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Tall deciduous shrubs offset delayed start of growing season through rapid leaf development in the Alaskan arctic tundra

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Abstract

Increasing temperatures in arctic regions are causing earlier spring snowmelt, leading to earlier plant emergence, which could lengthen the period of carbon uptake. Warming is also leading to a shift from graminoid to deciduous shrub-dominated tundra, and in many areas deciduous shrubs are becoming taller. As taller shrubs become increasingly dominant, arctic landscapes may retain more snow, which could lengthen spring snow cover duration and offset advances in the start of the growing season that are expected as a result of earlier spring snowmelt. As a consequence, deeper snow and later snowmelt in taller shrub tundra could delay plant emergence and shorten the period of carbon uptake. This study tracked leaf development of two abundant deciduous shrubs, *Betula nana* and *Salix pulchra,* and compared individuals along a natural shrub height gradient on the North Slope of Alaska. We measured spring snow depth and snow cover duration, bud and developing leaf nitrogen content, as well as the timing of budburst and leaf expansion. Taller deciduous shrubs in shrub-dominated communities had deeper snow surrounding them, and became snow-free 1 to 6 days later, delaying budburst by 2 to 12 days relative to shorter deciduous shrubs in graminoid-dominated communities. However, leaf development of tall shrubs caught up to that of short shrubs; occasionally, tall shrubs reached full leaf expansion 1 to 4 days *before* short shrubs, indicating more rapid leaf development. This convergence in the timing of later leaf development stages is potentially enabled by approximately 16% to 25% greater nitrogen in buds and developing leaves of taller shrubs compared with shorter shrubs. Our findings suggest that delayed snowmelt in areas dominated by taller shrubs may have a short-lived impact on the timing of leaf development, likely resulting in no difference in duration of peak photosynthetic period between tall and short stature shrubs.

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Introduction

Climate change has caused a particularly strong warming trend in the Arctic (Chapin et al., 2005; Serreze and Francis, 2006; IPCC, 2007), and spring snowmelt is occurring earlier in many arctic tundra regions (Stow et al., 2004; AMAP, 2012). Meta-analyses in northern ecosystems correlate increasing temperatures and earlier spring snowmelt with earlier plant emergence (Arft et al., 1999; Root et al., 2003; Wipf and Rixen, 2010). This phenomenon has been observed via field- (Starr et al., 2000; Wipf et al., 2009) and satellite-based studies (Myneni et al., 1997; Zhou et al., 2001; Zeng et al., 2011). The implication of a shift toward earlier plant emergence in arctic tundra ecosystems is not fully understood, but it could lengthen the period of maximum leaf area (Oberbauer et al., 1998), potentially increasing the amount of carbon sequestered by arctic plants within a given year (Euskirchen et al., 2006; Graven et al., 2013; Richardson et al., 2013).

In addition to an earlier start to the growing season, satellite studies suggest the Arctic has been "greening" over the past several decades (Bunn et al., 2007; Verbyla, 2008; Jia et al., 2009), which is likely due in part to the expansion and increasing dominance of deciduous shrubs (Jia et al., 2003). Expansion of deciduous shrubs into primarily graminoid-dominated tundra in the Alaskan Arctic is evident in comparative historical photo interpretation (Tape et al., 2006) and has been quantified in field surveys (Hinzman et al., 2005). Deciduous shrub expansion has been attributed to increases in air temperature (Walker et al., 2006), subsurface water flow (Naito and Cairns, 2011; Tape et al., 2012), and soil nutrient mineralization (Sturm et al., 2005). Findings from experimental manipulation studies suggest that deciduous shrubs will continue to expand and grow taller as arctic warming continues (Chapin et al., 1995; Wahren et al., 2005; Walker et al., 2006).

Many arctic tundra studies have focused on the impacts of increasing deciduous shrub dominance on snow and nutrient cycling dynamics. For example, tall stature deciduous shrubs are more efficient at trapping snow; deeper drifts surround them compared to shorter stature shrubs (Sturm et al., 2001, 2005; Myers-Smith and Hik, 2013). Deeper snowdrifts increase soil insulation, which increases winter microbial activity and nutrient mineralization (Schimel et al., 2004; Wahren et al., 2005; DeMarco et al., 2011). Because deciduous shrubs have been shown to be more efficient than many other arctic plants at taking up nutrients (Shaver and Chapin, 1991; Bret-Harte et al., 2001; Wookey et al., 2009), increased mineralization in this strongly nitrogen limited ecosystem allows deciduous shrubs to outcompete other plants (Chapin et al., 1995; Cornelissen et al., 2001; Shaver et al., 2001),

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creating a potential positive feedback for increasing deciduous shrub dominance (Sturm et al., 2005; Myers-Smith et al., 2011).

Further, it has been suggested that winter precipitation is also increasing in arctic regions (Serreze et al., 2000), contributing to deeper snowdrifts. Deeper snowdrifts lead to later snowmelt dates (Liston et al., 2002), which can delay timing of plant emergence (Borner et al., 2008), potentially shortening the growing season and delaying the period of photosynthetic activity. Thus, due to their tendency to increase spring snow cover duration, the increasing dominance of tall deciduous shrubs could delay plant emergence, thereby offsetting, at least to some extent, the earlier start to the growing season expected to continue with spring warming and earlier snowmelt.

Although several studies have explored how changing snow depth and spring snowmelt dates may affect plant phenology, most have been experimental, relying on snow removal (Oberbauer et al., 1998; Starr et al., 2000; Wipf et al., 2009) or artificial warming to simulate the impacts of early snowmelt (Wookey et al., 1993; Hartley et al., 1999; Aerts et al., 2006), and snow fences to simulate the impacts of greater snow depth and later snowmelt (Walker et al., 1999; Wahren et al., 2005). While snow manipulation studies are important for understanding potential implications of climate change on plant phenology, Wipf and Rixen (2010) suggested that such experimental techniques may deviate from natural scenarios by altering snow composition and compaction. Therefore, it is important to also include observations of how natural gradients in vegetation stature, and consequently snow depth, impact tundra plant phenology (Dunne et al., 2004; Hollister et al., 2005). Also, most plant phenological studies monitor the date on which some or all of the following life history events occur—snow-free, leaf budburst, flowering, and/or senescence dates (e.g., Molau and Molgaard, 1996)—yet intermediate leaf development stages, such as leaf expansion, can also be important from a carbon gain perspective (Johnson and Tieszen, 1976).

In this study, we monitored snow depth; timing of snowmelt; timing of leaf bud appearance, leaf budburst, leaf opening, and leaf expansion; as well as nitrogen contents of buds and emerging leaves for two species of deciduous shrubs (*Betula nana* and *Salix pulchra*, hereafter *B. nana* and *S. pulchra*) along a natural gradient of increasing shrub dominance (i.e., increasing aerial cover and stature) on the North Slope of Alaska. Because the rate of leaf development may affect timing of maximum photosynthetic capacity (Constable and Rawson, 1980) and thus carbon sequestration (Street et al., 2007), we quantified sequential leaf stages closely throughout the period of leaf development. Our goal was to gain an understanding of how shrub stature and associated snow dynamics impact the timing of leaf bud break and leaf development. Based on findings from previous studies (Sturm et al., 2001; Liston et al., 2002), we hypothesized that taller stature deciduous shrubs would undergo a delay in leaf development as a result of deeper snow and a delayed snow-free date.

Methods

STUDY SITES AND STUDY AREAS

Data sets were collected in early May through the end of July in 2011 and 2012 at three field sites (Fig. 1) within ~30 km of the Arctic Long Term Ecological Research (ARC LTER) site at Toolik Field Station in the northern foothills of the Brooks Range, Alaska (68°38′N, 149°34′W). Annual precipitation at Toolik is 200–400 mm, with 45% falling as snow; annual average air temperature is –10 °C (van Wijk et al., 2005) and average growing season air temperature is 7 °C (Johnson et al., 2000). We defined the growing season as the period from snow-free until senescence, which near Toolik extends from approximately late May/early June until mid to late August. Daily air temperature during the 2011 and 2012 growing seasons for sites used in this study can be found in Appendix Figure A1. Air temperatures at our sites were within the long-term average range of growing season air temperatures at Toolik (Johnson et al., 2000).

Sites were chosen in May 2010 to represent the most common shrub tundra types in the foothills of the Brooks Range (Hanson, 1953) as part of a larger research effort investigating the effects of shrub vegetation on associated arthropod and migratory songbird reproductive success (Rich et al., 2013). The three sites used in this study were: Toolik Lake Field Station (TLFS), Sagavanirktok River–Department of Transportation camp (SDOT), and Imnavait Creek (IMVT) (Fig. 1). Each of the three sites included two study areas dominated by different vegetation cover; one study area dominated by graminoids that also contained short deciduous shrubs (hereafter referred to as Open) and one study area dominated by deciduous shrubs (hereafter referred to as Shrub) (Fig. 2). Within each Open or Shrub study area, two 100 m transects were established, for a total of 12 transects (6 Open and 6 Shrub). Ten 1-m^2 quadrats were established at 10 m intervals along each transect. In early 2012, along each transect, wooden 2 × 6 inch boardwalks were installed low to the ground and a reasonable distance from quadrats. In this study, five 1-m^2 quadrats were randomly chosen along each transect, for a total of 60 quadrats (30 Open and 30 Shrub). In all 60 quadrats, individual *B. nana* and *S. pulchra* plants closest to the lower left corner of each quadrat were selected and an individual branch at the top of the canopy of each plant was labeled with an identification (ID) tag in the spring of 2011.

Together, the Open and Shrub areas represent a natural gradient of increasing shrub dominance, because the same deciduous shrubs (*B. nana* and *S. pulchra*) are found in all study areas, however, their percent cover and stature increase from low percent cover (~20%–30%) and short stature (>30 cm) in Open areas to higher percent cover (~40%–55%) and taller stature (ranging from 30 to 105 cm) in Shrub areas. Although there is topographical variation between sites (TLFS, IMVT, and SDOT), the study areas within each site (Open and Shrub) are not topographically different enough to cause significant differences in snow depths, thus differences in snow depth between Open and Shrub areas at each site are primarily caused by differences in vegetation height. See Appendix Table A1 for elevation ranges.

The Open areas at all three sites are similar to one another and are characterized by tussock-forming sedges interspersed with a variety of dwarf shrubs, forbs, and mosses, with average maximum deciduous shrub heights of approximately 16 cm (IMVT), 23 cm (TLFS), and 28 cm (SDOT). The three Shrub areas differ from one another and represent a gradient of shrub statures, with average maximum deciduous shrub heights of approximately 22 cm (IMVT), 35 cm (TLFS), and 84 cm (SDOT). The IMVT Shrub area is located in water tracks and represents vegetation typical of water track tundra as described in Chapin et al. (1988). The TLFS Shrub area is located near the Toolik Lake outlet (~200 m from the outlet) and represents vegetation typical of shrub tundra described in Shaver and Chapin (1991). The SDOT Shrub area is a riparian community (~200 m from the Oksrukuyik Creek), has tall and structurally complex shrubs, and represents vegetation typical of riverside shrub tundra as described in Giblin et al. (1991).

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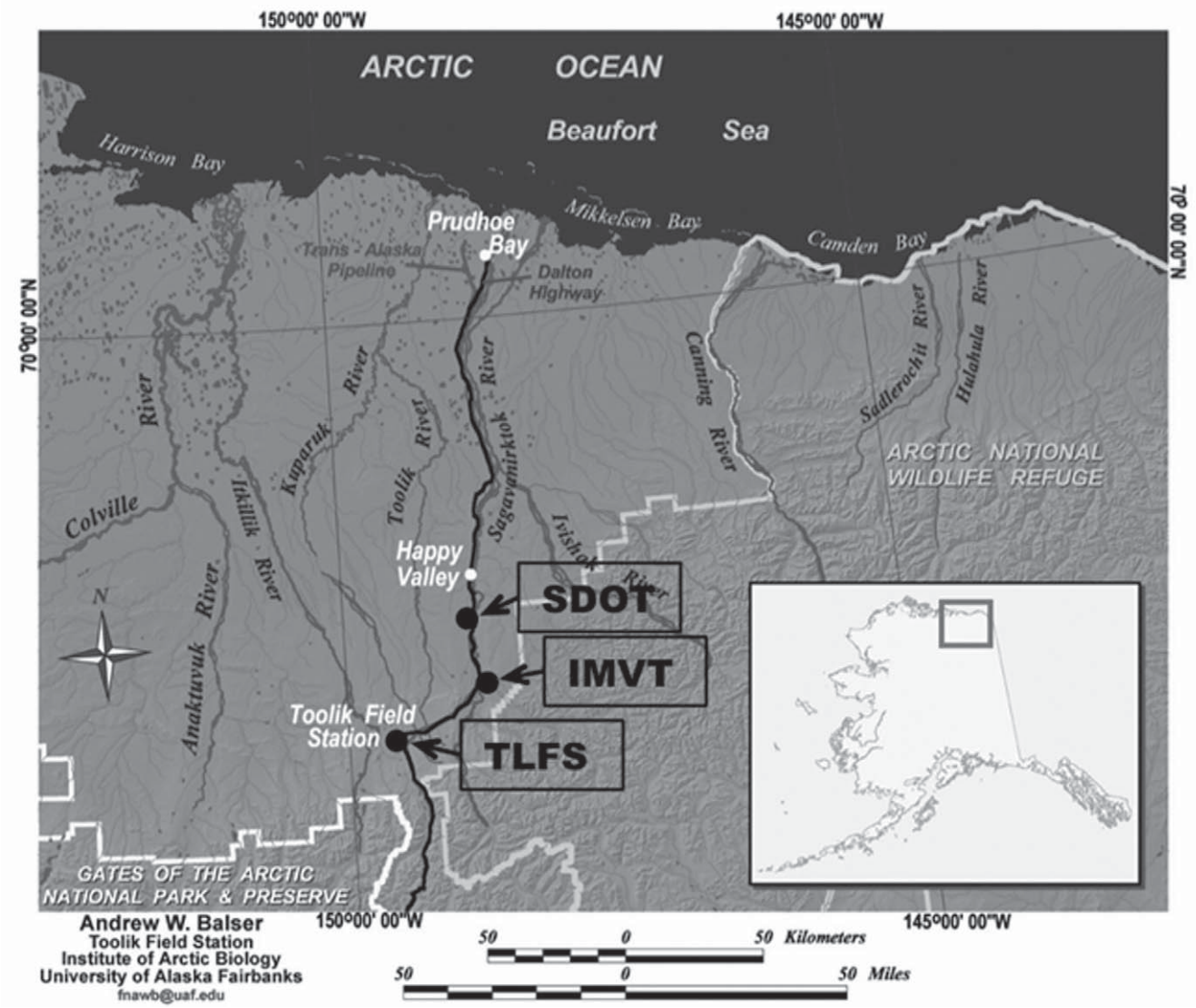

FIGURE 1. Map of Alaska and the North Slope of the Brooks Range (inset) showing the location of the three field sites near the Toolik Lake field station used in this study. TLFS = Toolik Lake Field Station; IMVT = Imnavait Creek; and SDOT = Sagavanirktok River–Department of Transportation.

SNOW DEPTH AND MELT

The day of year (DOY) on which each individual plant being monitored for leaf development (see Timing of Leaf Development section below) was snow-free (snow-free date) was recorded in 2011 and 2012. In addition to individual plant snow-free dates, in 2012 snow depth was measured every four to six days in each of the quadrats where individual plants were monitored, from 11 May until snow depth reached 0 cm (ca. 24 May to 5 June, depending on the site). Snow depth was measured at the center and four corners in all sixty 1-m^2 quadrats by pushing a 1 cm diameter aluminum pole into the snow until soil or moss surface was reached (for a total of 25 measurements per transect, per sampling date). The five snow depth values associated with each quadrat were averaged to give a mean quadrat value.

TIMING OF LEAF DEVELOPMENT

In 2011 and 2012, the timing of leaf development stages (described below and in Fig. 3) of individuals labeled with ID tags (see Study Sites section above) were monitored every two days, from the time each individual was snow-free until leaves were fully expanded (ca. 6 June to 30 June, depending on the species, site, and year) for a total of 60 *B. nana* and 60 *S. pulchra* monitored (n = 30 *B. nana* Open, 30 *B. nana* Shrub, 30 *S. pulchra* Open, and 30 *S. pulchra* Shrub). A modified version of the International Tundra Experiment (ITEX) phenology protocol (Molau and Molgaard, 1996) for *Salix* spp. was used, with the modification being that two additional leaf development stages (first leaf opening and first leaf expanded) were added to the existing ITEX protocol. For each *B. nana* and *S. pulchra* individual, the date on which the following four leaf development stages were reached for the first leaf on an individual labeled branch was recorded: (1) the appearance of the first leaf bud (first leaf bud, FLB), (2) when the first leaf became visibly distinct with green tissue splitting through bud scales (first leaf visible, FLV), (3) when the first leaf separated from the bud and individual leaves became apparent (first leaf opening, FLO), and (4) when the first leaf completely separated from the bud and expanded (first leaf expanded, FLE) (Fig. 3). This may not have always been the same leaf monitored

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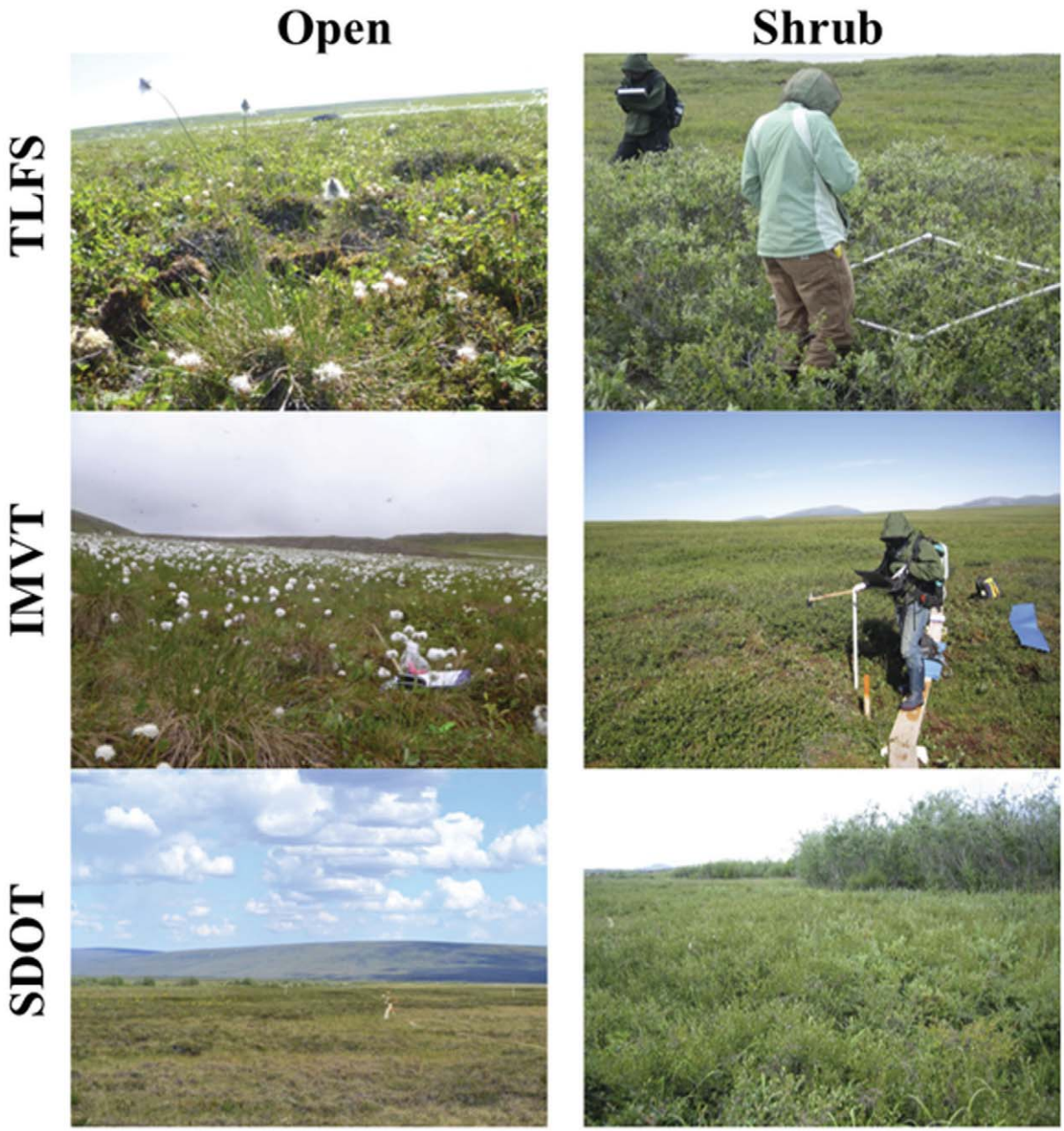

FIGURE 2. Examples of graminoid-dominated (Open) and deciduous shrub–dominated (Shrub) areas used in this study in the northern foothills of the Brooks Range, Alaska. See Figure 1 for site abbreviations.

at each stage, but the date the *first* leaf on the same branch reached each stage.

LEAF NUTRIENT CONTENT

Buds and leaves were collected for nutrient content analysis in 2012 from 25 May to 9 June at three times (corresponding to three leaf development stages: FLB, FLV, and FLO) from one *B. nana* and one *S. pulchra* individual located directly adjacent to each plant being monitored for timing of leaf development. A total of five bud or leaf samples per species, per leaf development stage, per transect were collected (n = 30 for each species, in each vegetation type, at each leaf development stage; for a total of 60 *B. nana* and 60 *S. pulchra* samples for each leaf development stage). Samples were placed in paper coin envelopes, air dried, and later dried in an oven at 60 °C for 24 hours. Samples were ground into a powder using a Mini-Beadbeater-16 ball mill (Bio Spec Products, Oklahoma, U.S.A.). Subsamples of approximately 10 mg were weighed into tin capsules, combusted at 950 °C, and analyzed for nitrogen content using a Thermo Scientific Flash 2000 CHN Analyzer (CE Elantech, New Jersey, U.S.A.). Because of equipment failure, there was only one sample available for data analysis for the FLB stage for *S. pulchra* from the IMVT Open area, thus data for IMVT Open *S. pulchra* were not included in statistical analysis.

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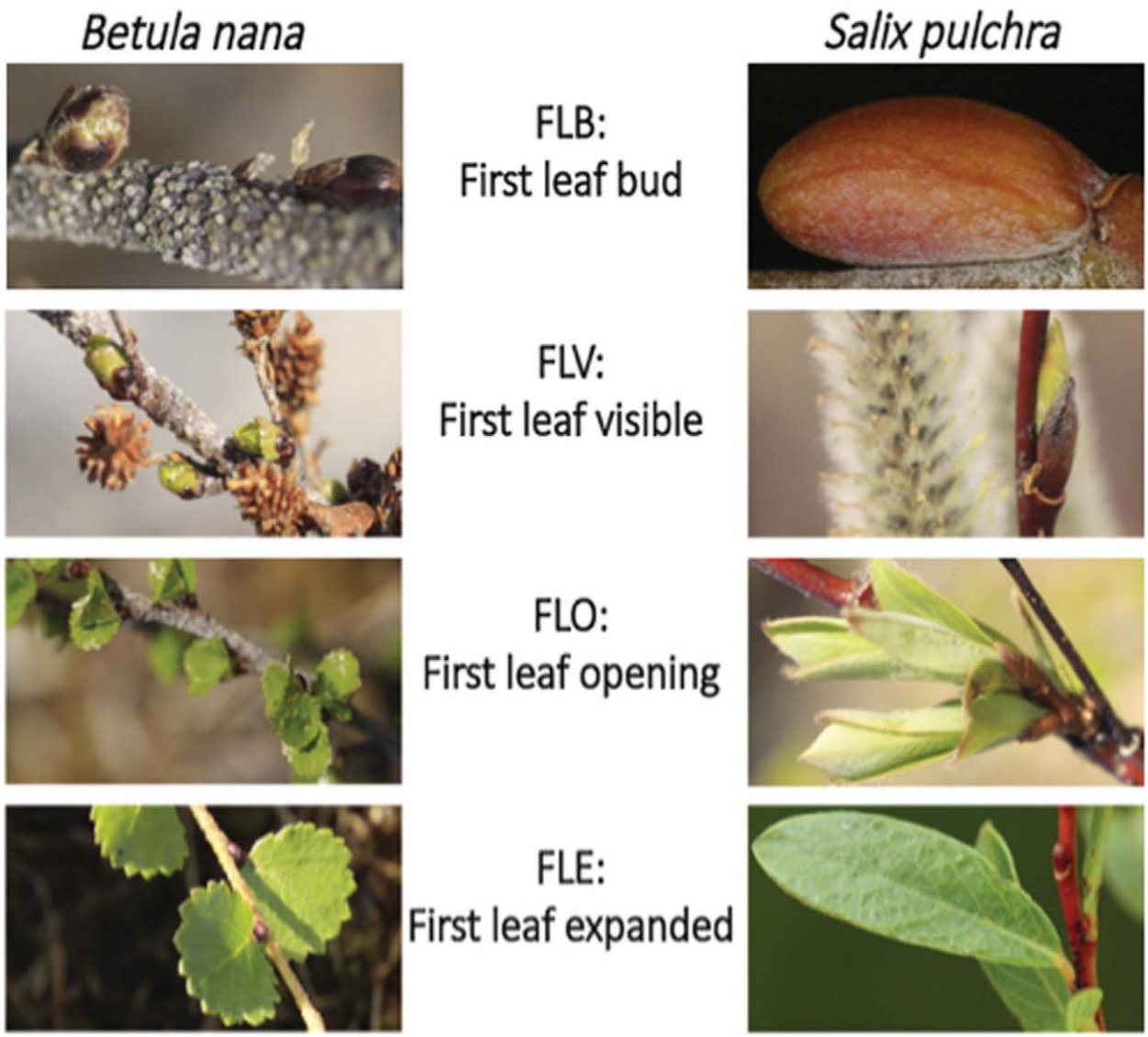

FIGURE 3. Examples of leaf development monitored for *Betula nana* and *Salix pulchra*. Photos courtesy of Jose Luciani, Florida International University.

STATISTICAL ANALYSIS

Because the same individual plants were tracked for leaf development and used for sample collection for nutrient analysis, repeated measures MANOVA was used with timing of leaf developmental stages or leaf nutrient content as the dependent variables and vegetation cover type (Shrub and Open) and site (TLFS, IMVT, and SDOT) as the main effects. For repeated measures multivariate between subject tests, we report Wilks's Lambda results. Because snow depth was measured repeatedly throughout 2012, and because snow-free date was monitored in both 2011 and 2012, a repeated measures analysis was performed on each data set separately, using a linear mixed-effects model, which included vegetation cover and site as the main effects. Quadrats were used as replicates for all data sets (n = 60; 30 Open and 30 Shrub). If the repeated model depicted a significant effect, means were compared using Tukey's honestly significant differences (Tukey's HSD) criterion. Statistical analysis was done in R (R Foundation for Statistical Computing v. 2.13.1, Vienna, Austria) and SAS (SAS Software, v. 9.2, SAS Institute, Cary, North Carolina, U.S.A.).

Results

SNOW DEPTH AND MELT

Depending on the site (i.e., TLFS, IMVT, and SDOT), snow depth (Fig. 4) ranged from 6 to 30 cm deeper in Shrub areas compared to Open areas from DOY 132 to 136 (12 May 2012 to 15 May 2012), and remained significantly deeper until the end of May (effect of cover: $F_{1,54} = 20.24$, $P < 0.0001$). The pattern of snow depth over time varied between site and cover type (i.e., Open and Shrub), driving a significant three-way interaction for the overall data set (effect of day × site × cover: $F_{10,100} = 1.94$, $P = 0.05$). The pattern of snow depth also differed over time and across sites (effect of day: $F_{5,50} = 128.84$, $P < 0.0001$; effect of day × site: $F_{10,100} = 9.98$, $P < 0.0001$) and cover type (effect of day × cover:

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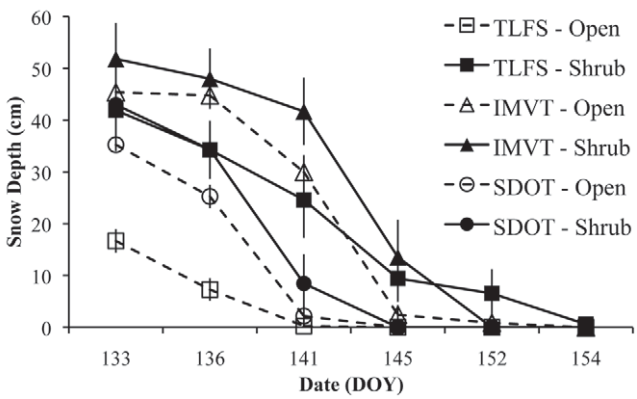

FIGURE 4. Average snow depth (cm) in 2012 throughout measurement period in Open (dashed lines and open symbols) and Shrub (solid lines and filled symbols) areas by site (TLFS = squares; IMVT = triangles; SDOT = circles). Error bars represent 1 SEM. See Figure 1 for site abbreviations.

$F_{5,50}$ = 4.69, P = 0.001). These significant interaction effects were driven by the differences in snow depth over time between sites and cover type. As can be seen in Figure 4, snow depth appears to have decreased at a fairly constant rate at TLFS, decreased more rapidly at SDOT after the second measurement date, and decreased even more rapidly at IMVT after the third measurement. There was also a significant interaction between site and cover type for the first two sample dates, driving a significant interaction for the overall data set (effect of site × cover: $F_{2,54}$ = 4.06, P = 0.02). The significant interaction of site × cover disappeared over time because, as snow melted, the magnitude of difference between sites and cover types decreased. Because the IMVT Open area actually had greater snow depths than TLFS or SDOT Shrub areas, there was also an effect of site on snow depth (effect of site: $F_{2,54}$ = 16.5, P < 0.0001).

Although there was variation from year to year and among the sites and cover types, the snow-free date for *B. nana* (Table 1) was approximately 1 to 6 days later in Shrub areas (depending on the site and year) as compared to Open areas (effect of year × site × cover: $F_{2,54}$ = 4.15, P = 0.02), which corresponds with deeper snow of Shrub areas (Fig. 4). This three-way interaction of year × site × cover was driven by the fact that there was no statistically significant difference in snow-free date between Shrub and Open cover type at SDOT in either year, nor at IMVT in 2012; but there were significant differences between cover types at TLFS in both years and at IMVT in 2011. There were also significant effects of year × site ($F_{2,54}$ = 19.63, P < 0.0001) and year ($F_{1,54}$ = 37.07, P < 0.0001), because *B. nana* was snow-free earlier in 2012 compared to 2011 at SDOT and TLFS, but later in 2012 at IMVT. Also, *B. nana* at IMVT was snow-free last compared to TLFS and SDOT, and whether TLFS or SDOT melted out first varied from year to year and between cover types. There was a significant interaction between site and cover type for *B. nana* in 2012 ($F_{2,54}$ = 4.31, P = 0.02), because in 2012 there was a significant difference in snow-free date between cover types at TLFS only. Although Shrub areas were snow-free later than Open areas in both years (effect of cover: $F_{1,54}$ = 25.69, P < 0.0001), the magnitude of difference between snow-free dates in Open and Shrub areas was greater at TLFS compared to IMVT or SDOT (effect of site: $F_{2,54}$ = 68.82, P < 0.0001).

As with *B. nana*, snow-free date for *S. pulchra* was later in Shrub areas compared to Open areas (Table 1), but this trend differed across sites and years (effect of year × site: $F_{2,54}$ = 10.68, P = 0.0001; effect of year: $F_{1,54}$ = 29.59, P < 0.0001). As with *B. nana*, this was driven by the fact that *S. pulchra* was snow-free earlier in 2012 compared to 2011 at SDOT and TLFS, but later in 2012 at IMVT. There was also a significant interaction between site and cover type for *S. pulchra* in 2011 (effect of site × cover 2011: $F_{2,54}$ = 3.4, P = 0.04), because there was a smaller magnitude of difference in snow-free date between cover type and sites for *S. pulchra* in 2012. Although the *S. pulchra* individuals in Shrub areas melted out later than Open areas in both years (effect of cover: $F_{1,54}$ = 41.21, P < 0.0001), as with *B. nana*, the magnitude of difference between snow-free dates for *S. pulchra* in Open and Shrub areas differed from site to site (effect of site: $F_{2,54}$ = 67.34, P < 0.0001). *S. pulchra* at IMVT were snow-free last compared to TLFS and SDOT, and whether TLFS or SDOT melted out first varied from year to year and between cover types.

TIMING OF LEAF DEVELOPMENT

Although there were differences among sites, years, and species, because *B. nana* and *S. pulchra* in Open areas were snow-free earlier (Table 1) due to shallower snow (Fig. 4), initial leaf development stages (e.g., first leaf visible [FLV] and first leaf opening [FLO]) occurred 2 to 12 days earlier (depending on the site) in Open areas as compared to Shrub areas (Figs. 5, part a, and 6, part a). However, individuals located in Shrub areas accelerated leaf development to such an extent that they reached the last leaf development stage (i.e., first leaf expanded [FLE]) only 2 days later

TABLE 1

Average snow free dates (day of year [DOY]) in 2011 and 2012 for *Betula nana* and *Salix pulchra*. Means are listed (±1 SEM) for Open and Shrub areas from three sites (IMVT, TLFS, and SDOT) near the Toolik Lake field station in northern Alaska. Different letters in parentheses next to mean indicate means within the row are significantly different (P < 0.05) from each other. See Figure 1 for site abbreviations.

		Site:	TLFS		IMVT		SDOT	
Variable	Species	Area:	Open	Shrub	Open	Shrub	Open	Shrub
SF Date 2011	*B. nana*		142 ± 0 (a)	144 ± 0.6 (b)	144 ± 0.4 (b)	148 ± 0 (c)	141 ± 0 (a)	142 ± 1 (a)
SF Date 2012	*B. nana*		136 ± 0.6 (a)	141 ± 1.1 (b)	146 ± 0.8 (c)	148 ± 1.1 (c)	140 ± 0.5 (b)	140 ± 0.5 (b)
SF Date 2011	*S. pulchra*		142 ± 0 (a)	145 ± 0.6 (b)	144 ± 0.4 (b)	148 ± 0.3 (c)	141 ± 0 (a)	142 ± 1 (a)
SF Date 2012	*S. pulchra*		136 ± 0.9 (a)	141 ± 1.3 (b)	145 ± 0.7 (b)	148 ± 1.3 (bc)	139 ± 0 (ab)	140 ± 0.6 (ab)

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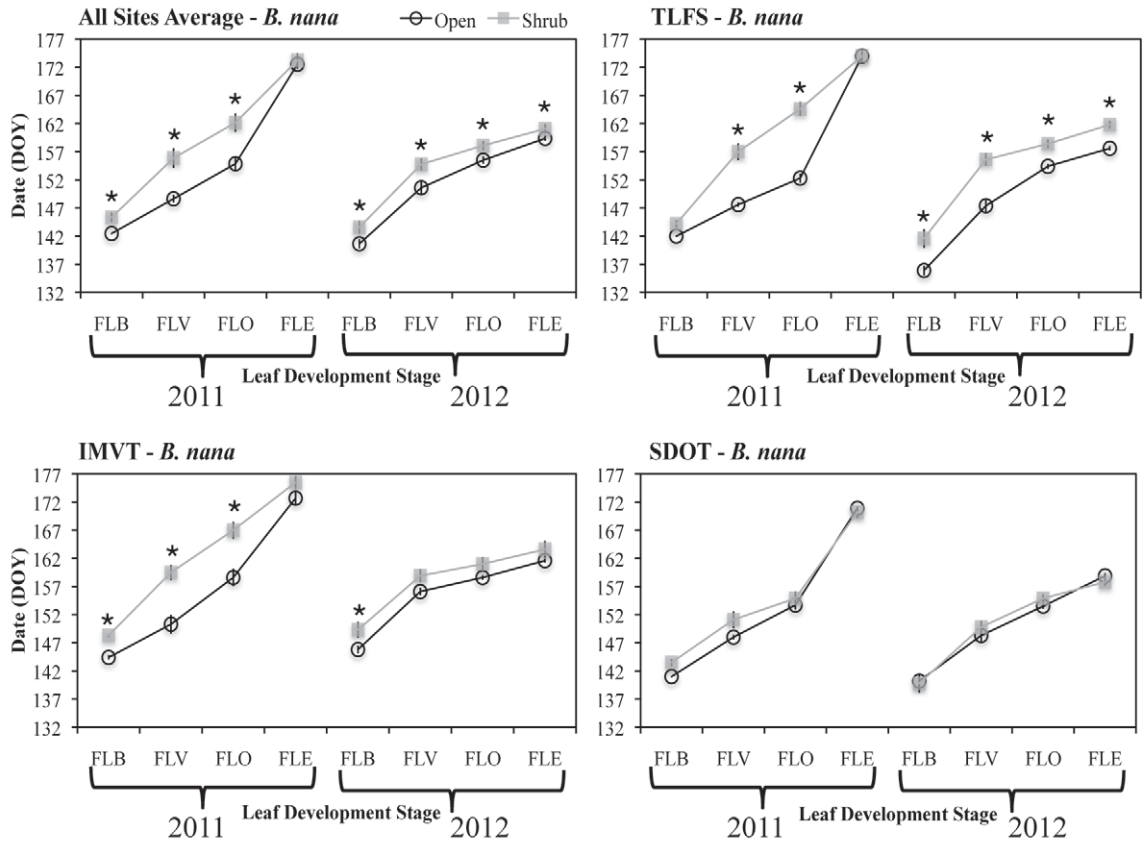

FIGURE 5. Average relative timing of leaf development stages (FLB = first leaf bud; FLV = first leaf visible; FLO = first leaf opening; and FLE = first leaf expanded) for *B. nana* in Open (white circles) and Shrub (gray squares) areas in 2011 and 2012 for (a) all three sites averaged; and at (b) TLFS, (c) IMVT, and (d) SDOT. Error bars represent 1 SEM. Asterisks (*) above symbols indicate a significant difference (P < 0.05) in time when leaf development stage was reached between Open and Shrub areas. See Figure 1 for site abbreviations.

or even 4 days *earlier* than those in Open areas. For instance, at TLFS in 2011, *B. nana* and *S. pulchra* reached FLO 12 and 10 days later (respectively) in Shrub areas compared to Open areas, but reached FLE 0 and 1 day later (respectively) (Figs. 5, part b, and 6, part b). And at SDOT in 2011, *B. nana* and *S. pulchra* reached FLV 2 and 5 days later (respectively) in Shrub areas compared to Open areas, but reached FLE 1 and 5 days *earlier* (respectively) (Figs. 5, part d, and 6, part d).

In both 2011 and 2012, the pattern of leaf development of *B. nana* over time differed between site and cover type, driving a significant three-way interaction for the overall data set (effect of leaf development stage × site × cover: 2011, $F_{6,104} = 4.83$, $P < 0.0002$; 2012, $F_{6,104} = 4.83$, $P < 0.0002$). In 2012, only the pattern of leaf development of *B. nana* differed between site and cover type (effect of site × cover: 2012, $F_{2,54} = 7.91$, $P = 0.001$) because shrubs at IMVT reached all leaf development stages in both Open and Shrub areas later than SDOT or TLFS in 2012 (Fig. 5), which corresponds with the later snow-free date at IMVT (Table 1). Differences between timing of leaf development stages FLV and FLO for *B. nana* between Shrub and Open areas were greatest at TLFS and IMVT in 2011 and at TLFS in 2012; and there was no significant difference in timing between cover types at SDOT in either year. Overall, in both 2011 and 2012, *B. nana* in Shrub areas reached the first three leaf development stages later than in Open areas (effect of cover: 2011, $F_{1,54} = 27.86$, $P < 0.0001$; 2012, $F_{1,54} = 28.70$, $P < 0.0001$) (Fig. 5, part a). For individual leaf development stages, in both years, *B. nana* in Shrub areas reached FLB, FLV, and FLO significantly later (2 to 12 days later depending on the site) than in Open areas, but there was a significant difference in timing at FLE in 2012 only (Appendix Table A2). In 2011, the effect of site was driven mostly by TLFS and IMVT (effect of site: 2011, $F_{2,54} = 13.11$, $P < 0.0001$), and by TLFS in 2012 (effect of site: 2012, $F_{2,54} = 55.75$, $P < 0.0001$). Differences between sites and years could also be affected by differences in air temperatures (Appendix Fig. A1). Although the difference in timing when leaf development stages were reached was not significant at SDOT, it is notable that although Open areas reached FLB and FLV leaf development stages 2 to 3 days earlier than Shrub areas, *B. nana* in SDOT Shrub areas reached FLE 1 day *before* those in Open areas, indicating an accelerated rate of leaf development (Fig. 5, part d).

For *S. pulchra*, there was a significant three-way interaction effect in 2011 only (effect of leaf stage × site × cover: 2011, $F_{6,104} = 2.53$, $P = 0.03$), because in 2011 there were significant differences in timing of leaf development stages being reached between Open and Shrub areas, but the stage at which the differences were significant differed among sites (Fig. 6). Overall, in both years, *S. pulchra* individuals in Shrub areas reached the first three leaf development stages later than *S. pulchra* in Open areas (effect of cover: 2011, $F_{1,54} = 11.17$, $P < 0.002$; 2012, $F_{1,54} = 6.45$, $P = 0.01$) (Fig. 6, part a). For individual leaf development in 2011, *S.*

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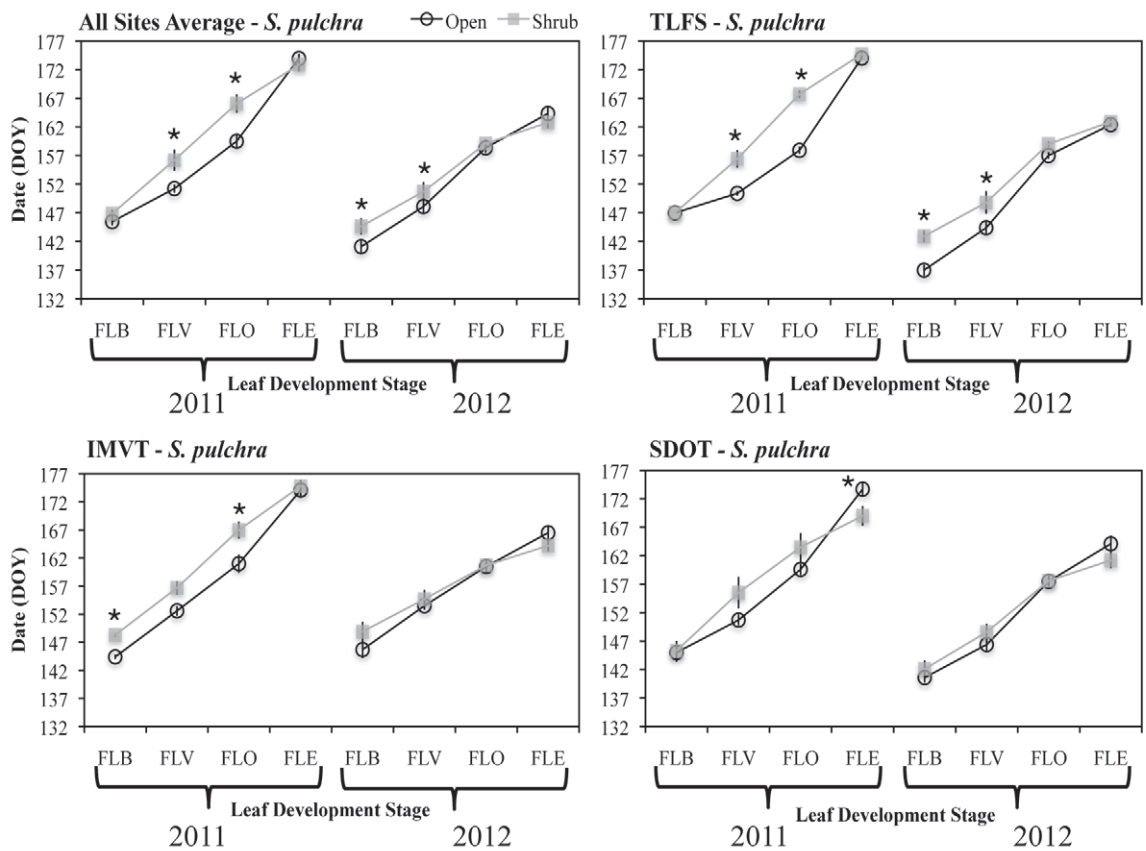

FIGURE 6. Average relative timing of leaf development stages (FLB = first leaf bud; FLV = first leaf visible; FLO = first leaf opening; and FLE = first leaf expanded) for *S. pulchra* in Open (white circles) and Shrub (gray squares) areas in 2011 and 2012 for (a) all three sites averaged; and at (b) TLFS, (c) IMVT, and (d) SDOT. Error bars represent 1 SEM. Asterisks (*) above symbols indicate a significant difference (P < 0.05) in time when leaf development stage was reached between Open and Shrub areas. See Figure 1 for site abbreviations.

pulchra in Shrub areas reached FLV and FLO significantly later (4 to 10 days later depending on the site) than in Open areas, but there was no significant difference in timing at FLB or FLE (Appendix Table A2). For individual leaf development in 2012, *S. pulchra* in Shrub areas reached FLB and FLV significantly later (2 to 6 days later depending on the site) than in Open areas, but there was no significant difference in timing of FLO or FLE. Effect of site in 2012 was driven by the fact that the only significant difference in timing of leaf development stages was at TLFS at FLB and FLV (effect of site: 2012, $F_{2,54} = 37.47$, $P < 0.0001$) (Fig. 6, part b). Similar to *B. nana*, differences between sites and years could also be due to differences in air temperature (Appendix Fig. A1). As with *B. nana*, *S. pulchra* in Open areas reached FLB and FLV leaf development stages earlier than Shrub areas at SDOT, but *S. pulchra* in SDOT Shrub areas reached FLE *before* those in Open areas—5 days in 2011 and 3 days in 2012—indicating an accelerated leaf development (Fig. 6, part d). *S. pulchra* in IMVT Shrub areas also reached FLE 2 days *before* those in Open areas in 2012 (Fig. 6, part c).

Figure 7, which depicts the relationship across species, sites, and years between the difference in snow-free dates and the difference in FLV and FLE dates (Shrub dates minus Open dates), shows that later snow-free dates for *B. nana* and *S. pulchra* in Shrub areas led to a later budburst relative to Open areas (FLV: $R^2 = 0.6$, $P < 0.01$), but did not significantly affect the date of leaf expansion (FLE: $R^2 = 0.21$, $P = 0.2$). Occasionally, even when snowmelt and budburst were delayed, taller shrubs in Shrub areas reached the leaf expansion stage before shorter shrubs in Open areas (Fig. 7).

LEAF NUTRIENT CONTENT

Although there were differences among sites, and at each leaf development stage, Shrub areas overall had higher percentage of nitrogen (%N) in developing leaves (e.g., first leaf visible [FLV] and first leaf opening [FLO]) of *B. nana* and *S. pulchra* as compared to Open areas (Fig. 8, part a). For instance, percentage of nitrogen in *B. nana* buds (measured at FLB) and leaves (measured at FLV and FLO) was generally higher in Shrub areas compared to Open areas (Fig. 8, part b) (effect of cover: $F_{1,33} = 20.22$, $P < 0.0001$), but this significance varied across individual leaf development stage (Appendix Table A3). Because %N for *B. nana* was actually lower in Shrub areas at TLFS for the first two leaf development stages, and because the pattern across the three leaf development stages differed from site to site, there was a significant effect of site (effect of site: $F_{2,33} = 9.22$, $P < 0.001$). Both IMVT and SDOT had higher %N in *B. nana* buds (measured at FLB) in Shrub areas compared to Open areas (the opposite was true for TLFS), and the overall %N in both Open and Shrub areas and magnitude of difference between cover types was greatest at SDOT. Both IMVT and SDOT had higher %N in *B. nana* leaves at FLV in Shrub areas compared to Open areas (the opposite was true for TLFS), but again, the overall %N and magnitude of difference between cover types was greatest

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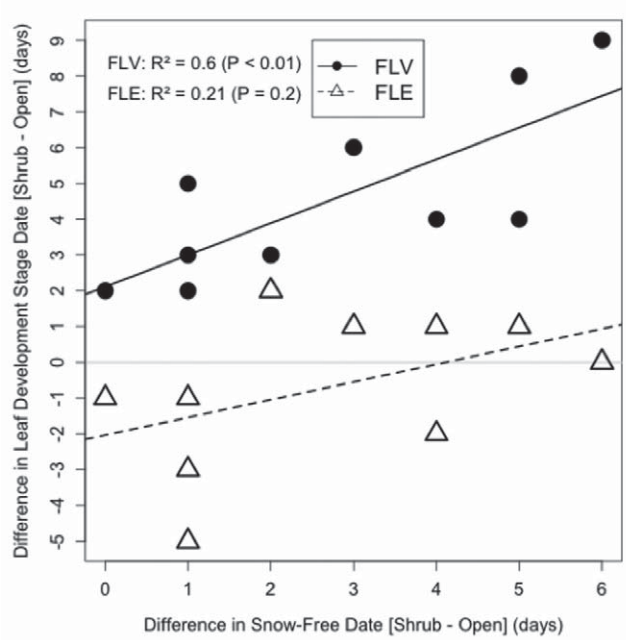

FIGURE 7. Across species, year, and site relationship between the difference in snow-free dates, and the difference in budburst (FLV = first leave visible; black circles) or leaf expansion dates (FLE = first leaf expanded; open triangles). Values indicate the number of days later (positive values) or earlier (negative values) each stage was reached in Shrub areas compared to Open areas [Shrub – Open]. Values below the gray line drawn at zero indicate Shrub areas reached that stage earlier, and values above this line indicate Shrub areas reached that stage later. Each point represents the average for a species (*B. nana* or *S. pulchra*) in one year (2011 or 2012) for an entire site (TLFS, IMVT, or SDOT).

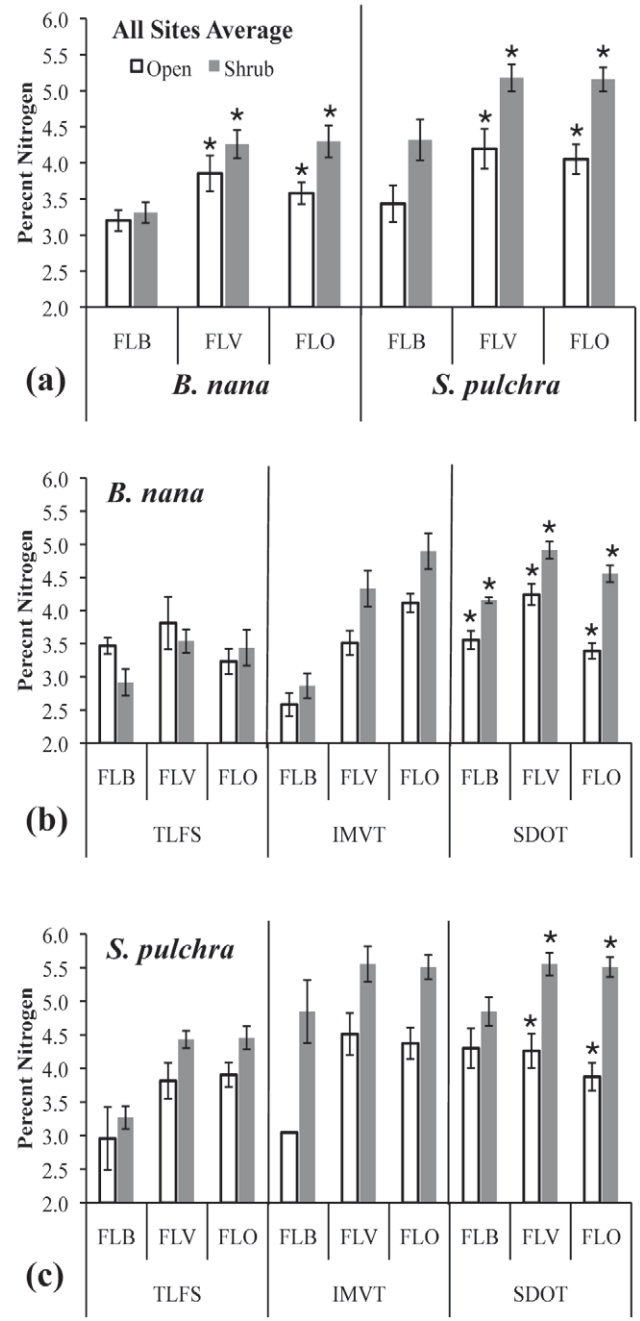

FIGURE 8. Average percent nitrogen in Open (white bars) and Shrub (gray bars) areas at each of the three leaf development stages measured: FLB = first leaf bud; FLV = first leaf visible; and FLO = first leaf opening for (a) *B. nana* and *S. pulchra* averaged across all sites; (b) *B. nana* separated for all three sites; and (c) *S. pulchra* separated for all three sites. Bars represent areas averages (n = 10 per bar where data was available). Error bars represent 1 SEM. Asterisks (*) above bars indicate a significant difference (P < 0.05) in percent nitrogen at that site and leaf development stage (note: at IMVT, there was not an adequate number of replicates at FLB stage at the Open area for statistical comparison; see Methods). See Figure 1 for site abbreviations.

at SDOT. At FLO, the pattern of %N in *B. nana* leaves changed from that of the previous two leaf development stages, where all three sites (including TLFS) had higher %N in *B. nana* leaves in Shrub areas compared to Open areas. As opposed to FLB and FLV, the %N at FLO was highest at IMVT Open and Shrub areas, but the magnitude of difference between cover types was still greatest at SDOT (Fig. 8, part b, and Appendix Table A3).

Although overall %N for *S. pulchra* was higher in Shrub areas compared to Open areas at all sites (effect of cover: $F_{1,32}$ = 16.99, P < 0.0002), the magnitude of difference between cover types differed from site to site at each leaf development (Fig. 8, part c), driving a significant site effect (effect of site: $F_{2,32}$ = 34.42, P < 0.0001) (Appendix Table A3). The difference between %N for *S. pulchra* in Open versus Shrub areas was greatest at IMVT at FLB, but because this data was not actually included in the statistical analysis (see Methods section), the main site effect was likely driven by the high %N at IMVT and SDOT Shrub areas and low %N at TLFS Shrub area. The magnitude of difference in %N for *S. pulchra* at FLV between cover types was greater at both IMVT and SDOT compared to TLFS, but was much greater at FLO at SDOT compared to either IMVT or TLFS (Fig. 8, part c, and Appendix Table A3).

The %N values in this study were higher than those reported for peak season biomass, likely because samples were collected prior to full leaf expansion (i.e., leaf bud and emerging leaf) (Chapin et al., 1980). Other studies in the Alaskan and Scandinavian Arctic have found that N concentrations in emerging leaves, shortly after snowmelt, tend to be high, and foliar N concentrations decrease as leaves continue to expand and arctic plants reach peak biomass (Chapin et al., 1975, 1980; Torp et al., 2010).

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Discussion

We found, similar to previous experimental and modeling studies (e.g., Sturm et al., 2001; Liston et al., 2002), that spring snowmelt was delayed where snowpack was deeper in our tall stature deciduous shrub–dominated communities. Our results supported our hypothesis in that later snowmelt did delay the initial stages of leaf development (e.g., budburst and leaf opening) for tall stature *B. nana* and *S. pulchra* in deciduous shrub–dominated communities relative to short stature individuals of the same species in graminoid-dominated communities. However, in contrast with our predictions, taller individuals reached *subsequent* leaf development stages (e.g., when the leaf fully expanded) at similar times, or even *before* the shorter *B. nana* and *S. pulchra* found in graminoid-dominated tundra. In other words, the delay in leaf development in taller shrubs was short-lived, and the difference in timing between tall and short stature shrub leaf development decreased, or even disappeared in some cases, by the time full leaf expansion occurred.

It is important to note that though snow-free dates were 1 to 6 days later in Shrub areas compared to Open areas, budburst dates (i.e., FLV) were 2 to 12 days later. Although we are not certain as to why the delay in budburst was twice that of the delay in snowmelt, it is possible that taller, more densely packed deciduous shrubs in Shrub areas shaded the soil, which could reduce soil temperatures relative to shorter, less densely packed deciduous shrubs in Open areas (Blok et al., 2010; Myers-Smith and Hik, 2013). This could lead to a slightly slower thawing of the active layer immediately following snowmelt in Shrub areas, which could delay water availability. Also, taller stature shrubs in deciduous shrub-dominated tundra likely have deeper roots due to deeper summer thaw depths (Shaver and Chapin, 1991; Bonfils et al., 2012), which means the active layer would need to thaw deeper relative to shorter stature shrubs in graminoid-dominated tundra before roots had access to liquid water essential for leaf opening (Billings and Mooney, 1968; Dale, 1988).

Similar to our findings, other studies have found trends of accelerated plant development offsetting the effects of a later spring snowmelt in alpine and arctic regions (Dunne et al., 2003; Borner et al., 2008). For instance, in their combined natural snow depth and snow fence manipulation experiment at Toolik Lake, Alaska, Borner et al. (2008) found that increased snow depth decreased the effective growing season length for both *B. nana* and *S. pulchra*. Yet, leaf senescence of these species occurred at relatively similar times regardless of snow depth and snowmelt date, suggesting that differences in the timing of early phenological stages diminished over the course of the growing season. However, because Borner et al. (2008) monitored only snow-free, budburst, and leaf senescence dates, the intermediate leaf stage at which the catch-up in development occurred was not known, nor was the mechanism driving the accelerated leaf development.

Although emergence and initial stages of leaf development of many species in the arctic tundra are cued by snowmelt and temperature (Pop et al., 2000; Hollister et al., 2005; Wipf et al., 2009), the rate of leaf expansion, shortly after leaves begin to open, is likely related to the amount of nitrogen in buds and emerging leaves (Radin and Boyer, 1982; Vos and Biemond, 1992). We surmise this relationship because it has been shown that enhanced nitrogen availability increases photosynthesis (Field and Mooney, 1983; Evans, 1989; Reich et al., 1998; Heskel et al., 2012), which increases metabolites important in leaf expansion (Dale, 1988). Therefore, one possible explanation for the accelerated leaf development of taller shrubs in our Shrub areas could be related to the fact that our taller shrubs had higher nitrogen contents (approximately 16% to 25% more) in their leaf buds and emerging leaves compared to the shorter shrubs of our Open areas.

There are several ways in which taller shrubs may have access to more nitrogen during the period of leaf expansion and bud formation. First, higher nitrogen of taller shrubs may be related to the fact that tall deciduous shrubs tend to grow in areas where soil conditions facilitate their growth (Tape et al., 2012). For instance, increased subsurface water flow in naturally occurring deciduous shrub–dominated tundra compared to graminoid-dominated tundra increases nutrient flow (Giblin et al., 1991; Shaver and Chapin, 1991) and access to nitrogen (Naito and Cairns, 2011; Bonfils et al., 2012; Chapin et al., 1988). Second, their inherently thicker snowpack insulates soils from freezing air temperatures during the winter, thereby enabling higher rates of winter soil mineralization (Schimel et al., 2004; DeMarco et al., 2011), which would enable higher leaf nutrient contents. For example, in their snow fence experiment in the Alaskan Arctic, Walsh et al. (1997) found that deeper snow led to higher nitrogen concentrations in leaves of *B. nana* and *Salix planifolia*. Finally, a delay in snowmelt has been shown to limit dilution of leaf nitrogen throughout the growing season (Körner, 1989; Welker et al., 2005). For these reasons, taller shrubs may have access to more nitrogen, which may allow for accelerated leaf development (Dale, 1988; Radin and Boyer, 1982; Vos and Biemond, 1992).

Regardless of the exact driving mechanism, accelerated leaf expansion may be important from a canopy carbon gain perspective for several reasons. First, phenological events for arctic plants tend to be compressed in time (i.e., rapid development) relative to plants growing in more southern locations (Post et al., 2008; Steltzer and Post, 2009). This rapid development of arctic plants (Billings and Mooney, 1968; Bliss, 1971) suggests that the expansion of the first leaf on an individual deciduous shrub likely corresponds with the expansion of most leaves on the entire canopy of that individual (Johnson and Tieszen, 1976). Second, when leaves are fully expanded is when they are near their maximum photosynthetic capacity (Constable and Rawson, 1980; Patankar et al., 2013). Therefore, accelerated leaf development could offset potential reductions in growing season carbon uptake by minimizing the effects of later snowmelt and delayed budburst. This is especially important in the Arctic, because the growing season is notoriously short and differences in canopy development of only a few days could significantly alter the tundra's annual carbon uptake potential (van Wijk et al., 2003). In fact, Euskirchen et al. (2006) suggested that for each day the growing season is extended in the arctic tundra, net carbon (C) uptake increases by 5.3 g C m^{-2} yr^{-1}. In addition, our findings have important implications for tundra fauna, since changes in tundra plant phenology associated with climate warming have been shown to create asynchrony in the timing of food resource availability for wildlife (Hoye and Forchhammer, 2008; Post et al., 2009).

Furthermore, deciduous shrub leaf expansion dates may be particularly important in the Arctic. At the beginning of the growing season, deciduous shrubs become photosynthetically active slightly later than other tundra plant functional groups (e.g., evergreens and sedges) (Starr and Oberbauer, 2003; Euskirchen et al., 2013). However, deciduous shrubs have higher peak season leaf area (van Wijk et al., 2005) and greater maximum rates of photosynthesis (Johnson and Tieszen, 1976; Oechel, 1989; Aerts, 1995) compared to other functional groups. Because of this, and because deciduous shrub dominance is expected to continue

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increasing in the arctic tundra (Walker et al., 2006; Pearson et al., 2013), changes in the timing of leaf expansion in deciduous shrubs may prove to be especially important for future carbon flux in the Arctic (Hobbie and Chapin, 1998).

Conclusions

Since the majority of studies examining the effect of shrub-induced delays in snowmelt on the timing of leaf development use experimental manipulations of snow depth, our study is important as it provides valuable supporting evidence through observations made along a naturally occurring gradient of increasing woody deciduous shrub (*B. nana* and *S. pulchra*) stature. We found that, relative to low stature shrubs of the same species in graminoid-dominated tundra, taller stature shrubs in shrub-dominated tundra were surrounded by deeper snowpack and experienced later snowmelt and delayed budburst. However, contrary to our hypothesis, the delay in leaf development was short-lived, and as a result both short and tall stature deciduous shrubs reached full leaf expansion on approximately the same date. Further, despite delayed budburst, tall shrubs occasionally reached full leaf expansion *before* short shrubs, suggesting an accelerated rate of leaf development. We also found that taller shrubs had higher bud and emerging leaf nitrogen compared to shorter shrubs, suggesting that environmental conditions conducive to taller shrubs are correlated with higher soil nitrogen availability, which may have further accelerated leaf development.

Although the intermediate leaf development stages monitored in this study may provide detailed temporal insight into the timing of canopy development as it controls timing in canopy carbon uptake (Johnson and Tieszen, 1976; Constable and Rawson, 1980; Patankar et al., 2013), we acknowledge that the short-term nature, small spatial scale, and novelty of this study should be taken into consideration in interpreting our results. Because this study was conducted over two years and in a single location, caution should be taken in extrapolating our findings to determine the potential impacts of observed pan-Arctic increases in deciduous shrub stature (Myers-Smith et al., 2011) on leaf and canopy development and canopy carbon gain. Further, the precise mechanisms involved in the accelerated leaf expansion of tall shrubs relative to short shrubs remains uncertain, and while our results are suggestive, we cannot conclusively state that increased nitrogen availability is the only mechanism driving accelerated leaf development. For these reasons, we believe high temporal resolution monitoring of leaf development, in both observational and experimental studies at more sites across the pan-Arctic, as well as a better mechanistic understanding of early season leaf expansion and canopy development across different types of tundra will be important to understanding the future consequences of the greening Arctic.

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APPENDIX

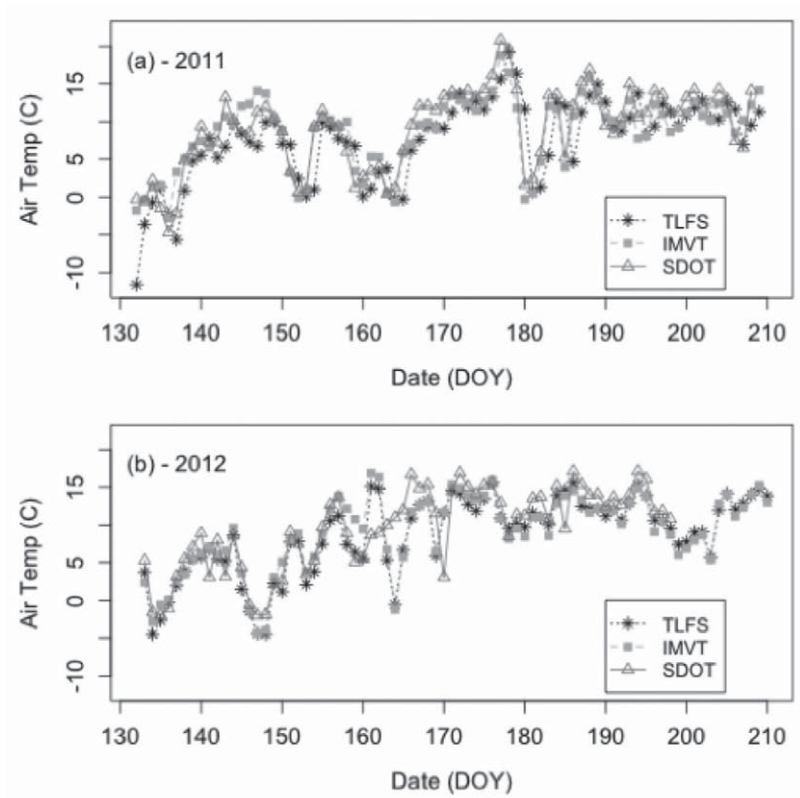

FIGURE A1. Average daily air temperature (°C) from 12 May to 28 July (DOY: 132 to 210) during the (a) 2011 and (b) 2012 field seasons at three sites (IMVT, TLFS, and SDOT) near the Toolik Lake field station in northern Alaska. See Figure 1 for site abbreviations.

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TABLE A1

Average, minimum, and maximum topographic elevation (in meters) at each site (TLFS, IMVT, and SDOT) and study area (Open and Shrub) used in this study. See Figure 1 for site abbreviations. Additional topographic maps can be found at http://toolik.alaska.edu/gis/index.php.

Site:	TLFS		IMVT		SDOT	
Area:	Open	Shrub	Open	Shrub	Open	Shrub
Average Elevation (m)	747	722	918	910	508	504
Minimum Elevation (m)	735	716	913	902	503	500
Maximum Elevation (m)	755	725	923	919	510	509

TABLE A2

Repeated measures MANOVA *P*- and *F*-values for main effects (Site and Cover) as well as their interaction comparing dates (day of year [DOY]) when leaf development stages (FLB, FLV, FLO, and FLE) were reached for *Betula nana* and *Salix pulchra* in 2011 and 2012 for Open and Shrub areas from three sites (IMVT, TLFS, and SDOT) near the Toolik Lake field station in northern Alaska. Direction of significant effects (S = Shrub and O = Open) are noted for means comparisons significant at *P* < 0.05. Any effect with a *P*-value < 0.05 is listed as NS. Degrees of freedom for leaf development stage = Cover: 1, 54; Site and Interaction: 2, 54. See Figure 1 for site abbreviations.

		Source:	Cover		Site		Interaction	
Species	Year	Leaf stage	*P* : effect	*F*	*P* : effect	*F*	*P*	*F*
B. nana	2011	FLB	< 0.0001 : S > O	22	< 0.0001 : IMVT > TLFS = SDOT	16.71	NS	
B. nana	2011	FLV	< 0.0001 : S > O	36.16	0.0027 : IMVT > TLFS = SDOT	6.6	0.0606	2.95
B. nana	2011	FLO	< 0.0001 : S > O	37.15	< 0.0001 : IMVT > TLFS > SDOT	16.79	0.0015	7.37
B. nana	2011	FLE	NS		0.003 : IMVT = TLFS > SDOT	6.48	NS	
B. nana	2012	FLB	0.0001 : S > O	16.75	< 0.0001 : IMVT > TLFS = SDOT	58.82	0.0038	6.19
B. nana	2012	FLV	< 0.0001 : S > O	31.23	< 0.0001 : IMVT > TLFS > SDOT	45.33	0.0013	7.57
B. nana	2012	FLO	< 0.0001 : S > O	19.11	< 0.0001 : IMVT > TLFS > SDOT	30	NS	
B. nana	2012	FLE	0.0066 : S > O	7.98	< 0.0001 : IMVT > TLFS = SDOT	17.36	0.0029	6.53
S. pulchra	2011	FLB	NS		NS		NS	
S. pulchra	2011	FLV	0.0002 : S > O	16.49	NS		NS	
S. pulchra	2011	FLO	< 0.0001 : S > O	29.5	NS		NS	
S. pulchra	2011	FLE	NS		0.0111 : IMVT = TLFS > SDOT	4.89	0.0278	3.83
S. pulchra	2012	FLB	< 0.0001 : S > O	19.33	< 0.0001 : IMVT > TLFS = SDOT	31.44	NS	
S. pulchra	2012	FLV	0.0038 : S > O	9.14	< 0.0001 : IMVT > TLFS = SDOT	30.22	NS	
S. pulchra	2012	FLO	NS		< 0.0001 : IMVT > TLFS = SDOT	13.84	NS	
S. pulchra	2012	FLE	NS		0.0065 : IMVT > TLFS = SDOT	5.54	NS	

TABLE A3

Repeated measures MANOVA *P*- and *F*-values for main effects (Site and Cover) as well as their interaction comparing percent nitrogen for *B. nana* and *S. pulchra* for each development stage measured (FLB, FLV, and FLO) for Open and Shrub areas from three sites (IMVT, TLFS, and SDOT) near the Toolik Lake field station in northern Alaska. Direction of significant effects (S = Shrub and O = Open) are noted for means comparisons significant at *P* < 0.05. Any effect with a *P*-value < 0.05 is listed as NS. Degrees of freedom for *B. nana* = Cover: 1, 33; Site and Interaction: 2, 33. Degrees of freedom for *S. pulchra* = Cover: 1, 32; Site and Interaction: 2, 32. See Figure 1 for site abbreviations.

		Source:	Cover		Site		Interaction	
Species	Variable	Leaf stage	*P* : effect	*F*	*P* : effect	*F*	*P*	*F*
B. nana	%N	FLB	NS		< 0.0001 : SDOT > TLFS = IMVT	25.01	0.0228	4.27
B. nana	%N	FLV	0.0096 : S > O	7.6	0.0087 : SDOT = IMVT > TLFS	5.53	NS	
B. nana	%N	FLO	0.0002 : S > O	17.36	0.0076 : IMVT > SDOT = TLFS	5.7	NS	
S. pulchra	%N	FLB	NS		< 0.0001 : SDOT = IMVT > TLFS	15.41	NS	
S. pulchra	%N	FLV	0.0002 : S > O	17.59	0.0403 : SDOT = IMVT > TLFS	3.6	NS	
S. pulchra	%N	FLO	< 0.0001 : S > O	35.62	0.0177 : SDOT = IMVT > TLFS	4.65	0.0065	8.6

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