1 Species and site differences influence climate-shrub growth responses in West Greenland

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3
4 Amanda B. Young^{1*}, David A. Watts^{2,3}, Alan H. Taylor^{1,3}, Eric Post^{2,3}

5
6 ¹Department of Geography
7 Pennsylvania State University
8 University Park, PA 16802
9 USA

10 Phone: +1(814) 863-7702

11 Fax: (814) 863-7943

12 E-mail: aby113@psu.edu

13
14 ²The Polar Center and Department of Biology
15 Pennsylvania State University
16 University Park, PA 16802
17 USA

18
19 ³Ecology Intercollege Graduate Degree Program
20 Pennsylvania State University
21 University Park, PA, 16802
22 USA

23
24 *Corresponding Author
25

Abstract

We examined the suitability of two deciduous arctic shrubs (*Salix glauca* L. and *Betula nana* L., hereafter *Salix* and *Betula*, respectively) for dendroclimatological analysis at two sites in West Greenland. Chronologies were successfully cross-dated, and the oldest covered the period 1954-2010 (Expressed Population Signal [EPS] >0.85, 1977-2010). Distinctive pointer years, also called micro-rings, including those from a known outbreak of the irruptive moth *Eurois occulta* L. (Lepidoptera: Noctuidae) that peaked in 2005, assisted in the dating process. Climate-growth analyses were performed in two ways: first, using correlation analysis between residual site-level chronologies and monthly and seasonal climate data, and second, using linear mixed effects models (LMM) with seasonal climate data and standardized chronologies for each individual. We used climate data for the current and previous years for a given growth ring for both analyses. Both analyses revealed differences in climate-growth response among species and among sites of contrasting topography. *Salix* ring widths from south facing slopes correlated positively with current year's summer temperatures, while those on gentle slopes associated negatively with current year's spring precipitation. *Betula* was only sampled at one site (flat), and displayed associations with temperature and precipitation in spring. Results from the LMM largely corroborated the correlations for *Betula* and *Salix* on south facing slopes. *Salix* at the flat site displayed significant associations with a large number of climate variables, most strongly previous year's summer and autumn temperatures, though precipitation in multiple seasons of the current and prior year did a better job of accounting for the variation in the data. Many dendrochronological studies in the Arctic illustrate clear summer temperature responses, but the majority were conducted on a single topographic position. Due to the heterogeneity of West Greenland's landscapes, it is important to examine individuals from varying topographies. We found that samples collected from south facing slopes do appear to respond positively to summer temperatures, while those on shallow slopes respond to a wider array of seasonal temperature and precipitation parameters. Accounting for these species and topographic differences, when sampling, is imperative for improving our understanding of how plant communities in the Arctic will respond to ongoing and expected warming.

Key Words: Arctic shrubs, vegetation dynamics, climate change, dendroclimatology, dendroecology, clonal plants

Introduction

Understanding how ecosystems have and will continue to respond to climate variability requires spatially explicit time series of temperature and precipitation data (Bradley, 2011). Time series of climate data from relatively dense networks of climate stations in more populated regions of the world have provided important insights into climatic variability and how the magnitude of recent climate change varies among regions (Hijmans et al., 2005). Recent temperature increases in the Arctic illustrate how the magnitude of warming varies regionally. Over the last several decades, the Arctic has warmed roughly twice as much as the global average (Trenberth et al., 2007), and this has led to pronounced localized changes in vegetation (Walker et al., 2006) that vary among Arctic climates (Post et al., 2009).

The Arctic as a whole has few spatially explicit time series of climate data compared to temperate regions (Hijmans et al., 2005). One approach for expanding knowledge of the spatial and temporal variation in historical climate in areas lacking highly-spatially resolved temperature data is to develop proxies to supplement the instrumental record (Mann et al., 1998). Past climatic variability has been reconstructed for parts of Greenland using climate proxies preserved in ice cores, which extend back to 100 ka (Andersen et al., 2004). The climate data preserved in ice cores has sub-annual (seasonal) resolution for some climate proxies and climate-associated parameters (e.g. snow accumulation, $\delta^{18}\text{O}$, CH_4 , and NO_2 [Alley, 2000; Blunier et al., 2002; Flückiger et al., 2004; Andersen et al., 2004]) and decadal to multidecadal resolution for others such as sea surface temperature and the Atlantic Multidecadal Oscillation (Dowdeswell and White, 1995; Chylek et al., 2012). However, the spatial resolution of ice core climate data is limited. Ice core-based climate data are derived from the Greenland ice sheet, often hundreds of kilometers from Greenland's terrestrial ecosystems, and are therefore unlikely to represent climate variability in heterogeneous local environments.

Tree ring widths are sensitive to climatic variability, and tree rings are commonly used as a climate proxy. However, with the exception of *Betula pubescens* Ehrh. in sheltered valleys in southwest Greenland (western coast between 60-63°N), trees are not present in most of ice-

free Greenland (Böcher, 1979; Kuivinen and Lawson, 1982; Fredskild and Ødum, 1990). The most abundant woody plants in much of inland Greenland are deciduous shrubs. Many shrub species form annual rings, and have the potential to be used as climate proxies (Myers-Smith et al., 2015a). In spite of this, little research on shrub growth has been conducted in arctic ecosystems to evaluate their potential as climate proxies compared with the abundant research on tree growth in temperate regions. Shrub species in both temperate and arctic ecosystems are known to produce annual rings, and have been used to reconstruct past precipitation and temperatures (Schweingruber and Poschlod, 2005; Schweingruber et al., 2013). For example, arctic shrubs provide a record of past climate variability in Siberia (Blok et al., 2011), Canada (Rayback and Henry, 2006), Svalbard (Weijers et al., 2012), mainland Scandinavia (Bär et al., 2006, Meinardus et al., 2011, Weijers et al., 2012), and High-Arctic Greenland (Forchhammer et al., 2008). Nonetheless, the Arctic remains understudied for dendrochronological climate reconstructions given the size of the region.

Greenland's terrestrial ecosystem represents a particularly infrequently studied part of the Arctic. In Zackenberg, NE Greenland, an approximately 50-75 year long shrub ring width chronology has been developed for *Salix arctica* Pall. (Wilson, 1964; Schmidt et al., 2006; Forchhammer et al., 2008; Schmidt et al., 2010). We are aware of only two studies, both recent, on secondary growth responses to climate in shrubs in the West Greenland region. Jørgensen et al. (2014) developed approximately 60 and 75 year long records of *Alnus viridis* (Chaix.) D.C. and *Salix glauca* L., respectively, and Hollesen et al. (2015) developed a nearly 90 year record of *Betula nana* L.; both studies demonstrate arctic shrub growth responses to maritime climates. *Betula nana* L. and *Salix glauca* L., hereafter *Betula* and *Salix*, are two of the dominant shrubs in our study area (Post and Pedersen, 2008). Both species have been successfully used for dendroecological and dendroclimatological investigations elsewhere (Blok et al., 2011; Meinardus et al., 2011; Buras et al., 2012).

The objectives of this study were to 1) determine if these two shrub species form annual growth rings that are amenable to reliable cross-dating in a continental climate in West Greenland and 2) conduct a climate-shrub growth analysis to determine how species and site differences mediate climate-shrub growth associations. We hypothesized that growth in both

Salix and *Betula* would be associated with temperature and precipitation, especially on the well-drained sites on steep south-facing slopes.

Materials and Methods

Study Site

The study area is located in West Greenland ca. 20 km northeast of Kangerlussuaq near Long Lake (*Aajuitsup Tasia*, 67.1 °N, 50.29 °W; Figure 1). The climate has frigid winters, cool summers, and low annual precipitation. Five months (May-September) have mean monthly temperatures above freezing (Figure 2; Klein Tank et al., 2002 [KNMI]). Most precipitation falls during the summer and estimates of total annual precipitation range from 131 to 338 mm, with a mean of 149 mm (Figure 2). Daily temperature measurements have been collected at the Kangerlussuaq airport (67.02 °N, 50.70 °W) since 1949 but missing values are common before 1973. Consequently, only data for the 1973-2010 period were used in our analysis. Missing monthly values from the data set (January-July in 1999) were interpolated using mean monthly temperatures for that month in the prior and subsequent 2 years. There were no missing values in the total monthly precipitation data for the period of 1977-2010, which was the period used for our analyses.

The study area is dominated by Low Arctic shrubland, a matrix of shrubs and patches of tundra forbs and grasses that create the mix of vegetation typical in terrain composed of mountain complexes of non-carbonate substrate (Walker et al., 2005). Common shrubs include three deciduous species (*Salix*, *Betula*, and *Vaccinium uliginosum* L.) and two evergreen species (*Rhododendron groenlandicum* (Oeder) Kron & Judd, and *R. lapponicum* (L.) Wahlenb.) In this study, we focused on *Salix* and *Betula* because they are locally dominant and also have circumpolar distributions. *Salix* is a highly polymorphic, dioecious erect shrub that is widespread throughout the Arctic, with the degree of polymorphism varying by region (Elven et al., 2011). It can attain heights between approximately 1.2 and 6 m tall, depending on habitat, and is an important food source for a variety of herbivores, including insects, birds, and mammals (Elven et al., 2011). *Betula* is a circumboreal-polar monoecious dwarf shrub that can grow in a variety of conditions, with maximum heights ranging from 0.4 to 1.20 m (Elven et al., 2011).

Field sampling

In May of 2011, we collected shrub samples from three sites around Long Lake (Figure 1). Long Lake is surrounded by a system of ridges running largely east-west; our goal was to sample the landscape to capture some of this heterogeneity. Therefore, we sampled two sites (Sites 1 and 3) on south facing aspects with large differences in slope and one on a southwest facing aspect (Site 2). Sites 1 and 2 are on gently sloping, low lying terrain near the northern and northeastern shores of Long Lake, respectively (Table 1). These sites consist of a matrix of *Betula* interspersed between taller *Salix* individuals, with several centimeters of litter accumulation beneath the shrub canopies. Site 3, in contrast, is on a steep, dry slope with sandy soils and negligible surface litter, and there is little vegetation other than *Salix* (Table 1). At all sites, we observed no obvious signs of locally heavy recent herbivory like feces or direct damage to plants. At each of Sites 1 and 2, we sampled *Salix* and *Betula* within one 10 X 100 m belt transect. Each transect was divided into ten 10 m² quadrats, and *Salix* and *Betula* were sampled in every other quadrat. This approach reduced the likelihood that sampled stems from different quadrats would be from the same clone, since both species can spread vegetatively from adventitious roots or shoots (De Groot et al., 1997; Stamati et al., 2007). We identified individual plants based on their margins and branching patterns and measured the largest (by basal diameter) stem for each individual. We then sampled the individuals with the five largest stems of each species from every other quadrat in each transect. Based on this approach, we deemed it highly unlikely that two samples represent the same individual. Because *Betula* was not present at Site 3, only *Salix* was sampled there. At this site, we collected the twenty largest stems of *Salix* from a population of spatially separated (>3 m between the edges of the clones) individuals. Stems selected for sampling were cut-off at the root collar for laboratory analysis.

Objective 1 - Chronology development

Samples were air dried and sanded to a high polish using progressively finer grades of sandpaper (120-1000 grit) until the cellular structures of the rings were visible under a binocular microscope. The ring boundaries of *Betula* were faint, so samples were stained with phloroglucinol to enhance boundary definition (Patterson, 1959). Samples were visually cross-dated using pointer years (Stokes and Smiley, 1968) along two to four clearly distinguishable

radii per sample ($\geq 90^\circ$ apart). A minimum of two radii per sample were used to identify partial and fully missing rings. After visual cross-dating, ring widths were measured with a Velmex measuring system and the program Measure J2X (VoorTech Consulting, 2007). The ring width measurements were then used to statistically evaluate visual cross-dating using COFECHA (Holmes, 1986; Grissino-Mayer, 2001). We then calculated the mean interseries correlation statistic ($\bar{r}$), expressed population signal (EPS), and mean sensitivity (MS) for each chronology using the *dplR* package (Bunn, 2008). EPS was calculated annually for each chronology with a 10 year window to identify periods with a running EPS (rEPS) > 0.85 (Wigley et al., 1984).

Ring width chronologies were developed by standardizing values in each sample to remove age-related growth trends (Fritts, 1976) using *dplR* (Bunn, 2008). Standardization functions included negative exponential ($n = 41$), linear regression ($n = 67$), and horizontal means ($n = 45$), with the choice of function based on best fit for each series. A standardized chronology was then developed for each species at each site and a pre-whitened residual chronology with the first order (i.e., lag-one) autocorrelation removed was used to identify climate-ring width relationships.

Objective 2 - Climate analyses

The relationship between shrub ring width and climate was determined by calculating correlation coefficients between the residual site-level chronologies and mean monthly temperature, total monthly precipitation, and seasonal temperature and precipitation using the *bootRes* package (Zang and Biondi, 2012). *bootRes* provides bootstrapped confidence intervals estimates for evaluating the significance of correlation coefficients. Correlation coefficients were calculated for the periods in each chronology with an EPS > 0.85 .

In addition to the traditional site chronology and development of correlation coefficients run on ring width data with autocorrelation removed, linear mixed effects models (LMM) with a first order autoregressive covariance structure were used to detect significant climatic variables influencing shrub ring growth for each of the species and sites using the *nlme* (Pinheiro et al. 2014) package in R version 3.1.2 (R Core Team, 2014). This second analytical approach allowed us to substantiate the results of the correlation analysis using an approach

that accounted for individual variation (Myers-Smith et al., 2015b). Standardized time series for two radii from each individual were averaged and used as the response variable in the LMM so that each individual, not each radius, would serve as a replicate. These data were normally distributed for *Salix* from Site 3 and for *Betula*; for *Salix* from Site 1/2, it was necessary to log+1 transform the standardized data to yield normality. Seasonal climate variables in each model were used as fixed effects after determining that collinearity was absent among these predictors (Freckleton, 2010), and we included individual stem as a random factor (Schmidt et al., 2006). The submodels were ranked by the sample size adjusted Akaike Information Criterion (AICc) (Burnham and Anderson, 2004), and we performed model averaging with the *MuMIn* package (Bartoń, 2012) on all submodels within two AICc of the best submodel. The model selection process was conducted using maximum likelihood estimation, and the reported effect sizes (parameter estimates) were based on restricted maximum likelihood estimation. We initially assessed quadrat as a higher level random factor for Sites 1 and 2, but because the variance estimate was near zero, we excluded it from our final models. Climate data from the period 1977-2010 were used for the LMM because of missing precipitation values in earlier years.

Results

Objective 1 – Construction of Chronologies

Betula and *Salix* are fully and semi-diffuse-porous species, respectively, and had clearly visible annual growth rings. Chronologies were successfully developed for *Betula* from Site 1 and *Salix* at Sites 1, 2, and 3. Due to the similarity in site conditions and the strong correlation between chronologies (Pearson's $r = 0.654$ [$p = <0.001$], Gleichläufigkeit [glk] of 0.86), the *Salix* samples from Sites 1 and 2 were combined into a single chronology.

There were two main challenges in cross-dating the samples. First, the three chronologies were short (40, 50, and 57 years for *Betula* 1, *Salix* 1/2, and *Salix* 3 chronologies, respectively; see Table 2). Moreover, the portions with an EPS >0.85 were even shorter (23, 34, and 30 years for chronologies, as above; see Table 2, Figure 3), and the rings were very narrow (*Betula* $\bar{x} = 0.204$ mm, *Salix* $\bar{x} = 0.334$ mm; Table 3). Second, multiple growth reductions

(pointer years) were present in most of the samples and occurred in 2005, 2000, 1996, and 1981/82 and served as markers for cross-dating (Table 3, Figures 3 and 4).

Mean inter-series correlations from COFECHA for the chronologies were moderate, from 0.48-0.60 (rbar range: 0.26-0.33) and stronger for portions that had an EPS >0.85 (rbar range: 0.27-0.41; Table 2). The chronologies had mean sensitivities that ranged from 0.33-0.39 (Table 2), suggesting that they are suitable for climate-growth analysis as these values are in the range used in previous studies on arctic shrubs (Schmidt et al., 2006; Jørgensen et al., 2014).

Objective 2 - Climate-Growth Relationships

Growth of both shrubs responded to climate, but each species differed in how climate influenced growth. The significant correlation coefficients ($p < 0.05$, see Figure 5) demonstrate that *Betula* ring widths had a negative response to the current year's spring temperature, whereas *Salix* responded to current year's summer temperature, but only at one site. *Salix* growth at this same site was also negatively correlated with mean monthly temperature for October of the previous year (Figure 5). Additionally, *Salix* at both sites had a positive correlation with September precipitation in the previous year, and *Betula* growth responded positively to the previous year's May precipitation. Both *Salix* and *Betula* showed negative growth responses to current year's spring precipitation despite the lack of responses to monthly precipitation.

Linear mixed effects models (LMM) broadly corroborated those significant climate responses found with correlations for all three of the chronologies (Table 4). Moreover, in each of the three LMMs, the climate factor with the highest z-value was also significant in the correlation analyses (Table 5); however, the significant climate variables were not always the same in both analyses. *Betula* at Site 1 showed nearly the same patterns as the correlations, with current year's spring temperature and previous year's spring and current year's summer precipitation influencing growth. Also, the effect size of the former factor was an order of magnitude greater than the latter two.

The full model for *Salix* at Site 1/2 revealed a large number of significant climate factors that influence growth, though only one of those factors had a large effect size (Table 5). Previous summer temperature had the largest (and negative) effect on growth, with previous

autumn and current year's winter temperatures having the next largest effect sizes. Though these factors were not significant in the correlation analysis, the upper limit of the confidence interval for previous summer temperature was only slightly above zero (Figure 5). Growth in *Salix* at Site 3 was influenced solely by the current year's summer temperature and the previous year's spring precipitation (Table 5), and the effect size of the former was nearly twice that of the latter. The results of these LMMs generally confirm those of the correlation analysis, with the LMM for *Salix* at Site 1/2 revealing additional climate parameters that significantly influenced growth, though the effect sizes for these parameters were small compared to values reported in a recent synthesis (Myers-Smith et al., 2015a).

Discussion

Betula and *Salix* shrubs from West Greenland can successfully be cross-dated and used for dendroclimatological analysis without using serial (Kolishchuk, 1990; Hallinger et al., 2010, Myers-Smith et al., 2015b) or microtome cross-sectioning (Cairns et al., 2012). The longest chronology with an EPS >0.85 was 33 years and extends back to 1977 (*Salix*, Site 1/2), 4 years less than the unbroken instrumental temperature record and the same length as the instrumental precipitation record. Because we sampled while the soil was still frozen, we could not sample belowground tissues that may have had a record of earlier growth. Excavation would have caused significant damage to the samples and disturbance to the site. Though the samples we collected do not extend beyond the instrumental climate record, *Betula* and *Salix* growth rings have the potential for climate reconstructions in West Greenland since the oldest individual stem in this study is 55 years old, while some individuals from the Disko Bay area north of our study region were approximately 75 years old (Jørgensen et al., 2014). Furthermore, conspecifics in Norway live to be over 90 and 70 years old for *Betula* and *Salix*, respectively (Meinardus et al., 2011; Buras et al., 2012). Future sampling during the growing season when the soils are not frozen would likely yield longer chronologies.

Ring widths in the wood samples had relatively high mean sensitivities (MS) (Table 2), because of the frequency of very narrow and partially missing rings. The years with very narrow rings corresponded with irruptive outbreaks of the moth *Eurois occulta* L. (Lepidoptera: Noctuidae) in the region. Documented outbreaks occurred in 2004/2005 (Post and Pedersen,

2008) and in 2010/2011 (Avery and Post, 2013), shortly before samples were collected in May 2011. In 2004/2005, the defoliation led to large leaf biomass reductions in *Betula* (87.1%) and *Salix* (97.8%) (Post and Pedersen, 2008). There was a reduction of ring growth in 2005 in both species at Sites 1 and 1/2, and during both 2004 and 2005 at Site 3, which corresponded to the outbreak observed by Post and Pedersen (2008) in 2004/2005 (Table 3, Figures 3 and 4).

In addition to the direct evidence of recent outbreaks, there is indirect evidence of an outbreak in the early 1980s (Fox et al., 1987). Moth larvae, of which *E. occulta* make up the largest proportion, are important in the diet of Lapland longspurs (*Calcarius lapponicus* L.) (Fox et al., 1987). In 1979, there was a high density of moth larvae on the landscape, and they comprised a major portion of nestlings' diet (Fox et al., 1987). By comparison, in 1984, overall breeding output was lower than in 1979, partly because moth larvae were far less abundant in 1984 (Fox et al., 1987). These results suggest that a large decline in the moth population may have occurred at some time in the interim. Our ring width record show narrow and partially missing rings in 1981 for both species at Sites 1 and 1/2 and in 1982 at Site 3, suggesting an outbreak occurred during these years. This highlights the potential for future research not only on climate reconstruction using shrub growth rings, but also on the assessment of possible relationships between outbreaks and climate, and even the possibility of exploring the spatial synchrony (Young et al., 2014) of these outbreaks throughout West Greenland.

Throughout the Arctic, numerous species of shrubs exhibit positive growth responses to summer temperatures (Rayback and Henry, 2006; Bär et al., 2008; Hallinger et al., 2010; Forbes et al., 2010; Blok et al., 2011; Buras et al., 2012; Macias-Fauria et al., 2012; Weijers et al., 2012; Buchwal et al., 2013; Jørgensen et al., 2014), though there are exceptions in the High Arctic (e.g. *Salix*; Schmidt et al., 2006; Zalatan and Gajewski, 2006). A recent synthesis demonstrated that the responses of arctic shrubs to climatic variability are dominated by correlations with summer temperature, most of which are positive relationships (Myers-Smith et al., 2015a). In our study area, only *Salix* responds positively to summer temperatures, and only on dry south facing slopes. Moreover, although *Salix* on gentle slopes showed a negative response to the previous year's summer temperature, this parameter is a comparatively poor predictor. If we

had made use of a limited set of climate predictors in our LMM (e.g. Myers-Smith et al., 2015a), previous summer temperatures would not have shown up in our final model.

Instead, the *Salix* in the flat site (Site 1/2) primarily showed very weak responses to precipitation in several different seasons (Table 5). The negative association between growth and current year's spring precipitation may indicate that springs with particularly heavy snowfall reduce growth (Schmidt et al., 2006, Schmidt et al., 2010), likely through a shortened growing season (Ernakovich et al., 2014). Interestingly, higher snowfall during the winter correlated positively with growth, suggesting that greater snow cover may have had a small insulating effect. Additionally, there was a small but significant positive association between precipitation during the summer months and ring width. A recent synthesis demonstrated that shrub growth was associated, both positively and negatively, with precipitation in some models, though the association with summer precipitation was only ever negative if significant (Myers-Smith et al., 2015). Nonetheless, the greatest increase in shrub abundance in response to warming occurred at wetter sites (Elmendorf et al., 2012). It may also be that greater summer precipitation increased growth via a lengthened, or at least not shortened (Ernakovich et al., 2014), growing season by reducing the advancement of senescence caused in part by seasonal declines in soil moisture (Oberbauer and Dawson, 1992).

Similarly to *Salix* in most of the Arctic, *Betula* from Siberia (Blok et al., 2011) and Norway (Meinardus et al., 2011) have shown a positive growth response to the current year's early summer temperatures. In contrast, *Betula* at our site showed no response to the current year's summer temperatures and had a negative response to current year's spring temperatures. Multiple potential mechanisms could be responsible for this pattern. Although we did not observe frost rings in our samples, we speculate that warm temperatures in the spring before leaves flush may increase the susceptibility of shrubs to spring frost events, potentially reducing annual growth (Inouye, 2000, Blok et al., 2015). Phenological differences between the species may be important here, as *Betula* opens its first leaves earlier in the spring (~3 days) compared with *Salix* (Post, 2013a). Although the mean differences in the dates of the first emergence of leaves are small, there may be years with exceptionally warm springs during which *Betula* leaves emerge enough before *Salix* leaves that they might be significantly more susceptible to

frost (Inouye, 2000). Moreover, because these data reflect differences in the onset of emergence, rather than peak leaf out, differences between the species in the duration of the leaf out process may also be important in influencing growth responses to spring temperatures (Post et al., 2008).

Alternatively, if warm springs lead to a lower near surface soil moisture later in the growing season, *Betula* may be more sensitive to this relative drought. Though both *Betula* and *Salix* can be deeply rooted compared with evergreen shrubs (Kummerow et al., 1983), *Betula* is more shallowly rooted than *Salix* and appears to acquire more of its resources near the soil surface (Nadelhoffer et al., 1996). Finally, because we did not sample *Betula* at a dry, warm site, it is possible that the differences between these two species are simply the product of the lack of spatial variation in the sampling of *Betula*; the spatial variation in climate-growth responses that is clearly evident in the *Salix* may also be present in *Betula*. There may be sites where *Betula* growth does respond positively to summer temperatures, as has been shown elsewhere (e.g. Blok et al., 2011). One potential cause of this variation among sites could be differences in the degree to which microsite variation buffers some individuals against broad scale climatic influence.

Many shrub species throughout the Arctic show little growth response to precipitation (Bär et al., 2008; Hallinger et al., 2010; Weijers et al., 2012), except where shrubs are growing in unusual microsite conditions (Bär et al., 2008; Hallinger et al., 2010). However, the results for *Betula* species are more ambiguous, with reports of both no significant response (Paradis et al., 2014) and positive (Blok et al., 2011; Keuper et al., 2012) growth responses to precipitation. Our chronologies from Sites 1 and 1/2 show a seasonal negative correlation with spring seasonal precipitation of the current year, while Site 3 does not. Furthermore, the LMM for *Salix* at Site 1/2 revealed not only the same negative response to spring precipitation, but also significant responses to precipitation in both the current and prior year. The LMM for Site 3 showed that only the previous spring's precipitation significantly influenced *Salix* growth. Site 3 is on a dry, warm south-facing slope, whereas Sites 1 and 1/2 are on relatively flat terrain that would remain comparatively wet and cool. Precipitation in the spring months falls largely as snow, and the negative correlation with spring precipitation on the shallow sloped sites could

have been due to lower angles of insolation than that of Site 3. Snow may persist longer on these sites in the spring, which could delay the onset of leaf out and decrease the length of the growing season, thereby reducing shrub growth (Bär et al., 2008; Wipf, 2010; Cooper et al., 2011). It should be noted, however, that many of these significant precipitation effects in the LMM had small effect sizes when compared with seasonal temperature effects (Table 5). Finally, though there were some differences between the results of the traditional correlation analysis and LMM approach, the most important seasonal climate parameter (in terms of increasing goodness-of-fit while maintaining parsimony) in the LMM also appeared to have similar importance in the correlation analysis.

Understanding how topographic position mediates the growth of shrubs is important in interpreting their responses to climatic variability and change. Due to the short stature of most arctic shrubs (<1 m), they are highly influenced by microsite conditions (e.g. aspect, elevation, landscape curvature). *Empetrum nigrum* ssp. *hermaphroditum* Hagerup. in Norway growing on south facing slopes experienced reduced growth due to heat stress during the warmest days of summer, while those on the north facing slopes benefited from these high temperatures (Bär et al., 2008). The timing of response may also shift due to elevation. For example, *Juniperus nana* Willd. growing at higher elevation showed positive monthly responses earlier in the summer (June) than individuals growing at low elevation (August), possibly due to high elevation individuals' need to develop as soon as conditions are adequate, while low elevation individuals experience a longer growing season (Hallinger et al., 2010).

Observations over the last 12 years in the study area (Post, 2013b) have shown an increase in the cover of both shrub species at small scales (~1 m²). At large scales, remote sensing data revealed large increases in both peak and time-indexed NDVI, which are estimates of total biomass and gross primary productivity, respectively (Masson-Delmotte et al., 2012). Much of these landscape-scale increases in biomass and productivity have been driven by an increase in woody plant abundance associated with increases in temperature in arctic and subarctic regions (Tape et al., 2006; Bhatt et al., 2010; Forbes et al., 2010; Naito and Cairns, 2011; Tremblay et al., 2012). Projections of climate change for West Greenland show increases

in both temperature and precipitation, the latter occurring through both larger and more frequent precipitation events, particularly during the growing season (Stendel et al., 2008).

Under these conditions, our results indicate that individual *Salix* ramets would benefit from these changes in climate more than those of *Betula* (Bret-Harte et al., 2001; Hollesen et al., 2015). However, microsite conditions as well as precipitation timing would influence annual growth (Bär et al., 2008; Blok et al., 2011). Although both species are deciduous shrubs, they have key differences in their life history strategies. *Betula* allocates carbon to both short and long shoots, so growth may not produce an even ring width in all ramets each year (Bret-Harte et al., 2001; Bret-Harte et al., 2002). On the other hand, *Salix* has only one type of shoot, and carbon is not partitioned, so annual ring widths are similar among ramets and relatively uniform (Bret-Harte et al., 2002). The positive correlation between *Salix* ramet growth and summer temperature (Site 3), and the absence of a similar association in *Betula* ramets, may reflect differences in allocation patterns. Physiological integration, which allows for genets to share resources among ramets through translocation, may be stronger in *Betula* than *Salix*. Hence, growth in any given ramet might poorly correlate with temperatures during the growing season because of the heterogeneity of other limiting resources (e.g. nutrients) or microtopographic influence on climate. In these instances, secondary growth may not be as reliable an indicator of the response to changes in climate as, for example, primary growth. Despite their different life history strategies, both species had a similar response to insect outbreaks. In the end, understanding how species-specific responses (cf. Bret-Harte et al., 2008) influence the way plant populations change over time is vital for reliable predictions of vegetation dynamics in a rapidly changing Arctic.

Conclusions

We suggest that an increase in *Betula* cover in a warmer climate may derive from increasing numbers of stems (ramets) in a genet (Bret-Harte et al., 2002) rather than an increase in the size of individual stems, as evidenced by the lack of a response to summer temperatures and the negative response to warmer springs. For *Salix*, warmer summers will elicit greater stem growth on dry, south-facing slopes. The processes contributing to the community level expansion of arctic shrubs are highly complex (Myers-Smith et al., 2011), and

accounting for the intra- and interspecific variation in secondary growth is needed to understand how communities are likely to change at multiple scales. Additionally, we found that serial sectioning was not necessary to capture the patterns of growth at these sites, mainly due to the occurrence of pointer rings created by periodic irruptive outbreaks of the moth, *E. occulta*. Our analysis demonstrates the continued potential for using shrub growth for climate reconstructions based on longer lived individuals and more spatially extensive sampling or studies of moth outbreak dynamics.

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Figure 1. Map of sites located on the eastern end of Long Lake (Aajuitsup Tasia), roughly 2-5 km from Russell Glacier, West Greenland. Data Source: Landsat 5 (NASA), Cryosphere Atlas (National Snow and Ice Data Center).

Figure 2. Climograph of Kangerlussuaq, West Greenland, with average monthly temperature in °C (red), and average total monthly precipitation in mm (blue). Data from Klein Tank et al., 2002, via KNMI's Climate Explorer website (climexp.knmi.nl).

Figure 3. Residual chronologies and sample size (number of individual shrubs) for Site 1 *Betula* (top), Site 1/2 *Salix* (middle), and Site 3 *Salix* (bottom). Solid lines on the residual chronology represent the portions that have a running expressed population signal (rEPS) >0.85. A known insect outbreak occurred in 2005 (vertical dashed line).

Figure 4. Images of *Betula* (upper) and *Salix* (lower) wood samples at 14x and 30x magnification. Note the small (micro) ring of the 2005 insect outbreak.

Figure 5. Correlations (grey bars) and significant correlations (black bars) between ring width series and climate parameters (monthly and seasonal mean temperature and total precipitation). Type I error rates were set at $\alpha = 0.05$. Analysis was conducted over a 20 month period encompassing the previous year (Capitals) and the current year (lower case) for the portion of each chronology with a rEPS >0.85.

Table 1. Site locations and microsite conditions, including latitude and longitude (decimal degrees), elevation (m), slope (degrees), aspect, and a description of the topography of the terrain.

Site	Latitude	Longitude	Elevation	Slope	Aspect	Topography
1	67.10486	50.34396	240	4	S	Long steady slope
2	67.10152	50.29398	218	4	WSW	Small rolling hills
3	67.08510	50.33027	382	30	S	Steep hillside

Table 2. Summary statistics for site chronologies for the entire series and the portion of the series with a running EPS (rEPS) >0.85. Listed are species, time interval, number of shrubs used in the analyses (# shrubs), total number of radii (# paths), mean interseries correlation statistic (rbar), expressed population signal (EPS), mean sensitivity (MS), autocorrelation of the 1st order for raw data (ARraw) and autocorrelation of the 1st order for the residual chronology.

Site	Species	Interval	# shrubs	# paths	rbar	EPS	MS	ARraw	ARres
1	<i>Betula</i>	1971-2010	15	33	0.288	0.809	0.344	0.392	0.075
1/2	<i>Salix</i>	1961-2010	42	92	0.307	0.918	0.389	0.427	-0.183
3	<i>Salix</i>	1954-2010	13	28	0.201	0.737	0.333	0.475	-0.050
rEPS>0.85									
1	<i>Betula</i>	1988-2010	15	33	0.393	0.907	0.350	0.387	-0.020
1/2	<i>Salix</i>	1977-2010	42	92	0.307	0.943	0.388	0.426	0.108
3	<i>Salix</i>	1981-2010	13	28	0.214	0.813	0.316	0.443	-0.073

Table 3. Comparison of average ring widths between all years excluding 2005 and the average 2005 insect outbreak ring for each site. Also shown are the mean ring widths (and standard deviations) in mm and the percent of samples with reduced growth in 2005 (% 2005).

Site	Species	Ring width		% 2005
		<i>All Years</i>	<i>2005 outbreak</i>	
1	<i>Betula</i>	0.204 (0.093)	0.106 (0.049)	100
1/2	<i>Salix</i>	0.242 (0.138)	0.089 (0.060)	100
3	<i>Salix</i>	0.565 (0.344)	0.598 (0.428)	71.4

Bracketed values are the standard deviation of the mean.

Table 4. Site specific linear mixed effects models (LMM) of seasonal climate variables that significantly influenced the growth of shrub rings. A t or p as the initial letter in the parameter name indicates temperature or precipitation, respectively, and lowercase letters for the climate variables represent the current year, while capitalized letters represent the previous year (djf/DJF = winter, mam/MAM = spring, jja/JJA = summer, and son/SON = autumn). Indiv. is the number of individual shrubs included in each model, while Obs. is the total number of ring width observations. R^2 is Nakagawa & Schielzeth's (2013) marginal R^2_{GLMM} , which summarizes the variance explained by the fixed factors. logLik is the log-likelihood statistic, AICc is the sample-size adjusted Akaike's Information Criterion, and BIC is Bayesian Information Criterion, and these are reported as the difference (Δ) between the full and intercept-only models using maximum likelihood estimation. Climate variables are fixed factors and are listed in descending order of their z-value.

Site	Species	Climate Variables	Indiv. (Obs.)	R^2	ΔlogLik	ΔAICc	ΔBIC
1	<i>Betula</i>	t.mam, P.MAM, p.jja	15 (399)	0.13	-36.51	67.02	55.05
1/2	<i>Salix</i>	p.mam, p.jja, p.djf, P.SON, T.JJA, P.JJA, T.SON, t.djf, p.son	42 (1112)	0.21	-93.86	169.73	124.72
3	<i>Salix</i>	t.jja, P.MAM	13 (380)	0.11	-27.36	50.73	42.84

Table 5. Parameter estimates (effect sizes) for fixed climate factors for full site specific linear mixed effects models (LMM) of shrub growth rings, with all significant factors included. A t or p as the initial letter in the parameter name indicates temperature or precipitation, respectively, and lowercase letters for the climate variables represent the current year, while capitalized letters represent the previous year (djf/DJF = winter, mam/MAM = spring, jja/JJA = summer, and son/SON = autumn). Adj. SE is the adjusted standard error of the mean, and z and p are the z-statistic and p-value of each fixed factor, respectively. Because all parameters in each final model had an importance value of 1, climate variables are instead listed in descending order of their z-value, and parameter estimates are based on restricted maximum likelihood estimation.

Site	Species	Parameter	Estimate	Adj. SE	z-value	p
1	<i>Betula</i>	(Intercept)	0.50000	0.13040	1.420	0.155
		t.mam	-0.02799	0.00581	3.662	0.000
		P.MAM	0.00233	0.00063	3.385	0.001
		p.jja	0.00105	0.00035	3.236	0.001
1/2	<i>Salix</i>	(Intercept)	1.12000	0.17980	4.745	0.000
		p.mam	-0.00289	0.00025	10.963	0.000
		p.jja	0.00118	0.00014	8.503	0.000
		p.djf	0.00395	0.00046	8.181	0.000
		P.SON	0.00145	0.00017	7.247	0.000
		T.JJA	-0.06633	0.00931	6.484	0.000
		P.JJA	0.00106	0.00017	5.888	0.000
		T.SON	0.02444	0.00472	4.376	0.000
		t.djf	0.00711	0.00188	3.242	0.001
		p.son	-0.00032	0.00017	2.163	0.031
		(Intercept)	-0.16650	0.15650	0.501	0.616
3	<i>Salix</i>	t.jja	0.11390	0.01555	6.429	0.000
		P.MAM	0.00225	0.00055	3.020	0.003

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