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**Title:** Declining growth of deciduous shrubs in the warming climate of continental western Greenland

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29 **Running Headline:** Declining growth of arctic shrubs

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33 **Summary**

- 34 1. Observational and experimental studies have generally shown that warming is associated with  
35 greater growth and abundance of deciduous shrubs in arctic ecosystems. It is uncertain,  
36 however, if this trend will persist in the future.
- 37 2. Our study examined growth responses of deciduous shrubs to climate change over the late 20<sup>th</sup>  
38 and early 21<sup>st</sup> centuries near Kangerlussuaq in western Greenland. We combined shrub  
39 dendrochronology, stable isotope analysis and weekly measurements of leaf gas exchange to  
40 examine the drivers of secondary growth in two widespread and dominant deciduous shrub  
41 species: *Salix glauca* and *Betula nana*.
- 42 3. *Betula* showed a dramatic growth decline beginning in the early 1990s, when correlations  
43 between growing season air temperature and growth shifted from neutral to strongly negative.  
44 *Salix* also showed a growth decline, but it began slightly later and was more pronounced among  
45 older stems. May-August mean air temperature of ~7°C appeared to be an important threshold.
- 46 4. Carbon isotope discrimination ( $\Delta^{13}\text{C}$ ) in  $\alpha$ -cellulose of *Salix* growth rings declined strongly during  
47 the period of reduced growth, suggesting drought-induced stomatal closure as a possible cause.  
48 Leaf gas exchange of *Salix* was also highly sensitive to seasonal variation in moisture availability.  
49 *Betula* growth declined more dramatically than *Salix*, but leaf gas exchange was less sensitive to  
50 moisture availability and there was less evidence of a  $\Delta^{13}\text{C}$  trend. We hypothesize that the  
51 dramatic *Betula* growth decline might reflect the combined effects of increasing moisture  
52 limitation, repeated defoliation during recent moth outbreaks and greater browsing by a  
53 growing muskoxen population.

54 Synthesis. Our findings contrast with widespread observations of increasing shrub growth in the  
55 Arctic and instead point to a potential decline in the flux of carbon into a pool with a long mean

56 residence time (wood). While our study area is warmer and drier than much of the Arctic, our  
57 results may serve as an early indicator of potential effects of rising temperature in other arctic  
58 ecosystems.

59 **Key Words:** *Betula nana*; carbon isotope; dendrochronology; herbivory; moisture limitation; *Salix*  
60 *glauca*; shrub-ring; stomatal conductance

## 61 **Introduction**

62 Deciduous shrub expansion in arctic tundra has been widespread in recent decades (e.g., Sturm  
63 et al. 2001; Tape et al. 2006; Myers-Smith et al. 2011; Hill & Henry 2011; Naito and Cairns 2011).  
64 Similarly, syntheses of experimental warming (Walker et al. 2006; Elmendorf et al. 2012a) and long-term  
65 plot-level monitoring studies (Elmendorf et al. 2012b) have generally shown increases in height and  
66 cover of deciduous shrubs throughout the tundra biome. However, several studies have also shown  
67 that shrub growth and abundance responses to warming depend upon soil moisture, with more positive  
68 responses observed in wetter areas (Elmendorf et al. 2012a; Elmendorf et al. 2012b; Myers-Smith et al.  
69 2015; Ackerman et al. 2017). These findings indicate that soil moisture may be an important mediator  
70 of shrub growth and abundance responses to warming, either directly (moisture limitation of  
71 photosynthesis, growth and/or reproduction) or indirectly (moisture effects on soil temperature, active  
72 layer depth, nutrient availability, etc.).

73 Arctic landscapes exhibit a wide variety of moisture regimes, as a result of variation in  
74 topographic position, snow distribution, soil type and the presence or absence of permafrost.  
75 Vegetation type is highly correlated with soil moisture, but it has long been thought that effects of soil  
76 moisture on arctic ecosystems are predominantly indirect, with vegetation productivity controlled by  
77 related factors such as nutrient availability (e.g., Chapin & Shaver 1985; Gold & Bliss 1995). Historically,  
78 moisture availability has not been thought to directly limit plant growth in most low arctic ecosystems  
79 (Oberbauer & Dawson 1992). However, plant water relations in arctic tundra are expected to change in  
80 response to rising air temperature, increasing evaporative demand and potential shifts in the amount  
81 and seasonality of precipitation. Annual air temperature on the west coast of Greenland is projected to  
82 be ~2°C warmer between 2021 and 2050 than it was between 1961 and 1990, with the greatest changes  
83 anticipated in winter and spring (Stendel et al. 2008). Precipitation is expected to increase in most areas  
84 of the Arctic, and an increase of 15% is predicted over the same time period in western Greenland  
85 (Stendel et al. 2008). Model projections of future climate scenarios are inherently uncertain due to  
86 differences in climate at regional scales. Moreover, climate models often lack direct observations  
87 required to evaluate model strength, especially in the Arctic. It is particularly uncertain whether greater

88 precipitation in the Arctic will compensate for the expected increase in evaporative demand associated  
89 with rising temperature. It is even more difficult to predict how changes in climate may lead to changes  
90 in soil moisture as a result of permafrost thaw.

91 Our study aimed to quantify the growth responses of arctic shrubs to climate change over the  
92 late 20<sup>th</sup> and early 21<sup>st</sup> centuries near Kangerlussuaq in western Greenland. We combined shrub  
93 dendrochronology, stable isotope analysis and weekly measurements of leaf gas exchange to examine  
94 the drivers of secondary growth in two widespread and dominant deciduous shrub species: *Salix glauca*  
95 and *Betula nana*. Recent work in our study area examined the sensitivity of coexisting *B. nana* and a  
96 dominant graminoid, *Poa pratensis*, to seasonal declines in moisture availability. Results showed that  
97 leaf gas exchange of *B. nana* was relatively insensitive to warm and dry conditions, compared to *P.*  
98 *pratensis*, which showed strong reductions in stomatal conductance ( $G_s$ ) at mid-day and during warm  
99 and dry periods (Cahoon et al. 2016a). Based on recent results in our study area, evidence from the  
100 literature indicating that summer air temperature is positively correlated with growth of arctic shrubs  
101 (Forbes et al. 2010; Macias-Fauria et al. 2012; Jørgensen et al 2015; Hollesen et al. 2015; but see Myers-  
102 Smith et al. 2015) and the general consensus that water availability does not strongly limit low arctic  
103 plant productivity, we hypothesized a positive and linear relationship between growing season air  
104 temperature and secondary growth of both shrub species. However, precipitation in our study area is  
105 very low (<250 mm/year), and evaporative demand is relatively high for the Arctic. Therefore, if  
106 moisture limitation is an important constraint on shrub growth anywhere in the Arctic, the  
107 Kangerlussuaq region is among the most likely locations.

## 108 **Materials and Methods**

### 109 Site Description

110 The study area (67.11°, -50.34°) is located ~ 150 km inland from the Greenland coast and ~20 km  
111 northeast of the village of Kangerlussuaq, Greenland. The landscape is composed of a mosaic of  
112 deciduous shrub and graminoid tundra. The dominant species are the deciduous shrubs, *Betula nana*  
113 (hereafter *Betula*) and *Salix glauca* (hereafter *Salix*), and the graminoids, *Poa* spp. and *Carex* spp. (Thing  
114 1984). Kangerlussuaq has a relatively dry, continental climate with mean annual precipitation of 229  
115 mm and mean annual temperature of -4.8°C, as estimated by the CRU TS 3.24.01 gridded climate  
116 dataset (1901-2015; Harris et al. 2014). July is the warmest month, with a mean air temperature of  
117 10.0°C. The study area is underlain by continuous permafrost and maintains only patchy snow cover  
118 during winter, with shallow snow (<20 cm depth) generally present among the deciduous shrubs and  
119 absent in areas dominated by graminoids. Soils in the study area thaw to a maximum depth of ~50 cm.

## 120 Estimates of Historical Shrub Growth and Water Relations

### 121 *Field Sampling*

122 Stem discs were collected from *Betula* and *Salix* as close as possible to the ground surface from  
123 a total of seven sites over a ten-year period (Table 1, Figure 1). Samples were collected from the largest  
124 stem of each selected shrub. The goal of sampling shrubs from numerous sites was to incorporate  
125 potential landscape variation in climate-growth relationships and produce shrub-ring chronologies  
126 representative of a relatively large area (~11 km<sup>2</sup>). Our goal was not to examine the magnitude and  
127 drivers of site-level variation, as these questions were addressed in an earlier study that included some  
128 of the same sites and samples (Young et al. 2016). Discs sampled in 2005 and 2007 were selected based  
129 on diameter in an effort to obtain the longest chronology possible (Haredalen, Kodalen and Storedalen  
130 sites). Discs collected during 2011 were selected by establishing a 100 m transect at each of the Long  
131 Lake 1, Long Lake 2 and Sandflugtsdalen sites (Young et al. 2016). Each transect was divided into ten 10  
132 m<sup>2</sup> quadrats and five stems each of *Salix* and *Betula* were cut at the root collar from every other  
133 quadrat. Discs sampled during 2014 were selected by establishing five 30 m parallel transects with stem  
134 discs of each species collected every 6 m along each transect (West site).

### 135 *Sample Selection*

136 The samples collected in 2005, 2007 and 2011 were sanded, stained, aged and measured with a  
137 sliding bench micrometer (Velmex Inc. Bloomfield, NY). A sub-set of samples from each site (Table 1)  
138 with the highest inter-series correlation were selected for re-measurement using the thin section and  
139 imaging method described below. Only one disc per shrub was included in our shrub-ring chronologies.  
140 However, serial sectioning was employed on a sub-set of the stems to ensure accurate dating, which  
141 was facilitated by the presence of clear marker rings associated with moth outbreaks in recent decades  
142 (Young et al. 2016). All of the samples collected from the West site in 2014 were analyzed using the thin  
143 section and imaging method. A sub-set of 9 discs of each species from the West site were selected for  
144 inclusion in the master chronologies with the objective of maximizing both chronology length and inter-  
145 series correlation.

### 146 *Ring Width Measurements*

147 Sample cutting and staining methods were adapted from Schweingruber and Poschlod (2005).  
148 Discs selected for measurement using the thin section and imaging method were soaked in water for a  
149 minimum of one hour to rehydrate the tissue. The bark was removed to improve cutting precision. Thin  
150 sections ~15-20 µm thick were cut from the discs using a GSL-1 sledge microtome and placed on glass  
151 slides. For samples that had previously been stained, the opposite face of the disc was sampled for thin

152 sections (~1 cm distant from the stained surface). A staining solution consisting of a 1:2 ratio of 1%  
153 Safranin to 1% Astra Blue was applied to each thin section and allowed to set for 1-2 minutes. Removal  
154 of the staining solution from the thin section was completed using a series of 10-15 washes with 95%  
155 anhydrous ethanol, followed by 3-5 rinses with absolute ethanol to complete sample dehydration. Thin  
156 sections were permanently adhered to the slides beneath glass cover slips using Canada Balsam and  
157 subsequently dried for 24 hours at 65°C. Slides were examined using a 10-45x stereo zoom microscope  
158 equipped with 5MP digital camera. A series of 9-40 images of adjacent portions of each disc were taken  
159 and stitched using Adobe Photoshop CS6 version 13.0 (Adobe Systems Inc., San Jose, CA). Annual ring  
160 widths were measured using Image J, version 1.48 (Rasband 1997). Ring widths were manually  
161 measured along four radii of each sample, cross-dated and subsequently averaged to produce one ring  
162 width series per sample. Rings formed during the year of sample collection were excluded, because we  
163 could not be certain of their completeness. A total of 42 *Betula* discs and 32 *Salix* discs were measured  
164 and included in the shrub-ring chronologies (Supplemental Figure 1). Length of the ring width series  
165 varied from 22 to 104 years for *Betula* and from 15 to 76 years for *Salix*. The ring width series were  
166 analyzed by species in COFECHA (Holmes 1983) to identify dating errors associated with missing rings or  
167 incorrect identification of latewood boundaries using a segment length of 26 years and an overlap of 13  
168 years. While partial rings were common, particularly for *Betula*, we detected very few completely  
169 missing rings.

#### 170 *Detrending*

171 Four different methods were used to examine implications of data processing decisions for  
172 trends in the shrub-ring chronologies and the strength of climate-growth correlations: no detrending,  
173 the negative exponential/negative linear method and both age and diameter regional curve  
174 standardization (RCS). No detrending involves constructing a chronology by computing the mean ring  
175 width for each year among all of the shrub-ring series. The negative exponential/negative linear method  
176 involves fitting either a negative exponential curve or a downward sloping line individually to each ring-  
177 width series (e.g., Fritts 2001). Age RCS involves aligning all of the ring width series by cambial age (age  
178 of the stem at the height of disc collection) and fitting an empirical curve to the relationship between  
179 ring width and cambial age to define the detrending curve. Our sample size (n=42 for *Betula* and n=32  
180 for *Salix*) was too small to support multiple curve age RCS, which has the advantage of fitting separate  
181 curves to slow and fast growing stems, the latter of which often show a more rapid decline in ring width  
182 with age, as new biomass is distributed around a rapidly increasing circumference (Briffa & Melvin  
183 2011). Finally, diameter RCS involves aligning all of the ring width series by size and fitting an empirical

184 curve to the relationship between ring width and the radius of the stem at the time when the ring was  
185 formed (Melvin 2004). This empirical curve is then used to detrend each ring width series. Aligning the  
186 ring widths by radius rather than age should account for differences in the rate of ring width decline  
187 with age in fast and slow growing stems and may, therefore, be a good alternative to multiple curve age  
188 RCS when sample size is too small to support fitting of multiple detrending curves. One of the key  
189 requirements of regional curve standardization (RCS) detrending is a large range of sample ages (for age  
190 RCS) or sample sizes (for diameter RCS) to ensure that age or radius are not confounded with calendar  
191 year when defining the detrending curve(s). This requirement was met by our datasets (Table 1).  
192 Detrending was performed in CRUST (Melvin & Briffa 2014) and shrub-ring chronologies were  
193 assembled as robust means of the ratios of observed to expected growth. Signal-free chronologies were  
194 produced by repeatedly dividing the raw ring widths by the detrended chronology with the aim of  
195 correcting for inadvertent removal of climate effects on growth during the detrending process (Melvin &  
196 Briffa 2008). Chronologies were truncated when the sample size dropped below nine, to mirror the  
197 number of discs contributing to the chronologies between 2011 and 2013, when data were only  
198 available for the West site. Standard dendrochronology statistics, such as the mean inter-series  
199 correlation ( $\bar{r}$ ), the expressed population signal (EPS) and the signal to noise ratio (SNR) were  
200 calculated for raw ring width and detrended data using the dplR package (Bunn 2008) in R 3.3.2 (R Core  
201 Team 2016).

#### 202 *Climate-Growth Analyses*

203 Growing season climate data within the study area (2008-2014) were collected by a station  
204 equipped with an air temperature and relative humidity sensor (CS215, Campbell Scientific, Logan, UT)  
205 housed within a radiation shield at 2 m height and a tipping bucket rain gauge (TE525, Texas Electronics,  
206 Dallas, TX) mounted at 1 m on a separate tripod. The sensors were scanned every 30 seconds and  
207 hourly means were logged to a CR1000 datalogger (Campbell Scientific, Logan, UT). Two sources of  
208 long-term climate data were examined for strength of correlation with our climate record for the study  
209 area and with our shrub-ring chronologies: the CRU TS 3.24.01 data for the grid cell nearest the study  
210 area (67.0 to 67.5°, -50.5 to -50.0°) and the Danish Meteorological Institute (DMI) climate record for  
211 Kangerlussuaq airport (Mernild et al. 2014). To identify which combination of climate data source and  
212 detrending method produced the strongest climate-growth correlations, static correlation analyses were  
213 performed using the treeclim package (Zang & Biondi 2015) in R. Monthly mean air temperature (May-  
214 August) of the growth year and the previous year were included in the analyses. Significance of the  
215 correlations was assessed through “exact” bootstrap resampling and  $\alpha=0.05$ .

216 The climate of Greenland is influenced by large-scale climate oscillations, such as the inter-  
217 related Arctic Oscillation (AO), North Atlantic Oscillation (NAO) and the Greenland Blocking Index (GBI).  
218 The AO and NAO are well-known climate modes that have been discussed extensively in the literature  
219 (e.g., Thompson and Wallace 1998). The GBI is an index of the geopotential height over the Greenland  
220 Ice Sheet (Fang 2004). Greater values of the GBI are associated with high pressure blocking, which  
221 corresponds with warm winters and warm and dry conditions during the growing season in the  
222 Kangerlussuaq region (Hanna et al. 2016). Monthly values of the AO, NAO and GBI during the growth  
223 year (January- August) and the previous year (January-December) were tested for strength of correlation  
224 with our shrub-ring chronologies, again using static correlation analyses in treeclim.

225 Having identified the optimum detrending method, climate data source and synoptic climate  
226 index, we conducted moving window analyses in treeclim to examine potential changes over time in the  
227 strength or sign of correlations between the shrub-ring indices and climate (monthly air temperature  
228 and monthly GBI for January through December of the previous year and January through August of the  
229 growth year). The window length was set at 20 years with a one-year step between windows.  
230 Significance was again assessed with exact bootstrap resampling (1000 iterations). Finally, to examine  
231 the potential for non-linear relationships between climate and growth, we conducted Random Forest  
232 regression analyses using the randomForest package (Liaw and Wiener 2002) in R. May-August mean air  
233 temperature and the precipitation sum for the growth year and the previous year were included as  
234 predictors. Climate data for these months were selected because they cover the entirety of the growing  
235 season, tended to be well-correlated with our shrub-ring chronologies and because perennial plants  
236 commonly use resources stored in the previous growing season to support growth in the current year  
237 (Chapin et al. 1990). May air temperature was included because it was strongly correlated with our  
238 shrub-ring chronologies and because conditions during May are an important determinant of growing  
239 season length in our study area (Post et al. 2016). Longer growing seasons may be associated with  
240 greater potential for mid-summer moisture limitation (Cahoon et al. 2016b), as a result of greater  
241 cumulative evapotranspiration and deeper soil thaw. Two variables were tested at each node and 1000  
242 trees were constructed in each analysis.

#### 243 *Alpha-cellulose Extraction and Carbon Isotope Analysis*

244 Three stem discs, representing three individuals of each species from each site, were selected  
245 for stable isotope analysis with the objective of maximizing the series length and inter-series correlation.  
246 Discs were sampled for isotope analysis using a micromill and a 0.9 mm cutting bit beneath a stereo  
247 zoom microscope. The same face of each disc sampled for thin sections was sampled for isotope



248 analysis. Wood was sampled at a constant depth (3 mm) around the complete circumference of each  
249 disc. Individual rings were often too narrow to sample. Therefore, samples were collected in 3-year and  
250 5-year increments for *Salix glauca* and *Betula nana*, respectively. Homogenized samples were stored in  
251 3 mL screw-top microcentrifuge tubes.

252 The carbon isotopic characteristics of cellulose and lignin are known to differ strongly (Benner et  
253 al. 1987). To ensure that chronologies of carbon isotope discrimination are not confounded by temporal  
254 variation in wood composition, it is important to extract cellulose for analysis. Alpha-cellulose was  
255 isolated from the homogenized wood tissue following the water-modified Brendel method (Brendel et  
256 al. 2000; Gaudinski et al. 2005). The  $\alpha$ -cellulose was dried overnight at 50°C and 0.3 mg subsamples  
257 were weighed into tin capsules. Analysis of  $\delta^{13}\text{C}$  in  $\alpha$ -cellulose was completed using an elemental  
258 analyzer (Costech 4010, Costech Analytical, Valencia, CA) coupled with a continuous-flow isotope ratio  
259 mass spectrometer (Thermo-Finnigan Delta Plus XP, Thermo Electron Corp., Waltham, MA). Carbon  
260 isotope discrimination ( $\Delta^{13}\text{C}$ ) was calculated as

$$261 \quad \Delta^{13}\text{C} = \frac{\delta^{13}\text{C}_a - \delta^{13}\text{C}_{shrub}}{1 + \delta^{13}\text{C}_{shrub}/1000}$$

262 where  $\delta^{13}\text{C}_a$  is the isotopic value of atmospheric  $\text{CO}_2$ , which has become progressively depleted due to  
263 combustion of isotopically light fossil fuels since the onset of the industrial revolution, and  $\delta^{13}\text{C}_{shrub}$  is  
264 the isotopic value of shrub-ring  $\alpha$ -cellulose. Annual  $\delta^{13}\text{C}_a$  values from 1928-2003 were acquired from  
265 McCarroll and Loader (2004). Linear extrapolation was used to estimate the  $\delta^{13}\text{C}$  values from 2004 to  
266 2013.

#### 267 Leaf Gas Exchange and Leaf $\delta^{13}\text{C}$

268 Measurements of instantaneous mid-day leaf gas exchange were made using a LI-COR 6400XT  
269 Portable Photosynthesis System (LI-COR Inc., Lincoln, NE, USA) on weekly intervals during the 2014  
270 growing season. The 2 x 3 cm opaque LED chamber typically enclosed 6 leaves and associated stems of  
271 *Betula* and 3 leaves and associated stems of *Salix*. On each sampling date, leaf gas exchange was  
272 measured on a single stem of 6 individuals of each species. Measurements were made in complete  
273 darkness and under saturating light conditions ( $1500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) at a leaf temperature of  
274 15°C. A reference  $\text{CO}_2$  concentration of 390  $\mu\text{mol/mol}$  was selected based on measurements of  
275 atmospheric  $\text{CO}_2$  in the study area. The flow rate was held constant at 300  $\mu\text{mol/s}$  and flow through the  
276 desiccant was manually adjusted to maintain a relative humidity of ~50%. Leaves were then collected  
277 and scanned fresh for measurement of projected leaf area using Image J version 1.48v.

#### 278 Stem Xylem Water Potential

279 During the 2014 growing season, stem xylem water potential measurements were conducted at  
280 mid-day on weekly intervals from mid-June to mid-August. The shoot was excised from the branch and  
281 sealed in a Pump-Up Chamber (PMS Instrument Company, Albany, OR). Pressure was increased within  
282 the chamber and a reading was taken the instant water was extruded from the xylem as observed with a  
283 hand lens.

## 284 **Results**

### 285 Identifying the Optimum Detrending Method, Climate Data Source and Synoptic Climate Index

286 Choice of detrending method had a limited effect on trends in the *Betula* chronology, but  
287 important effects on the *Salix* chronology (Supplemental Figure 2). In both species, examination of size  
288 (stem radius) and age effects on the ring widths revealed small, but potentially important effects  
289 (Supplemental Figure 3). Ring widths of both species tended to increase with stem radius and decrease  
290 initially with cambial age, although the apparent age effect in the *Salix* data was very small. Among the  
291 *Salix* chronologies, the raw ring widths, age RCS and diameter RCS all showed reduced growth during the  
292 past 15 years, while the negative exponential/negative linear method showed no evidence of an overall  
293 trend. In both species, diameter RCS produced chronologies that were more strongly correlated with  
294 the climate data, regardless of the climate data source (Supplemental Tables 1-3). Diameter RCS  
295 detrending also improved rbar and SNR slightly for *Betula* and strongly for *Salix* (Supplemental Table 4).  
296 Therefore, we restricted subsequent analysis to the diameter RCS chronologies. The CRU TS 3.24.01  
297 mean monthly air temperature data were similarly well correlated with the air temperature data for our  
298 study area and better correlated with our shrub-ring chronologies than the Kangerlussuaq airport data,  
299 regardless of detrending method (Supplemental Figure 4, Supplemental Tables 1 and 2). Both sources of  
300 monthly precipitation totals were poorly correlated with precipitation data from the study area and with  
301 our shrub-ring chronologies. We restricted subsequent analyses to the CRU TS 3.24.01 climate record,  
302 which had the additional benefit of covering the entirety of the *Betula* chronology. Of the synoptic  
303 climate indices examined (AO, NAO and GBI), the GBI was most strongly correlated with our shrub-ring  
304 chronologies (Supplemental Table 5) and was therefore retained in subsequent analyses.

### 305 Long-term Trends in Secondary Growth of *Betula nana* and *Salix glauca*

306 *Betula* growth showed an increasing trend from 1941 until the early 1990s, followed by a  
307 dramatic decline from the early 1990s to 2013 (Figure 2, Supplemental Figure 5). Initiation of the *Betula*  
308 growth decline in the early 1990s corresponded closely with strong increasing trends in both the GBI  
309 and growing season air temperature. Outbreaks of the defoliating moth, *Eurois occulta*, in 2004/2005  
310 (Post & Pedersen 2008) and 2010/2011 (Avery & Post 2013) may have exacerbated the *Betula* decline.

311 To examine the possibility that growth trends might depend upon the age (or size) of the stem, we  
312 divided the datasets approximately in half and produced separate chronologies for “old” and “young”  
313 stems (Figure 3). The *Betula* stems were older on average than the *Salix* stems. Therefore, a cut-off age  
314 of 50 years was used for *Betula*, while a cut-off of 30 years was used for *Salix*. For *Betula*, there was  
315 relatively little difference between the old (>50 yrs, n=21) and young (<50 yrs, n=21) chronologies,  
316 indicating the recent growth decline is generally not dependent on the age (or size) of the stem. To  
317 examine the possibility that growth trends might depend upon site, we produced chronologies for both  
318 species separately for each site (Supplemental Figure 6). The site-level chronologies showed universality  
319 in the recent *Betula* growth decline among the sites.

320 *Salix* similarly showed evidence of reduced growth in recent decades (Figure 2, Supplemental  
321 Figure 5), but the growth decrease began several years later than in *Betula*. Important differences  
322 emerged when the *Salix* dataset was broken down into old (>30 yrs, n=17) and young stems (<30 yrs,  
323 n=15). Inter-annual variability in growth was much greater in young stems and the recent growth  
324 decline was more apparent in older (generally larger) stems (Figure 3). Growth of the young *Salix* stems  
325 appeared to quickly recover from the moth outbreaks, with growth after each outbreak exceeding that  
326 immediately before the outbreak. When broken down by site, Sandflugtsdalen, Long Lake 1 and Long  
327 Lake 2 stood out as sites exhibiting fairly dramatic recent growth declines, while West and Haredalen  
328 showed much more limited trends (Supplemental Figure 6). *Salix* stems sampled at West and Haredalen  
329 were the youngest on average, again suggesting the recent *Salix* growth decline may be stronger in  
330 older stems.

### 331 Temporal Variation in the Strength and Sign of Climate-Growth Correlations

332 There was strong evidence that correlations between monthly air temperature and *Betula*  
333 growth have changed in recent decades (Figure 4). Prior to the early 1990s, correlations between air  
334 temperature and growth were generally weak. However, from the early 1990s to 2013, strong negative  
335 correlations emerged, particularly during February, March and August of the growth year and January  
336 through August of the previous year. It is important to note that there was almost a complete absence  
337 of positive correlations between air temperature and *Betula* growth between 1941 and 2013.

338 Similarly, there was evidence that correlations between the GBI and *Betula* growth have  
339 changed in recent decades. Prior to ~1990, the GBI was largely uncorrelated with growth. However,  
340 since the early 1990s, more positive values of the GBI, which correspond with warm and dry growing  
341 seasons in the Kangerlussuaq region (Hanna et al. 2016), have been associated with reduced *Betula*

342 growth. The months for which the GBI was most strongly correlated with *Betula* growth were January  
343 through March and August of both the growth year and the previous year.

344 The time period corresponding to the recent *Betula* growth decline is not the only instance of  
345 significant inverse air temperature-growth correlations in our shrub-ring chronology. A similar, but  
346 weaker, period of inverse correlations was observed in the 1960s, which is also a time when growing  
347 season air temperature was greater than the long-term mean and the GBI was consistently positive.

348 Correlations between monthly air temperature and *Salix* growth also showed evidence of a  
349 change in recent decades (Figure 5), with the exception of previous July air temperature, which was  
350 negatively correlated with growth throughout the chronology. Prior to ~1990, there were some  
351 significant positive correlations between *Salix* growth and air temperature during May through August  
352 of the growth year, but those correlations have deteriorated to become weak negative associations in  
353 recent decades. Similarly, positive values of the growing season GBI were associated with greater *Salix*  
354 growth between 1978 and the mid-1990s, but those associations shifted to become neutral or weak  
355 negative correlations over the last 15 years. As observed for *Betula*, there was some evidence that air  
356 temperature and GBI during the late winter have become negatively correlated with *Salix* growth in  
357 recent decades.

#### 358 Form of Relationships between Climate and Growth

359 Partial dependence plots from a Random Forest analysis provided further evidence of the  
360 negative relationship between growing season air temperature and growth of both *Betula* and *Salix*  
361 (Figure 6). The Random Forest analysis also revealed a weak positive correlation between growing  
362 season precipitation and *Betula* growth, despite our knowledge that the CRU TS 3.24.01 precipitation  
363 data are a crude representation of actual precipitation in our study area. There was some evidence of  
364 non-linearity in the relationship between air temperature and growth, as the decline tended to  
365 accelerate in both species when May-August air temperature exceeded ~7°C, which is almost exactly the  
366 long-term mean May-August air temperature for the study area in the CRU TS 3.24.01 dataset.

#### 367 Long-term Trends in $\Delta^{13}\text{C}$ of Shrub-ring $\alpha$ -cellulose

368 Chronologies produced using discs sampled for isotopic analysis were closely correlated with the  
369 overall *Betula* ( $r=0.89$ ) and *Salix* ( $r=0.96$ ) chronologies (Supplemental Figure 7). In *Betula*, there was  
370 evidence of a slight negative effect of age on  $\Delta^{13}\text{C}$  over the first ~40 years (Supplemental Figure 8). In  
371 *Salix*, there was no evidence that  $\Delta^{13}\text{C}$  of shrub-ring  $\alpha$ -cellulose was influenced by the age of the stem at  
372 the time the ring was formed. Carbon isotope discrimination in  $\alpha$ -cellulose of *Betula* rings showed a  
373 slight overall declining trend (Figure 7). Accounting for the small age effect (0.2‰ over 40 years,

374 Supplemental Figure 8) would tend to flatten the  $\Delta^{13}\text{C}$  trend prior to ~1980, while retaining a slight  
375 decreasing trend in recent decades. *Salix*, in contrast, showed a steep overall decline in  $\Delta^{13}\text{C}$  that began  
376 before the early 1990s growth decline, but accelerated during the period of reduced growth, amounting  
377 to an overall decrease of ~1.8‰.

#### 378 Seasonal Variation in Leaf Gas Exchange in Response to Changing Moisture Availability

379 The 2014 growing season was warm and dry, with a mean May-August air temperature of 7.4°C  
380 and total rainfall of 69 mm measured in the study area. Mean air temperature over the same time  
381 period at the Kangerlussuaq airport was 8.9°C making it the 7<sup>th</sup> warmest growing season in the DMI  
382 record since 1976. The CRU TS 3.24.01 dataset estimated a mean May-August air temperature of 8.3°C,  
383 making 2014 the 9<sup>th</sup> warmest growing season in the 115-year dataset. Most of the precipitation  
384 occurred during August, with only three measurable rain events in June and July of 2014 (Figure 8). The  
385 daily maximum atmospheric water vapor pressure deficit (VPD) declined slightly over the course of the  
386 growing season, while soil temperature generally increased and soil water content declined. Stem  
387 xylem water potential varied little between species and declined strongly over the course of the 2014  
388 growing season, reaching a mean seasonal minimum value of approximately -1.8 MPa in both species  
389 (Supplemental Figure 9). Stomatal conductance ( $G_s$ ) was positively correlated with soil temperature  
390 (*Salix*:  $r=0.41$ ; *Betula*:  $r=0.36$ ), as observed in other arctic plants (e.g., Dawson and Bliss 1989), and  
391 showed an increasing trend throughout the growing season in both species. The close correlation  
392 between  $G_s$  and soil temperature makes it challenging to detect the effect of moisture limitation, as  
393 seasonal minimum soil water content tends to coincide with seasonal maximum soil temperature. The  
394 late season rain events of 2014 offered an opportunity to examine the effects of increased moisture  
395 availability when soil water content was near the seasonal minimum. Both species showed increases in  
396  $G_s$  and net photosynthesis following August rainfall. The response of *Salix* was particularly dramatic,  
397 with more than a doubling of  $G_s$  between the July 19 and August 18 measurement dates, despite similar  
398 soil temperature.

#### 399 **Discussion**

400 Repeat photography (Tape et al. 2006), long-term plot-level monitoring (Elmendorf et al. 2012),  
401 experimental warming (Walker et al. 2006) and dendrochronology (Myers-Smith et al. 2015) have  
402 generally shown positive responses of shrubs to climate warming in the Arctic. There are exceptions,  
403 however, and researchers have shown that either direct or indirect effects of low moisture availability  
404 may be limiting shrub growth responses to warming in some regions of the Arctic (Myers-Smith et al.  
405 2015). Our shrub-ring,  $\Delta^{13}\text{C}$  and leaf gas exchange data suggest that rapid climate warming over the last

406 two decades in continental western Greenland has been associated with reduced growth of *Betula* and  
407 older stems of *Salix*, at least partially in response to the direct effects of moisture limitation. Our finding  
408 that radial growth of both species has been increasingly negatively correlated with the GBI in recent  
409 decades supports our argument that declining growth is at least partially related to increasing moisture  
410 limitation, as a positive phase of the GBI is associated with both warm and dry growing seasons in  
411 southwestern Greenland (Hanna et al. 2016).

412 Our observation that older *Salix* stems showed a more pronounced growth decline than younger  
413 *Salix* stems might reflect differences in stem size (particularly stem length). In our study area, even large  
414 diameter *Betula* stems tend to be relatively short, with leaves distributed along much of the stem. In  
415 contrast, large diameter *Salix* stems tend to be relatively long (and tall), with leaves concentrated near  
416 the ends of the branches. Resistance to xylem water flow increases in proportion to path length (e.g.,  
417 Ryan and Yoder 1997). Therefore, older, longer *Salix* stems may be more susceptible to moisture  
418 limitation than younger, shorter stems. Meanwhile, the architecture of *Betula* may limit differences in  
419 susceptibility between old and young stems. These effects of shrub architecture on water relations may  
420 be reinforced by differences in xylem anatomy between *Salix* and *Betula*. *Salix* is semi-ring porous, with  
421 large earlywood vessels, while *Betula* is diffuse porous, with much smaller vessel diameters. Larger  
422 diameter vessels tend to be more vulnerable to freezing and drought-induced cavitation (e.g., Hacke and  
423 Sperry 2001). The combination of a long path length with large vessels and leaves distributed near the  
424 ends of the stems may lead to greater susceptibility to moisture limitation in old, long *Salix* stems.

425 An important limitation of dendrochronology is that it generally only captures one aspect of  
426 plant growth (secondary stem growth). Meanwhile, plants are well known to shift allocation in response  
427 to changes in climate, often favoring growth of the organ responsible for acquiring the most limiting  
428 resource (Lambers et al. 2008; Ropars et al. 2017). In the case of moisture limitation, plants might  
429 allocate more resources to support fine root growth, while decreasing investment in foliage. In our  
430 study area, we hypothesize that leaf production might show a more dramatic decline since the early  
431 1990s than our shrub-ring chronologies, while fine root production might show a lesser decline.

432 Negative correlations between air temperature and growth of both species were found during  
433 the growing season and during late winter in recent decades. Our finding of negative correlations  
434 between growing season air temperature and radial growth contrasts strongly with numerous previous  
435 shrub-ring studies in the Arctic (e.g., Forbes et al. 2010; Ropars et al. 2015; Hollesen et al. 2015; Weijers  
436 et al. 2017; but see Myers-Smith et al. 2015). Young et al. (2016) similarly found negative correlations  
437 between February-April air temperature and growth of *Betula* at the Long Lake II sampling site. Our

438 study area has shallow and often discontinuous snow cover during winter, limiting the potential  
439 influence of snow on winter soil temperature and of snowmelt water on growing season soil moisture.  
440 Brief periods of above freezing air temperature, which are common in our study area during the late  
441 winter period (February and March), may be associated with freeze-thaw cycles, both aboveground and  
442 in shallow soil horizons, as a result of the limited snowpack. Freeze-thaw events may inflict mechanical  
443 or physiological damage to stems and/or fine roots (Cleavitt et al. 2008), potentially limiting growth  
444 during the subsequent growing season. Alternatively, negative correlations between late winter air  
445 temperature and growth could reflect the correlation between late winter and spring air temperature  
446 (Post et al. 2016), with spring air temperature being the more important driver of shrub growth. Warm  
447 springs may be associated with early initiation of the growing season, greater cumulative  
448 evapotranspiration, a deeper active layer and drier soil in mid to late summer.

449 Examination of the form of the relationship between May-August air temperature and growth  
450 highlighted a threshold temperature of  $\sim 7^{\circ}\text{C}$ , which corresponds very closely with the long-term mean  
451 for the study area in the CRU TS 3.24.01 dataset. Below  $7^{\circ}\text{C}$ , there was a weak correlation between air  
452 temperature and growth, while above  $7^{\circ}\text{C}$  growth of both species declined steeply with increasing  
453 temperature. Interestingly, *Betula* showed a greater growth decline, but more subtle evidence of  
454 moisture limitation at the leaf-level (limited long-term change in  $\Delta^{13}\text{C}$ ,  $\sim 50\%$  increase in  $G_s$  following late  
455 season rain). Meanwhile, *Salix* showed a lesser growth decline that was coupled with much greater leaf-  
456 level adjustments (long-term  $1.8\text{‰}$  decline in  $\Delta^{13}\text{C}$ , doubling of  $G_s$  following late season rain). We  
457 hypothesize these incongruent responses may reflect differences across species in the scale of their  
458 response to moisture limitation and in their recovery from herbivory.

459 *Salix* showed evidence of stomatal sensitivity to warm and dry conditions, both within the 2014  
460 growing season and over the last 20 years of climate warming. *Betula* showed evidence of similar  
461 responses, but was comparatively unresponsive to warm and dry conditions at the leaf-level, consistent  
462 with earlier findings in our study area (Cahoon et al. 2016a). However, plots dominated by *Betula*  
463 showed a decline in the normalized difference vegetation index (NDVI), which is closely correlated with  
464 leaf area, during warm and dry periods (Cahoon et al. 2016b). We hypothesize that *Salix* and *Betula* may  
465 exhibit contrasting responses to moisture limitation, with the former responding primarily at the leaf-  
466 level, by regulating  $G_s$ , and the latter responding at the canopy-level, by modifying effective leaf area  
467 (e.g., through leaf shedding or leaf curling). We further hypothesize that *Betula* may have decreased its  
468 investment in foliage and increased its investment in roots to a greater degree than *Salix* since the early  
469 1990s.

470 Outbreaks of the defoliating moth, *Eurois occulta*, were documented in the study area during  
471 2004/2005 and 2010/2011, well after the onset of the climate warming trend and the initiation of the  
472 growth declines. The 2004/2005 outbreak was associated with near complete defoliation (Post and  
473 Pedersen 2008) and the ring formed during the 2005 growing season was very narrow in both species.  
474 The 2010/2011 outbreak was less severe in terms of densities of trapped moth larvae and defoliation  
475 (Avery and Post, unpublished data) and radial growth of young *Salix* stems was much greater during  
476 2011 than during 2005. Meanwhile, *Betula* showed more limited radial growth in 2011 than in 2005,  
477 which could indicate that repeated defoliation may be exacerbating its growth decline. It is unknown  
478 whether the frequency or severity of *Eurois occulta* outbreaks may be related to climate warming.  
479 Historical observations suggest an outbreak may have occurred in 1981/1982 (Fox et al. 1987) and the  
480 rings of both species were narrower than expected based on climate conditions in 1982 (Gamm 2015;  
481 Young et al. 2016). If the last outbreak of *Eurois occulta* occurred more than 20 years prior to the two  
482 recent outbreaks, then it is possible that moth outbreaks in the study area may be increasing in  
483 frequency. Observations also indicate an increase in the local muskoxen population, from a single  
484 individual recorded in 1993 to approximately 40 individuals in 2015 (Post, unpublished data). Post and  
485 Pedersen (2008) showed that exclusion of large herbivores (caribou and muskoxen) had a strong  
486 positive effect on deciduous shrub abundance. Across the entire plant community, the strongest effects  
487 of herbivore exclusion on abundance were reported for *Betula*, not *Salix*, and from herbivory by  
488 muskoxen, rather than caribou (Post and Pedersen 2008). We hypothesize that the combined effects of  
489 increased muskoxen browsing, repeated defoliation by moths and a decline in moisture availability may  
490 be driving the dramatic *Betula* growth decline over the last ~20 years in our study area.

491 Our results contrast with widespread observations of positive effects of recent climate warming  
492 on the growth and abundance of deciduous shrubs in the Arctic (e.g., Tape et al. 2005; Forbes et al.  
493 2010; Macias-Fauria et al. 2012; Jørgensen et al 2015; Hollesen et al. 2015). The climate of continental  
494 western Greenland is among the warmest and driest in the Arctic (Supplemental Table 6; Supplemental  
495 Figures 10 and 11). In that sense, our results may serve as an early indicator of potential effects of  
496 climate warming on the productivity of other arctic ecosystems, as air temperature continues to rise and  
497 evaporative demand increases.

498 Arctic ecosystems have historically played a critical role in the global climate as strong sinks for  
499 atmospheric CO<sub>2</sub>, as evidenced by large C stocks in soils and permafrost (Tarnocai et al. 2009). At  
500 present, there is great concern that rising soil temperature may increase microbial activity and access of  
501 microbes to soil C stocks in thawing permafrost (e.g., Schuur et al. 2015). Vegetation productivity is



502 generally expected to increase and offset some of the respiratory C losses as the climate warms, but the  
503 effects of changing species composition and vegetation productivity on C uptake and storage are  
504 complex and not completely understood. Our results show a decline in the flux of C into a reservoir  
505 (wood) with a long mean residence time (Hobbie 1996), thereby raising important questions about the  
506 extent to which increases in vegetation productivity will offset C losses associated with rising soil  
507 temperature and thawing permafrost. A number of key uncertainties remain, including the relationships  
508 among main stem radial growth and whole plant productivity, competitive interactions, changes in  
509 deciduous shrub cover and changes in landscape greenness. These are important knowledge gaps that  
510 would benefit from future research, particularly in areas of the Arctic where moisture limitation is  
511 already, or may soon become, an important constraint on vegetation productivity.

#### 512 **Author Contributions**

513 CMG and PFS designed the study. CMG, ABY, DAW and EP collected shrub discs. CMG, AB and PFS  
514 performed thin sectioning and imaging. CMG analyzed shrub disc images, sampled discs for isotope  
515 analysis and extracted cellulose. CMG performed leaf gas exchange and water potential measurements,  
516 with training from SMPC and PFS. CMG and PFS analyzed the data. CMG drafted the manuscript. JMW  
517 co-chaired the graduate committee of CMG. PFS re-analyzed the data and re-drafted the manuscript.  
518 RJD performed the Pan-Arctic analyses. All authors contributed to revisions.

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#### 524 **Data Accessibility**

525 Data presented in this article have been archived in the Arctic Data Center (Sullivan  
526 2012): <https://arcticdata.io/catalog/#view/urn:uuid:3dc91064-7b8b-4308-b949-a361b7146baa>

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672  
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 674 **Table 1.** Breakdown of the timing and location of sample collection by species, along with number of  
 675 discs selected for thin sectioning, the range of ring width series length (years) and the range of stem  
 676 radius (mm, sum of the ring widths) at each site. The series length and stem sizes apply to the discs  
 677 selected for thin sectioning.

Storen	<i>Betula</i>	20	7	27-72	5.5-9.6	Early August 2007
		12	1	54	6.1	Late July 2005
Haredalen	<i>Betula</i>	17	5	56-75	5.5-15.8	Late July 2005
		13	3	53-79	11.8-11.9	Early August 2007
Kodalen	<i>Betula</i>	18	5	39-104	6.1-9.3	Early August 2007
		10	3	50-77	10.2-14.9	Late July 2005
Long Lake 1	<i>Betula</i>	25	9	31-56	4.7-6.4	Late May 2011
West	<i>Betula</i>	25	9	22-37	2.8-5.3	Late August 2014
<b>Overall</b>	<b><i>Betula</i></b>	<b>140</b>	<b>42</b>	<b>22-104</b>	<b>2.8-15.8</b>	
Haredalen	<i>Salix</i>	5	5	15-27	6.7-8.4	Late July 2005
Long Lake 1	<i>Salix</i>	25	5	32-35	5.5-12.3	Late May 2011
Long Lake 2	<i>Salix</i>	25	8	24-76	4.3-8.5	Late May 2011
West	<i>Salix</i>	25	9	23-31	4.0-7.8	Late August 2014
Sandflugtsdalen	<i>Salix</i>	50	5	33-56	12.6-20.9	Late May 2011

Overall	<i>Salix</i>	130	32	15-76	4.0-20.9
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**Figure Captions**

**Figure 1.** Locations of the seven sites from which shrub discs were collected near the margin of the Greenland Ice Sheet, inland from Kangerlussuaq in western Greenland.

**Figure 2.** Long-term trends in growing season air temperature, the Greenland Blocking Index (GBI) and secondary stem growth of *Betula nana* and *Salix glauca*. The air temperature data show an abrupt increase beginning in the early 1990s, corresponding with an increase in the GBI, which in turn is indicative of high pressure centered over the Greenland Ice Sheet. The increases in air temperature and GBI correspond with a dramatic growth decline in *Betula* that was exacerbated by two moth outbreaks (indicated by red circles). *Salix* shows evidence of lower growth during the recent warmer period, but the decline is not as dramatic as that of *Betula*. Grey shading indicates the 95% confidence intervals around the shrub-ring chronologies, while the black bars depict variation in the sample size over time.

**Figure 3.** The shrub-ring chronologies when divided into young (*Betula* n=21, *Salix* n=15) and old stems (*Betula* n=21, *Salix* n=17). For *Betula*, there is relatively little difference between the two chronologies, indicating the recent growth decline is generally not dependent on the age (or size) of the stem. For *Salix*, inter-annual variability in growth is much greater for young stems and the recent growth decline is much more apparent in older (generally larger) stems.

**Figure 4.** Moving window analyses designed to test for variation in the strength or sign of correlations between the *Betula* ring width indices and monthly air temperature and Greenland Blocking Index (GBI). Stars indicate significant correlations, while P-values in the right-hand column indicate oscillations that are greater than expected to occur by chance. Results show that increases in air temperature and GBI since the early 1990s are closely correlated with the *Betula* growth decline.

706 **Figure 5.** Moving window analyses designed to test for variation in the strength or sign of correlations  
707 between the *Salix* ring width indices and monthly air temperature and Greenland Blocking Index (GBI).  
708 Stars indicate significant correlations, while P-values in the right-hand column indicate oscillations that  
709 are greater than expected to occur by chance. Results show that increases in air temperature and GBI  
710 since the early 1990s have also been associated with reduced *Salix* growth.

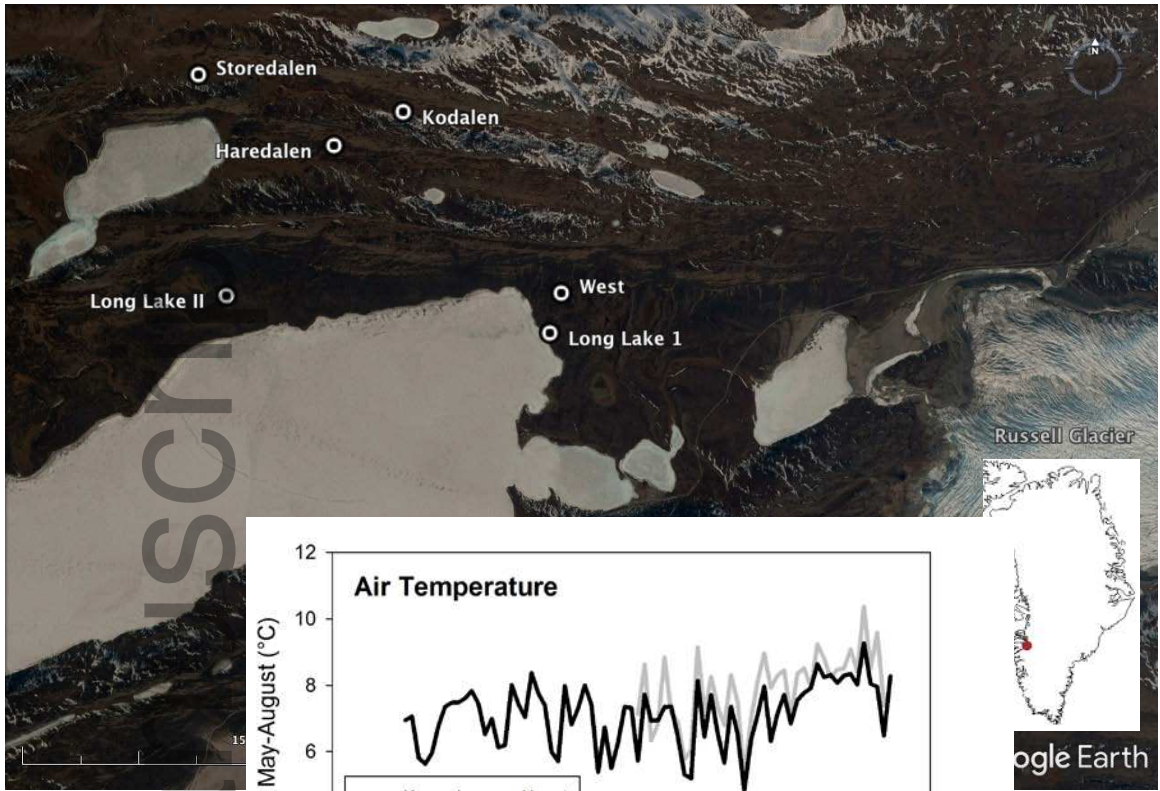
711 **Figure 6.** Partial dependence plots from a Random Forest analysis depicting the modeled effect of air  
712 temperature and precipitation on the ring width indices of *Betula* and *Salix*, when all other variables  
713 were held at their mean value. Results show a steep decline in growth of both species when May-  
714 August air temperature exceeds  $\sim 7^{\circ}\text{C}$ , which is very close to the long-term mean for the study area. The  
715 long-term precipitation data are considerably less reliable, but tend to show a positive correlation  
716 between growing season rainfall and growth. The bars show the distribution of the climate data during  
717 the *Betula* (black) and *Salix* (grey) chronologies.

718 **Figure 7.** Carbon isotope discrimination ( $\Delta^{13}\text{C}$ ) over time in  $\alpha$ -cellulose of the growth rings of *Betula* and  
719 *Salix*. Three stem discs from each of five sites were sampled for each species. *Betula* samples were  
720 pooled in 5-year increments, while *Salix* samples were pooled in 3-year increments. The year assigned  
721 to each sample was weighted based on the ring widths within each increment. The results show a steep  
722 decline in  $\Delta^{13}\text{C}$  during recent decades in *Salix*, which is consistent with stomatal closure to limit water  
723 loss in a warming climate. The *Betula*  $\Delta^{13}\text{C}$  data contain a small effect of stem age. Accounting for this  
724 age effect would tend to flatten the trend prior to 1980, while retaining a slight decreasing trend in  
725 recent decades.

726 **Figure 8.** Seasonal variation in the daily maximum atmospheric water vapor pressure deficit (VPD),  
727 precipitation, soil temperature, soil water content and mid-day leaf-level net photosynthesis and  
728 stomatal conductance of *Betula* (n=6) and *Salix* (n=6) at the West site during the 2014 growing season.  
729 Data show a seasonal increase in net photosynthesis and stomatal conductance with increasing soil  
730 temperature. *Salix* showed a strong increase in net photosynthesis and stomatal conductance  
731 immediately following rain events in August, supporting the interpretation that declining  $\Delta^{13}\text{C}$  over time  
732 may be indicative of increasing moisture limitation of growth.

733 **Figure 1.**





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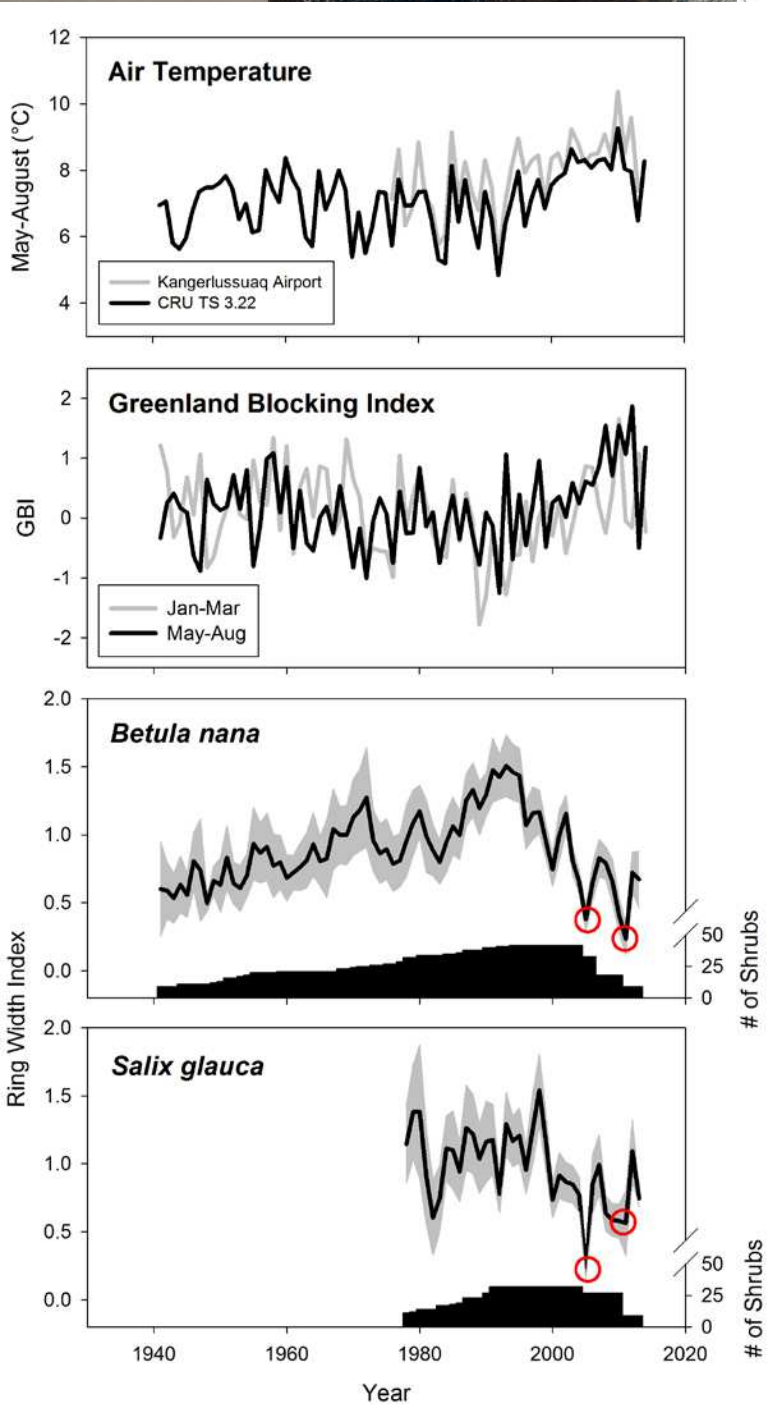
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Figure 2.



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761 **Figure 3.**

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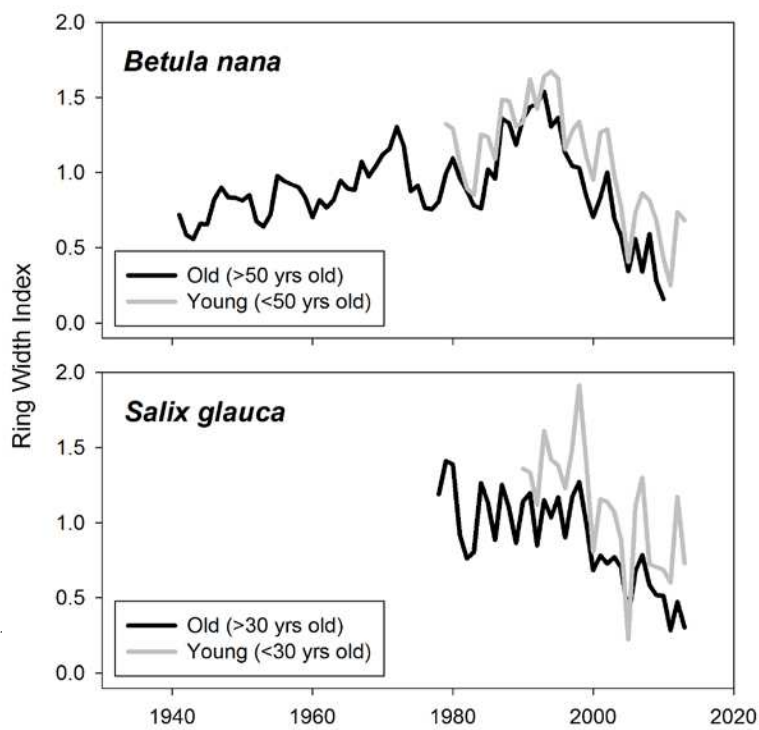
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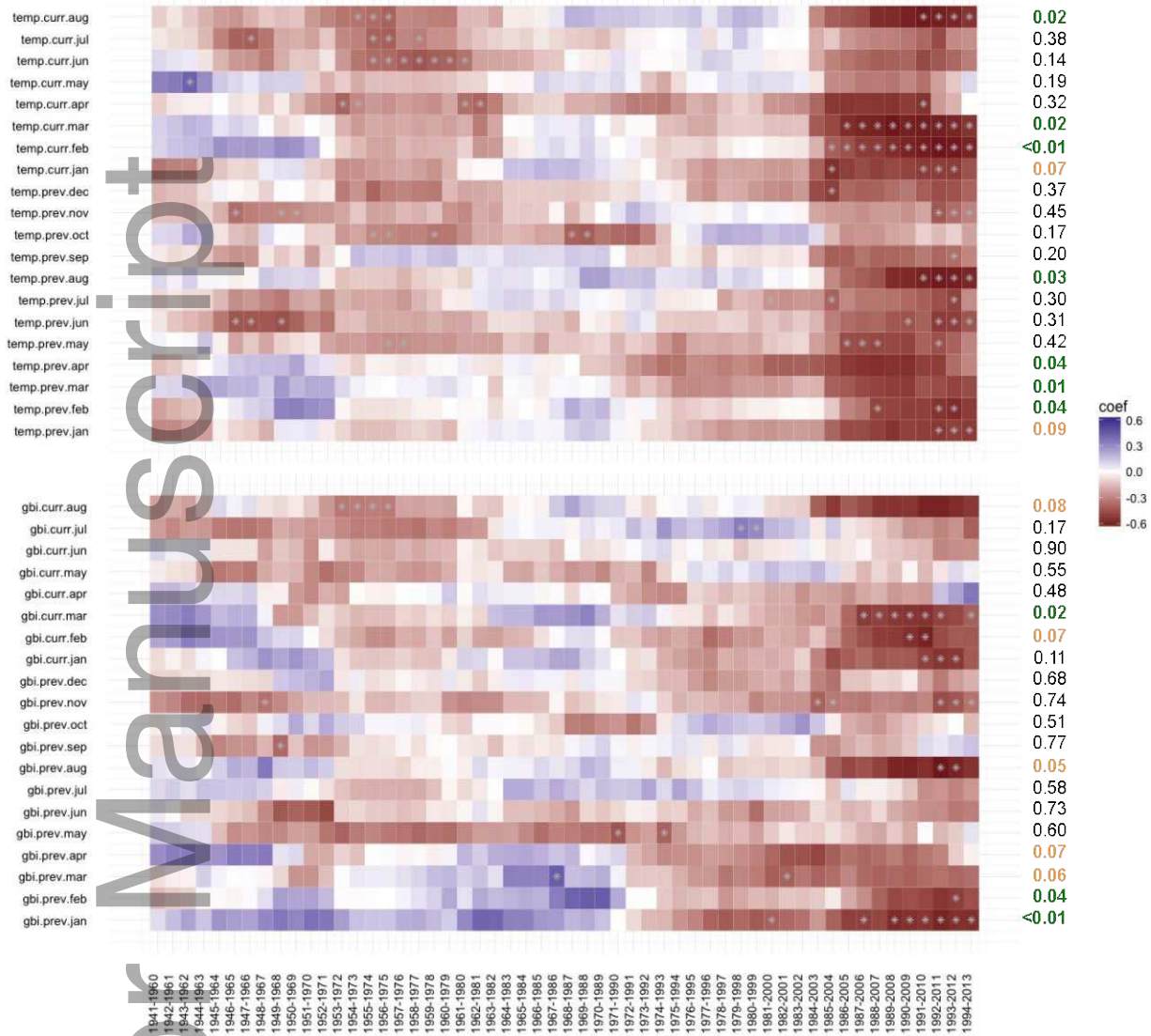
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**Figure 4.**

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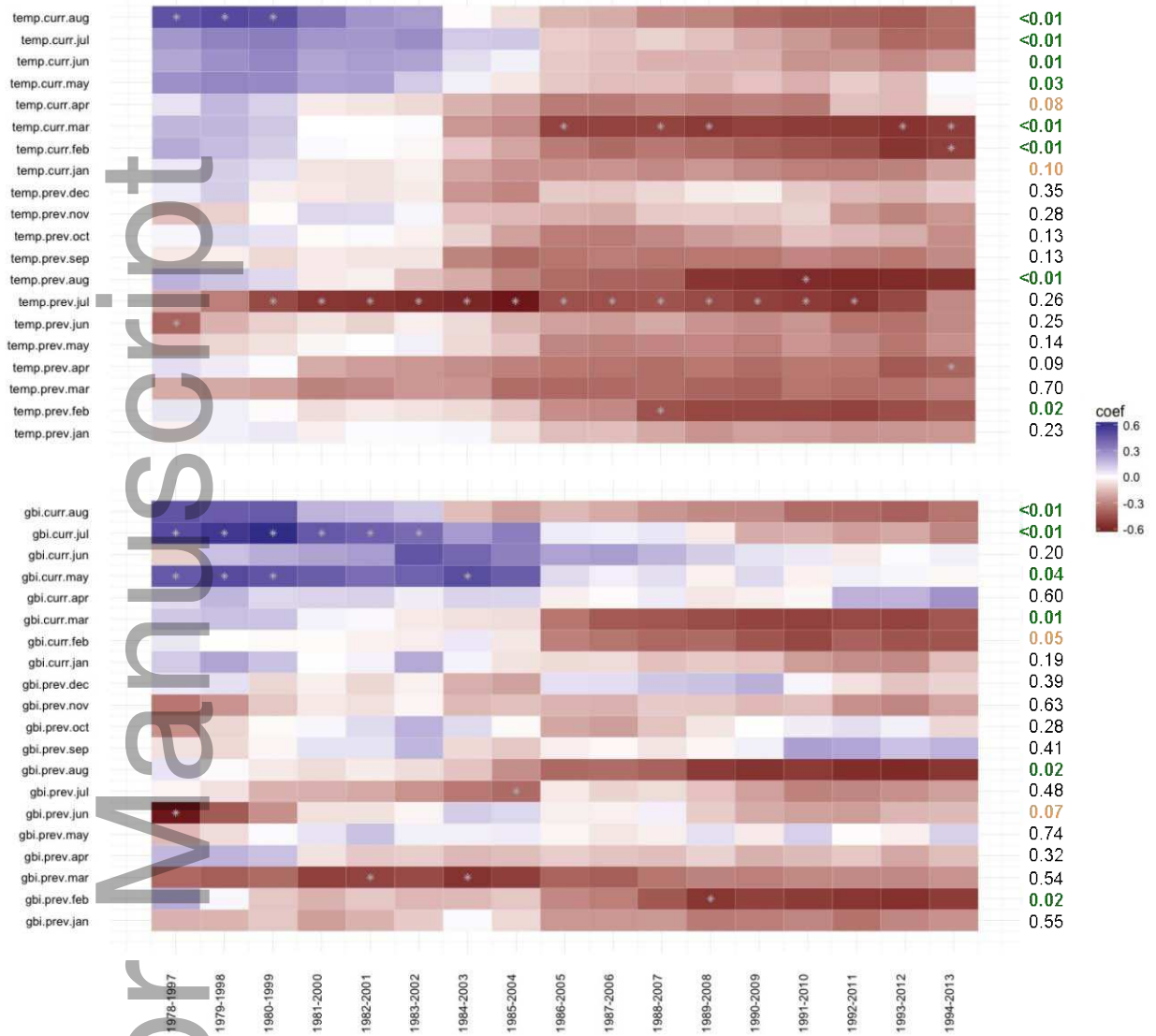
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Figure 5.



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Figure 6.

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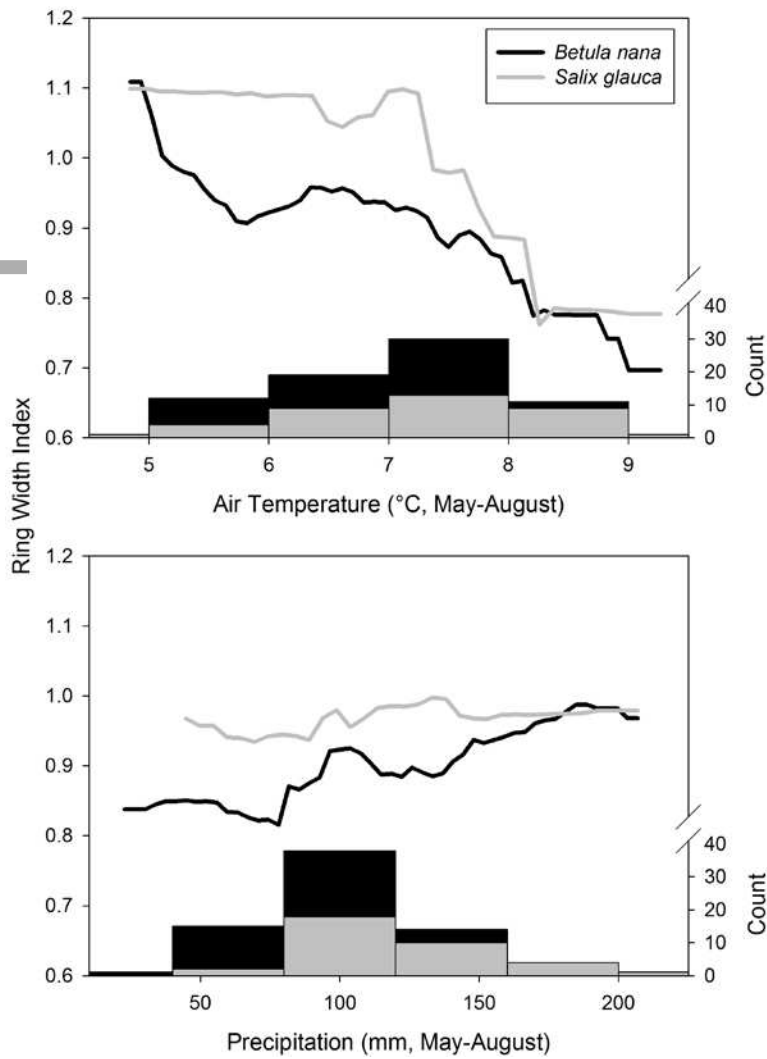
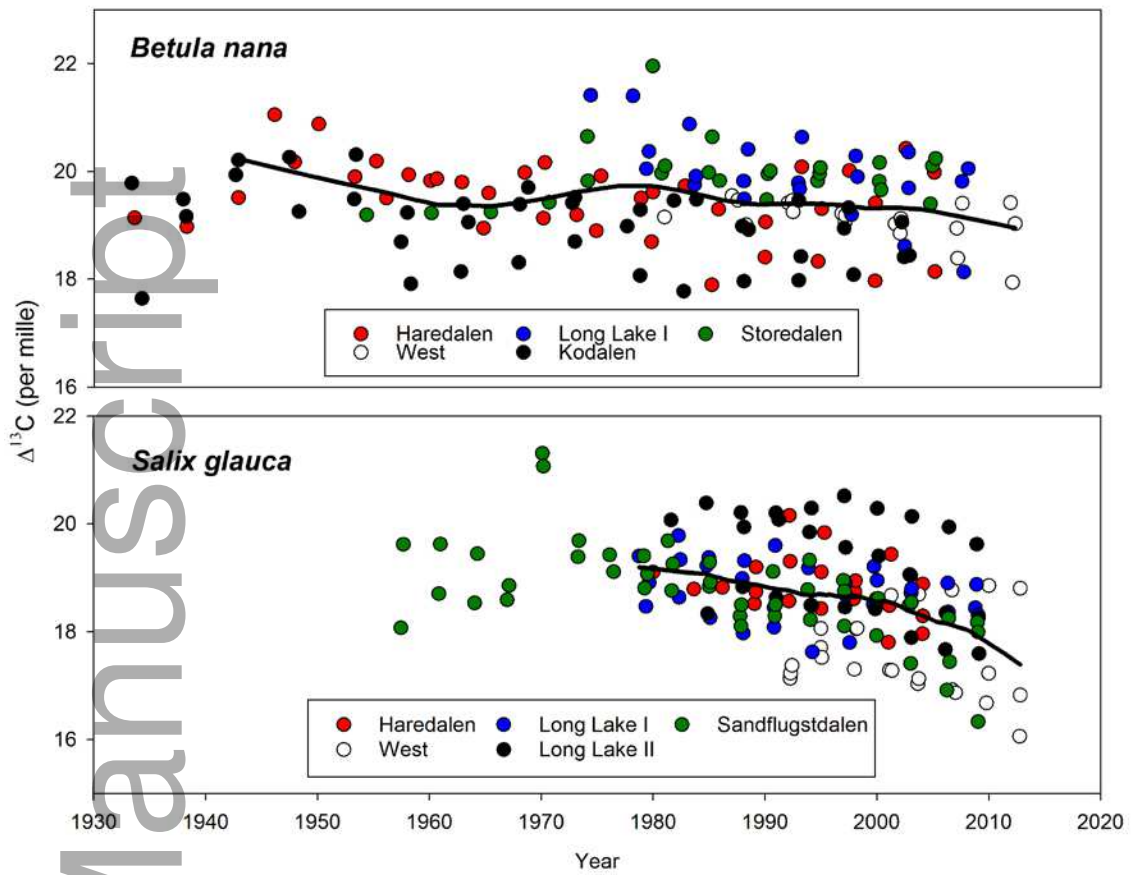


Figure 7.



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817 **Figure 8.**