferentially accumulates. We acknowledge that there is an element of pseudoreplication because all plots were within one tall birch patch, but since the patch was large, and the sampled shrubs were >10 m apart, we assume that these shrubs were independent of each other. Furthermore, the tall birch soil physical and biogeochemical values reported here are very similar to previous data from the full variety of tall birch patches across that landscape (Chu and Grogan 2010). We used larger sized plots in the tall birch ecosystem to account for the bigger size, canopy cover, and associated root biomass of the birch shrubs there. Plots were located away from the edge (>3 m) of the tall shrub patch in order to not to confound the experiment with potential differences in snow cover that accumulate at the edge of the shrub patch compared to within the patch.

Site differences in soil environmental and edaphic characteristics

Site differences in soil environmental and edaphic characteristics have previously been described in Vankoughnett and Grogan (2014). Briefly, both the snowfence and tall birch site showed a strong snow insulation effect on soil temperature in winter (5 cm depth). In particular, from 2006 to 2007 the snowfence insulating effect became evident in late December and was several degrees warmer (-5.5 vs -7.5 °C) than the control birch hummock plot, reaching maximum difference of 6.2 °C degrees in early February (-10.3 vs. -17.5 °C). Unlike the previous year, during 2007–2008 the snow accumulation effect did not become evident until late January indicating differences in snow accumulation between years, with the greatest separation between temperatures occurring in mid to late March (-20.5 vs. -13.5 °C for the control and snowfenced birch hummock, respectively). The tall birch site was generally ~ 5 °C warmer than the control in early January 2006–2007 (-2 vs. -7 °C), reaching a maximum difference of 9 °C in early February (-6 vs. -15 °C). A similar pattern was observed the second year (2007–2008), where the tall birch site was ~ 5 – 6 °C warmer than the

control birch hummock for much of the winter, reaching the greatest temperature separation of ~ 6 °C (-15 vs. -21 °C) in early February. On April 8th, 2007, mean snow depths were 29 (2), 87 (3) and 52 (3) cm (parentheses indicate standard errors), and 29 (1), 96 (3) and 62 (5) cm on May 05, 2008 in the birch hummock, snowfenced birch hummock and tall birch plots, respectively (Vankoughnett and Grogan 2014).

Both datalogger records of continuous volumetric water content and gravimetric measurements indicate that the tall birch organic layer soil moisture was drier than both of the birch hummock sites over the growing season (Vankoughnett and Grogan 2014). Furthermore, there were no site differences in either measure of moisture content in the uppermost mineral soil underlying the organic layer in each ecosystem (Vankoughnett and Grogan 2014).

Sample collection

To determine the influence of deepened snow on plant biomass and nitrogen pools of individual plant components among species, we removed the entire turf of soil plus associated vegetation above- and belowground (to a 10 cm soil depth) from each replicate plot (80 cm \times 80 cm and 40 cm \times 40 cm, for the tall birch and birch hummock sites, respectively) just prior to leaf senescence (between August 9–23, 2008). For both ecosystems, we assumed plant communities within each plot were representative of the overall vegetation at each site and therefore extrapolated the sampled biomasses of most species and growth forms directly up to 1 m² area. However, because we used different plot sizes (40 \times 40 cm and 80 \times 80 cm for the birch hummock and tall birch, respectively), there is potential for plant biomass inaccuracies between ecosystems due to scaling differences. Also, since each birch hummock plot was deliberately centered on a birch shrub and the nearest neighbor distance for *B. glandulosa* in the low birch hummock sites was outside of the plots, we calculated its overall areal biomass in those sites using a density of two birch plant ramets per m² that was determined for a previous study in the same research valley in order to not underestimate birch biomass (Zamin and Grogan 2012). *B. glandulosa* leaf litter production was measured by collecting leaves from senescing plants and the soil surface in randomly selected birch hummock and tall birch plots (2 m² and 1 m² areas respectively; $n = 4$) on Sept 5th, 2011, three years after initial biomass collection.

Sample processing

Intact vegetation from each tall birch and birch hummock plot was gently teased out from the soil to collect as much of the attached root system as possible, and then sorted to species and growth forms. Birch shrubs were sorted into shoot new growth (all leaves plus apical stem tissue produced in the current growing season as determined by colour change and complete budscars), shoot old growth (stem biomass from all previous years including secondary growth (shoot thickening)), below-ground stems (>5 mm diameter), coarse roots (2–5 mm diameter), and fine roots (<2 mm diameter). Birch below-ground stems and coarse roots were not observed in the mineral layer samples (top ~3–4 cm depth) of any plot.

Other vascular plant shoots were separated into shoot new growth (apical stem tissue in the current growing season, and leaves and inflorescences/fruits), shoot old growth, and fine roots (all were <2 mm diameter). All evergreen species leaves were included in the new shoot apical growth category to reduce sorting time, and although this compromises our ability to compare new and old shoot biomass categories for these species, it should not impact our capacity to determine site differences in their sum – total aboveground biomass (i.e. the main focus of our hypotheses). *Salix* spp. were rare but had distinctive ‘tap’ roots extending >20 cm down into the mineral layer. Graminoid species were sorted as a group into shoot new growth (leaves and inflorescences), shoot old growth (standing dead tissue, stem bases and rhizomes), and fine roots (all <2 mm diameter). The remaining material above the organic soil layer was sorted into mosses (all green living tissue), lichens, and surface litter (including leaf fragments, small twigs, dead moss tissue, and additional leaves found within the moss layer). Only living roots (on the basis of tissue turgor and colour) were included in the former category and were separated into fine roots (<2 mm diameter) and placed into an organic or mineral soil category depending on where they were found. Roots were rinsed with water to remove any adhering soil particles.

Total nitrogen pool analyses

Oven-dried (60 °C) shoot tissues and roots were ground for ~1 min to a fine powder with a centrifugal mill (Retsch, Germany), weighed out (~1 mg) into tin capsules (2 mm, Elemental Microanalysis Limited, UK)

and sent for total nitrogen analyses at the University of Waterloo Environmental Isotope Lab.

Statistical analyses

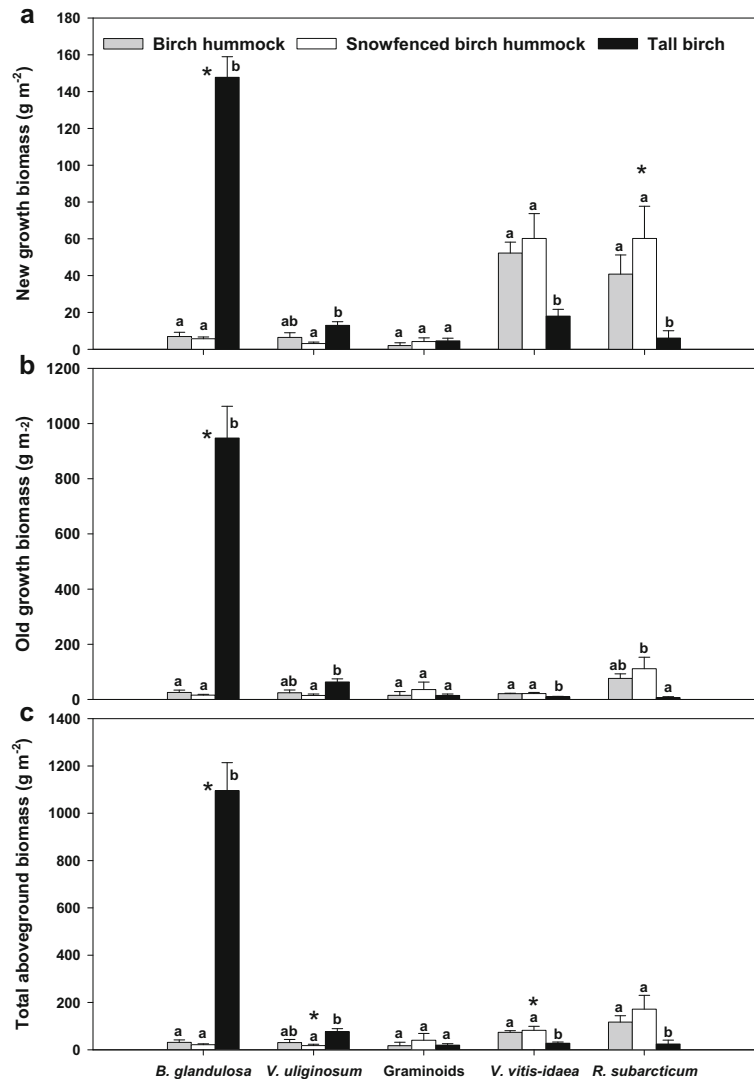
We tested for significant effects of site on plant biomass and nitrogen pools of each growth component that was identified to species using separate one way analyses of variance (ANOVAs). Multiple comparisons were analyzed using the Tukey-Kramer HSD test to identify significant differences between all pairwise combinations (JMP 12, SAS Institute). In addition, the Holm-sequential Bonferroni correction (Quinn and Keough 2002) was applied to all site comparisons for each species’ new growth, old growth, total growth, fine root biomass and nitrogen pools. All plant species biomass and nitrogen pool data were log transformed to meet the Shapiro-Wilks normality tests.

Results

Plant species biomass variation among sites

Total aboveground biomass in the tall birch site was dominated by *B. glandulosa* followed by mosses, lichens, *V. uliginosum*, *V. vitis-idaea*, *R. subarcticum*, and graminoids. The total vascular shoot to below-ground biomass ratio for each species at the tall birch site was ~1.2, ~1.4, ~2.4, ~3.1, and ~3.2 for *V. uliginosum*, *B. glandulosa*, *V. vitis-idaea*, *R. subarcticum*, and graminoids, respectively, resulting in a total vascular shoot to belowground biomass (including unidentified roots) ratio of ~0.78 at this site (Fig. 1c; Table 1). By contrast, the aboveground biomass of the birch hummock sites was generally dominated by lichens and mosses, followed by *R. subarcticum*, *B. glandulosa*, *V. vitis-idaea*, *V. uliginosum*, *A. polifolia* and graminoids. The total vascular shoot to belowground biomass ratio for each species at the birch hummock sites was ~0.75, ~1.7, ~2.3, ~3.4 and ~28.0, for the *B. glandulosa*, *V. uliginosum*, *R. subarcticum*, *V. vitis-idaea*, and graminoids, respectively, resulting in a total vascular shoot to belowground biomass (including unidentified roots) ratio of ~0.46 at these sites (Fig. 1c; Table 1). The control and snowfenced birch hummock sites did not differ in any plant biomass component, either above- or belowground (Fig. 1c; Table 1)

Fig. 1 Plant shoot new growth (a), old growth (b), and total aboveground (c) biomass (g m^{-2}) of the major vascular species at each site ($n = 5$; bars = S.E.). Species do not significantly differ among sites if they share the same superscript letters (ranging from a–c; $P < 0.05$; * indicates significance after Holm-Sequential Bonferroni correction is applied). Figure 1c is reproduced in figure format from Vankoughnett and Grogan, 2014 (Table S1)



Total vascular shoot new growth (i.e. apical biomass produced in the harvest year) was highest at the tall birch site (Fig. 1a, Table 1). In particular, new apical growth of *B. glandulosa* was 23× larger in the tall birch ecosystem than in either of the birch hummock sites (Fig. 1a, $F_{2,14} = 210.3$, $P < 0.0001$). In contrast, the evergreen species *R. subarcticum* and *V. vitis-idaea* together were the larger component of total vascular shoot new growth in the birch hummock sites ($F_{2,14} = 6.9$, $P = 0.009$ and $F_{2,14} = 10.1$, $P = 0.027$, respectively). Furthermore, new growth was similar among sites for Graminoids, while *V. uliginosum* new growth was highest at the tall birch site, but did not differ from the control birch hummock site (Fig. 1a, $F_{2,14} = 5.50$, $P = 0.0202$). The *B. glandulosa* and *R. subarcticum*

differences remained significant after the Holm-Sequential Bonferroni correction was applied.

We found similar corresponding patterns to the above for shoot old growth biomass among sites (Table 1). *B. glandulosa* shoot old growth was ~47× larger at the tall birch site ($F_{2,14} = 178.3$, $P = 0.0001$), the evergreens *R. subarcticum* and *V. vitis-idaea* dominated shoot old biomass at the birch hummock sites (Fig. 1b, $F_{2,14} = 4.9$, $P = 0.0276$ and $F_{2,14} = 6.4$, $P = 0.0127$, respectively). Graminoid old growth biomass did not differ among sites, while *V. uliginosum* old shoot growth was highest at the tall birch site (Fig. 1b; $F_{2,14} = 5.2$, $P = 0.0237$). Only the *B. glandulosa* difference remained significant after the Holm-Sequential Bonferroni was applied.

Table 1 Biomass (g m^{-2}) of total aboveground vascular plant new, old, and new + old growth, non-vascular plants, belowground vascular plants and surface litter mass at each site in late August 2008 ($n = 5$; parentheses indicate standard errors). Significant sitedifferences within rows are indicated by differences in superscript letters ranging from a-c ($P < 0.05$; *indicates significance in the species fine root category after Holm-Sequential Bonferroni correction is applied)

	Birch Hummock	Snowfenced Birch Hummock	Tall Birch	Statistical analysis
[‡] Total aboveground vascular				
New growth	121.0 ^a (11.7)	139.8 ^a (21.6)	189.6 ^b (15.6)	$F_{2,14} = 4.45, P = 0.0359$
Old growth	176.3 ^a (16.5)	209.5 ^a (51.0)	1055.4 ^b (123.1)	$F_{2,14} = 32.82 P < 0.0001$
New + Old growth	297.4 ^a (24.5)	349.2 ^a (68.3)	1245.0 ^b (131.0)	$F_{2,14} = 37.95 P < 0.0001$
Non-vascular				
Mosses	141.6 ^a (31.0)	310.8 ^a (70.8)	143.0 ^a (21.0)	
Lichens	227.4 ^a (61.5)	137.2 ^{ab} (22.0)	76.8 ^b (27.2)	$F_{2,14} = 5.03 P = 0.0259$
Total vascular plus non-vascular shoots	666.3 ^a (19.1)	797.2 ^a (75.6)	1464.8 ^b (126.0)	$F_{2,14} = 25.08 P < 0.0001$
Belowground vascular biomass				
Belowground stems (>5 mm)				
<i>Betula glandulosa</i>	23.9 ^a (8.8)	6.7 ^a (3.0)	565.3 ^b (126.5)	$F_{2,14} = 18.97, P = 0.0002$
Coarse roots (2–5 mm)				
<i>Betula glandulosa</i>	32.3 ^a (11.9)	7.1 ^a (3.1)	147.7 ^b (67.9)	$F_{2,14} = 7.36 P = 0.0082$
Fine roots (<2 mm)				
<i>Betula glandulosa</i>	1.8 ^a (0.6)	3.5 ^a (1.5)	43.7 ^b (17.8)	$F_{2,14} = 11.82 P = 0.0015^*$
<i>Vaccinium uliginosum</i>	17.7 ^a (7.4)	10.5 ^a (2.7)	65.1 ^b (19.8)	$F_{2,14} = 6.83 P = 0.0105^*$
Graminoids	1.4 ^a (1.0)	0.7 ^a (0.6)	5.9 ^a (2.6)	$F_{2,14} = 2.98 P = 0.0887$
<i>Vaccinium vitis-idaea</i>	25.5 ^a (2.5)	19.5 ^a (5.6)	11.4 ^a (3.5)	$F_{2,14} = 3.69 P = 0.0566$
<i>Rhododendron subarcticum</i>	51.2 ^a (18.7)	75.9 ^a (25.3)	8.0 ^b (4.6)	$F_{2,14} = 6.30 P = 0.0135^*$
<i>Andromeda polifolia</i>	8.5 (2.8)	6.7 (3.1)	0 (0)	
<i>Salix spp</i>	0 (0)	0 (0)	0.5 (0.5)	
Unidentified (organic soil)	533.9 ^a (128.4)	579.6 ^a (86.4)	824.5 ^a (129.0)	
^α Mineral soil roots	49.8 ^a (35.3)	16.4 ^a (10.9)	56.7 ^a (26.9)	
Total fine roots	689.9 ^a (114.5)	706.1 ^a (81.8)	1015.8 ^a (149.7)	
Total belowground biomass	741.3 ^a (105.0)	719.9 ^a (82.0)	1728.7 ^b (315.8)	$F_{2,14} = 8.49 P = 0.0052$
Total vascular plus non-vasc. Plant biomass	1407.6 ^a (87.2)	1517.1 ^a (140.5)	3193.5 ^b (411.1)	$F_{2,14} = 15.32 P = 0.0005$
Surface litter	1122.0 ^a (413.7)	835.4 ^a (294.0)	1088.4 ^a (192.7)	

^αOnly the uppermost 3–4 cm of the mineral layer were sampled[‡]Note that *Andromeda polifolia* and *Salix spp.* new, old, and total growth biomass were added to their respective categories for each site

As a result of these site differences in new and old shoot growth, total aboveground vascular shoot biomass (i.e. new plus old growth of all species) was ~4× larger in the tall birch site compared to the birch hummock sites (Table 1). Similar to new and old growth biomasses, total aboveground biomass was dominated by *B. glandulosa* at the tall birch site (Fig. 1c, $F_{2,14} = 80.9, P = <0.0001$), and by *R. subarcticum* and *V. vitis-idaea* at the low birch hummock sites (Fig. 1c, $F_{2,14} = 3.8, P = 0.0517$ and $F_{2,14} = 6.9, P = 0.0103$, respectively). *V. uliginosum* had

more biomass at the tall birch, but did not differ from the control birch hummock site (Fig. 1c, $F_{2,14} = 8.4, P = 0.0053$), while Graminoid total aboveground biomass did not differ among sites (Fig. 1c).

Although the *B. glandulosa* belowground stem and coarse root biomass components were larger in the tall birch site, neither the large proportions of unidentified fine roots nor the total fine root biomass differed among sites (Table 1). Species-identified fine root biomass (attached to shoots during harvest) comprised ~20 % of the total fine root biomass. Not surprisingly, the

species-identified fine root biomass was dominated by *R. subarcticum* and *V. vitis-idaea* in the low birch hummock sites, while *B. glandulosa*, Graminoid and *V. uliginosum* fine roots were all larger at the tall birch site (Table 1). Overall, total vascular plus non-vascular biomass was 2× larger in the tall birch site than in either of the birch hummock sites. Finally, although *B. glandulosa* senesced leaf litter production was ~10× larger in the tall birch plots than in the low birch hummock plots (44.3 (±11.8) and 4.3 (±1.2) g m⁻² means and standard errors respectively; $P < 0.015$), the total mass of dead leaf, small twig and moss litter on the

ground surface just prior to leaf senescence did not differ among sites (Table 1).

Plant species nitrogen pool variation among sites

The pattern of variation in shoot total nitrogen pools among species generally correlated with biomass components (Table 2), although differences in tissue nitrogen concentrations modified the magnitude of variation in some cases (App. Table 1). Nitrogen pools were generally dominated by the lichens and mosses in the birch hummock sites, and by *B. glandulosa* in the tall

Table 2 Nitrogen (N) pool (g m⁻²) of total aboveground vascular plant new, old, and new + old growth, non-vascular plants, belowground vascular plants and surface litter mass at each site in late August 2008 ($n = 5$; parentheses indicate standard errors).

Significant site differences within rows are indicated by differences in superscript letters ranging from a-c ($P < 0.05$; *indicates significance in the species fine root category after Holm-Sequential Bonferroni correction is applied)

	Birch Hummock	Snowfenced Birch Hummock	Tall Birch	Statistical analysis
[‡] Total aboveground vascular				
New growth	1.35 ^a (0.13)	1.44 ^a (0.20)	3.92 ^b (0.32)	$F_{2,14} = 41.40, P < 0.0001$
Old growth	1.09 ^a (0.07)	1.26 ^a (0.28)	6.74 ^b (0.88)	$F_{2,14} = 45.38, P < 0.0001$
New + Old growth	2.44 ^a (0.17)	2.70 ^a (0.46)	10.66 ^b (1.09)	$F_{2,14} = 55.99, P < 0.0001$
Non-vascular				
Mosses	1.19 ^a (0.30)	2.55 ^a (0.55)	1.58 ^a (0.26)	$F_{2,14} = 3.56, P = 0.0847$
Lichens	1.55 ^a (0.75)	0.89 ^a (0.14)	0.43 ^a (0.16)	
Total vascular plus non-vascular shoots	5.18 ^a (0.56)	6.14 ^a (0.68)	12.68 ^b (1.06)	$F_{2,14} = 29.70, P < 0.0001$
Belowground vascular biomass				
Belowground stems (>5 mm)				
<i>Betula glandulosa</i>	0.16 ^a (0.06)	0.05 ^a (0.02)	3.80 ^b (0.89)	$F_{2,14} = 15.29, P = 0.0007$
Coarse roots (2–5 mm)				
<i>Betula glandulosa</i>	0.20 ^a (0.07)	0.05 ^a (0.02)	0.97 ^b (0.44)	$F_{2,14} = 8.20, P = 0.0057$
Fine roots (<2 mm)				
<i>Betula glandulosa</i>	0.02 ^a (0.01)	0.02 ^a (0.01)	0.34 ^b (0.13)	$F_{2,14} = 14.72, P = 0.0007^*$
<i>Vaccinium uliginosum</i>	0.12 ^a (0.05)	0.06 ^a (0.02)	0.40 ^b (0.11)	$F_{2,14} = 6.72, P = 0.0110^*$
Graminoids	0.02 ^a (0.01)	0.01 ^a (<0.01)	0.04 ^a (0.02)	
<i>Vaccinium vitis-idaea</i>	0.17 ^a (0.02)	0.13 ^a (0.03)	0.09 ^a (0.03)	
<i>Rhododendron subarcticum</i>	0.29 ^{ab} (0.11)	0.42 ^a (0.15)	0.04 ^b (0.02)	$F_{2,14} = 3.41, P = 0.0675$
<i>Andromeda polifolia</i>	0.05 (0.02)	0.04 (0.02)	0 (0)	
<i>Salix spp</i>	0 (0)	0 (0)	0.01 (0.01)	
Unidentified (organic soil)	3.49 ^a (0.79)	3.83 ^{ab} (0.50)	6.63 ^b (0.87)	$F_{2,14} = 5.47, P = 0.0205$
^α Mineral soil roots	0.54 ^a (0.31)	0.11 ^a (0.07)	0.47 ^a (0.24)	
Total fine roots	4.47 ^a (0.70)	4.58 ^a (0.46)	8.02 ^b (1.04)	$F_{2,14} = 7.09, P = 0.0093$
Total belowground biomass	4.80 ^a (0.65)	4.67 ^a (0.46)	12.78 ^b (2.14)	$F_{2,14} = 9.41, P = 0.0035$
Total vascular plus non-vasc. Plant biomass	9.98 ^a (0.52)	10.81 ^a (1.06)	25.46 ^b (2.91)	$F_{2,14} = 18.94, P = 0.0002$
Surface litter	10.74 ^a (4.44)	8.47 ^a (3.09)	12.81 ^a (3.31)	

^α Only the uppermost 3–4 cm of the mineral layer were sampled

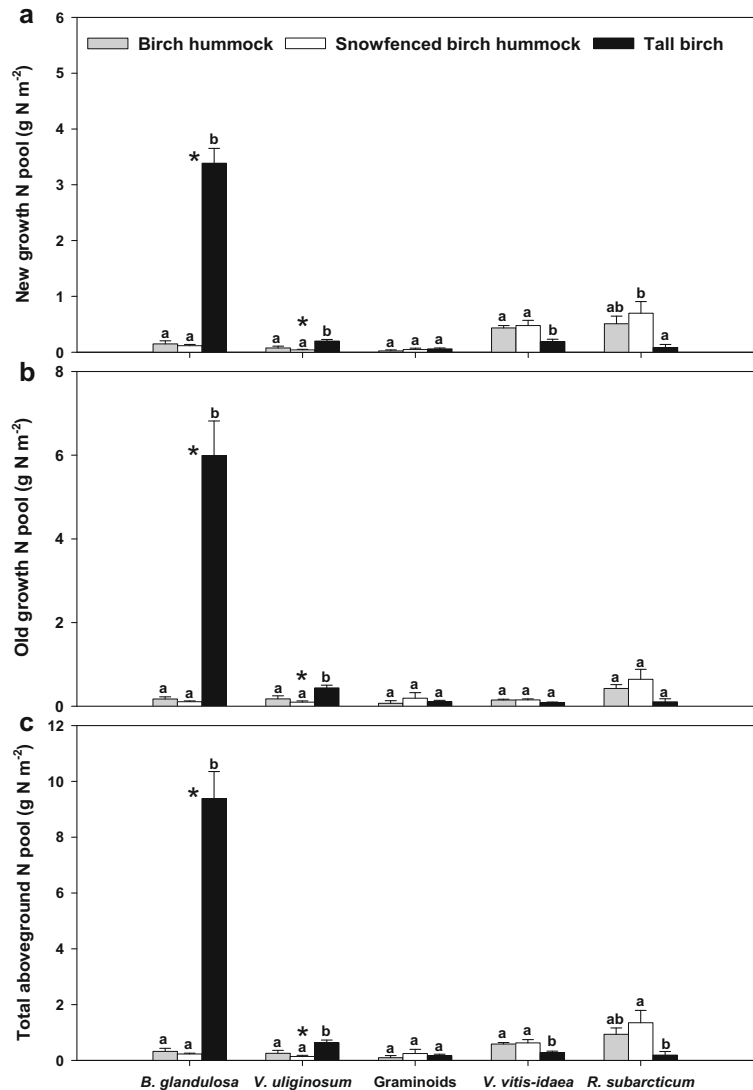
[‡] Note that *Andromeda Polifolia* and *Salix spp*. N pool new, old and total growth was added to their respective categories

birch ecosystem (Fig. 2; Table 2). Species nitrogen accumulation within shoot new and old growth components were highest in the tall birch site leading to greater aboveground nitrogen pools there (Fig. 2a, b). Total aboveground (i.e. new plus old shoots combined) birch nitrogen was at least 9× higher than any other species at the tall birch site, or than in the same species at either of the birch hummock sites (Fig. 2a, b, c). In particular, *B. glandulosa* new shoot growth nitrogen pool was ~25× larger at the tall birch site than at the birch hummock sites, respectively ($F_{2,14} = 185.8$, $P < 0.0001$). *V. uliginosum* also had a higher new shoot nitrogen pool at the tall birch site (Fig. 2a, $F_{2,14} = 10.72$, $P = 0.0021$), while *R. subarcticum* and *V. vitis-idaea* new shoot

nitrogen pools were greater at the birch hummock sites (Fig. 2a, $F_{2,14} = 4.7$, $P = 0.0310$ and $F_{2,14} = 6.1$, $P = 0.050$). However, only *B. glandulosa* and *V. uliginosum* remained significant after the Holm-Sequential Bonferroni correction was applied.

As with the new shoots nitrogen pool, *B. glandulosa* and *V. uliginosum* old growth nitrogen pools were highest at the tall birch site (Fig. 2b, $F_{2,14} = 73.0$, $P < 0.0001$ and $F_{2,14} = 9.3$, $P = 0.0021$, respectively). Furthermore, old shoot *V. vitis-idaea* and *R. subarcticum* nitrogen pools tended to be larger at the birch hummock sites (Fig. 2b; $F_{2,14} = 3.3$, $P = 0.071$ and $F_{2,14} = 3.2$, $P = 0.075$, respectively). *B. glandulosa* and *V. uliginosum* total aboveground nitrogen pools were

Fig. 2 Plant shoot new growth (a), old growth (b), and total aboveground (c) nitrogen (N) pools (g N m^{-2}) of the major vascular species at each site ($n = 5$; bars = S.E.). Species do not significantly differ among sites if they share the same superscript letters (ranging from a–c; $P < 0.05$; *indicates significance after Holm-Sequential Bonferroni correction is applied)



highest at the tall birch site (Fig. 2c, $F_{2,14} = 148.6$, $P < 0.0001$ and $F_{2,14} = 9.8$, $P = 0.0030$, respectively), and *R. subarcticum* and *V. vitis-idaea* total aboveground nitrogen pools were larger in the birch hummock sites (Fig. 2c, $F_{2,14} = 4.1$, $P = 0.0453$ and $F_{2,14} = 5.8$, $P = 0.0177$). Only *B. glandulosa* and *V. uliginosum* remained significant after the Holm-Sequential Bonferroni was applied. Graminoid new shoot, old shoot and total aboveground nitrogen pools did not differ among sites. Overall total aboveground vascular plant nitrogen pools across all species in new plus old shoot growth components were $\sim 4\times$ larger at the tall birch site than at the birch hummock sites, resulting in $\sim 2\times$ more total vascular plus non-vascular plant nitrogen at the former site (Table 2).

The total fine root nitrogen pool was almost twice as large in the tall birch ecosystem compared to the birch hummock sites (Table 2) due to larger biomass (Table 1) and a slightly higher mean tissue nitrogen concentration (App. Table 1). Nitrogen pools in *B. glandulosa* belowground stems, coarse, and fine roots, as well as *V. uliginosum* fine roots, and the unidentified fine roots within the organic layer were all higher in the tall birch compared to the birch hummock sites, together resulting in a $\sim 2.5\times$ larger total belowground biomass nitrogen pool in the tall birch site (Table 2). On the other hand, *R. subarcticum* fine root nitrogen pools were larger at the birch hummock sites (Table 2). Finally, the total pool of nitrogen in both aboveground and belowground plant tissues across all vascular species was $\sim 3\times$ greater in the tall birch than in either of the birch hummock sites, resulting in $\sim 2.5\times$ more total plant (vascular plus non-vascular) nitrogen in that ecosystem (Table 2).

Discussion

The influence of experimentally deepened snow on plant species production and nitrogen accumulation in the low birch hummock ecosystem

Experimentally deepened snow did not significantly enhance production or nitrogen accumulation by deciduous shrubs or any other plant species (Figs. 1, 2), rejecting Hypothesis I and challenging the prediction of the Snow-Shrub Feedback Hypothesis (Sturm et al. 2001, 2005b). We had anticipated that the deepened snow would enhance birch shrub production and nitrogen pool accumulation because we had already

determined in the same plots that the snowfences cause a very large late spring thaw pulse of soil solution ammonium, phosphate and dissolved organic nitrogen and phosphorus (Buckeridge and Grogan 2010). However, despite this large pulse of nutrients, our earlier study demonstrated that deepened snow did not enhance isotopic ^{15}N nitrogen uptake by birch shrubs (or any other species) two years after its addition (Vankoughnett and Grogan 2014). Our study here reflects the impact of deepened snow on birch shrub growth (and other species) after four years, and similar to the isotopic ^{15}N nitrogen experiment, it may have been too short in duration to detect differences that could ultimately occur. After all, significant birch shrub growth responses to chronic high level nutrient additions generally take several years (Chapin et al. 1995; Zamin and Grogan 2012), and therefore a lack of response to much more moderate nutrient increases within the timeframe of our study may not be surprising. Alternatively, there are several reasons why deepened snow alone may not enhance shrub biomass or nitrogen accumulation, whatever the time-scale. Greater surface runoff from deeper snow cover may enhance leaching losses of the late spring nutrient pulse. Furthermore, birch shrub nutrient uptake seems to begin at least several weeks after snowmelt (Larsen et al. 2012) long after the late spring nutrient pulse takes place, suggesting that this species may not be able to directly acquire nutrients during the pulse period. Nevertheless, experimentally deepened snow over a similar timeframe to our study has enhanced *Salix* and *Betula* shrub growth in N. Alaska (Bret-Harte, pers. Comm.). Overall, we can conclude that there was no significant effect of deepened snow over four years at our site, and therefore there may be substantial spatial and temporal heterogeneity in the impact of the snow-shrub feedback on shrub growth across the Arctic.

Biomass and production in tall birch as compared to birch hummock ecosystems

Both total above- and belowground plant biomass and production were substantially higher in the tall birch compared to the low birch ecosystems, mainly due to *B. glandulosa* (Table 1, Fig. 1). *B. glandulosa* new production (i.e. new apical shoot growth), old growth biomass, belowground stem, coarse root, and fine root components were $\sim 23\times$, $\sim 48\times$, $\sim 37\times$, $\sim 7.5\times$, and $\sim 16\times$ larger at the tall birch site than at the birch hummock, respectively, supporting Hypothesis II (Fig. 1, Table 1).

Preliminary growth ring counts indicated that the old shoot mean age of harvested *B. glandulosa* ($n = 5$) was greater in the tall birch (taken from shrubs located away from the shrub patch edge (>3 m) than in the birch hummock sites (51 (± 6.3) and 36 (± 2.8) years respectively; $P < 0.04$), and likewise for the oldest belowground stems (66 (± 6.5) and 37 (± 2.2) years respectively; $P < 0.002$) (P. Grogan, *unpubl. data*). Thus, older age may partly explain the larger *B. glandulosa* biomass at the tall birch compared to the birch hummock sites, but the much greater magnitude proportional differences in shoot biomass and production suggests that other factors are also important.

Very few previous studies have completed a careful quantification of both above- and belowground biomass and production in tall and low shrub tundra ecosystems. Total vascular plus non-vascular plant aboveground biomass per unit area in *Salix*-dominated tall shrub tundra and in acidic tussock tundra of northern Alaska (1393 and 708 g m⁻² respectively) (See Table 11 in Shaver and Chapin 1991) were very similar to our tall birch and birch hummock sites respectively (Table 1 - Total aboveground vascular plus non-vascular shoot biomass values). Nevertheless, at the growth form level, these analogous ecosystems clearly differed between the two locations. Proportionally, the Alaskan tall shrub site was more strongly dominated by the deciduous shrub, and had almost no evergreen shrubs or lichens, and $\sim 3\times$ more moss than our tall birch site (Shaver and Chapin 1991). By contrast, the acidic tussock tundra ecosystem had at least $3\times$ more graminoids than our low birch hummock sites. Furthermore, new apical stem production (and total vascular aboveground net primary production) in the Alaskan ecosystems (See Fig. 4 and Table 11 from Shaver and Chapin 1991) were similar in magnitude to the analogous ecosystems at our site (Table 1 - Total aboveground vascular new growth) despite their very differing community structures. To the best of our knowledge, ours is the first study to carefully harvest and quantify species belowground biomass in these two ecosystem-types. For example, Shaver and Chapin (1991) did not measure fine root biomass but derived values from other literature and used these to estimate total plant biomass for the two ecosystems at values almost identical to ours. Clearly, despite differences in growth form proportional abundances and species evenness, these analogous tall shrub ecosystems in Alaska and Canada are similar in terms of biomass and production – both above- and belowground, and

likewise for the analogous low shrub acidic tussock tundra and birch hummock ecosystems.

Surprisingly, even though total vascular shoot old growth biomass was $\sim 5\times$ larger at the tall birch site, our results suggest that total vascular new shoot growth was only $\sim 50\%$ greater (Table 1). In other words, the overall production per unit shoot biomass (ratio of new apical growth relative to old shoot biomass) in the birch hummock sites (0.69) was much higher than in the tall birch site (0.18). Interestingly, just as in our study, total vascular new apical stem production was only a little greater in the tall shrub compared to the low shrub vegetation in the Alaskan sites (130 and 105 g m⁻², respectively – Fig. 4, Shaver and Chapin 1991), even though the total aboveground biomass differed by at least a factor of 2.5. We undoubtedly overestimated evergreen shrub new growth because we included all previous years' leaves with the current year's production, and underestimated total *B. glandulosa* new growth because we did not include secondary stem thickening (see Methods). Nevertheless, the large *B. glandulosa* old shoot biomass at the tall birch site is clearly an important factor contributing to the low production ratio, not just in terms of its calculation, but also reflecting the general pattern of increasing proportional allocation of photosynthate to maintenance respiration in more woody ecosystems (Odum 1969).

Nitrogen cycling in tall birch as compared to birch hummock ecosystems

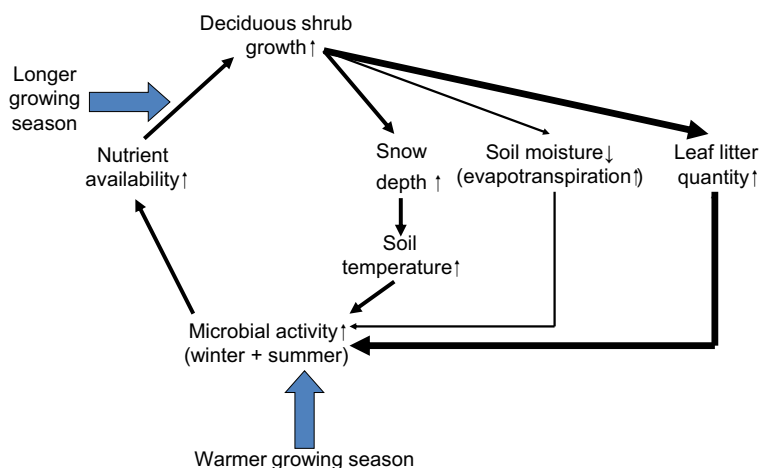
Annual nitrogen cycling in the tall birch ecosystem was clearly faster than in the low birch hummock ecosystem. Total nitrogen accumulation across all plant species in new shoot growth, and in total fine roots, at the end of summer were $2\times$ higher in the tall birch ecosystem than the birch hummock sites (totaling ~ 12 and ~ 6 g N per m², respectively; Table 2), and soil nitrogen availability (NH₄, DON) is also generally higher in the tall birch plots than in the birch hummock sites (Vankoughnett and Grogan 2014). The absence of snowfence manipulation effects on soil nutrient pools, plant production or ¹⁵N nitrogen accumulation demonstrates that deeper snow alone cannot explain this pattern (Vankoughnett and Grogan 2014). Since the tall birch patch in our study was not located in an area of obvious seasonal water flow that would enhance nutrient supply (Chapin et al. 1988), and nitrogen accumulation within the snow column (deepened or ambient) is negligible (Buckeridge

and Grogan 2010), our results suggest that the higher tall birch nutrient cycling may be a result of an internal feedback mechanism. In particular, litter inputs may provide a strong positive feedback promoting shrub growth and expansion that could act in concert with the snow-shrub feedback (by providing more substrate for decomposition in the warmer soils beneath deepened snow in winter) or independently by stimulating summertime decomposition (Fig. 3). Leaf (and presumably fine root) litter production within a plant community is largely determined by the deciduous and graminoid species (Chapin and Shaver 1996). *B. glandulosa* new apical shoot growth was $\sim 23\times$ larger in the tall birch site compared to the birch hummock sites, and this species strongly dominated the tall birch plant community while mosses, lichens and evergreen shrubs dominated the low birch community. Therefore, it is not surprising that *B. glandulosa* leaf production mass was $\sim 10\times$ greater at the tall birch site, we can reasonably assume that total leaf litter production at the tall birch site must also have been substantially larger than at the birch hummock sites.

Despite these fundamental differences in litter production, we found no differences in surface litter mass or nitrogen among sites (Tables 1, 2) in the samples that were collected late in the growing season just prior to leaf senescence. These latter samples represent the residual litter from the previous year's input that had been subject to decomposition over the preceding fall, winter, and summer seasons. Together, the substantially higher leaf litter production at the tall birch site, but absence of site differences in residual (pre-senescence) surface litter mass at the end of the growing season directly imply that

litter decomposition was much faster in the tall birch ecosystem over the previous year. A similar logic applies to nitrogen cycling in that the residual surface litter nitrogen concentration is half of the tall birch and birch hummock new shoot concentrations (App. Table 1), suggesting that the much larger litter mass produced in the tall birch site results in a correspondingly larger release of nitrogen from senesced tissues into the plant available pool each year. Furthermore, we already know that in situ instantaneous nitrogen cycling rates at our study sites are typically $3\times$ larger and faster in the tall birch ecosystem just before leaf senescence in late summer - when litter substrate might be most limiting (Buckeridge et al. 2009). Laboratory incubations also indicate higher rates of net nitrogen mineralization in tall shrub soils as compared to tussock tundra soils (Weintraub and Schimel 2003; Chu and Grogan 2010). Finally, we know that birch shrubs in the tall birch ecosystem can acquire newly incorporated nitrogen and use it to contribute to new growth within two years (Vankoughnett and Grogan 2014). The multiyear field data that we report here are important because, when combined with findings from previous studies, they provide evidence that *annual* nitrogen cycling is more rapid in tall birch ecosystems, thus supporting Hypothesis III that larger litter production could be an important internal positive feedback promoting the relatively high deciduous shrub growth rates in tall shrub ecosystems. However, further evidence is needed to fully support our conclusion. Nevertheless, this conclusion is consistent with, and complements, a recent study of litter decomposition rates across a gradient from low to tall deciduous shrub vegetation in Alaskan tundra (DeMarco et al.

Fig. 3 Shrub-soil-microbial activity feedback loops that may enhance nutrient availability and promote shrub growth (adapted from Sturm et al. 2005a, b). Potential influences of climate change are indicated by blue arrows



2011). Interestingly, on the basis of a common garden incubation experiment with all the principal species at our site, these authors concluded that differences in litter quality are very small and therefore are likely to have relatively little impact compared to the differences in litter quantity on decomposition rates across a snow depth gradient.

The litter quantity and other potential feedbacks that may enhance deciduous shrub proliferation as the arctic climate warms are illustrated in a conceptual diagram (Fig. 3). In addition to site differences in litter quantity, the tall birch microclimate in the winter as well as in summer may be more favorable for decomposition. Although winter soil temperatures were generally similar in the snowfenced birch hummock and tall birch sites, spring soil nitrogen availability was clearly higher at the tall birch than in the snowfenced birch hummock site (Vankoughnett and Grogan 2014). Thus, deepened snow had little impact alone, but the combination of warmer subnivean soil temperatures (coupled with microbial access to relatively large quantities of litter) may have enhanced decomposition and nitrogen availability (Fig. 3). Conversely, summer soil temperatures at the tall birch site were 1.5–2° C cooler than the birch hummock sites from mid-June through to early and late-July (at 2 cm and 5 to 10 cm, respectively), presumably due to soil shading during the maximum solar radiation phase reducing soil temperatures (Blok et al. 2010). It has been suggested that decreased summer soil temperatures will reduce nitrogen mineralization rates (McFadden et al. 1998; Sturm et al. 2001), but if so, this effect is clearly temporally limited at our site. Furthermore, lab incubation studies of Alaskan tundra soils of differing organic matter quality imply that mineralization is more dependent on microbial access to high quality substrate than such small changes in temperature (Nadelhoffer et al. 1991). In contrast to soil temperature, soil volumetric water content was substantially different (~25 % lower) in the tall birch site over the growing season (Vankoughnett and Grogan 2014), presumably at least in part as a result of higher evapotranspiration associated with rapid shrub growth. If soil moisture levels in low birch hummock tundra can be high enough to inhibit microbial activity at some stages in the growing season, the drying effect associated with tall birch vegetation may favor faster rates of soil organic matter and litter decomposition, suggesting another potential positive feedback to increased shrub growth (Fig. 3).

Spatial distribution of tall shrubs and the potential for change

Tall shrub vegetation generally occurs in patches across the tundra landscape (Shaver and Chapin 1991) where conditions favor enhanced nutrient cycling/productivity such as areas of preferential water flow, or downwind of relatively high elevation locations where snow accumulates and protects the shoots from winter damage (Tape et al. 2006, 2012). Unlike many tall birch patches in our study landscape, the particular site we used was not located in or near any obvious seasonal surface water flow or source of wind protection. Nevertheless, the soil physical and biogeochemical values reported here are very similar to those from the full variety of tall birch patches across that landscape (Chu and Grogan 2010), suggesting that our results are widely applicable. We focused our study on this particular tall birch patch because we were interested in interpreting our results in the context of the climate warming potential for increases in shrub density in landscape areas that have a similar hydrology and topography to current birch hummock (i.e. low shrub) tundra. Vegetation transitions from low birch to tall birch ecosystems in stable landscapes must ultimately be driven by factors that enhance productivity/nutrient cycling. These factors may be split into two groups - those that are driven by internal feedbacks associated with the vegetation itself (e.g. snow-trapping, shading, evapotranspiration, litter quantity – Fig. 3), and those that are the ultimate external causes regulating the spatial distribution of tall shrubs such as topography, hydrology, or changing climate. As indicated earlier, the shrubs in our tall birch site were ~50 % older than at the low birch sites, suggesting some heterogeneity in the history of herbivory (Zamin and Grogan 2013), disease or fire disturbances across the landscape that has affected shrub demography (Myers-Smith et al. 2011). While the cause of higher shrub biomass at the tall birch site was not determined, our biogeochemical comparison strongly suggests that the internal positive feedback associated with larger quantities of litter can enhance nitrogen cycling and therefore promote deciduous shrub production in tall birch tundra.

Conclusions

Our results revealed that within the four year timeframe of this study, deepened snow cover alone did not

enhance deciduous birch shrub growth and nitrogen accumulation, but that other factors associated with increased stature and density of deciduous shrubs, such as litter quantity, may interact with the deeper snow cover there to promote shrub production. Total nitrogen accumulation in new apical shoot growth and fine roots just prior to senescence was clearly higher in the tall birch than the birch hummock sites (totaling ~12 and ~6 g N per m², respectively). Some nitrogen in those pools is lost in leaf litter and root turnover, and therefore the net annual plant nitrogen uptake from soil each year would be lower. Nevertheless, these data suggest that about double the amount of nitrogen is needed to maintain annual primary production in the tall birch ecosystem compared to the birch hummock ecosystem. Overall, our results indicate that deepened snow alone has little impact on birch growth, and strongly suggest that the much larger litter production in tall birch ecosystems is an important internal feedback that may or may not interact with the deeper snow in tall shrub tundra to promote birch growth.

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