

# From Intra-plant to Regional Scale: June Temperatures and Regional Climates Directly and Indirectly Control *Betula nana* Growth in Arctic Alaska

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## ABSTRACT

Tundra shrubs reflect climate sensitivities in their growth-ring widths, yet tissue-specific shrub chronologies are poorly studied. Further, the relative importance of regional climate patterns that exert mesoscale precipitation and temperature influences on tundra shrub growth has been explored in only a few Arctic locations. Here, we investigate *Betula nana* growth-ring chronologies from adjacent dry heath and moist tussock tundra habitats in arctic Alaska in relation to local and regional climate. Mean shrub and five tissue-specific ring width chronologies were analyzed using serial sectioning of above- and below-ground shrub organs, resulting in 30 shrubs per site with 161 and 104 cross sections from dry and moist

tundra, respectively. *Betula nana* growth-ring widths in both habitats were primarily related to June air temperature (1989–2014). The strongest relationships with air temperature were found for ‘Branch2’ chronologies (dry site:  $r = 0.78$ , June 16, DOY = 167; moist site:  $r = 0.75$ , June 9, DOY = 160). Additionally, below-ground chronologies (‘Root’ and ‘Root2’) from the moist site were positively correlated with daily mean air temperatures in the previous late-June (‘Root2’ chronology:  $r = 0.57$ , pDOY = 173). Most tissue-specific chronologies exhibited the strongest correlations with daily mean air temperature during the period between 8 and 20 June. Structural equation modeling indicated that shrub growth is indirectly linked to regional Arctic and Pacific Decadal Oscillation (AO and PDO) climate indices through their relation to summer sea ice extent and air temperature. Strong dependence of *Betula nana* growth on early growing season temperature indicates a highly coordinated allocation of resources to tissue growth, which might increase its competitive advantage over other shrub species under a rapidly changing Arctic climate.

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**Key words:** *Betula nana*; dendroclimatology; shrub rings; serial sectioning; shrub parts; northern Alaska; temperature; PDO index; AO index; sea ice extent.

## INTRODUCTION

As the Arctic warms, shifts in tundra vegetation composition, productivity and abundance are occurring across the northern latitudes (Beck and Goetz 2011; Epstein and others 2021). These changes are primarily associated with the most dominant woody plants in the tundra biome—arctic shrubs (Myers-Smith and others 2011; Tape and others 2012). However, the response of tundra shrub growth to climate change is variable at the pan-Arctic scale (Buchwal and others 2020), resulting in complex spatiotemporal patterns of tundra ‘greening’ and ‘browning’ across the north (Phoenix and Bjerke 2016; Bhatt and others 2017; Myers-Smith and others 2020).

Different spatiotemporal patterns of greening and browning across the Arctic might be driven by local differences in habitat characteristics that affect shrub growth. Landscape heterogeneity including geomorphology, soil properties, snow distribution, permafrost and local climate are closely interconnected and can drive variable tundra greening rates (Lara and others 2018; Chen and others 2021). For instance, Ropars and others (2015) showed that growth of *Betula glandulosa* differs across topographic features, with snowbed sites favoring shrub growth in comparison with terraces and hilltops in a forest-tundra ecotone in northern Québec. Further, in northern Alaska, tundra greening has been positively associated with the lengthening of the growing season, particularly in wetter locations (Arndt and others 2019). These findings suggest that within landscapes, distinct habitat types that vary along moisture gradients (that is, dry, moist and wet tundra) might provide localized controls on shrub responses to regional climate forcing. Although different climate–shrub growth responses to warming have been reported in Pan Arctic studies of different populations (Myers-Smith and others 2015; Buchwal and others 2020), the effects of localized habitat conditions remain uncertain. Hence, direct plant-level measurements across a range of habitats are necessary for a mechanistic and empirically based understanding of tundra shrub growth patterns.

Spatiotemporal patterns of greening and browning across the Arctic might also be driven by large-

scale atmospheric circulation in the Arctic. Alaska straddles a dynamic climate zone between the Arctic and North Pacific Oceans and its regional climate is driven by the configuration of large-scale atmospheric-ocean systems that advect air masses with specific temperature and moisture properties (Bieniek and Walsh 2017). These circulation regimes vary on interannual to decadal time scales and induce characteristic climate patterns observed in the coupled modes of the Arctic Oscillation (AO) or Pacific Decadal Oscillation (PDO) climate indices (Mantua and others 1997; Thompson and Wallace 1998). Several tree-ring series show high sensitivity to large-scale climate indices, including boreal trees (for example, D’Arrigo and others 1993; Lange and others 2020). However, their application to tundra shrub studies is limited in space and time (for example, Aanes and others 2002; Welker and others 2005a; Weijers and others 2017; Buchwal and others 2019), despite recognized effects of PDO/AO on sea ice extent and regional climate (Screen and Francis 2016; Kim and others 2020) that might impact shrub growth.

Typically, above-ground growth rings are used in shrub dendrochronology studies (Myers-Smith and others 2015; Buchwal and others 2020) and differences in allocation of carbon to above-ground production and below-ground stems and roots in arctic shrubs is poorly recognized. However, in a warmer and drier Arctic, allocation strategies might constitute a key-component for tundra shrub survival and biome projections. For example, as in trees, some species in dry habitats might invest more in below-ground growth and deeper root systems to enhance survival under warmer climate conditions (Canadell and others 1996), but also to potentially augment their carbon fixation capacity. Resolving organ-specific traits is possible when both above-ground stems and below-ground tissue are harvested and analyzed, allowing tissue-specific climate analyses and comparisons of growth which could provide a retrospective assessment of carbon allocation priorities in response to climate variability (Ropars and others 2017).

Shrub dendrochronology is an effective method to directly evaluate their growth in the context of both local and regional climate and ecophysiological drivers (Schweingruber and Poschod 2005). Timeseries of individual growth rings can be applied to delineate climate–shrub relationships from annual to centennial (Weijers and others 2017; Hantemirov and others 2011; Hollesen and others 2015; Opała-Owczarek and others 2020), and even millennial timescales (Gaglioti and others 2017). To date, site-specific climate–growth studies in the

Alaskan Arctic have focused on *Alnus* (Tape and others 2012) and *Salix* spp. (Ackerman and others 2017, 2018; Andreu-Hayles and others 2020). However, *Betula nana* (dwarf birch), together with *Betula glandulosa*, is one of the primary deciduous shrub species growing in the Arctic. Because of its high abundance and relatively advanced age, the species has been used in dendrochronological studies across the tundra biome, including Greenland (Büntgen and others 2015; Hollesen and others 2015; Young and others 2016; Nielsen and others 2017; Gamm and others 2018), Canada (Ropars and others 2015; Andruko and others 2020), Siberia (Blok and others 2011; Li and others 2016) and alpine Scandinavia (Weijers and others 2018), but not yet in Alaska.

Here, we investigate *Betula nana* growth sensitivity to climate in arctic Alaska. We explore climate–growth relationships at different spatial–temporal scales, from individual plant parts to local and regional climatology using dendrochronological tools. Specifically, we address the following questions:

1. What are the relationships between climate and *Betula nana* growth in Northern Alaska, and how do they vary between shrubs growing in dry and moist habitats? We hypothesized that shrubs from the dry tundra habitat are less responsive to summer temperature than shrubs from the moist tundra habitat because their growth is moisture limited, rather than temperature limited.
2. Do *Betula nana* growth-ring responses to climate differ between tissue type, that is, between above- versus below-ground plant parts? We hypothesized that below- and above-ground shrub growth would not be perfectly coupled, because of potential differences in allocation to below- and above-ground tissues across the growing season.
3. Are *Betula nana* growth rings a suitable proxy for local and/or regional climate? We anticipated that, through potential coupling between local and Pan Arctic climate variables (such as PDO, AO index and/or sea ice extent), *Betula nana* growth-ring chronologies would be a suitable proxy for regional climate signals.

## METHODS

### Study Site

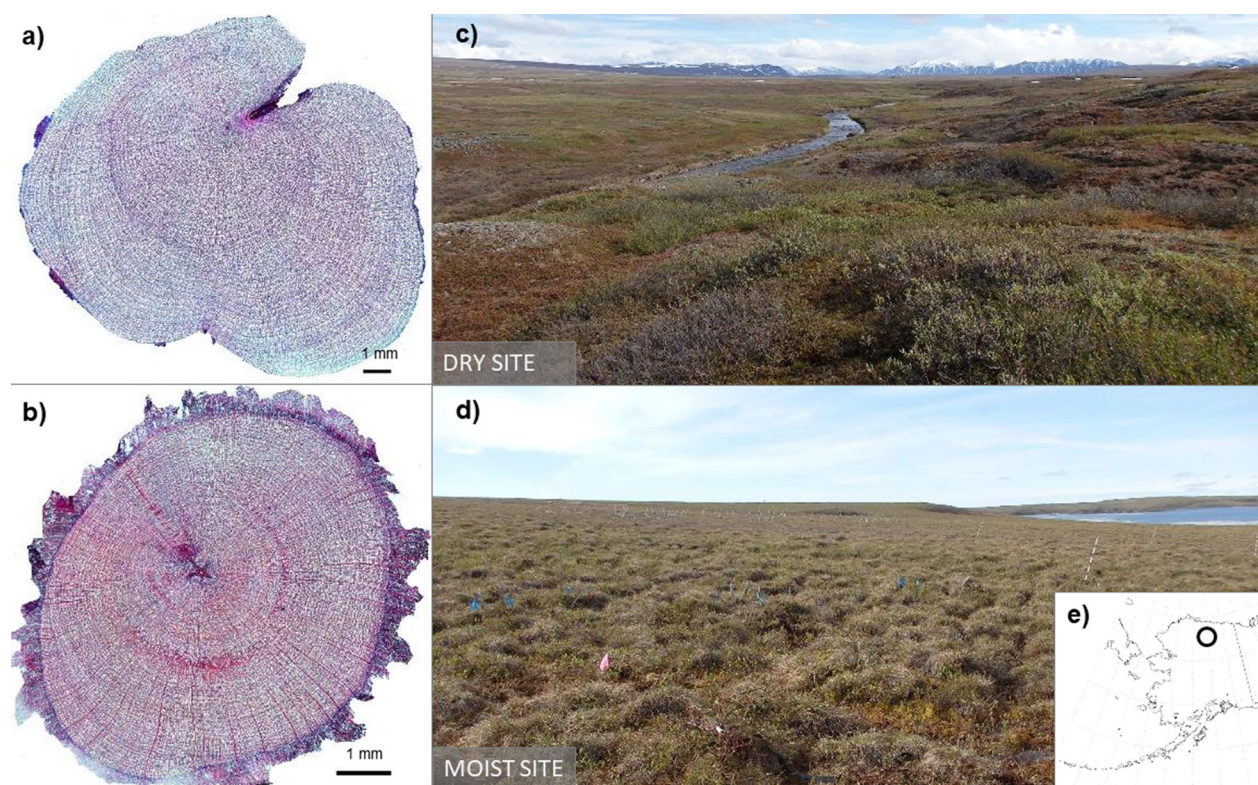
The study was conducted approximately 1 km south of Toolik Field Station in northern Alaska

(68°38'N, 149°38'W, 760 m a.s.l.) at one of the US ITEX (International Tundra Experiment) study sites (Welker and others 1997). This site represents a Low Arctic ecosystem in the northern foothills of the Brooks Range (Figure 1). *Betula nana* shrubs were sampled in two habitats with contrasting moisture conditions, located about 400 m apart. The first, hereafter referred to as 'dry site,' was a dry tundra habitat and the second was the moist tussock tundra, hereafter referred to as 'moist site.' Soil moisture varied because of the underlying sediments; the dry site was located on rocky glacial outwash, while the moist site was located on glacial till (Hamilton 2003). The moist site is characterized by shallower active layer depths and colder soil temperatures than the dry site (Welker and others 2005b). Weekly soil temperature measurements performed in year 2016 (from June to mid-September) with a use of a pin thermometer (with 10 random measuring points in each habitat) showed that the moist site was colder by 2.5 °C, 3.4 °C, 3.9 °C and 2.2 °C in June, July, August and September, respectively (Figure S1).

The mean annual and mean summer (June–July–August) air temperatures at the study area are – 8.1 °C (sd = 1.8) and 9.2 °C (sd = 1.3), respectively (1989–2014) (Environmental Data Center Team 2020). The warmest and coldest months are July and January with mean monthly temperatures of 11.3 °C (sd = 1.7) and – 22.6 °C (sd = 5.5), respectively. Mean annual precipitation is approximately 312 mm (Hobbie and others 2017).

### Shrub Sampling and Processing

*Betula nana* sampling was conducted during three growing seasons (at the end of summer 2014, and in the summers of 2015 and 2016) in both the dry and moist study sites. At each site, 30 shrubs were sampled at a minimum distance of 5 m apart. We applied a serial sectioning method (Kolishchuk 1990; Appendix A) to at least 10 shrubs per site, with a minimum of five cross sections per individual shrub acquired from both above- and below-ground shrub parts (Table S1). Specifically, we aimed to acquire at least two below-ground and two above-ground shrub parts, each sampled at least 10 cm apart. A stem-base (if present) or main shoot-base section was cut. Root collars were typically characterized by wood with intermingled stem and root tissues and were not sectioned. In total, 161 and 108 cross sections were acquired from the dry and moist site, respectively, whereby 39% (dry site) and 24% (moist site) represented a below-ground shrub part (that is, roots only).



**Figure 1.** Example of *Betula nana* thin sections from the **a** dry (root section) and **b** the moist (stem section) habitat; **c** densely vegetated tussock tundra (moist site) with relatively unified shrub cover; **d** dry heath tundra with patchy shrub cover with isolated shrub individuals; **e** study area location (black circle) in northern Alaska.

All individual shrub cross sections were categorized into five groups: (i) 'Root' for below-ground cross sections acquired up to 20 and 10 cm below the root collar for shrubs from the dry and moist sites, respectively; (ii) 'Root2' for below-ground cross sections acquired more than 20 and 10 cm from the root collar for shrubs from the dry and moist sites, respectively; (iii) 'Stem' for stem or main shoot base cross sections sectioned just above the root collar for shrubs from both sites; (iv) 'Branch' and (v) 'Branch2' for above-ground cross sections sampled up to 20 cm (Branch) and above 20 cm from the root collar (Branch2) for shrubs sampled at both sites. Because of shorter root lengths in the moist site, the threshold between below-ground parts was placed at a shallower depth than in the dry site.

Annual *Betula nana* growth rings were analyzed using thin sections. Cross-sectional cuts were performed using a GSL-1 sledge microtome, and thin sections were prepared using a standard double staining protocol (that is, with Safranin and Astrablue dyes) (Schweingruber and Poschold 2005). In total, 567 radii were measured from the dry site shrubs and 308 radii from the moist site

shrubs (Appendix A). Cross-dating between the above-ground vs. below-ground shrub parts was performed, as well cross-dating between individual shrubs within a habitat. For this procedure, radial measurement series were cross dated first within each cross section, and later between cross sections of an individual shrub. Finally, growth series were cross dated between shrubs from each habitat type, and averaged for the dry and moist sites. A quality check of the visual cross-dating was performed using COFECHA (Holmes 1983; Grissino-Mayer 2001).

### Site- and Organ-Specific Chronologies

Cross-dated growth-ring measurements from a single cross section were standardized to remove non-climatic growth trends, such as age-related trends. Because shrubs were sampled across three growing seasons, each chronology was truncated at year 2014. Each growth series was detrended using a cubic spline in 'dplR' package (Bunn and others 2018) in R version 3.6.3 (R Core Team 2020). The default frequency response of a spline was 0.50 at a wavelength of 0.67 multiplied by series length in years. After detrending, all individual growth

curves (that is, ring width indices, RWI) were averaged at the shrub level within each site and used to compute mean dry and moist site chronologies.

In addition to site-specific chronologies (that is, dry vs. moist site), five shrub organ-specific chronologies were computed for each site: 'Root2,' 'Root,' 'Stem,' 'Branch' and 'Branch2' chronology. For this purpose, all cross sections assigned to each organ-specific group (see above) were averaged first at the individual shrub level and second at the site level. A minimum of 8 and a maximum of 28 individual shrubs were included in organ-specific chronology (Figure 2). To evaluate the quality of both raw (that is, arithmetic mean) and standardized chronologies, descriptive statistics were calculated (Table S2, Appendix A). This includes the expressed population signal (EPS) that measures the reliability of the chronology based on inter-series correlations and sample size, with  $EPS > 0.85$  generally considered as a reliable value (Wigley and others 1984).

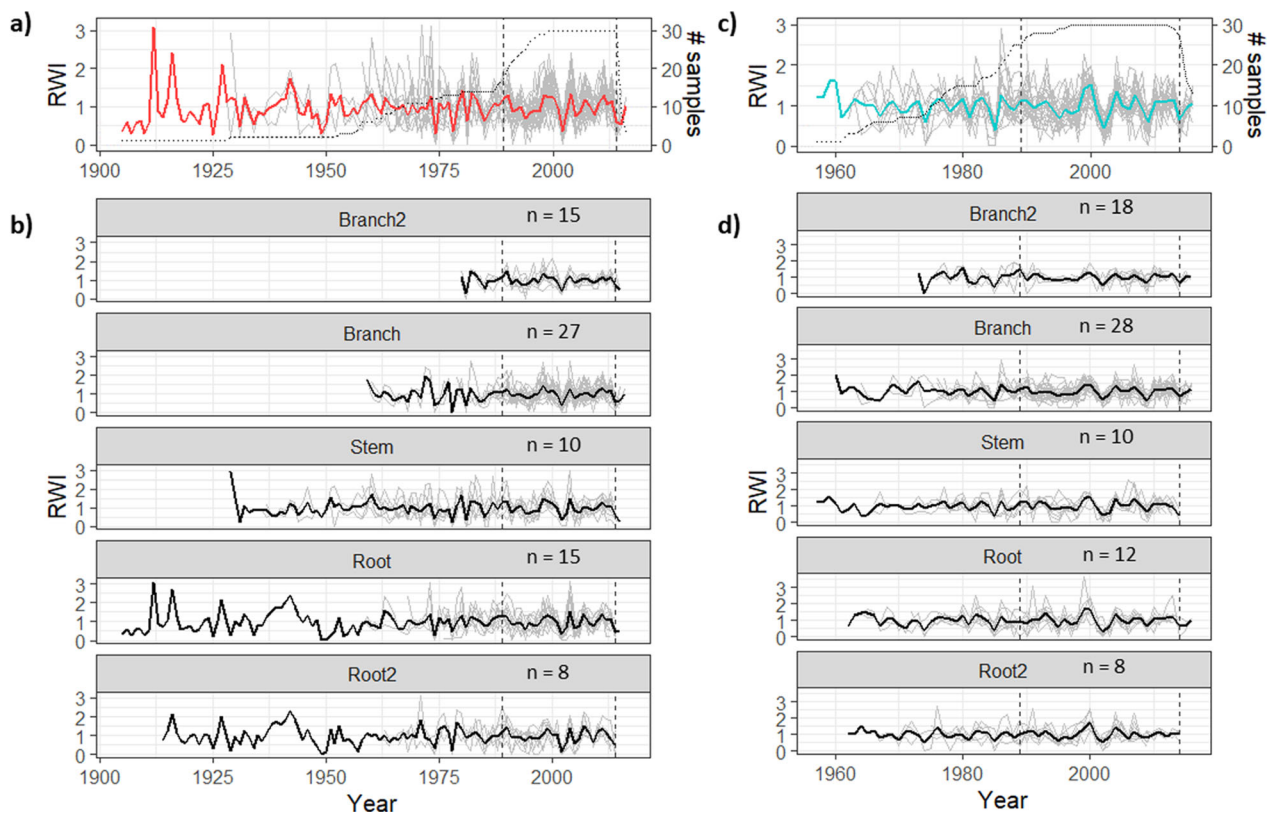
## Climate Data

Daily and monthly air temperature and monthly precipitation totals were obtained from Toolik Field Station (TFS) (Environmental Data Center Team 2020) and the Long-Term Ecological Research Network (LTER; Shaver 2019), and cover the period 1989–2014. One gap in daily air temperature data was recognized (from day 21 to 144 in the year 2004) and retained in the dataset. Daily mean air temperature values were used to calculate the mean sum of growing degree-days (GDD) during the summer (that is, June–to–August) months (1989–2014):

$$GDD = \sum_{i=1}^n (T_D - T_B)$$

where  $i$  represents each day where the daily mean temperature ( $T_D$ ) was greater than our defined base temperature threshold ( $T_B$ ). A range of base temperatures from 0 °C to 12 °C were used.

For moving correlation analyses and structural equation modeling CRU TS4.02 (Harris and Jones



**Figure 2.** Standardized *Betula nana* chronologies from the dry (a, b) and the moist (c, d) site from Toolik Lake area. Mean site chronologies for the dry (a, red line) and the moist (c, blue line) site are presented in bold. Organ-specific chronologies are presented for the dry (b) and the moist (d) site in black bold. Vertical dashed lines indicate study period (1989–2014), whereas dashed horizontal lines (a, c) illustrate sample size. RWI—ring width index; n—number of shrubs.

2019), air temperature and precipitation data were used. The data were obtained for the half-grid cell centered at 68.75°N latitude and 149.75°W longitude. Additionally, for spatial correlation analyses we used ERA5 monthly temperature data (Hersbach and others 2020) acquired via KNMI Climate Explorer (Trouet and van Oldenborgh 2013).

To test the sensitivity of *Betula nana* growth to drought conditions, we calculated the Standardized Precipitation and Evapotranspiration Index (SPEI) for the period 1980–2014 using TFS climate data in the R ‘spei’ package (Beguería and Vicente-Serrano 2017). The SPEI is a multi-scalar drought index (Vicente-Serrano and others 2010) that uses precipitation and temperature data in a water balance calculation (Thornthwaite 1948) where high (low) SPEI index represents wet (dry) conditions. We calculated a two-month SPEI index to provide the best estimate of soil water content where, for example, July SPEI represents the index over the period June to July. For structural equation models (period 1980–2014), SPEI was calculated using CRU TS4.02 temperature and precipitation data.

We also used monthly and seasonal mean values of the PDO (Mantua and others 1997) and AO indices (Thompson and Wallace 1998). Monthly mean sea ice extent (SIE) data for the Beaufort Sea were obtained from the National Snow and Ice Data Center, whereby a sea ice concentration threshold of 15% defines the ice margin (Fetterer and others 2017).

## Climate–Growth Relationships

Climate–growth relationships were analyzed at each site using standardized chronologies and climate variables. Bootstrapped correlation coefficients using mean monthly climate variables (TFS air temperature and precipitation) were calculated for the mean dry and moist site chronologies, as well as with the organ-level chronologies (1989–2014). Correlations for standardized chronologies at a site level were also performed with SPEI and the GDD time series. Additionally, bootstrapped correlations between the mean site-level chronologies and the PDO and AO indices were calculated for 1989–2014.

Moving correlation analyses were computed to investigate the long-term stationarity of *Betula nana* chronologies at a site level to air temperature and precipitation (CRU TS4.02 data; Appendix A). Both bootstrapped correlations (with 1000 iterations) and moving correlations were performed with current year months (January to August) and previous year monthly variables (starting from the

previous June) using the R ‘treeclim’ package (Zang and Biondi 2015). Also, simple linear regression was used to calculate the slope of *Betula nana* growth response (1989–2014) to June temperatures, using raw and standardized chronologies from both sites.

To establish which part of the month influences growth of a specific shrub organ, Pearson’s correlation coefficients were calculated between all organ-specific chronologies and TFS daily mean temperatures and precipitation (1990–2014), computed over a fixed 20-day window. Shorter window lengths were also tested, but as they can produce spurious correlations we used a 20-day window length for the mean daily temperature analyses. Analyses covered the period from day 153 of the previous year (1 June) and day 274 of the current year (30 September). Correlations were performed using the ‘dendroTools’ package in R (Jevšenak and Levanič 2018).

Spatial correlations were calculated to investigate the long-term spatial relationship between *Betula nana* chronologies (from both sites using plant mean chronologies) and regional air temperatures (1979–2014). Spatial correlations were computed between standardized chronology at a site level and ERA5 mean monthly air temperatures. Correlation maps were obtained for the area 52°–80°N and 120°–180°W using the Royal Netherlands Meteorological Institute (KNMI) Climate Explorer (Trouet and van Oldenborgh 2013), with a Monte Carlo approach to assess confidence intervals.

## Structural Equation Modeling

Structural equation models (SEMs) (Rosseel 2012) were used to investigate the strength of potential causal relationships between seasonal pan-regional and regional climate variables and *Betula nana* shrub growth. Climate variables that related significantly to shrub growth in bootstrapped correlations were included in the SEMs (that is, air temperature, precipitation, SPEI, PDO and AO index). Additionally, we integrated Beaufort sea ice extent (SIE) data as a proxy for a local open/closed oceanic moisture source (Klein and others 2015; Bailey and others 2021) and because of its potential coupled influence with regional temperature (Buchwal and others 2020) and relation to the PDO (Lindsay and Zhang 2005) and AO climate indices (Ogi and others 2016). Before SEMs were computed, pairwise relationships between monthly and seasonal climatic variables and indices were investigated using correlation matrices (Figure S3). Finally, separate SEMs incorporating climatic

variables from the previous autumn (that is, from previous September to November) and current summer months (that is, from June to August) were fit for the dry and moist site. For all SEMs, standardized mean site chronologies were used as the response variable for the period 1980–2014, that is, period covering monthly satellite observation for sea ice extent. For comparison, all paths, including nonsignificant ones, were retained in each SEM. All data that were unrepresented by an index value were normalized prior to the SEMs analyses. Multicollinearity between the predictors was assessed using variance inflation factor. Direct effects in each SEM were represented by standardized partial regression coefficients. The goodness of fit of each SEM was determined using Chi-square p value, CFI and AIC statistical tests, and the model was considered to have a good fit if  $P > 0.05$ , which indicates that model is consistent with the data. Marginal  $R^2$  was reported for each sub-model. All analyses were performed using 'lavaan' package (Rosseel 2012) in R.

## RESULTS

### Quality of Chronologies

Mean *Betula nana* shrub age was similar at both study sites averaging 39 (sd = 22) and 36 (sd = 10) years for the dry and the moist site, respectively. Shrubs were older at the dry site where the maximum age was 110 years (Figure 1b, Table S1), whereas the maximum age was 58 years at the moist site. Ten shrubs in the dry site (33%) and six in the moist site (20%) had at least one growth ring missing from an entire individual shrub. The maximum number of missing rings per individual shrub was three rings for both sites (Table S1). Mean ring width was larger from shrubs in the dry site (0.132 mm; max = 0.209) compared to the moist site (0.078 mm; max = 0.121). The time period covered by at least three individual shrubs was 1953–2014 and 1962–2014 for the dry and the moist site, respectively. Radial growth between standardized chronologies from the dry and the moist site was strongly coherent ( $r = 0.79$ ,  $p < 0.001$ ) for the study period (1989–2014). Both mean site chronologies had EPS > 0.94, whereas organ-specific chronologies had lower EPS values for the below-ground parts (between 0.764 and 0.861) compared to above-ground parts (between 0.805 and 0.949) (Table S2). Mean inter-series correlation was  $r = 0.348$  for the dry site and  $r = 0.384$  for the moist site.

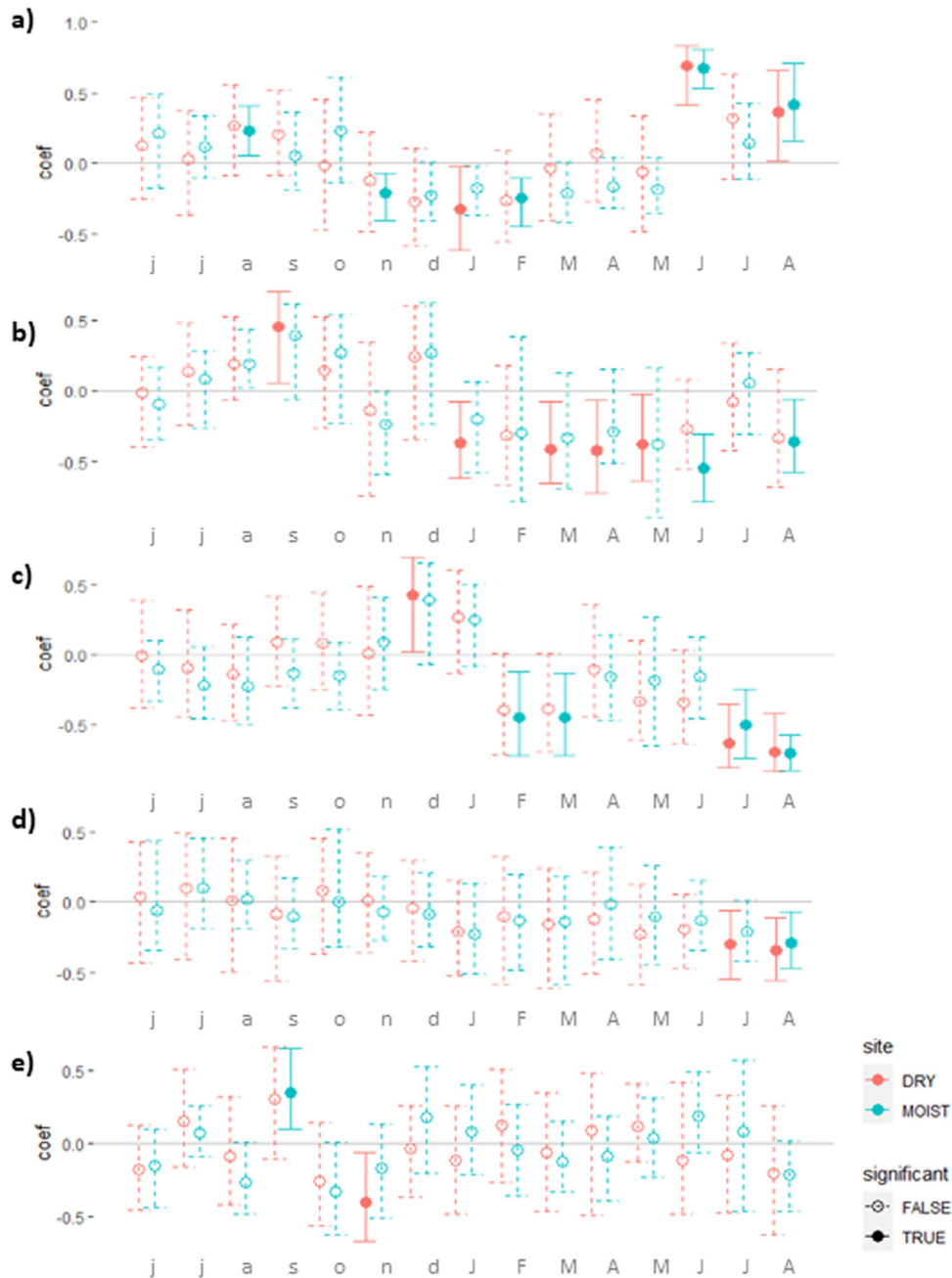
## Climate–Growth Relationships

### Site-Specific Chronologies

Climate–growth relationship analyses performed with TFS monthly mean climate variables (1989–2014) revealed the highest correlations between *Betula nana* growth and June temperature (Figure 3a). This positive relationship equaled  $r = 0.68$  (confidence Intervals (CI) = [0.39:0.84]) for the dry site and  $r = 0.67$  (CI = [0.52:0.80]) for the moist site. The strength of these relationships increased slightly with higher June growing-degree days (GDD) (Figure 4a), whereby the highest coefficients at the dry site were observed with the number of June GDD > 7 °C ( $r = 0.73$ ,  $P < 0.05$ ), and at the moist site with GDD > 8 °C ( $r = 0.72$ ,  $P < 0.05$ ) (Table S3). Notably, the strength of the correlation between radial growth and June GDD began to decrease with temperatures > 8 °C at the dry site, whereas it remained strong at the moist site for GDD temperatures > 10 °C ( $r = 0.72$ ,  $P < 0.05$ ) (Figure 4a). For every 1 °C increase in June air temperature, simple linear regression models (1989–2014) predicted a shrub ing-width increase of 11.1% (SE = 3%) and 12.2% (SE = 3%) for the dry and the moist site, respectively (Figure 4b–c).

Radial growth in both chronologies was also positively associated with August temperature, but correlations with July temperature were not significant at either site. Weaker but significant relationships were found between the growth of shrubs at the moist site and previous August temperature ( $r = 0.23$ ; CI = [0.06:0.40]), previous November temperature ( $r = -0.21$ ; CI = [-0.40: -0.06]), and current February temperature ( $r = -0.23$ ; CI = [-0.42: -0.09]). Additionally, for the shrubs growing at the dry site only, there was a significant negative correlation with current January temperature ( $r = -0.33$ ; CI = [-0.62: -0.04]) (Figure 3a). Moving correlation analyses revealed that both the positive relationship between growth and June temperature, and the negative relationship between growth and January temperatures, were more pronounced at the dry than at the moist site over a long-term period (1960–2014) (Figure S2).

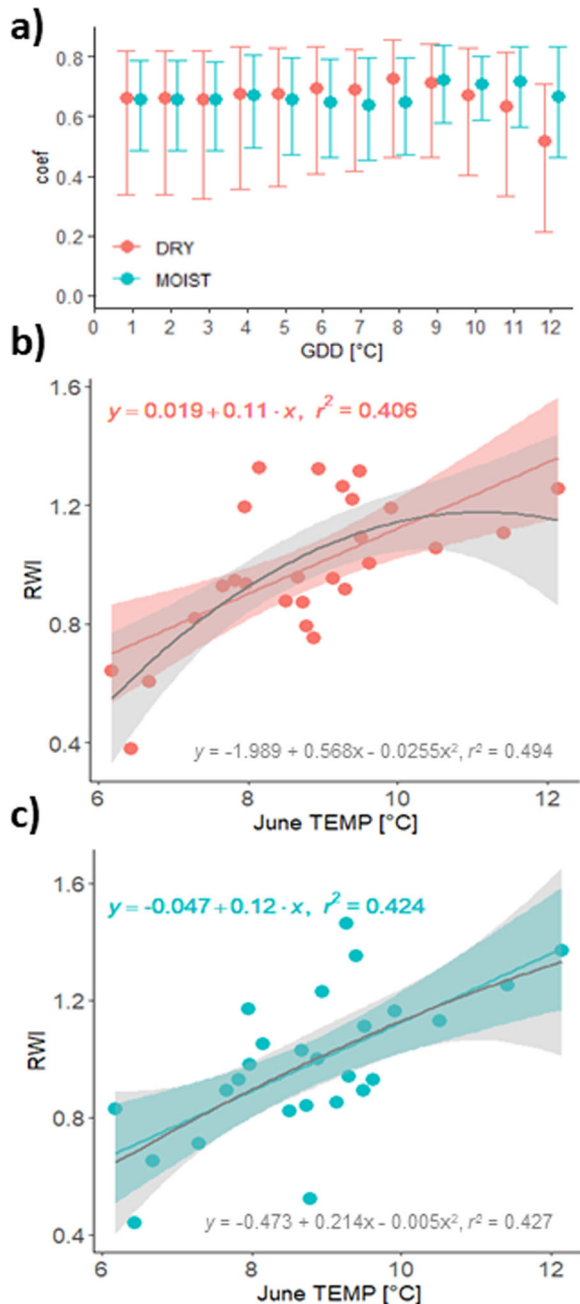
Mean radial growth of *Betula nana* at both sites was negatively associated with precipitation in the current year (Figure 3b). Radial growth in the moist site was negatively associated with June ( $r = -0.54$ ; CI = [-0.76: -0.28]) and August ( $r = -0.35$ ; CI = [-0.58: -0.05]) precipitation. In the dry site, *Betula nana* growth was negatively correlated with January ( $r = -0.36$ ; CI = [-



**Figure 3.** Bootstrapped correlation coefficients between standardized *Betula nana* chronology from the dry (red) and the moist (blue) site from Toolik Lake area and monthly **a** air temperature, **b** precipitation, **c** SPEI (scale = 2), **d** PDO and **e** AO index computed for the common period (1989–2014). Significant coefficients ( $P < 0.05$ ) together with associated confidence intervals (at the level of 95%) are marked with solid lines and filled dots. Monthly climatic variables include previous year (small letters, from June) to current year (capital letters, to August).

0.60:– 0.07]) and March-to-May precipitation, but positively correlated with previous September precipitation ( $r = 0.46$ ; CI = [0.06:0.72]). Additionally, shrub growth in both sites had negative relationships with July SPEI ( $r = -0.63$  and  $r = -0.51$  for the dry and moist site, respectively) and August SPEI ( $r = -0.70$  and  $r = -0.71$  for the dry

and moist site, respectively) (Figure 3c). Also, shrub growth at the dry site was negatively correlated with July PDO ( $r = -0.30$ ; CI = [– 0.56:– 0.06] and August PDO ( $r = -0.34$ ; CI = [– 0.57:– 0.11]). At the moist site, this relationship between growth and PDO was significant only for August ( $r = -0.29$ ; CI = [– 0.47:– 0.07]) (Fig-



**Figure 4.** a) Bootstrapped correlation coefficients between the dry (red) and the moist (blue) site *Betula nana* chronologies and various growing degree days (GDD) thresholds for the period (1989–2014); linear (color line) and quadratic (grey line) fits between June temperature and b) dry and c) moist site *Betula nana* growth (RWI, ring width index).

ure 3d). The relationship between *Betula nana* growth and previous November AO index was negative at the dry site ( $r = -0.39$ ; CI =  $[-0.66; -0.06]$ ). In contrast, the relationship between *Betula nana* growth at the moist site and

previous September AO index was positive ( $r = 0.34$ ; CI =  $[0.07; 0.63]$ ).

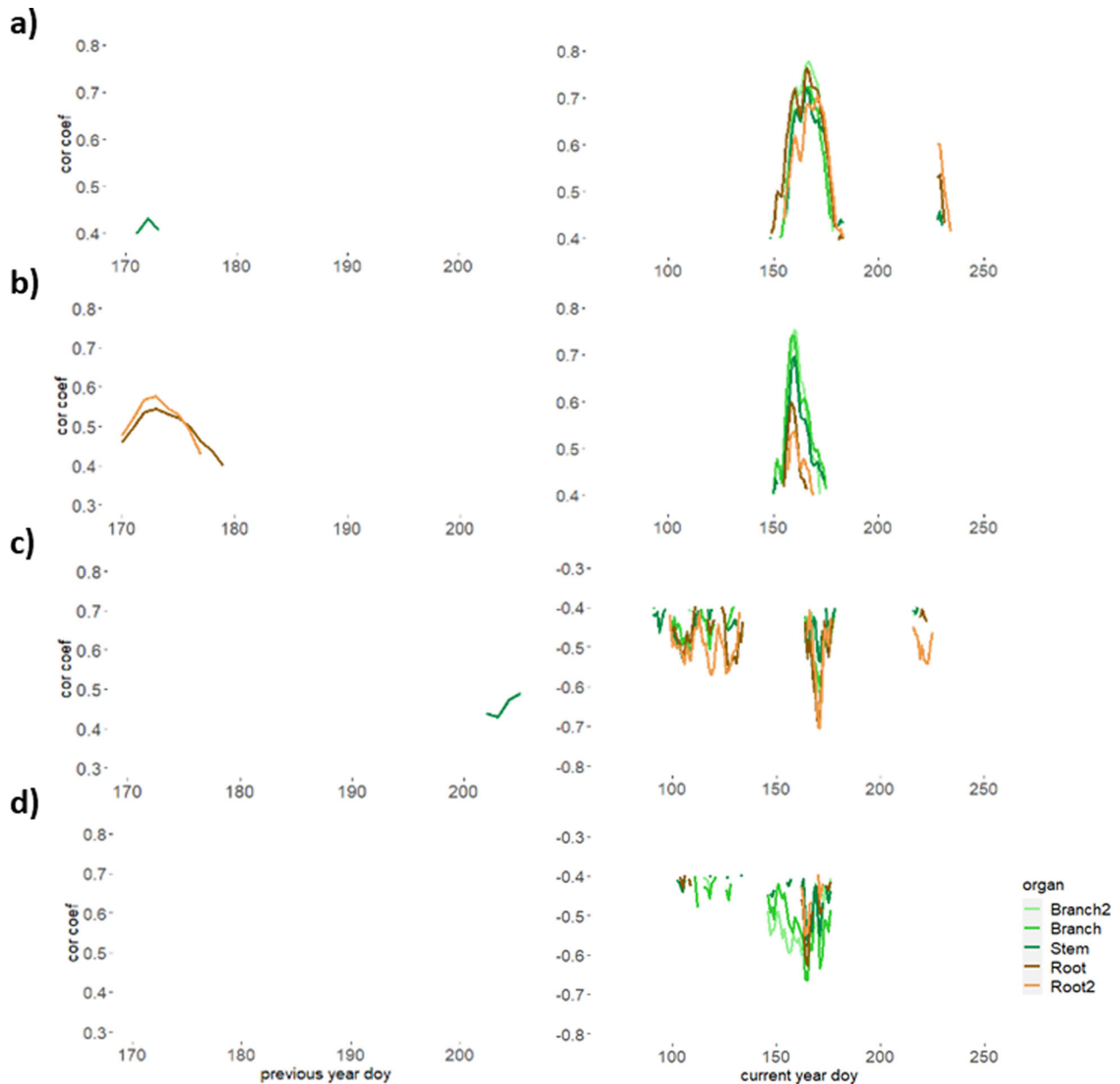
#### Organ-specific chronologies

Organ-specific chronologies revealed consistent correlations between *Betula nana* ring growth and mean monthly June temperatures at both sites (Figure S4); however, further temporal insights were revealed by moving correlation analyses using daily data (Fig. 5a–b). *Betula nana* growth at the dry site was positively associated with daily mean air temperature averaged over a 20-day period from the end of May (DOY = 150) to the end of June (DOY = 180), whereas for *Betula nana* growing at the moist site, this period was ten days shorter and ended on June 19 (DOY = 170). All organ chronologies, except for ‘Root2’ at the moist site, showed the strongest positive correlation coefficients with daily mean air temperature over the period June 8 (DOY = 159) through June 20 (DOY = 171) (Figure 5a–b). The strongest correlation coefficients for shrub growth at both sites were found for ‘Branch2’ chronologies (dry site:  $r = 0.78$ , June 16, DOY = 167; moist site:  $r = 0.75$ , June 9, DOY = 160). Additionally, growth in three of the dry site chronologies (‘Stem,’ ‘Root’ and ‘Root2’) was positively associated with temperature in the second part of August. In contrast, both below-ground chronologies (that is, ‘Root’ and ‘Root2’) from the moist site were positively correlated with daily mean air temperatures in the second part of the previous June, with the maximum correlation found for the ‘Root2’ chronology and daily mean air temperature for the previous June 22 ( $r = 0.57$ , pDOY = 173). Positive relationships between *Betula nana* growth in the dry site and previous year temperatures were observed only for the ‘Stem’ chronology and previous year’s mid-June daily mean air temperatures (Figure 5a).

Moving correlation analyses using daily precipitation data and organ-specific chronologies revealed negative relationships between shrub growth at both sites with June precipitation (Figure 5c–d). The strongest negative correlation with June precipitation was found for the ‘Root’ chronology at the dry site ( $r = -0.71$ , June 19, DOY = 170) and for the ‘Branch’ chronology at the moist site ( $r = -0.67$ , June 14, DOY = 165).

#### Spatial Correlation Analyses

Spatial correlation analyses indicated a significant positive relation between *Betula nana* chronologies from both sites and regional June air temperatures (1979–2014) (Figure 7). The extent of this rela-



**Figure 5.** Moving window correlation with (a, b) mean daily air temperatures and (c, d) precipitation (including current and previous year) for organ specific *Betula nana* chronologies from (a, c) the dry and (b, d) the moist site for the common period (1989–2014). Mean daily temperatures and precipitations were calculated for 20-day intervals using TFS climate data. Only significant ( $P < 0.05$ ) correlation coefficients are shown; doy—day of the year. Please note various Y-axis scales on the c and d panels between previous and current years.

tionship was especially pronounced across Alaska's North Slope and the neighboring Yukon territory, with correlation coefficients up to  $r = 0.6$  ( $P < 0.05$ ), as well as a weaker positive signal ( $r = 0.3$ ;  $P < 0.05$ ) with surface air temperature over the southern Beaufort Sea for the dry site. Additionally, there was a significant negative relationship between growth from both the dry and the moist site and current January temperature, with

the strongest signal evident in the interior of Alaska and northeastern Pacific Ocean (Figure S6), suggesting large-scale seasonal climate controls on *Betula nana* radial growth in the Toolik Lake area.

#### SEMs

The SEMs highlighted complex relationships between local summer temperature and regional climate. SEMs using either summer only or previous

autumn variables explained 21% and 22% of variance in inter-annual radial growth variation in the dry (Figure 8) and in the moist (Table S4) *Betula nana* chronologies, respectively. The SEMs further confirmed the strong positive relationship between shrub growth and June to August (JJA) temperature ( $\beta = 0.53$ ,  $P = 0.003$ ). Significant negative relationships were also revealed between summer Beaufort sea ice extent and summer temperatures ( $\beta = -0.31$ ,  $P = 0.050$ ) (1980–2014) (Figure 8a), and between previous autumn sea ice extent and current summer temperature ( $\beta = -0.36$ ,  $P = 0.023$ ) (Figure 8b). Moreover, SEMs highlighted a significant positive relation between summer PDO ( $\beta = 0.32$ ,  $P = 0.022$ ) and AO ( $\beta = 0.47$ ,  $P = 0.001$ ) indices on sea ice extent (Figure 8a), as well a positive impact of the previous autumn PDO index ( $\beta = 0.46$ ,  $P = 0.002$ ) on summer sea ice extent (Figure 8b). No significant effect of SPEI on shrub growth was recognized in the SEMs.

## DISCUSSION

### June Temperature Signal

Our analyses collectively demonstrate the high sensitivity of *Betula nana* growth to June temperature at both the plant and tissue level, and across both habitats. These findings are consistent with the spatially coherent June temperature sensitivity of *Salix pulchra* (Ackerman and others 2018), and mixed *Salix* spp. shrubs on Alaska's North Slope (Andreu-Hayles and others 2020). However, while a positive relation between tundra shrub growth and summer temperature is commonly observed (Myers-Smith and others 2015), our analyses also reveal that *Betula nana* was less sensitive to July temperature at the plant level compared to June, despite July being the warmest month of the year (Figure 3a). Indeed only weak relationships were found between July temperature and the dry sites 'Branch,' 'Stem,' and 'Root2' growth chronologies (Figure S4). These findings contrast with a nearby study of growth of *Alnus viridis* individuals, that showed sensitivity to both June and July temperatures (Tape and others 2012), and highlight variable, shrub-specific, growth sensitivities to climate.

We identified a critical temperature sensitivity period for *Betula nana* growth in mid-June (8 to 20 June). This period is slightly earlier than was observed for *Salix pulchra* from a nearby riparian site (end of June, Ackerman and others 2017), and shorter than for *Salix* spp. across the North Slope (31 May to early July, Andreu-Hayles and others

2020). However, the consistent June sensitivity signal among these studies suggests that regional to large-scale factors, such as temperature, are the primary drivers initiating shrub radial growth across northern Alaska, with local conditions being of secondary importance (for example, Bår and others 2008).

Notably, the coherent June temperature signal among our tissue-specific chronologies suggests that *Betula nana* has strong control over allocation to growth across different tissue types. These findings complement research in northern Sweden that proposed consistent plant resource economics across species' organs in a subarctic flora (Freschet and others 2010), and suggests that growth-ring patterns of *Betula nana*, especially at dry sites, can potentially be upscaled to represent whole plant performance. However, we acknowledge that further studies across a range of habitats and moisture gradients are required to verify this assumption, including comparison with other shrub species, which in the case of more diverse growth strategies between plant tissues and lower developmental plasticity in secondary growth might be less competitive than *Betula nana* (Bret-Harte and others 2002). For example, many tree-specific studies have revealed different patterns of growth allocation, indicating that growth trajectories might vary between plant organs (for example, Berntson and others 1995; Litton and Giardina 2008; Poorter and others 2012), which might apply to secondary growth of some tundra shrub species as well.

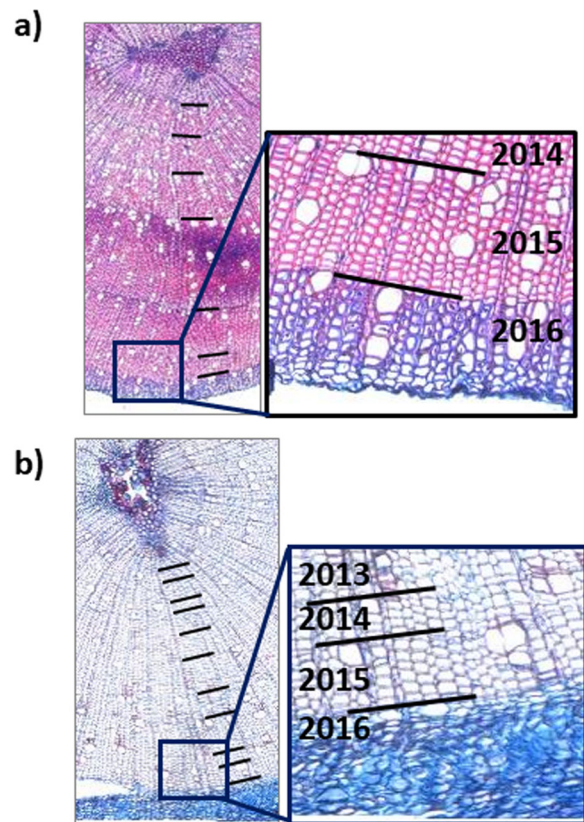
### Previous June Matters for Below-ground Growth in the Moist Site

At the moist site only, previous year June temperatures were positively related to growth for the 'Root' and the 'Root2' chronologies, specifically, temperatures from ca. June 19 (DOY = 170) to June 29 (DOY = 180) of the previous year (Figure 5b). For the 'Root2' chronology from the moist site, the previous year June temperature was of higher importance than the current year's June temperature. These findings suggest that below-ground growth of *Betula nana* in the moist sites relies on reserves stored in the second part of the previous June, that is, produced just after the peak of growth that is usually observed in mid-June. We might expect most reserves to be developed during maximum light abundance when the photoperiod is the longest, that is, mid-June in the Alaskan Arctic, and thus beneficial for tundra plant growth (Chapin and Shaver 1985).

To the contrary, positive growth relationships with previous June air temperatures were only weakly observed at the dry site and ‘Stem’ chronology (Figure 5a), where a potentially longer growing season might allow *Betula nana* shrubs to complete their growth using the current year’s photosynthate. It is widely recognized that conditions preceding the growing season, including in the previous year, can positively influence the current year’s radial growth of boreal trees (Babst and others 2013). In the case of tundra shrubs, this lag effect might relate to higher storage production in previous summers with favorable thermal conditions, or potentially higher microbial activity and nutrient availability during dormancy and/or early spring. For instance, tundra shrub growth in our study area was previously found to rely on stored reserves (Chapin and others 1986), and our study suggests that this specifically relates to the below-ground plant parts of *Betula nana* at the moist site. Growth of these parts, that is, the ‘Root’ and the ‘Root2’ chronologies, benefits from warmer conditions of the previous year and hence can potentially overcome less favorable growing conditions (such as colder soils) in the moist site. Moreover, our observation that moist site shrubs invest in multiple finer roots, thus potentially investing in more below-ground biomass than shrubs at the dry site, which invest in one main root, could further explain why more stored reserves are required for secondary growth of the below-ground tissues at the moist site. Additionally, shrubs in the moist tundra can potentially benefit from higher late winter net nitrogen mineralization rates compared to the dry site (Schimel and others 2004).

### Habitat Differences

Mean growth-ring widths for *Betula nana* from the dry site were almost double the size of those from the moist site, suggesting more favorable growing conditions and a longer growing season in the dry site. Similarly, a recent study revealed both an earlier start and a later end to the growing season for dwarf shrub tundra (that is, dry habitat) as compared to tussock tundra sites (moist habitat) across the North Slope of Alaska (Kelsey and others 2021). We also found a longer correlative period between shrub growth and daily temperature at the dry site (Figure 5a), further suggesting a longer period for cambial activity at the dry site compared to the moist. Our initial observations in the ‘Branch2’ tissues suggest that ring formation is more developed at the end of June in the dry site than in the moist site (Figure 6). Thus, despite high



**Figure 6.** Cambial activity observed in upper branch (that is, ‘Branch 2’) *Betula nana* cross sections from the (a) dry and (b) the moist site on June 28, 2016. The two examples show the most advanced cambial activity stages observed along entire branch circumference and were chosen among five randomly sampled shrub individuals in each habitat. Black horizontal lines delimit annual growth rings.

habitat coherence in the timing of maximum correlation between air temperature and secondary growth in both habitats, cambial activity is more advanced in the dry site, probably because of earlier onset of cambial activity. In part, this might also reflect a combination of the dry tundra site being snow-free earlier than the moist site, due to wind-scouring during winter (Welker and others 1997), as well as consistently warmer summer soil temperatures at the dry site (Figure S1).

Warmer soils in the dry site can enhance deeper thaw depth and potentially higher microbial activity (Schimel and others 2004), greater N availability thus favoring below-ground shrub growth in the dry tundra. Indeed, soil temperature in the moist site was on average 3 °C colder than in the dry site, and even at the end of the growing season stayed below 5 °C (Figure S1). Lower and less variable ambient temperature for below-ground tissue growth at the moist site could also be

the result of shading by dense shrub vegetation (Blok and others 2010), in contrast to the more sparsely vegetated dry heath tundra community. It has long been recognized that the soil environment is more important than the aerial environment in determining the range of productivity in tundra plants (Bell and Bliss 1978; Chapin and Shaver 1985), but shrub-growth studies are still lacking long-term comparisons with soil conditions. Thus, future studies should aim to evaluate shrub growth differences across habitats, specifically focusing on shrub growth-soil temperature and soil moisture interactions, preferably over a longer time scale.

Comparing shrub growth sensitivity to climate between dry and moist habitats is valuable for understanding the extent to which moisture might limit shrub growth (Ackerman and others 2017; Gamm and others 2018; Buchwal and others 2020; Francon and others 2020). In contrast to a previous study of *Betula nana* in Siberia (Li and others 2016), we found birch growth to be either insensitive to summer precipitation or negatively correlated with summer precipitation. Moreover, shrub growth at both sites was negatively correlated with summer SPEI, suggesting that radial growth of *Betula nana* was not constrained by moisture availability during our study period. There was no significant increase in mean summer air temperatures in the Toolik Lake region between 1989 and 2014 (Hobbie and others 2017). Thus, conditions for *Betula nana* growth might be relatively more stable in the Toolik region than in locations where summer climate warming is more apparent. However, the strength of the relationship between June temperature and growth at the dry site decreased with GDD temperatures  $> 8^{\circ}\text{C}$  (Figure 4a), whereas the threshold was  $> 10^{\circ}\text{C}$  at the moist site. These observations indicate that moisture might become more important for *Betula nana* growth at our dry site under warmer conditions in the future, in contrast to the moist site where moisture availability is less limiting. Hence, despite high coherence of *Betula nana* growth to June temperature revealed at both habitats, future studies should not overlook the importance of moisture on tundra shrub growth across biome.

### Impacts of Regional Climate on *Betula nana*

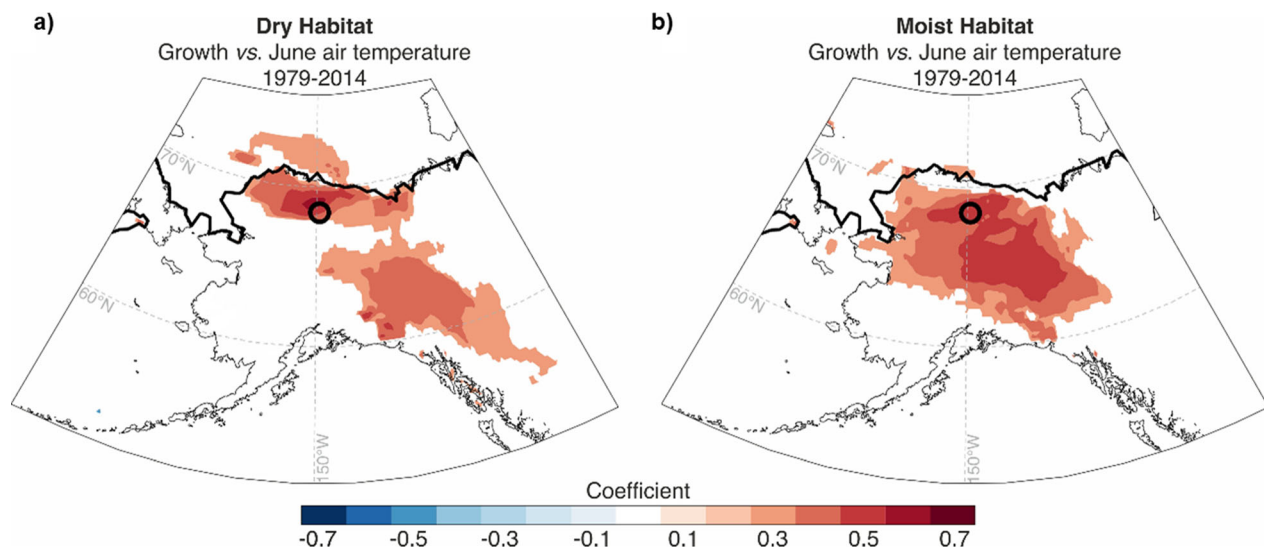
Our analyses demonstrate the ability of *Betula nana* to respond to, and archive, June air temperature changes within their annual growth rings. Specifically, for every  $1^{\circ}\text{C}$  increase in June air temperature we found an increase of 16.8 microns

(SE = 3.7; dry site) and 11.5 microns (SE = 2.2; moist site) in *Betula nana* mean ring widths, that is, an increase of 13.5% and 14.8%, respectively. This strong temperature-modulated response, combined with their relatively ubiquitous distribution, also highlights the potential application of *Betula nana* as a proxy for local and regional summer climate. While *Betula nana* chronologies are relatively short compared to tree rings, some of our specimens were 110 years old (Table S1) and extend beyond the available instrumental climate record.

Our coupled regional analyses show that Beaufort Sea ice extent has been an important factor modulating summer air temperatures over the North Slope, and thereby *Betula nana* growth (Figures 7 and 8). Sea ice conditions regulate the surface energy balance through the sea ice-albedo effect, typically resulting in warmer North Slope summers when ice is less extensive, and vice versa (Drobot and Maslanik 2003). Additionally, dynamic sea ice-atmospheric interactions can affect air temperatures across the North Slope (Wendler and others 2010) and influence transport of moisture from the ice-free portions of the Beaufort Sea into the Toolik Lake region (Klein and others 2015).

In particular, the strength and position of the Beaufort High (BH) governs regional sea ice conditions and is well expressed in the Arctic Oscillation (AO). For instance, low-ice summers typically occur when the BH is well defined over Arctic Canada (negative AO) and strong easterlies export ice out of the Beaufort Sea, thus increasing North Alaskan air temperatures (Figure 7) (Drobot and Maslanik 2003). These interactions might represent a potential mechanism for our observed link between the AO index, Beaufort SIE and *Betula nana* growth in our SEMs (Figure 8) and add to the growing body of empirical evidence that shows declining sea ice in this sector of the Arctic promotes shrub growth through regional warming (Bhatt and others 2014; Buchwal and others 2020).

Sea ice also controls the exchange of moisture between the ocean and the atmosphere (Klein and others 2015; Bailey and others 2021). The long-term negative relationship between winter Beaufort SIE and precipitation (Figure S3h) likely reflects increased open (ice-free) waters that supply precipitation to the North Slope (Klein and others 2015; Mellat and others 2021). However, there was no such link during summer in our SEMs (Figure 8), despite a negative relation between summer precipitation and *Betula nana* growth (Figure 3). These findings further suggest that *Betula nana* growth in the Toolik Lake region has been related



**Figure 7.** Spatial correlations between June surface air temperature (ERA5 data) and standardized *Betula nana* chronology from the (a) dry and (b) moist site. All correlations were computed for the period 1979–2014. All shaded contours are significant at the 95% level. Black circle indicates the Toolik study area, and the thick black lines depict the mean sea ice extent over the corresponding period (Fetterer and others 2017).

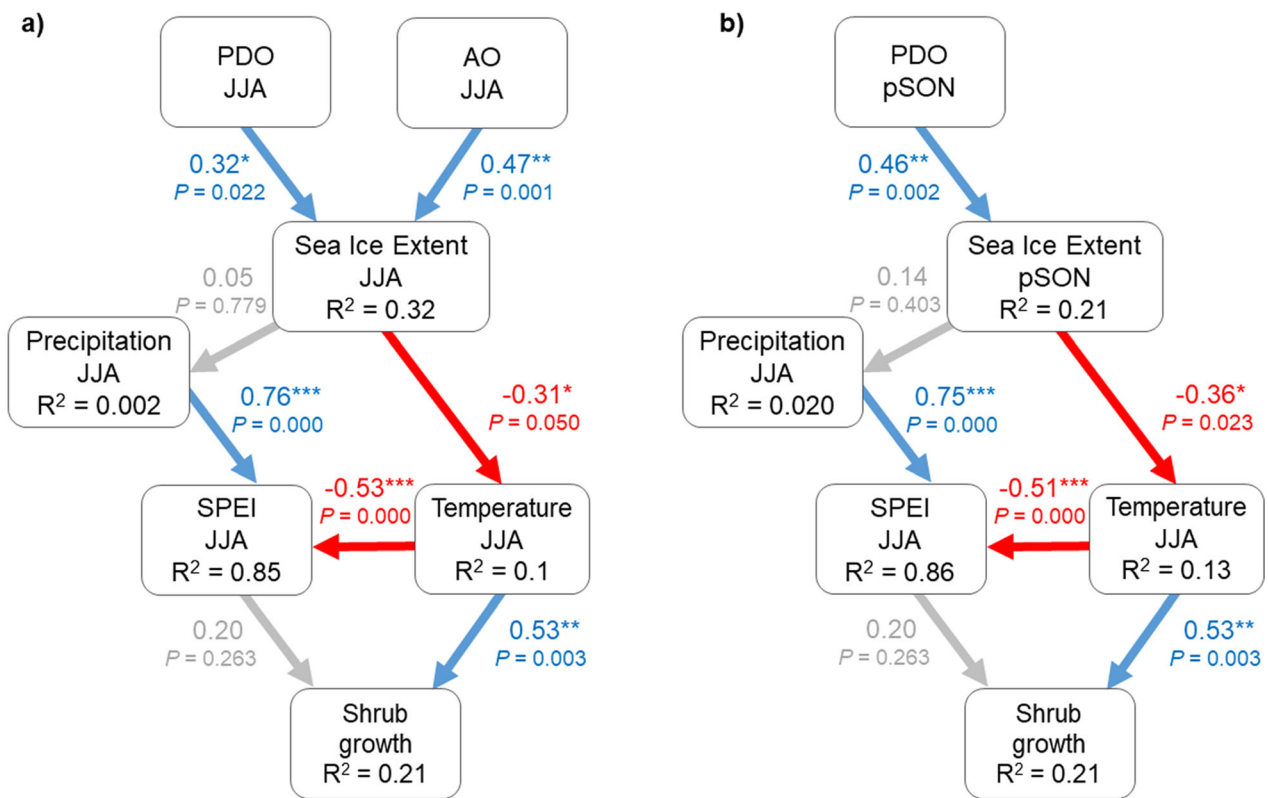
to Beaufort sea-ice variability through its effect on air temperatures, rather than local moisture variability, although this could change in the future as climate warms (Buchwal and others 2020) and moisture source transport patterns change (Mellat and others 2021).

Moisture limitation in northern Alaska has also been linked recently to divergent phases of the PDO (Lange and others 2020), and several Alaskan tree-ring series also captured PDO temperature and/or precipitation fluctuations (D'Arrigo and others 2001; Ohse and others 2012). We found that enhanced summer *Betula nana* growth was associated with a negative PDO phase (1980–2014) (Figure 3). Accordingly, over the same period we also found that negative PDO was associated with warmer surface air temperatures in North Alaska (Figure S5a), and thus, our PDO–shrub relationships are consistent with the positive temperature–growth responses we observed among all chronologies. However, the relationship between the PDO and surface climate in northern Alaska is variable and nonlinear. For instance, while the summer PDO–temperature relationship was negative in north Alaska between 1980 and 2014; the relationship was positive over the extended instrumental period from 1948 to 2020 (Figure S5b). Similarly, the relationship between *Betula nana* growth and mean monthly precipitation was generally positive (or neutral) for the period between 1960 and 1977, but became negative after about 1978, when enhanced *Betula nana* growth

was associated with reduced precipitation (Figure S2c). Notably, the timing of these switches coincided with a well-documented PDO regime shift in 1978 from a negative to positive phase (Hare and Mantua 2000). Hence, while our observed PDO–climate–shrub responses are coherent (1980–2014), the complex spatial–temporal surface expression of the PDO limits the ability of *Betula nana* to accurately capture its inherent variability over longer timescales (Figure 8 and Figure S3). However, these findings do not detract from the suitability of *Betula nana* as a credible proxy for summer air temperature, which is ultimately a more valuable indicator for assessing past climate changes and the processes driving them (for example, sea ice extent).

## CONCLUSIONS

High coherency of *Betula nana* shrub growth to a narrow window of June temperature was revealed in northern Alaska, across two diverse habitats and among below- versus above-ground plant tissues. *Betula nana* growth was especially sensitive to mid-June temperature, with below-ground shrub growth in the moist site also responding positively to previous year June temperatures. This strong dependence of *Betula nana* growth on temperature conditions in the early growing season indicates a high degree of control by the plant for coordinated allocation of resources to growth of its various organs, and might confer a competitive advantage.



**Figure 8.** Structural equation models (SEMs) relating shrubs growth (RWI—ring width index, 30 shrubs) from the dry site with local and pan-regional (a) summer and (b) previous autumn and summer climate for the period 1980–2014. Red and blue arrows indicate significant positive and negative relationships, respectively. Grey arrows indicate nonsignificant relationships. PDO—Pacific Decadal Oscillation index; AO—Arctic Oscillation index; SPEI—Standardized Precipitation Evapotranspiration Index; JJA—June–July–August; pSON—previous September–October–November. Sea ice extent refers to the Beaufort Sea; Model statistics: summer model (chisq = 13.13; df = 12; P value = 0.360; CFI = 0.988; AIC = 413.98), previous autumn–current summer model (chisq = 8.89; df = 8; P value = 0.352; CFI = 0.989; AIC = 414.28). \*— $P < 0.05$ ; \*\*— $P < 0.01$ ; \*\*\*— $P < 0.001$ . Results for the moist site were qualitatively similar and are shown in Table S4.

Results at the organ level were largely consistent with those obtained for the mean plant-level chronologies, but enabled more detailed insight into subtle differences in radial growth strategies between the shrubs from two sites and among the shrub parts. For example, in the moist site, the positive correlation between previous June and July air temperature and the below-ground chronologies was only revealed at the organ-level time series, when daily temperature variables were used.

Our coupled analyses show that Beaufort sea ice extent affects *Betula nana* growth by modulating Alaska's North Slope summer air temperatures, rather than through sea ice impacts on terrestrial moisture availability. A number of previous studies also documented a strong dependence of *Betula nana* growth on summer air temperature across

various arctic habitats (for example, Blok and others 2011; Ropars and others 2015; Hollesen and others 2015). In combination with our study on the coherent growth response of *Betula nana* tissues to June temperature, it suggests that this species could be a suitable proxy for summer temperature in other geographically similar areas of the Arctic, where instrumental records are either short in duration or not available. However, we acknowledge that our shrub sampling was spatially limited to one area, and future studies should focus on a wider range of *Betula nana* habitats to adequately assess and constrain its response to warmer and drier climates. We also recommend the inclusion of synoptic-scale climatic variables in future climate–shrub growth analyses to trace causal, yet often indirect, relationships between climate and shrub growth at a given tundra location.

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## DATA AVAILABILITY

The mean growth curves for individual shrubs (raw series) and standardized chronologies for each site used in this study are available at The International Tree-Ring Data Bank (ITRDB): moist site (Alaska AB, ITRDB AK189): <https://www.ncei.noaa.gov/access/paleo-search/study/36433> dry site (Alaska DB, ITRDB AK190): <https://www.ncei.noaa.gov/access/paleo-search/study/36434>

## REFERENCES

- Aanes R, Sæther BE, Smith FM, Cooper EJ, Wookey PA, Øritsland NA. 2002. The Arctic oscillation predicts effects of climate change in two trophic levels in a high-arctic ecosystem. *Ecology Letters* 5:445–453.
- Ackerman D, Griffin D, Hobbie SE, Finlay JC. 2017. Arctic shrub growth trajectories differ across soil moisture levels. *Global Change Biology* 23:4294–4302.
- Ackerman DE, Griffin D, Hobbie SE, Popham K, Jones E, Finlay JC. 2018. Uniform shrub growth response to June temperature across the north slope of Alaska. *Environmental Research Letters* 13:044013.
- Andreu-Hayles L, Gaglioti BV, Berner LT, Levesque M, Anchukaitis KJ, Goetz SJ, D'Arrigo A. 2020. A narrow window of summer temperatures associated with shrub growth in Arctic Alaska. *Environmental Research Letters* 15:105012.
- Andruko R, Danby R, Grogan P. 2020. Recent growth and expansion of birch shrubs across a low Arctic landscape in continental Canada: Are these responses more a consequence of the severely declining caribou herd than of climate warming? *Ecosystems* 23:1362–1379.
- Arndt KA, Santos MJ, Ustin S, Davidson SJ, Stow D, Oechel WC, Tran TTP, Graybill B, Zona D. 2019. Arctic greening associated with lengthening growing seasons in Northern Alaska. *Environmental Research Letters* 14:125018.
- Babst F, Poulter B, Trouet V, Tan K, Neuwirth B, Wilson R, Carrer M, Grabner M, Tegel W, Levanic T, Panayotov M, Urbinati C, Bouriaud O, Ciais P, Frank D. 2013. Site- and species-specific responses of forest growth to climate across the European continent. *Global Ecology and Biogeography* 22:706–717.
- Bailey H, Hubbard A, Klein ES, Mustonen KR, Akers PD, Marttila H, Welker JM. 2021. Arctic sea-ice loss fuels extreme European snowfall. *Nature Geoscience* 14:283–288.
- Bär A, Pape R, Bräuning A, Löffler J. 2008. Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences. *Journal of Biogeography* 35:625–636.
- Beck PSA, Goetz SJ. 2011. Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: ecological variability and regional differences. *Environmental Research Letters* 6:045501.
- Beguieria S, Vicente-Serrano SM. 2017. SPEI: calculation of the standardised precipitation-evapotranspiration index. Version 1.7, R package. <http://cran.r-project.org/web/packages/SPEI/index.html>
- Bell KL, Bliss LC. 1978. Root growth in a polar semidesert environment. *Canadian Journal of Botany* 56:2470–2490.
- Berntson GM, Farnsworth EJ, Bazzaz FA. 1995. Allocation, within and between organs, and the dynamics of root length changes in two birch species. *Oecologia* 101(4):439–447.
- Bhatt US, Walker DA, Walsh JE, Carmack EC, Frey KE, Meier WN, Moore SE, Parmentier FJW, Post E, Romanovsky VE, Simpson WR. 2014. Implications of Arctic Sea Ice Decline for the Earth System. *Annual Review of Environment and Resources* 39:57–89.
- Bhatt US, Walker DA, Raynolds MK, Bieniek PA, Epstein HE, Comiso JC, Pinzon JE, Tucker CJ, Steele M, Ermold W. 2017. Changing seasonality of panarctic tundra vegetation in relationship to climatic variables. *Environmental Research Letters* 12:055003.
- Bieniek PA, Walsh JE. 2017. Atmospheric circulation patterns associated with monthly and daily temperature and precipitation extremes in Alaska. *International Journal of Climatology* 37:208–217.
- Blok D, Heijmans MMPD, Schaepman-Strub G, Kononov AV, Maximov TC, Berendse F. 2010. Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Global Change Biology* 16:1296–1305.

- Blok D, Sass-Klaassen U, Schaepman-Strub G, Heijmans MMPD, Sauren P, Berendse F. 2011. What are the main climate drivers for shrub growth in Northeastern Siberian tundra? *Biogeosciences* 8:1169–1179.
- Bret-Harte MS, Shaver GR, Chapin FS III. 2002. Primary and secondary stem growth in arctic shrubs: implications for community response to environmental change. *Journal of Ecology* 90:251–267.
- Buchwal A, Weijers S, Blok D, Elberling B. 2019. Temperature sensitivity of willow dwarf shrub growth from two distinct High Arctic sites. *International Journal of Biometeorology* 63:167–181.
- Buchwal A, Sullivan PF, Macias-Fauria M, Post E, Myers-Smith I, Stroeve JC, Blok D, Tape KD, Forbes BC, Ropars P, Lévesque E, Elberling B, Angers-Blondin S, Boyle JS, Boudreau S, Boulanger-Lapointe N, Gamm C, Hallinger M, Rachlewicz G, Young A, Zetterberg P, Welker JM. 2020. Divergence of Arctic shrub growth associated with sea ice decline. *Proceedings of the National Academy of Sciences* 117(52):33334–33344.
- Bunn A, Korpela M, Biondi F, Campelo F, Mérian P, Qeadan F, Zang C, Pucha-Cofrep D, Wernicke J. 2018. dplR: Dendrochronology Program Library in R. R package version 1.6.9. <https://CRAN.R-project.org/package=dplR>
- Büntgen U, Hellmann L, Tegel W, Normand S, Myers-Smith I, Kirdyanov A, Nievergelt D, Schweingruber FH. 2015. Temperature-induced recruitment pulses of arctic dwarf shrub communities. *Journal of Ecology* 103:489–501.
- Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze E-D. 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* 108:583–595.
- Chapin FS, Shaver GR, Kedrowski RA. 1986. Environmental controls over carbon, nitrogen and phosphorus fractions in *Eriophorum vaginatum* in Alaskan tussock tundra. *Journal of Ecology* 74(1):167–195.
- Chapin FS, Shaver GR. 1985. Arctic. In: Chabot BF, Mooney HA, Eds. *Physiological Ecology of North American Plant Communities*. New York, London: Chapman and Hall. pp 16–40.
- Chen Y, Hu FS, Lara MJ. 2021. Divergent shrub-cover responses driven by climate, wildfire, and permafrost interactions in Arctic tundra ecosystems. *Global Change Biology* 27(3):652–663.
- D'Arrigo RD, Cook ER, Jacoby GC, Briffa KR. 1993. NAO and sea surface temperature signatures in tree-ring records from the North Atlantic sector. *Quaternary Science Reviews* 12(6):431–440.
- D'Arrigo RD, Villalba R, Wiles G. 2001. Tree-ring estimates of Pacific decadal climate variability. *Climate Dynamics* 18:219–224.
- Drobot SD, Maslanik JA. 2003. Interannual variability in summer Beaufort Sea ice conditions: Relationship to winter and summer surface and atmospheric variability. *Journal of Geophysical Research: Oceans* 108(C7):3233.
- Environmental Data Center Team. 2020. Meteorological monitoring program at Toolik, Alaska. Toolik Field Station, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775. [http://toolik.alaska.edu/edc/abiotic\\_monitoring/data\\_query.php](http://toolik.alaska.edu/edc/abiotic_monitoring/data_query.php)
- Epstein HE, Walker DA, Frost GV, Raynolds MK, Bhatt U, Daanen R, Forbes B, Geml J, Kaarlejarvi E, Khitun O, Khomutov A, Kuss P, Leibman M, Matyshak G, Moskalenko N, Orekhov P, Romanovsky VE, Timling I. 2021. Spatial patterns of arctic tundra vegetation properties on different soils along the Eurasia Arctic Transect, and insights for a changing Arctic. *Environmental Research Letters* 16:014008.
- Fetterer F, Knowles K, Meier WN, Savoie M, Windnagel AK. 2017. Sea Ice Index, Version 3. [G02135/seaiice\_analysis/Sea\_Ice\_Index\_Regional\_Monthly\_Data\_G02135\_v3.0]. Boulder, Colorado USA. NSIDC: National Snow and Ice Data Center. <https://doi.org/10.7265/N5K072F8>. [access date: May 20, 2020]
- Francon L, Corona C, Till-Bottraud I, Carlson BZ, Stoffel M. 2020. Some (do not) like it hot: shrub growth is hampered by heat and drought at the alpine treeline in recent decades. *Annals of Botany* 107(4):1–11.
- Freschet GT, Cornelissen JHC, van Logtestijn RSP, Aerts R. 2010. Evidence of the 'plant economics spectrum' in a sub-arctic flora. *Journal of Ecology* 98(2):362–373.
- Gaglioti BV, Mann DH, Wooller MJ, Jones BM, Wiles GC, Groves P, Kunz ML, Baughman CA, Reanier RE. 2017. Younger-Dryas cooling and sea-ice feedbacks were prominent features of the Pleistocene-Holocene transition in Arctic Alaska. *Quaternary Science Reviews* 169:330–343.
- Gamm CM, Sullivan PF, Buchwal A, Dial RJ, Young AB, Watts DA, Cahoon SMP, Welker JM, Post E. 2018. Declining growth of deciduous shrubs in the warming climate of continental western Greenland. *Journal of Ecology* 106:640–654.
- Grissino-Mayer HD. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research* 57:205–221.
- Hamilton TD. 2003. Glacial Geology of the Toolik Lake and upper Kuparuk River regions. In: Walker DA, Ed. *Biology Papers*, University of Alaska 26, Fairbanks, AK: University of Alaska, Institute of Arctic Biology. p 24p.
- Hantemirov R, Shiyatov S, Gorlanova L. 2011. Dendroclimatic study of Siberian juniper. *Dendrochronologia* 29:119–122.
- Hare SR, Mantua NJ. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47(2–4):103–145.
- Harris IC, Jones PD. 2019. CRU TS4.02: Climatic Research Unit (CRU) Time-Series (TS) version 4.02 of high-resolution gridded data of month-by-month variation in climate (Jan. 1901–Dec. 2017). Centre for Environmental Data Analysis, University of East Anglia Climatic Research Unit, 01 April 2019. <https://doi.org/10.5285/b2f819124257c4188b181a4d8b0a46bff>.
- Hersbach H, Bell B, Berrisford P, Hirahara S, Horányi A, Muñoz-Sabater J, Nicolas J, Peubey C, Radu R, Schepers D, Simmons A, Soci C, Abdalla S, Abellan X, Balsamo G, Bechtold P, Biais G, Bidlot J, Bonavita M, De Chiara G, Dahlgren P, Dee D, Diamantakis M, Dragani R, Flemming J, Forbes R, Fuentes M, Geer A, Haimberger L, Healy S, Hogan RJ, Hólm E, Janisková M, Keeley S, Laloyaux P, Lopez P, Lupu C, Radnoti G, de Rosnay P, Rozum I, Vamborg F, Villaume S, Thépaut JN. 2020. The ERA5 global reanalysis. *Quarterly Journal of the Royal Meteorological Society* 146:1999–2049.
- Hobbie JE, Shaver GR, Rastetter EB, Cherry JE, Goetz SJ, Guay KC, Gould WA, Kling GW. 2017. Ecosystem responses to climate change at a Low Arctic and a High Arctic long-term research site. *Ambio* 46:160–173.
- Hollesen J, Buchwal A, Rachlewicz G, Hansen BU, Hansen MO, Stecher O, Elberling B. 2015. Winter warming as an important co-driver for *Betula nana* growth in western Greenland during the past century. *Global Change Biology* 21:2410–2423.
- Holmes R. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43:69–78.

- Jevšenak J, Levanic T. 2018. dendroTools: R package for studying linear and nonlinear responses between tree-rings and daily environmental data. *Dendrochronologia* 48:32–39.
- Kelsey KC, Pedersen SH, Leffler AJ, Sexton JO, Feng M, Welker JM. 2021. Winter snow and spring temperature have differential effects on vegetation phenology and productivity across Arctic plant communities. *Global Change Biology* 27(8):1572–1586.
- Kim H, Yeh SW, An SI, Song SY. 2020. Changes in the role of Pacific decadal oscillation on sea ice extent variability across the mid-1990s. *Scientific Reports* 10:17564.
- Klein E, Cherry J, Cable J, Noone D, Leffler J, Welker JM. 2015. Arctic cyclone water vapor isotopes support past sea ice retreat recorded in Greenland ice. *Scientific Reports* 5:10295.
- Kolishchuk V. 1990. Dendroclimatological study of prostrate woody plant. In: Cook ER, Kairiukstis LA, Eds. *Methods of dendrochronology applications in the environmental sciences*, . Dordrecht: Kluwer Academic Publishers. pp 51–55.
- Lange J, Carrer M, Pisarcic MFJ, Porter TJ, Seo J-W, Trouillier M, Wilmking M. 2020. Moisture-driven shift in the climate sensitivity of white spruce xylem anatomical traits is coupled to large-scale oscillation patterns across northern treeline in northwest North America. *Global Change Biology* 26:1842–1856.
- Lara MJ, Nitze I, Grosse G, Martin P, McGuire D. 2018. Reduced arctic tundra productivity linked with landform and climate change interactions. *Scientific Reports* 8:2345.
- Li B, Heijmans MMPD, Berendse F, Blok D, Maximov T, Sass-Klaassen U. 2016. The role of summer precipitation and summer temperature in establishment and growth of dwarf shrub *Betula nana* in northeast Siberian tundra. *Polar Biology* 39:1245–1255.
- Lindsay RW, Zhang J. 2005. The Thinning of Arctic Sea Ice, 1988–2003: Have We Passed a Tipping Point? *Journal of Climate* 18:4879–4894.
- Litton CM, Giardina CP. 2008. Below-ground carbon flux and partitioning: Global patterns and response to temperature. *Functional Ecology* 22(6):941–954.
- Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of American Meteorological Society* 78:1069–1079.
- Mellat M, Bailey H, Mustonen K-R, Marttila H, Klein ES, Gribanov K, Bret-Harte MS, Chupakov AV, Divine DV, Else B, Filippov I, Hyöky V, Jones S, Kirpotin SN, Kroon A, Markussen HT, Nielsen M, Olsen M, Paavola R, Pokrovsky OS, Prokushkin A, Rasch M, Raundrup K, Suominen O, Syvänpää I, Vignissin SR, Zarov E, Welker JM. 2021. Hydroclimatic Controls on the Isotopic ( $\delta^{18}\text{O}$ ,  $\delta^2\text{H}$ , d-excess) Traits of Pan-Arctic Summer Rainfall Events. *Frontiers in Earth Science* 9:651731.
- Myers-Smith IH, Forbes BC, Wilmking M, Hallinger M, Lantz T, Blok D, Tape KD, Macias-Fauria M, Sass-Klaassen U, Lévesque E, Boudreau S, Ropars P, Hermanutz L, Trant A, Collier LS, Weijers S, Rozema J, Sa Rayback, Schmidt NM, Schaepman-Strub G, Wipf S, Rixen C, Ménard CB, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen V, Welker J, Grogan P, Epstein HE, Hik DS. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* 6:45509.
- Myers-Smith IH, Elmendorf SC, Beck PSA, Wilmking M, Hallinger M, Blok D, Tape KD, Rayback SA, Macias-Fauria M, Forbes BC, Speed JDM, Boulanger-Lapointe N, Rixen C, Lévesque E, Schmidt NM, Baittinger C, Trant AJ, Hermanutz L, Collier LS, Dawes MA, Lantz TC, Weijers S, Jorgensen RH, Buchwal A, Buras A, Naito AT, Ravolainen V, Schaepman-Strub G, Wheeler JA, Wipf S, Guay KC, Hik DS, Vellend M. 2015. Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change* 5:887–891.
- Myers-Smith IH, Kerby JT, Phoenix GK, Bjerke JW, Epstein HE, Assmann JJ, John C, Andreu-Hayles L, Angers-Blondin S, Beck PSA, Berner LT, Bhatt US, Bjorkman AD, Blok D, Bryn A, Christiansen CT, Hans J, Cornelissen C, Cunliffe AM, Elmendorf SC, Forbes BC, Goetz SJ, Hollister RD, De Jong R, Lorant MM, Macias-Fauria M, Maseyk K, Normand S, Olofsson J, Parker TC, Parmentier F-JW, Post E, Schaepman-Strub G, Stordal F, Sullivan PF, Thomas HJD, Tømmervik H, Treharne R, Tweedie CE, Walker DA, Wilmking M, Wipf S. 2020. Complexity revealed in the greening of the Arctic. *Nature Climate Change* 10:106–117.
- Nielsen SS, von Arx G, Damgaard CF, Abermann J, Buchwal A, Büntgen U, Treier UA, Barfod AS, Normand S. 2017. Linking spatio-temporal variability of climate, xylem anatomical features, and growth of *Betula nana* from Western Greenland. *Arctic, Antarctic and Alpine Research* 49(3):359–371.
- Ogi M, Rysgaard S, Barber DG. 2016. Importance of combined winter and summer Arctic Oscillation (AO) on September sea ice extent. *Environmental Research Letters* 11:034019.
- Ohse B, Jansen F, Wilmking M. 2012. Do limiting factors at Alaskan treelines shift with climatic regimes? *Environmental Research Letters* 7:015505.
- Opala-Owczarek M, Owczarek P, Łupikasza E, Boudreau S, Migala K. 2020. Influence of climatic conditions on growth rings of *Salix uva-ursi* Pursh from the southeastern shore of Hudson Bay, Subarctic Canada. *Arctic, Antarctic and Alpine Research* 52(1):87–102.
- Phoenix GK, Bjerke JW. 2016. Arctic browning: extreme events and trends reversing arctic greening. *Global Change Biology* 22:2960–2962.
- Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* 193(1):30–50.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Ropars P, Lévesque E, Boudreau S. 2015. How do climate and topography influence the greening of the forest-tundra ecotone in northern Quebec? A dendrochronological analysis of *Betula glandulosa*. *Journal of Ecology* 103(3):679–690.
- Ropars P, Angers-Blondin S, Gagnon M, Myers-Smith IH, Lévesque E, Boudreau S. 2017. Different parts, different stories: climate sensitivity of growth is stronger in root collars vs. stems in tundra shrubs. *Global Change Biology* 23(8):3281–3291.
- Rosseel Y. 2012. lavaan: An R package for structural equation modeling. *Journal of Statistical Software* 48:1–36.
- Schimel JP, Billbrough C, Welker JM. 2004. Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology and Biochemistry* 36:217–227.
- Schweingruber FH, Poschod P. 2005. Growth rings in herbs and shrubs: life span, age determination and stem anatomy. *Forest Snow and Landscape Research* 79:195–415.

- Screen JA, Francis JA. 2016. Contribution of sea-ice loss to Arctic amplification is regulated by Pacific Ocean decadal variability. *Nature Climate Change* 6:856–860.
- Shaver G. 2019. A multi-year DAILY weather file for the Toolik Field Station at Toolik Lake, AK starting 1988 to present. ver 4. Environmental Data Initiative. <https://doi.org/10.6073/pasta/ce0f300cdf87ec002909012abefd9c5c> (Accessed 2021-02-01).
- Tape KD, Hallinger M, Welker JM, Ruess RW. 2012. Landscape heterogeneity of shrub expansion in Arctic Alaska. *Ecosystems* 15:711–724.
- Thompson DW, Wallace JM. 1998. The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. *Geophysical Research Letters* 25(9):1297–1300.
- Thornthwaite CW. 1948. An approach toward a rational classification of climate. *Geographical Review* 38(1):55–94.
- Trouet V, van Oldenborgh GJ. 2013. KNMI climate explorer: a web-based research tool for high-resolution paleoclimatology. *Tree Ring Research* 69:3–13.
- Vicente-Serrano SM, Beguería S, López-Moreno JI. 2010. A Multi-scalar drought index sensitive to global warming: The Standardized Precipitation Evapotranspiration Index - SPEI. *Journal of Climate* 23:1696–1718.
- Weijers S, Buchwal A, Blok D, Löffler J, Elberling B. 2017. High Arctic summer warming tracked by increased *Cassiope tetragona* growth in the world's northernmost polar desert. *Global Change Biology* 23(11):5006–5020.
- Weijers S, Beckers N, Löffler L. 2018. Recent spring warming limits near-treeline deciduous and evergreen alpine dwarf shrub growth. *Ecosphere* 9(6):e02328.
- Welker JM, Molau U, Parsons AN, Robinson C, Wookey PA. 1997. Response of *Dryas octopetala* to ITEX manipulations: A synthesis with circumpolar comparisons. *Global Change Biology* 3:61–73.
- Welker JM, Rayback SA, Henry GHR. 2005a. Arctic and North Atlantic oscillation phase changes are recorded in the isotopes ( $\delta^{18}\text{O}$  &  $\delta^{13}\text{C}$ ) of *Cassiope tetragona* plants. *Global Change Biology* 11:997–1002.
- Welker JM, Fahnestock JT, Sullivan PF, Chimner RA. 2005b. Leaf mineral nutrition of Arctic plants in response to warming and deeper snow in northern Alaska. *Oikos* 109:167–177.
- Wendler G, Shulski M, Moore B. 2010. Changes in the climate of the Alaskan North Slope and the ice concentration of the adjacent Beaufort Sea. *Theoretical and Applied Climatology* 99(1):67–74.
- Wigley TML, Briffa KR, Jones PD. 1984. On the average value of correlated time-series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology* 23:201–213.
- Young AB, Watts DA, Taylor AH, Post E. 2016. Species and site differences influence climate-shrub growth responses in West Greenland. *Dendrochronologia* 37:69–78.
- Zang C, Biondi F. 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. *Ecography* 38:431–436.