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Decomposition of Senesced Leaf Litter is Faster in Tall Compared to Low Birch Shrub Tundra

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Abstract

Many Low Arctic tundra regions are currently undergoing a vegetation shift towards increasing growth and groundcover of tall deciduous shrubs due to recent climate warming. Vegetation change directly affects ecosystem carbon balance, but it can also affect soil biogeochemical cycling through physical and biological feedback mechanisms. Recent studies indicate that enhanced snow accumulation around relatively tall shrubs has negligible physical effect on litter decomposition rates. However, these investigations were no more than 3 years, and therefore may be insufficient to detect differences in inherently slow biogeochemical processes. Here, we report a 5-year study near Daring Lake, Canada, comparing *Betula neoalaskana* foliar litter decay rates within unmanipulated and snowfenced low-stature birch (height: ~ 0.3 m) plots to test the physical effect of experimentally deepened snow, and within tall birch (height: ~ 0.8 m) plots to test the combined physical and biological effects, that is, deepened snow plus strong birch dominance. Having corrected for carbon gain by the colonizing decomposers, actual litter carbon loss increased by approximately 25% in the tall birch relative to both low birch sites. Decay of lignin-like acid unhydrolizable litter residues also accelerated in the tall birch site, and a similar but lower magnitude response in the snowfenced low birch site indicated that physical effects of deepened snow were at least partially responsible. In contrast, deepened snow alone did not affect litter carbon loss. Our findings suggest that a combination of greater litter inputs, altered soil microbial community, enhanced soil nutrient pools, and warmer winter soils together promote relatively fast decomposition of recalcitrant litter carbon in tall birch shrub environments.

Key words: Arctic; *Betula*; climate warming; deepened snow; litter decomposition; deciduous shrubs; long-term investigation.

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Highlights

- Tall birch shrub tundra promotes relatively fast litter decomposition rates
- Tall birch shrubs promote fast decomposition of recalcitrant litter compounds
- Biological feedback mechanisms are driving decay patterns in tall birch tundra

Introduction

Climate warming is currently leading to vegetation changes in many Arctic tundra regions (Goetz and others 2005; Jia and others 2006; Forbes and others 2010; Epstein and others 2012; Tremblay and others 2012; Ju and Masek 2016). Deciduous shrubs in particular have increased growth and groundcover during the last 30–50 years (Tape and others 2006; Elmendorf and others 2012; Myers-Smith and others 2015). These relatively tall shrubs are able to alter key ecosystem functions, such as carbon and energy balances, but they may also affect biogeochemical cycling (Shaver and others 2001; Chapin and others 2005; Sturm and others 2005; DeMarco and others 2014b). The snow-shrub feedback hypothesis predicts that accumulation of wind-blown snow by tall shrubs creates a favorable microclimate with warmer and less dynamic soil temperatures that promotes wintertime litter and soil organic matter decomposition rates, and hence soil nutrient availability, which ultimately stimulates shrub growth in a positive feedback-loop (Sturm and others 2001; Sturm and others 2005). For example, soil nitrogen (N) mineralization rates can double under experimentally deepened snow (Schimel and others 2004); leading to enhanced spring nutrient pulses (Buckeridge and Grogan 2010) and summer soil solution N pools (DeMarco and others 2011; Semenchuk and others 2015). Growth of deciduous shrubs is particularly responsive to fertilizer additions (Chapin and others 1995; Jonasson and others 1999; Zamin and others 2014), suggesting that feedback mechanisms that promote nutrient availability, such as the proposed snow-shrub feedback, will also stimulate their growth. However, recent studies show that the physical effect of enhanced snow accumulation on foliar litter decomposition is negligible (Aerts and others 2012; Myers-Smith and Hik 2013; DeMarco and others 2014a; Christiansen and others 2017). Nevertheless, only few studies have attempted to disentangle the effects of physical and biological feedbacks associated with tall deciduous shrub dominance on litter decomposition in Arctic tundra (DeMarco and others 2014a), limiting our current understanding of how these deciduous shrubs affect tundra ecosystem function now, and in a changing climate.

Deciduous shrubs have evolved to promote localized soil fertility by producing larger quantities of litter with greater nutrient contents than low-stature evergreen shrubs (Hobbie 1996; Hobbie and others 2000; DeMarco and others 2014a; Vankoughnett and Grogan 2016), and deciduous shrub litter generally decomposes faster (McLaren and others 2017; but see DeMarco and others 2014a). Therefore, in comparison to low-stature evergreen shrub and tussock tundra, tall shrub-dominated communities support larger and different soil microbial communities (Wallenstein and others 2007; Buckeridge and others 2010b; McMahon and others 2011) that promote relatively high soil N mineralization rates (Buckeridge and others 2010b; DeMarco and others 2011). Together, these nutrient-related features may help to transform litter carbon chemistry in ways that render the decaying litter more decomposable (Wickings and others 2012). For example, faster nutrient cycling and/or greater nutrient availability can stimulate microbial litter decomposition by supplying N for exoenzyme production (Schimel and Weintraub 2003), or by priming the degradation of recalcitrant carbon substrates (Kuzyakov and others 2000) that would otherwise accumulate during the litter decay process (Chapin and others 2002). Therefore, a biological feedback mechanism associated with the relatively large quantity and distinctive chemical quality of tall deciduous shrub litter could be more important than the proposed physical snow accumulation effect in explaining how tall deciduous shrubs promote their own growth and expansion in tundra landscapes (DeMarco and others 2014a).

Here, we incubated *Betula neoalaskana* leaf litter in situ over a 5-year period within the soil of unmanipulated and snowfenced low-stature birch (height: $\sim$ 0.3 m) hummock tundra, and in tall birch (height: $\sim$ 0.8 m) shrub tundra containing similar plant species composition, but differing relative abundances, as the low-stature birch sites. We selected *B. neoalaskana* as litter material for logistical convenience. Our experimental design allowed us to test the direct effect of experimentally deepened snow (physical effect), and to compare the impact of deepened snow alone to the overall combined effects of a taller and denser birch shrub

ecosystem (combined physical and biological effect), on litter decomposition rates. We hypothesized that litter decomposition rates over the 5-year incubation period would be: (H1) fastest in the tall birch site; (H2) unaffected by the deepened snow treatment alone; and (H3) that decomposition of recalcitrant lignin-like compounds would be fastest in the tall birch plots.

Materials and Methods

Site Description

This study took place from August 2006 to September 2011 near the Terrestrial Ecosystem Research Station (TERS) at Daring Lake (64°52′N, 111°34′W), Northwest Territories, Canada. The study area has a mean annual air temperature of − 9°C with diel temperatures ranging from − 40°C in January to +20°C in July. Annual rainfall from June to October is about 140 mm, with annual snowfall from October to June corresponding to half of that (climate data are 1996–2011 averages; Bob Reid and Steve Kokelj, unpublished data). Snow depth generally remains below 10 cm until December and autumn air temperatures are very cold so soils have frozen before the onset of substantial snow accumulation. All sites are situated within 300 m of each other in the middle of a gently sloping valley (~ 4 km^2) enclosed by an esker and bedrock outcrops. The soils in the study area are well drained with no water table and underlain by continuous permafrost with no visible thaw or degradation activity (*pers. obs.*).

In the fall of 2006, we selected two mesic shrub ecosystems: low-stature birch hummock and tall dense birch shrub tundra. Both shrub vegetation types are abundant across the circumpolar Arctic, covering 20.6 and 18.3% of the total non-glaciated Low Arctic (Circumpolar Arctic Vegetation Map, subunits S1 and S2, respectively, in subzones D and E combined; Walker and others 2005). Figure S1 shows photographs of the study area.

Low-stature birch hummock vegetation (from here on 'low birch') is abundant across the valley in our study area and contains hummocks (10–30 cm in height) with the deciduous birch shrub *Betula glandulosa* Michx. (height < 40 cm) covering 10–30% of the ground surface but only accounting for about 7% of the total plant biomass due to its relatively low frequency (1–2 ramets m^{-2}; Zamin and others 2014). In contrast, the evergreen shrubs *Rhododendron subarcticum* Harmaja (formerly *Ledum decumbens* Ait.) and *Vaccinium vitis-idaea* L., mosses *Aulacomnium turgidum* Wahlenb. and *Sphagnum* spp., and lichens *Cladonia* spp. and *Cetraria* spp. dominate the aboveground biomass (Zamin and others 2014). Other plants at lower densities include the deciduous *Vaccinium uliginosum* L., evergreen *Andromeda polifolium* L., forb *Rubus chamaemorus* L., and sedge *Eriophorum vaginatum* L (Nobrega and Grogan 2008; Buckeridge and others 2010b).

Tall birch vegetation patches sporadically occur across the valley in areas where deep snow patches accumulate during winter or where there is seasonal surface flow from snowmelt. For this study, we chose a relatively large approximately 40 × 130 m patch of about 80 cm tall and dense (~ 90% cover) birch shrubs (from here on 'tall birch' site) located around 300 m from the low birch sites, and growing in mesic soil conditions with no obvious surface water flow. The vegetation is dominated by the dense cover of *B. glandulosa* shrubs but contains a similar understory composition as found in the low birch sites (Buckeridge and others 2010b), although with sporadic occurrences of tall willow *Salix spp.* and a complete lack of the evergreen shrub *Andromeda polifolia* L.

Experimental Setup

Our experimental design comprises three sites with five plots each: low birch with ambient snow, low birch with experimentally deepened snow, and tall birch with ambient relatively deep snow. Unmanipulated low birch plots were located in low birch vegetation during the summer of 2004, and have previously served as 'control' plots in other studies (Buckeridge and Grogan 2008; Buckeridge and others 2010a; Buckeridge and Grogan 2010; Vankoughnett and Grogan 2014). Simultaneously, five replicate snowfences (15 m long, 1.2 m high) were constructed in similar low birch vegetation and topography. Peak ambient snow depth in the low birch plots is typically 31 ± 2 cm, while the snowfences uniformly enhance snow accumulation to peak depths of 92 ± 3 cm within 3 m of each fence. Snow accumulation is usually 58 ± 3 cm in our tall birch plots (all snow depths are 2007–2009 averages). Compared to the unmanipulated low birch plots, complete snowmelt usually is delayed 1–2 weeks in the snowfenced low birch plots, and about 1 week in the tall birch plots (Nobrega and Grogan 2007).

Soil active layer thaw depth is similar across the three sites, with the unmanipulated and snowfenced low birch plots reaching 64 ± 6 and

71 ± 3 cm in early August, respectively (Christiansen, unpublished 2014 data), and the tall birch site reaching 67 ± 4 cm (Elyn Humphreys unpublished 2014 data).

Soil Temperature and Moisture Time-Series

Soil temperatures at 2–5 cm depth, and soil moisture integrated over 0–5 cm depth, were logged every 4 h from 1 September 2007 to 1 September 2011 using thermocouples (n = 3 per treatment; one probe at 5 cm depth and two probes at 2 cm depth; the average used as composite for temperature across 2–5 cm depth), and moisture probes (n = 2 per treatment), respectively, connected to dataloggers (instrumentation from Campbell Scientific, Australia).

We divided each year into autumn (1 September through 30 November), winter (1 December through 31 May), and growing season (1 June through 31 August) periods, and used monthly and seasonal probe averages of temperature and moisture data in the statistical analyses. In addition, we calculated cumulative degree-days as the sum of average diel temperatures within a given season or across all measurement years.

Litterbag Preparation, Incubation, and Processing

We incubated senesced leaves of *B. neoalaskana* Sarg. (Alaska Paper Birch) in all three sites on 21 August 2006. We used *B. neoalaskana* litter, as it was readily available in large amounts in time for our litterbag preparation, similar to other tundra litter decomposition studies (Hobbie and Chapin 1996; DeMarco and others 2014a). All litter was collected near Fairbanks, Alaska, while still attached to trees but after leaf color had changed and the petiole had begun abscission. Litter was air-dried, well mixed, and separated into about 1 g samples, which were then weighed, and subsequently sewn into small mesh bags (2 mm mesh size on both sides, 8 × 8 cm bag size).

In low and tall birch tundra, litter is typically found well-mixed into the moss and upper organic soil horizons. Accordingly, we cut slots at approximately 45° with a serrated knife and inserted the litterbags so that they were located across 0–5 cm depth below the green–brown transition in the moss layer between hummocks and hollows (low birch sites) or between birch shrubs (tall birch site). Our measurements therefore reflect the integrated litter decomposition dynamics across the upper 5 cm of the organic soil horizon. A total of 10 bags were inserted into each plot initially and a random selection of 2–4 bags were subsequently harvested in late August of 2007 and 2008, and in early September of 2011. Figure S1 shows photographs of retrieved litterbags.

After harvest, we carefully removed the litter material from the mesh bags and gently rinsed the litter with deionized water to remove any soil particles, foreign litter and in-grown roots. We cut roots and any attached mycorrhizal hyphae networks so that only material inside litterbags remained while discarding root and hyphae material growing outside of bags. Litter and root material from each bag was then oven-dried separately at 60°C until constant weight (minimum of 48 h), and the final mass recorded before grinding the litter material (MF 10, #40 mesh screen; IKA-Werke GmbH & Co. KG, Staufen, Germany).

Litter Carbon, Nitrogen, and Phosphorus Content

Litter sub-samples (40 mg) were analyzed for total *C* and *N* content using an Elementar VARIO Micro Cube elemental analyzer (Elementar Analysensysteme, Hanau, Germany), n = 2–4 bags per plot per year. Other sub-samples (200 mg; n = 2–3 bags per plot per year) were acid-digested (Parkinson and Allen 1975) before determining total *P* content colorimetrically (Kuo 1996) using automated flow analysis (Autoanalyzer 3; Braun-Leubbe, Norderstadt, Germany). The remaining litterbag material was pooled among selected replicates within the same site and harvest year to generate 3–4 independent samples of sufficient mass (500 mg) for determination of proximate *C* fractions using a series of sequential H_2SO_4 digestions (that is, the fiber forage analytical technique; Ryan and others 1990) in an Automated Fiber Analyzer (ANKOM Technology, Macedon, New York, USA). This yielded the following proximate *C* extractives: cell solubles (that is, carbohydrates, lipids, pectin, starch, and soluble proteins), hemicelluloses (including bound proteins), cellulose, and lignin-like acid unhydrolyzable residues (AUR), that is, the remnant recalcitrant compounds after sequential digestion of the fractions listed above.

Finally, 6–9 subsamples of homogenized leaves that had not been incubated in the field were included in each of the analyses listed above to determine initial litter *C*, *N*, *P*, and proximate *C* fraction contents. Furthermore, we determined *C*, *N*, and *P* contents of fully senesced local *B. glan-*

dulosa litter obtained in the fall of 2012 by gently shaking shrub branches into large plastic bags in both the low and tall birch sites (n = 6 per site). In addition, we estimated birch leaf litter production in the unmanipulated low birch and tall birch sites in September 2011, collecting leaves from senescing plants and the soil surface in 2 and 1 m^2 subplots, respectively (n = 4). All

Litter Calculations

We calculated the fraction of initial mass remaining using the equation $M_r = \frac{M_t}{M_0}$, where M_r is the fraction of total litter mass remaining at time t (years after incubation), M_t is total litter mass (g) remaining at time t, and M_0 is initial total litter mass (g). The fractions of initial C, N, and P remaining were calculated as $CNP_r = \frac{M_t \times CNP_t}{M_0 \times CNP_0}$, where CNP_r is the fraction of litter C, N, or P remaining at time t, M_t and M_o are as described above, CNP_t is the concentration of litter C, N, or P remaining at time t, and CNP_0 is the initial litter concentration of C, N, or P. The proximate fiber forage C fractions were calculated in similar fashion, but using average C fraction concentrations per site and harvest year due to the pooled litterbag material approach used for this analysis.

Assuming a single exponential decay relationship for litter mass loss over time, we modelled litter decay as $M_t = M_0 \times e^{-kt}$, where M_t, t and M_0 are as described above, e is the base of the natural logarithm, and k is the exponential decay constant ($year^{-1}$).

Fine-root (including ectomycorrhizal (ECM) fungi) and soil microbial biomass pools are larger in the tall birch site (Buckeridge and others 2010b; Vankoughnett and Grogan 2014), and thus microbes, primarily fungi, growing into the leaf litter could potentially bias litter mass loss data. Therefore, we modelled microbial growth using a modified litter C relationship adapted from Manzoni and others (2010) that relates microbial biomass C (MBC) increases as a function of litter C loss. Briefly, $G = (1 - \lambda_c)eD$, where G is microbial growth rate, D is decomposition flux, λ_c is fraction of D lost through leaching, and e is microbial carbon use efficiency. Assuming negligible litter C leaching (for example, C leaching losses averaged $\sim$ 3% across 41 plant species; Schreeg and others 2013), microbial growth is equal to eD, where e is approximated as a function of the initial litter C/N ratio (Manzoni and others 2010). Microbial C and N stoichiometry and e are assumed constant across sites and through time. If at any time litter N_t exceeded litter N_0 (due to immobilization of N from the surroundings), we adjusted the calculated MBC for this additional N import according to a fixed MBC/N ratio (12.4; mean of litter decomposer C/N ratios in polar regions, Table 2; Manzoni and others (2010) and references therein). We consider this a relatively conservative approach as soil microbial C/N ratios are lower in the tall birch site relative to the low birch sites (MBC/n = 12.1 and 14.3, respectively; Vankoughnett and Grogan 2014), and microbes therefore likely metabolize C more efficiently in the tall birch plots (Manzoni and others 2008).

Statistical Analyses

All statistical analyses were performed using SAS 9.2 (SAS Institute, Cary, NC, USA). Prior to each analysis, we tested data by visual inspection of distributions. When necessary, data were either log or square root transformed to achieve variance homogeneity. Post analysis, we tested model validity by visual inspection of the distribution of residuals, as well as residuals plotted against predicted values.

We tested for differences among sites (unmanipulated low birch, snowfenced low birch, and unmanipulated tall birch) on litter decomposition rates and C, N, and P content using single repeated measures linear mixed effects models for each variable, using PROC MIXED in SAS. For each elemental analysis, we used the plot average per harvest year as a single datum in the corresponding statistical model. For all models, we specified *plot* and harvest *year* as separate random factors with *year* also set as repeated factor within *plot*. *Site* was a fixed main effect, with *year* as an additional fixed main effect and the interaction term between site and year (*site* × *year*). Based on this full model, we used the LS MEANS procedure (approximated t test of fixed effect least square means) to *post-hoc* test for significant differences using sequential Holm-Bonferroni adjusted P values (Holm 1979) between all sites within each harvest year. Covariance structure was determined using the two-model fit criteria AIC-output from PROC MIXED (Littell and others 1996).

This statistical analysis assumes that any differences in litter properties become proportionally greater with increasing time over the 5 years of the study (—that is, that any changes are linear over time).

Results

Site Differences in Microclimate

The snowfences enhanced winter soil temperatures by an average of about 2°C relative to the unmanipulated low birch hummock site ($t_{1,6}$ = − 4.07,

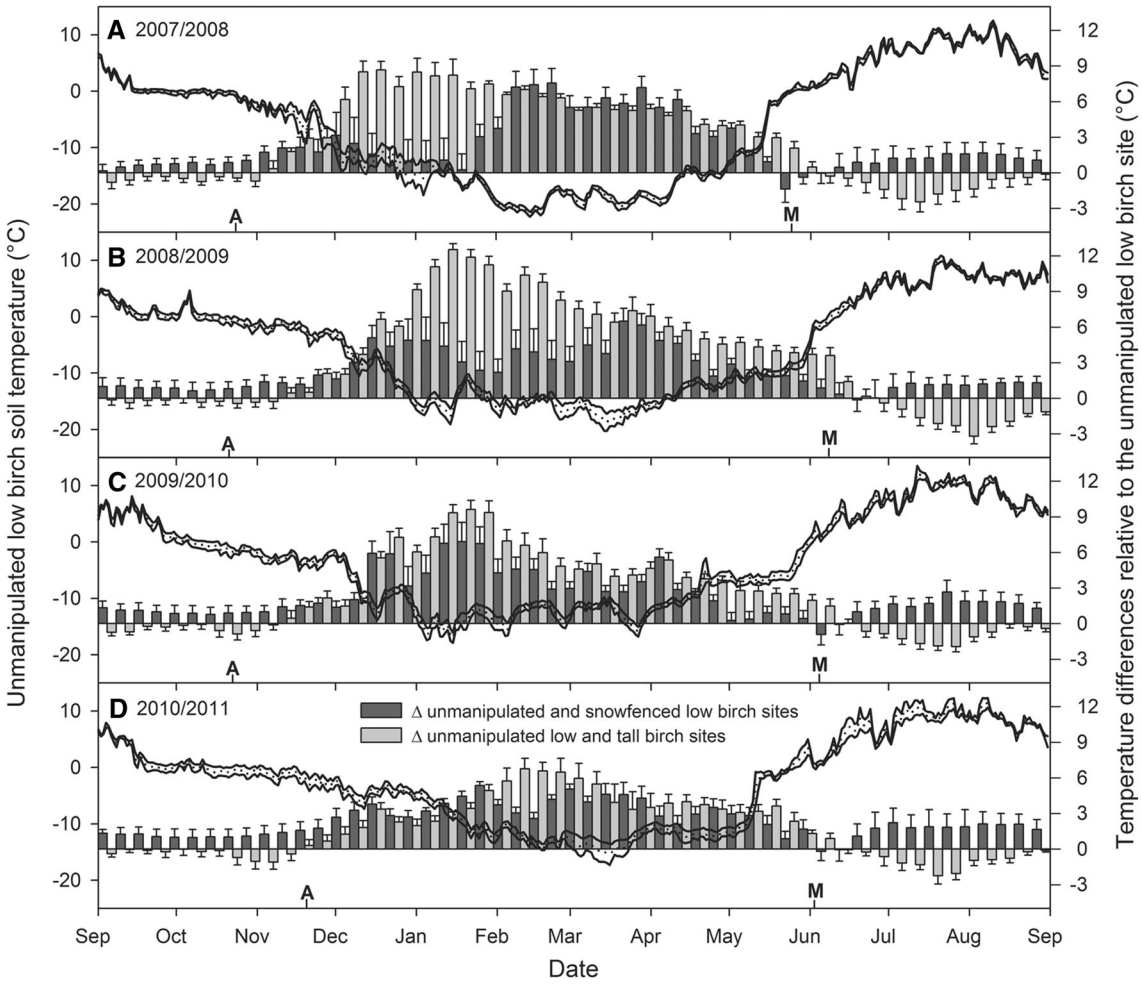

Figure 1. Weekly soil temperature differences (integrated 2–5 cm depth) between the unmanipulated low birch site compared to either the snowfenced low birch (dark bars) or unmanipulated tall birch (light bars) sites from September 2007 to September 2011 (n = 3 probes per site; ± 1 S.E; data range on right side Y-axis). Diel soil temperatures in the unmanipulated low birch site are indicated by the dotted lines (see left side Y-axis) with 95% CI shown as lines. First day of continuous snow accumulation is indicated by ''A'', and first day of complete snowmelt is indicated by ''M'' according to records from a nearby meteorological station, located ~ 1 km away in broadly similar but more wind-exposed vegetation.

$P \leq 0.001$; Figure 1), leading to a 20% decrease in cumulative total winter degree days in the snowfenced plots ($t_{1,6} = -4.07$, $P \leq 0.001$; Table 1). However, the tall birch site had the warmest winter soils of all, with average soil temperatures over the 2007–2010 winters being about 5°C and about 3°C warmer than the unmanipulated ($t_{1,6.12} = -8.99$, $P \leq 0.001$) and snowfenced ($t_{1,6.12} = -4.94$, $P \leq 0.001$) low birch sites, respectively. In contrast, we detected no site differences in growing season or autumn mean soil temperatures or degree-days (Figure 1 and Table 1) or when analyzing each month separately with comparisons across all sites.

We observed a strong trend of increasing autumn and winter soil temperatures across all three sites through successive years of the study (Table 1). Multiple air temperature records at the site indicate that this was due to increasingly warmer autumn air temperatures during those years, leading to warmer soils at the time of continuous snow accumulation (Table S1) and thereby warmer winter soils. Maximum winter snow accumulation, as indicated by April snow depth, was relatively consistent (30–40 cm) throughout the study period (Bob Reid, unpublished data not shown).

Volumetric soil water content (VWC) was generally similar across both unmanipulated and snowfenced low birch sites during all growing seasons, except during bulk snowmelt in early June where snowmelt was typically delayed approximately 1–2 weeks in the snowfenced plots (Figures 1 and S2). In contrast, VWC in the tall birch site was consistently about 1/3 lower than in the

Table 1. Seasonal Mean Soil Temperatures (Integrated 2–5 cm depth) and Cumulative Degree Days from 1 September 2007 to 1 September 2011 in the Three Experimental Shrub Tundra Sites: Unmanipulated Low Birch, Snowfenced Low Birch, and Unmanipulated Tall Birch

Year	Winter (1 December–31 May)			Growing season (1 June–31 August)			Autumn (1 September–30 November)		
	Low birch	Snowfenced low birch	Tall birch	Low birch	Snowfenced low birch	Tall birch	Low birch	Snowfenced low birch	Tall birch
Mean seasonal temperature (°C)									
2007–2008	− 14.4 ± 0.2	− 12.9 ± 0.6	− 9.2 ± 0.4	7.7 ± 0.6	8.1 ± 0.3	7.1 ± 1.5	− 1.3 ± 0.4	− 0.6 ± 0.5	− 0.7 ± 0.6
2008–2009	− 13.1 ± 0.4	− 10.7 ± 0.5	− 6.4 ± 0.6	6.4 ± 0.5	6.5 ± 0.3	5.4 ± 0.8	− 0.2 ± 0.1	0.6 ± 0.3	0.0 ± 0.3
2009–2010	− 10.4 ± 0.3	− 8.0 ± 0.4	− 5.8 ± 0.5	7.9 ± 0.5	8.4 ± 0.2	7.3 ± 0.7	0.3 ± 0.1	1.1 ± 0.3	0.3 ± 0.3
2010–2011	− 8.8 ± 0.1	− 6.11 ± 0.2	− 5.3 ± 0.7	7.9 ± 0.3	8.9 ± 0.4	7.4 ± 0.6	0.4 ± 0.0	1.2 ± 0.2	0.3 ± 0.2
Average	**− 11.7 ± 0.7**[a]	**− 9.4 ± 0.8**[b]	**− 6.4 ± 0.5**[c]	7.5 ± 0.3	8.0 ± 0.3	6.8 ± 0.5	− 0.2 ± 0.2	0.6 ± 0.3	0.0 ± 0.2
Seasonal degree-days									
2007–2008	− 2640 ± 41	− 2358 ± 100	− 1682 ± 81	705 ± 53	742 ± 24	652 ± 138	− 114 ± 33	− 50 ± 43	− 63 ± 58
2008–2009	− 2390 ± 78	− 1952 ± 82	− 1163 ± 104	587 ± 50	598 ± 24	494 ± 73	− 16 ± 15	56 ± 30	− 3 ± 26
2009–2010	− 1883 ± 61	− 1452 ± 78	− 1049 ± 97	726 ± 41	774 ± 20	671 ± 69	23 ± 9	100 ± 28	29 ± 26
2010–2011	− 1609 ± 21	− 1112 ± 28	− 963 ± 125	730 ± 24	820 ± 36	684 ± 59	35 ± 4	111 ± 19	30 ± 20
Cumulative	**− 8523 ± 199**[a]	**− 6873 ± 288**[b]	**− 4296 ± 589**[c]	2748 ± 164	2934 ± 84	2284 ± 352	− 72 ± 60	217 ± 119	14 ± 108

Values are means ± 1 S.E. (n = 3 temperature probes per treatment), and statistically significant results of repeated measures linear mixed analyses across the entire monitoring period are shown in bold with different site means indicated by differing superscript letters ($P \leq 0.001$).

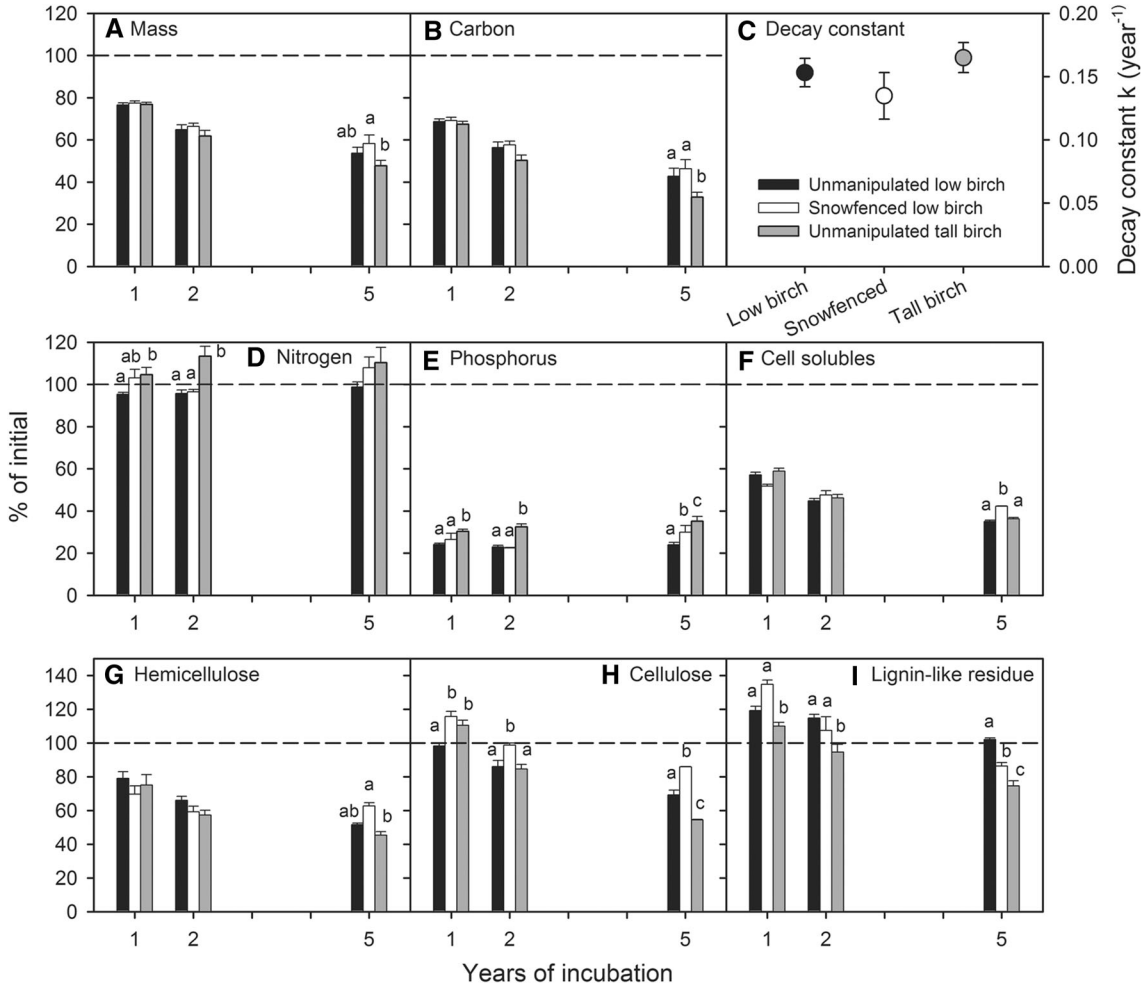

Figure 2. Effects of 5 years of in situ incubation on *B. neoalaskana* leaf litter **A** total mass, **B** carbon, **C** mass decay constant *k*, **D** nitrogen, **E** phosphorus, **F** cell solubles, **G** hemi-cellulose, **H** cellulose, and **I** lignin-like residues in the unmanipulated low birch (black bars), snowfenced low birch (white bars), and unmanipulated tall birch (grey bars) tundra sites. All values are site means (n=5 in (**A–E**); and n=3–4 in (**F–I**); ± 1 S.E.) and are shown as % of initial (non-incubated) litter content, except in (**c**) which is shown as k year^{-1}. Cell solubles are soluble cell carbohydrates, lipids, pectin, starch, and proteins. Litter carbon was corrected for calculated changes in microbial biomass carbon over the study, but litter mass was not (see ''Materials and Methods''). In each panel and within each harvest year, bars sharing a lowercase letter in common are not significantly different from each other ($P \leq 0.05$). No lowercase letters indicate that all site means were similar in that year. Note the different scaling of the *Y*-axes.

low birch sites during each growing season (Figure S2), similar to single date gravimetric soil water contents from the same low and tall birch sites in late summer (Buckeridge and others 2010b).

Site Differences in Incubated Litter Mass, Carbon, Nitrogen, and Phosphorus Dynamics

Across all three sites, litter mass remaining was about 77% of the initial incubated mass after the first year, and decreased to 64% remaining across all sites after 2 years (Figure 2A). Site differences became apparent after 5 years, with litter mass declining to 55–58% remaining at the unmanipulated and snowfenced low birch sites, and to 48% remaining at the tall birch site. The mass and *C* content of the remaining litter (uncorrected for litter microbial biomass *C*, MBC) were both significantly lower at the tall birch site compared to the snowfenced low birch site ($t_{1,34.7} = 2.9$, $P < 0.02$; and $t_{1,32} = -3.17$, $P = 0.01$, respectively; Figure 2A, Table S2). Similarly, there was a strong trend for less litter *C* (uncorrected for MBC) remaining in the tall birch compared to the ambient low birch site ($t_{1,34.7} = -2.17$, $P = 0.07$; Table S2) after 5 years.

Litterbags incubated for 5 years in the tall birch site contained approximately 4 times more root and

associated ectomycorrhizal hyphal biomass than either of the low birch sites (unmanipulated low birch site; $t_{1,12} = 2.09$, $P = 0.05$; and snowfenced low birch site; $t_{1,12} = 2.37$, $P = 0.04$, respectively), whereas there was no difference between the two low birch sites (Table S2). The modelling of litter MBC growth revealed that after 5 years of incubation, the tall birch site contained significantly less litter *C* than either of the low birch sites (unmanipulated low birch site; $t_{1,39} = 2.57$, $P = 0.04$; and snowfenced low birch site; $t_{1,30.9} = -3.44$, $P < 0.01$, respectively; Figure 2B), with no difference between the two low birch sites. After 5 years, the tall birch site litter tended to have about 22–25% more MBC than either of the low birch sites (unmanipulated low birch site; $t_{1,39} = 2.28$, $P = 0.08$; and snowfenced low birch site; $t_{1,39} = 2.17$, $P = 0.1$, respectively; Table S2).

Litter *N* increased, or tended to increase, in the tall birch site, relative to the unmanipulated low birch site (1st year, $t_{1,19.3} = 2.5$, $P = 0.05$; 2nd year, $t_{1,13.1} = 2.76$, $P = 0.03$; and 5th year, $t_{1,25.9} = 2.22$, $P = 0.1$, respectively), whereas there was no snowfence effect on litter *N*-dynamics in the low birch sites.

Litter *P* content declined very strongly over the first year of incubation with reductions of 70–75% across all three sites (Figure 2E). Litter incubated in the tall birch site had consistently more *P* remaining than either of the low birch sites across all harvest years (unmanipulated low birch site: 1st year, $t_{1,21.5} = 3.21$, $P = 0.01$; 2nd year, $t_{1,13.5} = 4.17$, $P < 0.01$; and 5th year, $t_{1,29.4} = 4.44$, $P < 0.01$; and snowfenced low birch site: 1st year, $t_{1,21.5} = 2.95$, $P < 0.02$; 2nd year, $t_{1,13.5} = 3.29$, $P < 0.01$; and 5th year, $t_{1,29.4} = 2.37$, $P < 0.05$, respectively), and the snowfenced low birch site contained more litter *P* than the unmanipulated low birch site but only after 5 years ($t_{1,29.4} = -2.07$, $P < 0.05$; Figure 2E).

Site Differences in Incubated Litter Carbon Chemistry

Litter incubated in the snowfenced low birch site retained more soluble cell contents after 5 years relative to the other two sites (unmanipulated low birch site: $t_{1,29} = -3.95$, $P < 0.01$; and tall birch site; $t_{1,29} = -3.36$, $P < 0.02$; Figure 2F). Likewise, hemi-cellulose loss was also relatively low in the snowfenced site compared to the other two sites after 5 years of decomposition (unmanipulated low birch site: $t_{1,29} = -2.16$, $P = 0.08$; and tall birch site: $t_{29} = -4$, $P < 0.01$; Figure 2G). These patterns were also observed in cellulose degradation, which was substantially and consistently reduced in the snowfenced low birch site relative to the unmanipulated low birch site during all harvest years (1st year, $t_{1,29} = -4.11$, $P < 0.01$; 2nd year, $t_{1,29} = -5.57$, $P < 0.01$; and 5th year, $t_{1,29} = -5.22$, $P < 0.01$, respectively, Figure 2H), and after 2 and 5 years of decomposition when compared to the tall birch site (2nd year, $t_{1,29} = -5.57$, $P < 0.01$; and 5th year, $t_{1,29} = -10.63$, $P < 0.01$, respectively). Cellulose degradation in the tall birch site was significantly less than in the unmanipulated low birch site over the first year of incubation ($t_{1,29} = 2.71$, $P = 0.03$), but subsequent processes reversed this pattern resulting in significantly lower litter cellulose content in the tall birch site relative to the low birch site after 5 years ($t_{1,29} = -5.22$, $P < 0.01$).

During all harvest years, the tall birch site litter lost more lignin-like AUR relative to the low birch sites (unmanipulated site; 1st year, $t_{1,29} = -2.99$, $P = 0.03$; 2nd year, $t_{1,29} = -5.16$, $P < 0.01$; and 5th year, $t_{1,29} = -5.31$, $P < 0.01$; and snowfenced site; 1st year, $t_{1,29} = -3.89$, $P < 0.01$; 2nd year, $t_{1,29} = -4.78$, $P < 0.01$; and 5th year, $t_{1,29} = -2.48$, $P = 0.05$, respectively, Figure 2I). The loss of these lignin-like residues was also significantly greater in the snowfenced low birch site compared to the unmanipulated low birch site, but only after 5 years of incubation ($t_{1,29} = 3.00$, $P = 0.03$).

Site Differences in Litter Production and Chemistry

The initial (that is, non-incubated samples) *B. neoalaskana* litter contained about 25% more *N* ($\boldsymbol{t}_{1,14} = 5.08$, $P < 0.01$; and $\boldsymbol{t}_{1,14} = 4.88$, $P < 0.01$) and consequently had lower *C*/*N* ratios ($\boldsymbol{t}_{1,14} = -5.51$, $P < 0.01$; and $\boldsymbol{t}_{1,14} = -5.15$, $P < 0.01$) than fully senesced native *B. glandulosa* litter obtained from both the low and tall birch sites, respectively. In contrast, the *P* contents of *B. neoalaskana* and *B. glandulosa* litter did not differ significantly (Table 2). For additional biochemical properties of the *B. neoalaskana* leaf substrate used in litterbags, see Table S3.

Leaf litter production was 10 times greater in the tall birch site relative to the low birch site ($\boldsymbol{t}_{1,6} = -5.76$, $P = 0.001$), whereas leaf chemical quality was overall similar across the low and tall birch shrub sites (Tables 1 and S3).

Tables S2 and S4 show biochemical properties of the incubated litterbags.

Discussion

Our results indicate that the local environment under tall birch shrubs promotes faster litter *C*

Table 2. Initial Litter Biochemical Properties of the Common *B. neoalaskana* Leaf Substrate Used in Litterbags, as well as Properties of Local Fully Senesced *B. glandulosa* Litter (Dominant Deciduous Shrub in the Study Area) Collected from Both the Low and Tall Birch Shrub Study Sites

Litter type	%*C*	%*N*	%*P*	*C*/*N*	*C*/*P*	*N*/*P*	Leaf litter production (g m^{-2})
B. neoalaskana (incubated litter)	48.9 ± 0.1	0.57 ± 0.01[a]	0.15 ± 0.01	86.7 ± 1.8[a]	347 ± 31	4 ± 0.42	–
B. glandulosa (low birch shrub tundra)	51.4 ± 1.0	0.46 ± 0.02[b]	0.10 ± 0.04	112.1 ± 4.5[b]	830 ± 237	7.3 ± 2	4.3 ± 1.2[a]
B. glandulosa (tall birch shrub tundra)	51.1 ± 0.8	0.47 ± 0.01[b]	0.10 ± 0.01	109.4 ± 3.2[b]	556 ± 75	5 ± 0.55	44.3 ± 11.8[b]

Data are means (n = 6–9; ± 1 S.E.), with significant differences (P ≤ 0.05) indicated by differing superscript letters.

decomposition and greater *N* and *P* immobilization. This suggests two positive feedback mechanisms that could contribute to the recently observed deciduous shrub expansion across the Arctic (Elmendorf and others 2012; Myers-Smith and others 2015): (1) biological effects associated with tall birch versus low birch differences in leaf-litter inputs and the decomposer community (DeMarco and others 2014a); and (2) physical effects related to snow accumulation and winter microclimate (Sturm and others 2005). In the following sections, we discuss the basis for these feedbacks according to our results and those of others.

Litter Decomposition Processes in Tall Versus Low Birch Tundra

The tall birch plots reduced litter *C* by 22–28% compared to both low birch sites, supporting H1 that litter decomposition rates are faster in tall birch environments. It took 5 years for this site-specific effect to occur, and even then the statistical significance of the tall birch site ($P < 0.05$) was only apparent after correcting for MBC growth into the litter. However, note that our statistical analysis assumes that any differences in litter properties become proportionally greater over the 5 years of incubation, and therefore it is possible that significant changes appeared as early as in years 3 or 4 where we did not sample litterbags. Using similar *B. neoalaskana* litter, DeMarco and others (2014a) found no significant difference in *C*-loss rates between adjacent Alaskan low and high shrub sites after 3 years. Together, this suggests that the effects of taller and denser shrub vegetation on foliar litter decomposition are slow, and that they apply to the more recalcitrant litter *C* pools which otherwise tend to become part of the SOM pool. This conclusion highlights the fundamental concern that short-term tundra manipulation studies (1–3 years) that focus primarily on the fast-decomposing litter *C* pool may not be able to reveal important biogeochemical features of changing Arctic vegetation and its impact on *C* cycling. Therefore, longer-term investigations, such as this study, are critical for improving our understanding of how fast- *and* slow-decomposing *C* pools will react to changes in their abiotic and biotic surroundings in the future.

Phosphorus losses from the incubated litter in all the sites over the first year amounted to almost ¾ of initial *P* content. The absence of a tall birch effect suggests that this process was largely physical rather than biologically mediated. Phosphorus losses of a similar magnitude have previously been observed over one cold season for *B. glandulosa* litter incubated in Subarctic woodland (Moore 1984) and in Arctic tundra (Christiansen and others 2017). In addition, rainfall leaching of senescing *B. neoalaskana* leaf *P* during autumn in Alaska is almost as large as observed in our study (Chapin and Moilanen 1991). Together, these results suggest that the broadly similar litter *P* losses across all three sites occurred in autumn, shortly after incubation. Foliar litter *N* is generally much less soluble than *P* (Schreeg and others 2013), and the incubated litter immobilized *N* during all harvest years in the tall birch plots, but remained consistently close to the initial *N* content in the unmanipulated and snowfenced low birch sites. Consequently, both the *N* and *P* contents of the incubated litter were always larger in the tall birch plots.

Total vascular plant biomass (above- and belowground) and annual birch new shoot growth are 3 and 23 times greater, respectively, in our tall birch site compared to the two low birch sites (Grogan 2012; Vankoughnett and Grogan 2016), leading to 10 times more leaf litter production (Table 2). In addition, microbial biomass *C*, soluble organic *C*

(DOC) and all *N* pools (total *N*, microbial biomass *N*, and soluble organic and inorganic *N* forms), as well as flux-rates of DOC production, microbial *N* cycling, and *N* mineralization are all substantially larger at the tall birch site (Buckeridge and others 2010b; Chu and Grogan 2010; Vankoughnett and Grogan 2014). By contrast, native *B. glandulosa* litter nutrient contents were similar across the low and tall birch sites, suggesting that although the incubated *B. neoalaskana* leaves had higher *N* content compared to the native litter, it is unlikely that feature affected site-differences in decomposition rates.

Generally, tall deciduous shrub patches are often found in areas where nutrient supply is enhanced by flowing water (Chapin and others 1988). Localized subsurface water flow during the growing season could potentially be a driver of soil microbial decomposition rates and shrub growth in our tall birch site. Nevertheless, over 10+ years, we have been unable to demonstrate this. In fact, soil moisture (0–10 cm depth) is consistently lower in the tall birch site relative to the low-stature birch sites (Figure S2), possibly due to enhanced evapotranspiration. Accordingly, the greater decomposition rates under these tall birch shrubs are likely due to an internal biological feedback mechanism where greater leaf litter inputs in autumn prime organic matter decomposition (Kuzyakov and others 2000; Vankoughnett and Grogan 2016). At our tall birch site, this in-turn promotes faster nutrient cycling rates (Buckeridge and others 2010b), and supports a different and larger microbial community (Buckeridge and others 2010b; Chu and others 2011) compared to the low-stature birch shrub sites.

Physical Effects Associated with Snow Accumulation have Negligible Effect on Overall Foliar Litter Decay

Our experimentally deepened snow treatment in low birch vegetation had no effect on leaf litter mass or *C*, supporting H2 that snow accumulation by itself has little or no impact on litter decomposition rates. Similarly, 1, 2, 3 and 4 years of experimentally deepened snow did not significantly affect mass or *C* loss of *B. glandulosa* litter on Disko Island, Greenland (Christiansen and others 2017), *B. nana* (Walker and others 1999) and *B. glandulosa* litter (DeMarco and others 2014a) in Alaska, or *B. nana* litter in Abisko, Northern Sweden (Aerts and others 2012). Additionally, experimental snow reduction did not affect *B. pubescens* litter decay in Umeå, Northern Sweden (Bokhorst and others 2013).

Tundra landscapes are notoriously heterogeneous at all spatial scales within and across ecosystems. To account for plot variability, we sampled 2–4 litterbags per plot and sampling year. Additionally, our study, and the studies referenced above, used experimental designs with 5–24 plots per treatment, suggesting that the lack of treatment effects was not an artefact of plot heterogeneity or low replication. In conclusion, tundra litter decomposition remains profoundly temperature-inhibited even when deepened snow raises mean winter soils by up to 4°C as in the snowfence studies referenced above. By contrast, our comparison of the low and tall birch sites clearly indicates differences in litter decomposition rates that may be a result of biological differences between these vegetation-types alone, or a consequence of those differences acting in combination with the deeper snow associated with taller stature shrubs.

Biological and Physical Effects Combine to Enhance Lignin Decay in Tall Birch Tundra

Five years of litter decomposition in the tall birch site significantly reduced the content of lignin-like acid unhydrolizable residues (AUR) by 27 and 14% relative to the unmanipulated and snowfenced low birch sites, respectively. Because these lignin-like residue losses were greater in the snowfenced low birch site compared to the unmanipulated low birch site, warmer winter soil temperatures due to deepened snow were at least partly responsible for the observed decay of lignin-like residues in the tall birch site, supporting H3 that tall shrub environments promote decay of recalcitrant *C*-compounds.

Why would warmer, yet still frozen, winter soil temperatures under deepened snow enhance degradation of lignin-like residues in foliar litter? When soils freeze, liquid water becomes exceedingly rare and consequently limits microbial activity (Elberling and Brandt 2003). Increasing soil temperatures from − 10 to − 5°C therefore greatly affects soil C mineralization rates (Mikan and others 2002), primarily due to greater unfrozen water availability (Öquist and others 2009). Additionally, microbial decomposition of recalcitrant litter *C* compounds is more temperature-sensitive compared to fast-turnover *C* (Erhagen and others 2013) due to greater activation energies associated with enzymatic degradation of recalcitrant lignin-like organic material (Ågren and Wetterstedt 2007; Conant and others 2011). Thus, several physiochemical features associated with freezing suggest that decay of lignin-like residues in particular should indeed be relatively sensitive to sub-zero increases in temperatures.

Fungi are more active than bacteria at freezing temperatures (McMahon and others 2009) and they dominate tundra soils during winter (Schadt and others 2003), including in our study area (Buckeridge and others 2013). Soil fungal biomass is enhanced under tall deciduous shrub patches (Deslippe and others 2011), also across our low and tall birch sites (Buckeridge and others 2010b), and because fungi are the primary lignin decomposers (Osono 2007), a more dominant fungal community could be driving greater lignin decay rates during both winter *and* summer in the tall birch site. In contrast, late-winter fungal biomass is similar across our two low birch sites (Buckeridge and Grogan 2008), suggesting that temperature differences are the primary driver of lignin decomposition here. Thus, our study clearly demonstrates that decomposition of lignin-like residues in litter is enhanced by deepened snow alone (snowfenced low birch site), and by the combination of physical and biological impacts of a taller and denser shrub ecosystem (Figure 2I).

The lignin-like residues increased (up to ~ 20–30%) over the first incubation year, after which they generally declined. Lignin is a highly irregular plant polymer primarily found in plant cell walls whereas microorganisms do not synthesize or contain lignin (Higuchi 1990). How then could the lignin-like residue pool increase during the first year of incubation? AUR is a proximate fraction containing both lignin and other recalcitrant plant cell constituents such as cutins and tannins as well as many cellulose complexes bound to these compounds (Preston and others 1997). Fungal and bacterial cell walls contain complex melanin and/or chitin structures, which are mostly unhydrolyzable (resembling humic acids; Saiz-Jimenez 1996), and therefore end up in the SOM pool (Kögel-Knabner 2002). These recalcitrant or humic microbial products are therefore also likely to occur in the AUR fraction that we isolated via chemical extraction. In absolute terms, the increase in lignin-like residues over the first year was relatively small (35 mg on average), whereas in comparison the loss of soluble *C* fractions amounted to 250–300 mg during the same period (Table S4). Nevertheless, although the magnitudes of enhanced AUR losses in the snowfenced low birch and tall birch plots are small, our study clearly demonstrates that decay of both recalcitrant plant *and* microbially-derived compounds increased. Lignin represents about 30% of the total atmospheric *C* sequestered into plant biomass every year (Boerjan and others 2003), and enhanced decay rates of this otherwise highly recalcitrant *C* compound is likely to affect future litter and SOM cycling rates and thus ecosystem *C* storage over the longer-term.

Revisiting the Snow-Shrub Hypothesis: Are Biotic Controls More Important than Abiotic Controls in Driving Shrub-Soil Feedbacks?

We have demonstrated two positive feedback mechanisms by which deciduous shrubs may promote their own expansion. Although these mechanisms are consistent with the proposed snow-shrub feedback hypothesis (Sturm and others 2005), our results clearly indicate that any effect of warmer winter soils due to deepened snow alone (that is, without tall shrubs) on leaf litter *C* loss is likely to be insignificant, at least over a five-year period. Consequently, we conclude that it is the combined biological effects of a more fertile soil environment that promote foliar litter (and soil) nutrient cycling in tall birch shrub ecosystems during both summer *and* winter, leading to the positive feedback mechanisms promoting expansion of tall shrubs (Figure 3). In contrast, the physical effect of a deepened snow cover, and a warmer winter soil microclimate, enhances decay rates of the more recalcitrant litter compounds but to a lesser extent than the combined biological (see above) and physical features of tall shrubs. Vankoughnett and Grogan (2014) observed no difference in birch shrub uptake of tracer ^{15}N over a two-year period when comparing the unmanipulated and snowfenced low birch plots used in our study, but they did find significantly greater birch shrub ^{15}N uptake in the tall birch site. The feedbacks demonstrated in our results here, together with the above conclusion, strongly suggest that deciduous shrub expansion driven by climate warming will primarily occur in and around existing tall shrub-dominated communities (Myers-Smith and others 2011).

Soil microbial communities are inherently different between tundra ecosystems with few low shrubs and taller shrub-dominated tundra (Wallenstein and others 2007; McMahon and others 2011), including our low and tall birch sites (Chu and others 2011). Specialized physiologies of ecosystem-specific microbial communities, adapted to local litter inputs and soil edaphic properties, are likely to play an integral part in how tall shrubs promote litter decomposition. For example, microbial exoenzyme activity is stimulated by litter quantity and quality inputs (Hernández and Hobbie 2010), supporting the hypothesis that larger inputs of deciduous leaf litter, with correspondingly lower

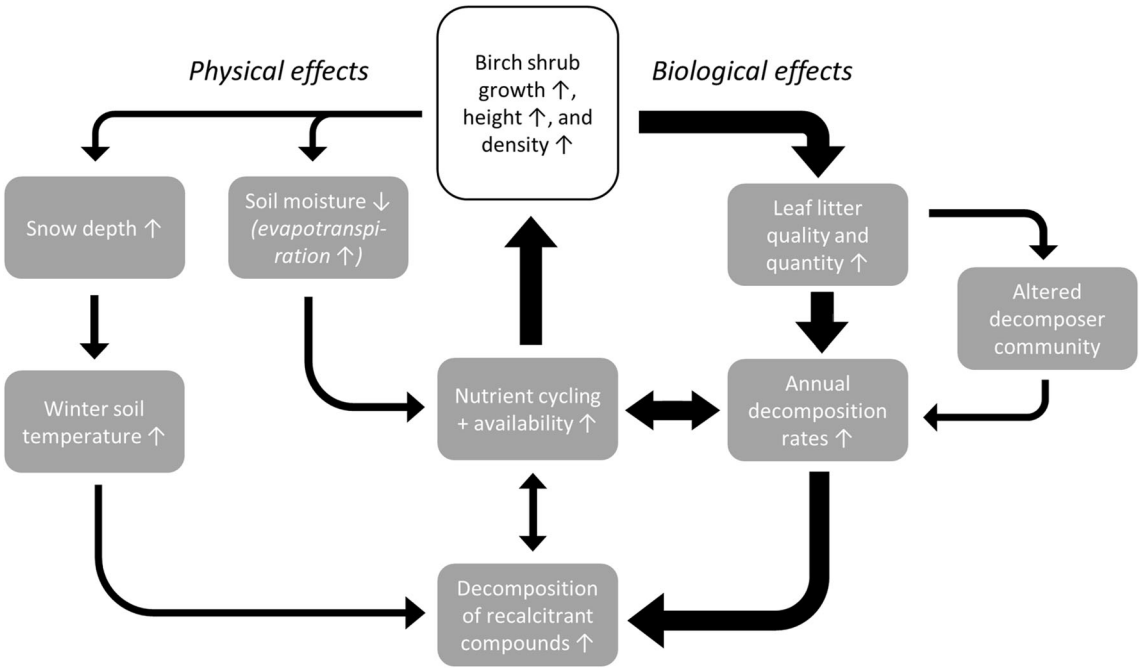

Figure 3. Predicted feedbacks resulting from enhanced growth of birch shrubs to form relatively tall and dense deciduous shrub patches. Factors are split into physical (left) and biological (right) effects, with arrow widths indicating the magnitude of the effect between the linked factors. The predicted feedbacks are based on the results of this study and previous research (see main text for detailed discussion of feedbacks).

proportions of recalcitrant evergreen litter, and the associated biotic feedbacks (Figure 3), is the primary driver of foliage decay rates in tall birch-dominated ecosystems (DeMarco and others 2014a). This biotic plant-soil mechanism is very likely also the driver of recently observed tundra soil *C* loss associated with shrub and tree growth (Wilmking and others 2006; Hartley and others 2012; Parker and others 2015; Sørensen and others 2017), emphasizing the large influence that tall shrubs may exert on key ecosystem functions such as carbon and nutrient mobilization and storage. In conclusion, biotic feedbacks associated with tall and dense shrub vegetation exert a stronger control over nutrient availability and nutrient cycling than changes in the physical winter microenvironment alone, and these plant-soil dynamics are likely to become increasingly important in determining shifts in vegetation within Arctic tundra ecosystems as the climate warms further.

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