Uniform shrub growth response to June temperature across the North Slope of Alaska

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Abstract

The expansion of woody shrubs in arctic tundra alters many aspects of high-latitude ecosystems, including carbon cycling and wildlife habitat. Dendroecology, the study of annual growth increments in woody plants, has shown promise in revealing how climate and environmental conditions interact with shrub growth to affect these key ecosystem properties. However, a predictive understanding of how shrub growth response to climate varies across the heterogeneous landscape remains elusive. Here we use individual-based mixed effects modeling to analyze 19,624 annual growth ring measurements in the stems of Salix pulchra (Cham.), a rapidly expanding deciduous shrub. Stem samples were collected at six sites throughout the North Slope of Alaska. Sites spanned four landscapes that varied in time since glaciation and hence in soil properties, such as nutrient availability, that we expected would modulate shrub growth response to climate. Ring growth was remarkably coherent among sites and responded positively to mean June temperature. The strength of this climate response varied slightly among glacial landscapes, but in contrast to expectations, this variability was not systematically correlated with landscape age. Additionally, shrubs at all sites exhibited diminishing marginal growth gains in response to increasing temperatures, indicative of alternative growth limiting mechanisms in particularly warm years, such as temperature-induced moisture limitation. Our results reveal a regionally-coherent and robust shrub growth response to early season growing temperature, with local soil properties contributing only a minor influence on shrub growth. Our conclusions strengthen predictions of changes to wildlife habitat and improve the representation of tundra vegetation dynamics in earth systems models in response to future arctic warming.

Introduction

Woody shrubs are expanding in arctic tundra, with cascading effects on terrestrial carbon balance and wildlife habitat (Tape et al 2006, Myers-Smith et al 2011). Establishing the drivers of shrub expansion is therefore key to predicting future shifts in both ecosystem and community processes at high latitudes, where half of Earth’s terrestrial organic carbon is stored (Tarnocai et al 2009, Hugelius et al 2014). Recent meta-analyses (Myers-Smith et al 2015a, Martin et al 2017) suggest that shrub growth variability is driven by temperature and precipitation, and modified by ecosystem properties like soil moisture and nutrient status. However, very few empirical studies have tested these ideas by measuring shrub growth on decadal timescales across landscapes with varying ecosystem properties.

One overarching ‘master’ variable controlling ecosystem properties in arctic Alaska is the time since last glaciation. Due to the heterogeneous nature of glacial advance and retreat in this region, adjacent watersheds can vary in landscape age by more than an order of magnitude (Hamilton 2003). This patchwork of glacial histories gives rise to spatial variation in ecosystem properties among landscapes. Older glacial landscapes have greater plant biomass, cation exchange capacity, soil acidity, and net nitrogen mineralization...
(Hobbie and Gough 2002, Hobbie et al 2002, Walker et al 2014). Because of these legacy effects of glaciation, Oswald et al (2014) argue that glacial history is a key regional control on vegetation response to future climate changes. Nitrogen availability, the strongest limiting factor to plant growth in the region, varies widely among landscapes of different ages. For example, Hobbie and Gough (2002) found 10 times greater rates of annual net nitrogen mineralization in an older landscape (120 000–60 000 years since glaciation) compared to an adjacent younger landscape (25 00–11 500 years since glaciation). Therefore, it may be expected that shrub growth is more responsive to climate variability in older glacial landscapes where nitrogen limitation is less severe (Chapin 1983, Chapin et al 1995, Whittinghill and Hobbie 2011, Walker et al 2014, Shaver et al 2014).

Within glacial landscapes, variability in local soil conditions has further consequences for vegetation response to climate. For example, while shrub growth often responds positively to growing season temperature, temperature-induced moisture limitation may constrain growth during particularly hot years at drier locations such as uplands (Ackerman et al 2017, Gamm et al 2017). Such local variability in soil conditions interacts with regional glacial geology and broad-scale climate patterns to create a hierarchical structure of controls on tundra vegetation growth (Myers-Smith et al 2015a). This hierarchy poses a major challenge to building a predictive understanding of arctic shrub growth.

Dendroecology, the study of annual growth increments in woody plants, has become a popular method within the last two decades for analyzing climate response of arctic vegetation (See studies included in Myers-Smith et al 2015a, Young et al 2016, Ackerman et al 2017, Gamm et al 2017). This method is particularly well-suited for arctic tundra, since many plant species are long-lived and interannual climate is highly variable. Further, the use of individual-based mixed effects models in the analysis of dendroecological data yields estimates of the strength of controls on shrub growth across all levels of the aforementioned hierarchy (Myers-Smith et al 2015a, Myers-Smith et al 2015b). In contrast to the traditional site-level standardization approach that extracts a uniform growth signal shared among individuals at a site, the mixed-modeling approach maintains information related to the variability in climate response among individuals (Galván et al 2014). Therefore, this method is ideal for comparing individualistic climate responses of shrubs sampled from distinct glacial landscapes and from multiple microsites within those landscapes (Galván et al 2014, Myers-Smith et al 2015b).

In this study, we present results of dendroecological analysis from six populations of Salix pulchra (cham.) on the North Slope of Alaska. This work builds on a prior study by Ackerman et al (2017) that revealed shrub growth sensitivity to mean June temperature at upland and riparian sites within a single glacial landscape. Diminishing marginal growth gains to increasing temperature were evident only at the upland site, a potential indicator of temperature-induced moisture limitation during particularly warm years. Here we explore whether such patterns hold at a regional scale encompassing four landscapes ranging in age from 14 000 to over 900 000 years since glaciation. We use individual-based mixed modeling to test two hypotheses:

1. Shrub growth on older glacial landscapes will respond more strongly to climate variability, because older landscapes are less nitrogen-limited.

2. In upland areas (but not in riparian areas), shrubs will show diminishing marginal growth gains in response to increasing temperature, because fewer soil resources such as moisture are available in upland areas to facilitate elevated growth in warm years.

Methods

During the summers of 2015 and 2016, we sampled six populations of Salix pulchra (cham.) on the North Slope of Alaska across four landscapes of different glacial ages, ranging between 14 000 and >900 000 years old (figure 1). Within two of the landscapes, Kuparuk and Inigok, we replicated our sampling of 40 stems at both upland and streamside riparian sites. Within the other two landscapes, Itkillik and Roche Moutonee in the Brooks Range, we sampled only from upland sites. Detailed description of the geologic histories of the sampling sites can be found in the references in table 1. At each site, shrub sampling protocol (including serial sectioning along the stem), microscope slide preparation, image-based ring width measurements, and cross-dating were conducted following methods described by Ackerman et al (2017). In total, we cross-dated 19 624 annual ring (i.e. secondary stem growth) measurements across 184 individuals to assemble the ring width dataset. Measurements from the Kuparuk landscape have been previously published (Ackerman et al 2017), while data from the rest of the landscapes are presented here for the first time. For visualization purposes, traditional dendroecological standardization (following Ackerman et al 2017) was used to calculate time-stable ring width indices for each individual, and site-level chronologies were calculated as the median of all ring-width index values available in a given year (figure 2). We ran a principal component analysis of the six site-level chronologies to assess coherence in the growth signal among the sites.

Expanding on the more traditional dendroecological standardization approaches used in Ackerman
Figure 1. Landscape age in the circumpolar Arctic tundra (a) and on the North Slope of Alaska (b), where Salix pulchra were sampled across four glacial landscapes. At the Kuparuk (c) and the Inigok landscapes, S. pulchra were sampled from both upland and riparian positions. Only upland samples were taken at the Brooks Range and Itkillik landscapes. Landscape age data was provided by Raynolds and Walker (2009).

Table 1. Characteristics of four glacial landscapes sampled across the North Slope of Alaska for this project. Basal diameter, stem length, stem age, and stem elongation rate represent mean (standard error) values for shrub individuals sampled in each landscape. Geology reference 1 = Badding et al 2013; 2 = Hamilton 2003; 3 = Walker et al 2014; 4 = Hobbie and Gough 2002, 5 = Hobbie et al 2002, and 6 = Carter 1981.

| Site          | Latitude, Longitude | Landscape age (years) | Populations sampled | Basal diameter (mm) | Stem length (cm) | Stem age (years) | Stem elongation rate (cm/year) | Geology reference |
|---------------|---------------------|-----------------------|---------------------|---------------------|------------------|------------------|-------------------------------|------------------|
| Brooks Range  | 68.375, −149.295    | 14 000                | Upland              | 19.04 (1.62)        | 111.4 (9.5)      | 26.14 (1.38)     | 4.48 (0.15)                   | 1                |
| Itkillik      | 68.641, −149.614    | 21 000                | Upland              | 16.13 (0.60)        | 82.0 (2.6)       | 30.52 (1.95)     | 3.06 (0.22)                   | 2, 3, 4, 5       |
| Kuparuk       | 68.660, −149.423    | 500 000               | Riparian & upland   | 23.83 (1.90)        | 122.7 (8.6)      | 31.17 (1.68)     | 4.50 (0.42)                   | 2, 3             |
| Inigok        | 70.000, −153.097    | >900 000              | Riparian & upland   | 14.06 (0.66)        | 82.6 (3.4)       | 24.31 (1.00)     | 3.70 (0.07)                   | 6                |

et al (2017), we used linear mixed effects modeling to analyze the raw, unstandardized ring width data of individual shrubs. Compared with traditional methods, mixed effects modeling is more effective in preserving individual-level variation in shrub growth while accounting for the influence of intrinsic factors, such as stem age, on ring width (Galván et al 2014, Myers-Smith et al 2015b). We used the R package nlme (Pinheiro et al 2014) to run our models, with ring width (log transformed to achieve normality of residuals) as the response variable, individual shrub as a random effect, and a first-order autocorrelation structure.

To determine which climate variables to test as fixed effects in our model, we used the R package treeclim (Zang and Biondi 2015) to correlate growth chronologies from each site with monthly climate variables including precipitation and minimum, mean, and maximum temperatures. Climate data for Kuparuk, Itkillik, and the Brooks Range landscapes come from Toolik Field Station (Environmental Data Center Team 2017), which is within 50 km of each of these sites and has continuously monitored climate conditions since 1989. Climate data for Inigok come from the NOAA Climate Divisional Dataset for the North Slope of Alaska (NOAA, Vose et al 2014),
a regional climate monitoring product, as no individual meteorological station has a continuous multi-decadal record of climate near Inigok. Monthly climate variables found to be significant predictors of shrub growth across multiple sites were selected for inclusion as fixed effects. The other fixed effects were stem length, glacial landscape (categorical, 4 levels), and position (categorical, 2 levels: upland or riparian). We included a term for the interaction between climate variables and glacial landscape, to test whether shrub response to climate varied among landscapes (Hypothesis 1). We also tested for second-order relationships between significant climate variables and shrub growth, to account for potential decreasing marginal growth gains in response to increasing temperature. A negative second-order relationship between temperature and ring width would be consistent with temperature-induced moisture limitation during warm growing seasons (Ackerman et al 2017). Finally, we tested for an interaction between this second-order relationship and position, to determine whether temperature-induced moisture limitation was stronger at the upland sites (Hypothesis 2). We ran the model for ring width measurements from 1989–2014, the common period between the shrub growth measurements and the instrumental record across all sites.

After running the full model described above, we tested a more parsimonious model that excluded terms not found to be statistically significant at alpha = 0.05. To compare the full model with the parsimonious model, we used both the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC), which imposes a stronger penalty for increasing model complexity.
In our individual-based mixed modeling analysis of the raw ring width measurements, the parsimonious model (AIC = 5568, BIC = 5562) was preferred over the full model (AIC = 5584, BIC = 5691). Both models explained 45% of the variability in ring width, using Nakagawa and Schielzeth’s (2013) calculation of conditional R². Therefore, we focus on results of the parsimonious model, but we present complete output for both models in table 2.

June T was the climate variable with the greatest effect size on ring width. Further, there was a statistically significant interaction between June T and glacial landscape. However, in contrast to our prediction arising from Hypothesis 1, the strength of this interaction did not vary systematically with landscape age. For example, shrub growth was most sensitive to climate in the youngest landscape, Brooks Range, while shrub growth was least sensitive to climate in the second youngest landscape, Itkillik. Shrub growth sensitivities to June T at the two oldest landscapes were intermediate. There was also a negative second-order relationship between ring width and June T, which is consistent with temperature-induced moisture limitation of growth in warm growing seasons. However, in contrast to our expectation in Hypothesis 2, the strength of this temperature-induced moisture limitation did not vary by position within the landscape (upland versus riparian), because position itself was not a significant term in the model.

Longer stems were positively associated with ring width, while stem age was negatively associated with ring width (table 2). Though position was not included as a significant term in the parsimonious model, it should be noted that position was correlated with stem length, which was a significant predictor of ring width (figure 4; table 3). Riparian shrubs had greater mean ring widths than upland shrubs. Mean annual stem elongation was also greater for riparian individuals than for upland individuals, as stem age did not differ across populations (table 3).

Discussion

Our analysis revealed an overwhelming effect of June temperature on shrub growth, despite substantial variation in ecosystem properties (e.g. pH, soil moisture, nitrogen availability) associated with glacial landscape age and position (Chapin et al 1988, Hobbie and Gough 2002, Hobbie et al 2002, Walker et al 2014, Ackerman et al 2017). Contrary to our expectation in Hypothesis 1, shrubs growing on older glacial landscapes were not more sensitive to climate variability, though shrub response to climate did vary slightly among landscapes. Contrary to our expectation in Hypothesis 2, within-landscape shrub response to climate did not vary based on position (upland versus riparian). Temperature-induced moisture limitation (as indicated by a negative, second-order relationship between temperature and ring width) was evident across our entire set of samples, regardless of position. At the site level, interannual shrub growth was remarkably coherent across the North Slope (figure 2), likely driven by the strength of the June temperature signal.

Table 2. Fixed effect coefficient estimates for the parsimonious and full mixed models predicting Salix pulchra ring width (mm, log-transformed) across the North Slope of Alaska. The parsimonious model was preferred based on both AIC and BIC. Conditional R² (Nakagawa and Schielzeth 2013) was 0.45 for both models. Temperatures (T) are in units of °C, and stem age is measured in years.

| Parameter                          | Parsimonious model | Full model               |
|-----------------------------------|--------------------|--------------------------|
|                                   | AIC = 5568, BIC = 5562 | AIC = 5584, BIC = 5691   |
| Intercept                         | −4.42 0.244 < 0.001 | −4.36 0.271 < 0.001      |
| June mean T                        | 0.324 0.048 < 0.001 | 0.329 0.049 < 0.001      |
| (June mean T)^2                    | −0.007 0.001 0.01  | −0.006 0.003 0.028      |
| May minimum T                      | −0.035 0.003 < 0.001| −0.035 0.003 < 0.001    |
| Stem length                        | 0.018 0.001 < 0.001 | 0.016 0.001 < 0.001     |
| Landscape Inigok                   | 0.87 0.152 < 0.001  | 0.88 0.169 < 0.001      |
| Landscape Itkillik                 | 1.064 0.165 < 0.001 | 1.046 0.165 < 0.001     |
| Landscape Kuparuk                  | 1.005 0.151 < 0.001 | 1.04 0.168 < 0.001      |
| Stem age                           | −0.035 0.002 < 0.001| −0.035 0.002 < 0.001    |
| June mean T×Landscape Inigok       | −0.069 0.017 < 0.001| −0.079 0.019 < 0.001    |
| June mean T×Landscape Itkillik     | −0.102 0.017 < 0.001| −0.101 0.017 < 0.001    |
| June mean T×Landscape Kuparuk      | −0.086 0.016 < 0.001| −0.096 0.018 < 0.001    |
| Position_upland                   | Not included       | −0.028 0.082 0.73       |
| (June mean T)^2×Position_upland   | Not included       | −0.001 0.001 0.21       |

Figure 4. Stem length correlates with mean ring width in individuals from Inigok and Kuparuk, where both upland and riparian populations were sampled. Riparian individuals had longer stems and larger ring widths than upland individuals.
Mean June temperature was the only climate variable to significantly affect individual shrub growth in all six populations sampled, and in all cases it provided the strongest growth signal of any climate variable (figure 2). This coherence in climate response across the North Slope contrasts with a meta-analysis (Myers-Smith et al. 2015a) that found significant variability in shrub response to climate at both regional and local scales. However, the studies included in this meta-analysis are largely single-site investigations with varied methodologies not designed to test for uniformity-versus-heterogeneity in climate response among sites. The uniform climate response we found in shrubs across the North Slope emphasizes the importance of consistency in sampling and measurement protocols, as outcomes of shrub dendroecological analyses vary based on the specific measurement techniques used (Myers-Smith et al. 2015b). For example, climate sensitivity of shrub growth appears greater when ring measurements are taken at the root collar compared with higher up the stem (Ropars et al. 2017). In our analysis, we used serial sectioning (Myers-Smith et al. 2015b) to ensure that the June temperature signal in the shrubs we sampled was indicative of secondary growth throughout the stem, not just in a specific part of the stem (e.g. the root collar).

Shrub climate response varied among glacial landscapes, indicated by a significant interaction between landscape and June T. However, the strength of this interaction was not systematically related to landscape age. Shrubs in older landscapes reported to have greater nitrogen availability did not respond more strongly to June T than shrubs in older landscapes reported to have lower nitrogen availability (Whittinghill and Hobbie 2011). This outcome did not support Hypothesis 1, perhaps due to the difficulty of measuring nitrogen availability for plants in tundra soils. Although older landscapes have greater net nitrogen mineralization rates (Hobbie et al. 2002), this may not be the best indication of nitrogen availability, as some tundra plant species can use organic forms of nitrogen (Schimel and Chapin 1996, Schimel and Bennett 2004). Additionally, other factors associated with landscape properties (e.g. pH, herbivory rates, disturbance regimes, availability of other nutrients, etc.) may impact shrub climate response more than nitrogen availability or landscape age per se.

Within-landscape variability in position (upland versus riparian) did not alter shrub climate response, nor was its main effect a significant predictor of ring width. However, stem length, which was partially determined by position, was positively correlated with ring width. Favorable landscape positions such as riparian zones tend to host taller shrubs with greater growth rates (Ackerman et al. 2017). In turn, taller shrubs have stronger climate responses (Myers-Smith et al. 2015a), perhaps due to release from competition with shorter conspecific neighbors (Saccone et al. 2017). Therefore, while position was not directly useful in modeling shrub growth, stem length, often an indirect effect of position, was a highly significant predictor of secondary growth. Separating the often correlated effects of shrub size and position within the landscape would not have been possible using a traditional site-based chronology approach to the analysis of our ring width data, as individual (within-site) variability in stem size would have been lost. Our mixed modeling approach thus provided unique ecological insight on the importance of shrub size and competition in growth variability (Myers-Smith et al. 2015a, Myers-Smith et al. 2015b, Young et al. 2016).

We found evidence of temperature-induced moisture limitation of shrub growth, indicated by the negative second-order relationship between ring width and June T. In other words, shrubs across the North Slope showed decreasing marginal growth gains in response to increasing June T. This second-order relationship did not depend on shrub position within the landscape. This result differs from findings by Ackerman et al. (2017), who found temperature-induced moisture limitation at a dry upland site, but not at a nearby moist riparian site. The contrasting results described in the present study may be due either to greater individual replication, or to the difference in model specification, which here includes more individual-level information (e.g. stem length). Alternatively, the standardization procedure used by Ackerman et al. (2017) may have removed low-to-medium-frequency variability in ring-width index that would be diagnostic of temperature-induced moisture limitation at both sites, given the monotonic increase in mean June air temperature on the North Slope in recent decades (NOAA). In this study, we avoided this potential issue by analyzing raw ring width data using an individual-based model, which preserved growth variability at all temporal frequencies and maintained shrub-level information in the model (Galván et al. 2014, Myers-Smith et al. 2015a, Myers-Smith et al. 2015b). Regardless of the exact cause of the discrepancy, our results further support the idea that greater

| Position  | Basal diameter (mm) | Mean ring width (mm) | Stem length (cm) | Stem age (years) | Stem elongation rate (cm/year) |
|----------|---------------------|----------------------|------------------|------------------|-------------------------------|
| Upland   | 12.391 (0.530)      | 0.182 (0.003)        | 66.825 (2.399)   | 25.626 (1.396)   | 2.938 (0.150)                 |
| Riparian | 22.643 (1.464)      | 0.301 (0.005)        | 125.589 (5.912)  | 28.159 (1.271)   | 4.952 (0.300)                 |

Table 3. Shrub characteristics from upland and riparian populations. Shrubs included in these results were sampled from the Kuparuk and Inigok landscapes, where shrubs at both positions were sampled. Riparian shrubs were generally larger and faster growing than upland shrubs. Values are reported as means (standard errors) of individual shrub measurements. All differences between upland and riparian shrubs were significantly different at the alpha = 0.05 level, except for stem age (p = 0.18).
temperatures do not always lead to consistent increases in shrub growth, due to interactions with other limiting resources such as moisture (Ackerman et al., 2017, Gamm et al., 2017).

The early season response in secondary stem growth across all our sites is consistent with the findings of Chapin and Shaver (1989), who showed that biomass accumulation in the leaves and twigs of deciduous shrubs was restricted to the early growing season. Shaver (1986) found that secondary growth accounts for half of aboveground net primary productivity in Salix shrubs from the region (the other half being stem elongation and leaf growth). Therefore, we can infer that almost all aboveground net primary productivity in Salix occurs early in the growing season. Radville et al. (2016) also documented early season peaks in belowground productivity of tundra communities near Kangerlussuaq, Greenland, though phenology of deciduous shrub roots in particular were not reported.

Our results suggest that as June temperatures continue to warm, shrub growth will increase across all glacial landscapes of the North Slope. Based on allometric relationships between secondary stem growth and aboveground biomass, large shrubs with high growth rates will add proportionally more biomass in response to increased temperatures than smaller shrubs (Berner et al., 2015, Ackerman et al., 2017). Consequently, areas favorable for large shrubs, such as riparian zones and water tracks, may continue to yield improved habitat quality for shrub-reliant species such as moose and ptarmigan (Tape et al., 2010, Tape et al., 2016). Greater aboveground shrub biomass in these areas may also impact rates of soil carbon turnover, and increased secondary stem growth in particular affects water balance (Bret-Harte et al., 2002). Across both riparian and upland habitats, biomass increase may be limited by soil moisture in particularly warm growing seasons.

The robust and highly coherent shrub growth response to temperature early in the growing season raises prospects for climate reconstruction using a multi-proxy approach. Otolith growth in long-lived fish of tundra lakes has been introduced as an effective annually-resolved climate proxy beyond latitudinal treeline (Black et al., 2013, Torvinen, 2017). In contrast to the June signal embedded in the shrub rings, otolith growth in lake trout (Salvelinus namaycush) on the North Slope of Alaska responds positively to mean August air temperature (Black et al., 2013, Torvinen, 2017). June and August air temperatures in this region are not correlated ($R^2 = 0.02, p = 0.44$ for the period 1989–2014; NOAA). Therefore, reconstructing past temperature conditions over the course of entire growing seasons necessitates the use of both shrub and otolith proxies, which are each tuned to distinct, uncorrelated periods of the growing season. We believe the prospects for such a multi-proxy reconstruction are strong, given the large range overlap between S. namaycush and deciduous shrubs in the Arctic. Multi-proxy climate reconstruction in the Arctic would be useful because of the poorly resolved spatial-temporal climate record during the instrumental period (Overland et al., 2004, Simmons and Poli, 2015, Cowtan and Way, 2014, Simmons et al., 2017). On the North Slope of Alaska, for example, the NOAA divisional dataset (NOAA) incorporates data from just a single inland meteorological station. Multi-proxy reconstructions from the North Slope could be used to evaluate spatial patterns in climate where instrumental data are lacking.

**Conclusion**

Our dendroecological analysis of S. pulchra revealed remarkable coherence in secondary growth and climate response across four glacial landscapes of the North Slope of Alaska. June mean temperature was the dominant control on annual shrub growth at all sites. Shrub response to climate varied slightly among glacial landscapes, but there was no systematic correlation between landscape age and climate sensitivity of shrub growth. Position (upland versus riparian) had no direct effect on growth, though taller shrubs, more common in riparian areas, had higher growth rates. As June temperatures continue to increase, deciduous shrubs are likely to continue expanding across all glacial landscapes of the North Slope. However, this expansion may be limited by temperature-induced moisture limitation in particularly warm years. Together, these outcomes highlight the preeminence of climate in controlling shrub growth variability across the North Slope. When combined with future climate scenarios, our model of shrub growth may strengthen predictions of changes to habitat structure and improve the representation of tundra communities in dynamic vegetation models.

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