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Temperature sensitivity of willow dwarf shrub growth from two distinct High Arctic sites

Agata Buchwal[1] · Stef Weijers[2] · Daan Blok[3] · Bo Elberling[4]

Abstract

The High Arctic region has experienced marked climate fluctuations within the past decades strongly affecting tundra shrub growth. However, the spatial variability in dwarf shrub growth responses in this remote region remains largely unknown. This study characterizes temperature sensitivity of radial growth of two willow dwarf shrub species from two distinct High Arctic sites. The dwarf shrub *Salix arctica* from Northern Greenland (82°N), which has a dry continental High Arctic climate, is linked with *Salix polaris* from central Svalbard (78° N), which experiences a more oceanic High Arctic climate with relatively mild winters. We found similar positive and significant relationships between annual growth of both *Salix* dwarf shrub species and July–August air temperatures (1960–2010), despite different temperature regimes and shrub growth rates at the two sites. Also, *Salix* dwarf shrub growth was significantly negatively correlated with Arctic and North Atlantic Oscillation (AO/NAO) indices; *S. arctica* from Northern Greenland was negatively correlated with previous autumn (AO index) and current summer AO and NAO indices, and *S. polaris* with the summer NAO index. The results highlight the importance of both local and regional climatic drivers for dwarf willow shrub growth in harsh polar desert habitats and are a step in the direction of identifying and scaling changes in plant growth across the High Arctic.

Keywords *Salix arctica* (Pall.) · *Salix polaris* (Wahlenb.) · Greenland · Svalbard · Climate sensitivity · AO/NAO index

Introduction

In recent decades, tundra vegetation greenness has increased at many Arctic sites, which has been documented by remotely-sensed proxies, as the normalized difference vegetation index (NDVI) (Myneni et al. 1997; Jia et al. 2003; Walker et al. 2012). This increase has mainly been associated with increased shrub growth in response to warmer summers (Forbes et al. 2010; Blok et al. 2011; Macias-Fauria et al. 2012; Tape et al. 2012; Weijers et al. 2018) and has furthermore been confirmed by site-specific experimental and monitoring observations on tundra shrubs, typically over relatively short (less than two decades) time-scales (e.g., Walker et al. 2006; Elmendorf et al. 2012; Bjorkman et al. 2015; Prevéy et al. 2017). Large-scale patterns under field conditions are more difficult to confirm and growth response studies of shrubs of the same species across large regional and pan-regional scales and longer time-scales are rare (but see Weijers et al. 2012).

Recent studies reported a heterogeneous pattern in shrub growth responses to a changing climate (Elmendorf et al. 2012; Tape et al. 2012; Myers-Smith et al. 2015; Ropars et al. 2015) including evidences of shrub growth decline (Gamm et al. 2018). Climate sensitivity of shrub growth was found to be greatest at the boundary between the Low and High Arctic, and greater for taller than shorter shrub species (Myers-Smith et al. 2015). Additionally, Arctic vegetation is

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getting taller (Bjorkman et al. 2018) which will further influence albedo changes and global heat flux (Pearson et al. 2013). This inconsistent growth response of tundra shrubs across the Arctic requires detailed studies, at both site- and species-specific levels, to gain insight in the mechanisms controlling shrub growth over longer time scales. However, extreme northern sites are especially understudied (Metcalfe et al. 2018), although these areas are expected to experience the largest climatic changes in the decades to come (Kirtman et al. 2013). Therefore, it is important to test the impact of climate warming on High Arctic shrub growth, especially as secondary growth of these shrubs may not only reflect annual growth rates of the respective species, but also past fluctuations in annual vascular plant production at the community level (Le Moullec et al. 2018).

Many studies have recently concluded that tundra shrub growth at high latitudes is limited primarily by growing season temperatures (for example: Forbes et al. 2010; Blok et al. 2011; Buchwal et al. 2013; Myers-Smith et al. 2015; Weijers et al. 2017). In contrast, *Salix arctica* growth was found to be related with snow precipitation in NE Greenland (74° N), suggesting that shrub growth may not be exclusively related to air temperatures (Schmidt et al. 2006, 2010). In addition, winter temperatures in the Arctic have been shown to be an important driver for *Betula nana* shrub growth (Hollesen et al. 2015). Therefore, comparisons of shrub growth sensitivity to climate between sites across climate gradients are an important new step in terms of linking site-specific observations to regional vegetation responses to climate changes (Prevéy et al. 2017).

Very few chronologies covering recent decades are available from the extreme High Arctic (> 75° N; see Weijers et al. 2010, Weijers et al. 2017). This is both due to the remoteness of those sites as well as the numerous growth constraints caused by the harsh environmental conditions that northernmost woody plants represent (cf. Schweingruber et al. 2013), which often lead to incomplete or missing rings and crossdating difficulties. Willow shrubs are among the most widespread tundra woody plants, but their growth has not yet been compared across genus and locations in the extreme High Arctic. Specifically, *Salix arctica* (Pall.) is among the most northerly occurring woody plant species in the world and its dendrochronological potential in the High Arctic was already recognized in the nineteenth century (Kraus 1874). *S. arctica* exhibits clear but irregular growth rings and is known to reach ages of about 130 years (Kraus 1874; Polunin 1955; Polunin 1958). Studies on that species were conducted for example on Axel Heiberg Island (ca. 79°N) (Beschel and Webb 1963), Cornwallis Island (74° N) (Warren Wilson 1964), and Ellesmere Island (82° N and 81° N; Woodcock and Bradley 1994, Savile 1979), all in the Canadian High Arctic, as well as in Eastern Greenland, Zackenberg (74° N) (Schmidt et al. 2006, 2010). In parallel, in the European High Arctic

(Spitsbergen, Svalbard 77°–78° N), the dendroclimatological potential of another willow shrub was recently recognized and described for the dwarf willow shrub *Salix polaris* Wahlenb. (Buchwal et al. 2013; Owczarek and Opała 2016). Thus, with the spatial distribution of *Salicaceae* shrubs in the northernmost regions of the Arctic, regional variability in climatic controls on that genus' growth can be assessed. This is further relevant for assessing *Salix* dwarf shrubs potential and role in future snow redistribution, water balance, permafrost thaw and forage availability (cf. Myers-Smith et al. 2011) in the most extreme and climatically diverse High Arctic ecosystems.

This study aims to characterize the temperature sensitivity of two dominant dwarf willow shrub species from two strongly contrasting High Arctic sites (continental vs. oceanic). We tested weather radial growth of different dwarf shrub species from the same genus, is characterized by similar temperature sensitivity, despite potential species-specific growth requirements and site-specific conditions in two remote High Arctic locations. Additionally, to account for a part of variance in shrub growth not explained by temperature and in relation to the recent findings highlighting strong relationship between High Arctic dwarf shrub growth and large-scale atmospheric circulation patterns (Weijers et al. 2017), we compared our two *Salix* chronologies with the Arctic and North Atlantic Oscillation (AO/NAO) indices (Hurrell 1995). Although the two indices are highly correlated, the AO index is expected to influence weather patterns in Northern Greenland more, whereas NAO index signature is more prominent in the lower polar latitudes. Specifically, the NAO index relates to a redistribution of atmospheric mass between the Arctic and the subtropical Atlantic, and swings from one phase to another, producing large changes in, for example, heat and moisture transport between the Atlantic and neighboring continents (Hurrel et al. 2003). The positive phase of the NAO index was found to be associated with a significant increase in storminess in the Spitsbergen region (Hurrell 1995; Hurrell and Van Loon 1997), as well rain-on-snow events (Putkonen and Roe 2003). The related AO index accounts for a significant larger fraction of the variance in Northern Hemisphere surface air temperatures and has been identified as the dominant empirical orthogonal function of winter sea-level pressure variability for the Northern Hemisphere poleward of 20° N (Thompson and Wallace 1998; Deser 2000). Moreover, signatures of both NAO and AO index are reflected in numerous tree (D'Arrigo et al. 2003) and selected shrub (Aanes et al. 2002; Welker et al. 2005; Weijers et al. 2017) growth chronologies.

We hypothesized (1) a similar climate-growth response of *Salix* dwarf shrubs with respect to temperature despite the differences in climate between the two High Arctic sites and (2) that dwarf shrub growth of both species is controlled indirectly and in a similar manner by larger-scale climatic features, such as the AO and NAO atmospheric circulation patterns.

Material and methods

Study sites and shrub sampling

Jørgen Brønlund Fjord is located on Peary Land, which is a peninsula in northern Greenland about 700 km south of the North Pole and thereby the most northerly ice-free region in the world. Peary Land reaches from Independence Fjord in the south to the northernmost point of Greenland's mainland and the Arctic Ocean in the North.

Peary Land is mountainous polar desert with generally a growing season lasting 1 month (July) and an annual precipitation sum usually less than 100 mm per year (Bennike 1987). The mean annual air temperature in the central part of the fiord is − 16.2 °C (sd = 1.1 °C) as computed for the period 1960–2010 (Table 2). Mean winter temperature (previous December
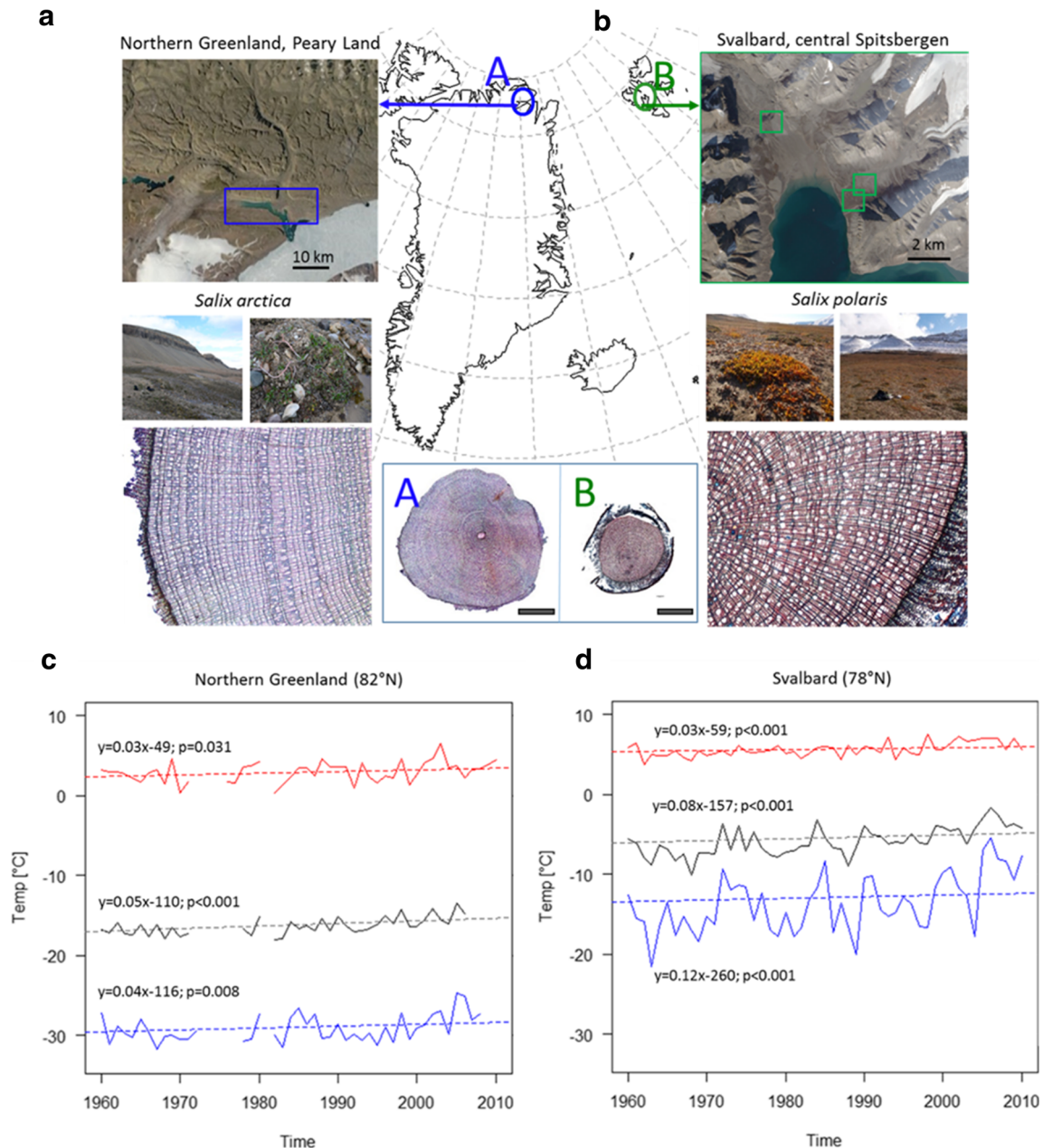
Fig. 1 The High Arctic study locations and species (**a** and **b**), and climate (**c** and **d**). **a** *Salix arctica* shrub and cross-section from Northern Greenland (Peary Land) - vicinity of Jørgen Brønlund Fjord (82°N); and **b** *Salix polaris* shrub and cross-section from central Spitsbergen, Svalbard - vicinity of Petuniabukta (78°N). Cross-section black scale bars indicate 2 mm. Satellite images: Google Maps (Peary Land)/ Norwegian Polar Institute (Spitsbergen). Mean temperatures (**c** and **d**): annual temperature (black solid line), winter temperature (previous December-current February; blue solid line) and summer temperature (July–August; red solid line). Dashed lines represent linear trends. See "Material and Methods" for temperature data sources

- current February, pDJF) is - 29.1 °C (sd = 1.7 °C). The warmest month is July and the coldest February with average temperatures of 3.7 °C (sd = 1.5 °C) and − 30.1 °C (sd = 2.9 °C), respectively. All temperature averages for Peary Land were computed based on CRUTEM4 and DMI datasets (with gaps, see below).

The summer (JJA) is relatively mild with typically 40–60 days without frost, a low relative humidity and periods with strong and dry foehn-like winds. Due to the very limited precipitation, the area is characterized as "desert-like" with very sparse vegetation developed only in limited micro-sites where melting snowdrifts and creeks supply water in summer (Holmen 1957). In lowlands and on slopes with running meltwater from snowdrifts, a thin soil layer up to 20 cm, but mostly less than 5 cm, is formed.

S. arctica is characterized as one of the earliest (mid-June) flowering plant in Peary Land, growing in micro-habitats such as snow-beds, slopes, and riversides (Holmen 1957). At the study site, mainly isolated individuals are found that prostrate from a central stem and are usually less than 15 cm in height.

Shrub sampling in Peary Land, Northern Greenland, was conducted along a transect beside the 25 km long Jørgen Brønlund Fjord (82°07′ N; 33° 04′ W to 82° 03′ N; 32° 00′ W), which consists of an inner 15 km long and 2 km wide part running east-west and an outer 10 km long and up to 3 km wide section running northwest-southeast. Here 11 intact *S. arctica* individuals were collected at five locations in July 2014. Sampling locations consisted of relatively moist plots, i.e., along the creeks or downstream from snowbed areas where individual willow shrubs were observed (Fig. 1a). Samples were taken within valley bottom sites and alluvial fans at elevations below 200 m above sea level (Suppl. Table 1). Maximum distance between the sampling sites in Northern Greenland was 18 km and one to three shrubs were collected from each site. Only mature and apparently healthy individuals were sampled. Additionally, to investigate the shrubs' temperature sensitivity over a longer time-scale, we attempted to sample relatively old individuals.

S. polaris samples from the Svalbard archipelago were collected in central Spitsbergen (78° 44′ N; 16° 27′ E to 78° 42′ N; 16° 40′ E), in the Petuniabukta area located in the northernmost part of Billefjorden, which is the northeastern part of Isfjorden (Fig. 1b). According to the long-term and homogenized climate data from Svalbard Airport (Nordklim dataset 1.0, 08/01 KLIMA 2001; DNMI 2018; www.eklima.no), mean annual temperature for central Spitsbergen is − 5.8 °C (sd = 1.8 °C), as computed for the period 1960–2010. Mean winter temperature (previous December - current February, pDJF) for central Spitsbergen is − 13.7 °C (sd = 3.6 °C). The warmest month is July and the coldest February with average temperatures of 6.2 °C (sd = 1.0 °C) and − 15 °C (sd = 4.2 °C), respectively. The climate in the Petuniabukta area is characterized by more continental conditions than Svalbard Airport, where the long-term climate station is located (Rachlewicz

and Styszyńska 2007; Láska et al. 2012), but is still under influence of the West Spitsbergen Current, which brings warm water and shapes relatively mild winters in this part of the High Arctic, much warmer than those in Peary Land. Mean annual precipitation in the study location is usually not higher than 200 mm (DNMI 2018), which is twice as high as that at our site in Northern Greenland.

S. polaris is a mat-forming prostrate dwarf shrub species, usually smaller than 10 cm in height. The species commonly dominates the middle and northern arctic tundra zones. It often grows on fine texture substrates (www.svalbardflora.no). *S. polaris* is one of the most widely distributed woody species on Svalbard and its stands can be found in harsh polar desert habitats, including glacier moraines.

Sampling in central Spitsbergen was conducted at three locations in Petuniabukta vicinity: i) an edge of the Hørbye glacier forefield (two shrubs), ii) Ebbadalen valley bottom prone to aeolian and niveo-aeolian activity (four shrubs) and iii) gentle slope of an alluvial fan in Ebbadalen prone to seasonal wash-out (four shrubs) (Suppl. Table 1). Maximum distance between any two sampling locations was 6 km (Fig. 1b). Shrubs were selected from a broader sample pool (i.e., more than 30 shrubs) collected in central Spitsbergen in mid-August 2010. For this study, ten shrubs were selected by choosing the oldest individuals from each location that cover the study period (1960–2010). Six individuals were previously sectioned, measured, cross-dated and incorporated into the *S. polaris* site chronology, as published in Buchwal et al. (2013); however, in the current study, these shrubs were used for the calculation of climate-growth relationships over a longer time scale.

Thin-sections preparation and growth rings measurements

Although a limited number of shrubs were collected from each study area, individuals were carefully inspected and sectioned at both below- and aboveground plant segments in accordance with basic principles of serial sectioning (Kolishchuk 1990). The sectioning consisted of the extraction of 1-cm long fragments from the main root and up to two main aboveground shoots at a mean distance of 2–3 cm apart from each other. Bent or injured shrub parts were not sectioned. From each plant fragment, a thin section of 15–20 μm of thickness was cut with a sledge GSL1-microtome and later stained by a mixture of Safranin and Astra Blue (Gärtner et al. 2014). This was done to highlight lignified and unlignified tissues, and to enable the identification of narrow and irregular ring boundaries. As *S. polaris* from central Svalbard (Fig. 1b) was characterized by narrower rings and greater growth irregularities, a larger amount of cross-sections were prepared per shrub for this species than for *S. arctica* from Greenland. In total 30 stained micro-slides were prepared from Northern Greenland and 117 from central Svalbard material following a standard protocol (Schweingruber and Poschlod 2005). Sequential images

were taken from each micro-slide under 25× magnification for regular cross-sections and under × 50 magnification for irregular individuals. This was done using a Leica DFC420C camera connected to a Leica DM4500B microscope. Images were stitched together in Adobe Photoshop (Adobe Systems Incorporated, USA) to form a single high-resolution image for each cross-section, required for accurate annual ring-border recognition and ring-width measurements. The latter were performed along a minimum of three radii for each cross-section, using manual path in WinCell (Regent Instruments, Canada).

Cross-dating and chronology development

Cross-dating of raw ring width measurements of the two willow shrub species was performed separately for each species in four independent steps: Firstly, radial measurement series were cross-dated within cross-sections. This was supplemented by careful visual inspection of irregular and partially missing rings within complete cross-section. Secondly, the cross-dated radial growth curves were averaged for each cross-section and then cross-dated and averaged per shrub individual. In a third step, the resulting mean shrub series were cross-dated and averaged per sample location. In the final step, the resulting mean growth series were cross-dated at site level, which resulted in a final willow shrub chronology for each High Arctic site. Quality check of visual cross-dating was performed during the third and fourth steps using COFECHA (Holmes 1983; Grissino-Mayer 2001). Additionally, both locally missing rings (i.e., missing in some part of the shrub) and completely missing rings (rings that were not detected in a particular shrub but found in another shrub) were quantified for each shrub individual (Table 1, Suppl. Table 1). Furthermore, recognition of continuously missing outer rings (CMOR; Wilmking et al. 2012) was performed for both dwarf shrub species.

For the Peary Land site, ten *S. arctica* shrubs from five locations, 24 cross-sections (from one to four cross-section per plant) and 77 radii (from four to 12 radii per shrub) were successfully cross-dated (Table 1). Based on their low inter-series correlations with other shrubs, one shrub with clear growth suppression in the outermost rings and six cross-sections were excluded from further analyses.

For central Spitsbergen, all 117 *S. polaris* cross-sections prepared from ten willow shrubs were successfully cross-dated and further analyzed. In total, two to 19 thin-sections were prepared per shrub and a total of 420 radii measured (i.e., from eight to 74 radii per shrub) (Table 1). Ring-widths were measured along three to six radii within each *S. polaris* cross-section to support the detection of incomplete (wedging) and locally absent rings, which are frequent in this species (Buchwal et al. 2013).

After cross-dating, two raw site chronologies were computed, one for each willow shrub, using an arithmetic mean.

Data standardization

Raw growth ring-width measurements after cross-dating were standardized to remove possible non-climatic age-related and/or biologically induced growth trends. The juvenile phase growth trend, i.e., a sharp decline in ring-widths with increasing stem diameter during early stage of shrub growth, was visible in *S. arctica* growth curves, but not in *S. polaris* (Fig. 2; Suppl. Fig. S1). To evaluate climate-growth responses of shrubs from two distant High Arctic sites in a comprehensive way both chronologies were standardized.

To retain the low-frequency component in our growth data, we used a regional curve standardization (RCS) method to standardize raw tree-ring series by calculating an empirical age-related growth curve and by dividing each mean cross-section series by this growth trend (Briffa et al. 1992; Briffa and Melvin 2011). The single-curve RCS chronologies are often affected by what is known as "modern sample bias" (Melvin 2004; Sullivan et al. 2016), which can emerge when a population of trees (here shrubs) is composed of both young fast-growing and older slow-growing individuals. This artifact was not present in either chronology (Suppl. Fig. S8), most likely due to relatively homogeneous age distribution within the shrub individuals of both species.

As a result of RCS detrending ring-width indices (RWI) were generated. These were then averaged at the individual shrub level. Shrub means were than averaged at the site level using bi-weight robust means to calculate two standardized site chronologies, one for each shrub species. Autocorrelation was removed from the chronologies through whitening of the time-series using autoregressive coefficients prior to averaging. For comparison results for both raw and standardized data are shown.

We calculated the following descriptive statistics, commonly used in dendrochronology, for the quality evaluation of both chronologies: i) the mean correlation (i.e., inter-series correlation) between individual growth curves and a master chronology (r), ii) mean pairwise correlation between all cross-sections (rbar.tot), iii) mean correlations between mean cross-section series within individual shrub (rbar.wt), and iv) mean inter-series correlation between all mean shrub series (rbar.bt). Analyses were computed in R (version 3.2.5) using the dplR package (version 1.6.4) (Bunn 2008; Bunn et al. 2016). Other statistics included computation of: v) the expressed population signal (EPS), vi) signal-to-noise ratio (snr), vii) mean sensitivity (MS), viii) Gini coefficient (Gini) as well ix) first-order autocorrelation, i.e., AR(1) (Table 1).

Climate-growth relationship analyses

The period 1960–2010 (50 years) was used for climate-growth relationship analyses as this period was characterized by at least three individual shrubs in both study areas (Table 1) with a stable common signal (i.e., EPS > 0.85). Climate-growth

Table 1 Characteristics and descriptive statistics of the High Arctic willow shrub chronologies. Chronology statistics relate to raw and rcs-detrended (RWI) chronologies of both species. *r*, Mean interseries correlation between individual growth curve and a master chronology; *rbar.tot*, mean pairwise correlation between all cross-sections; *rbar.wt*, mean correlation between growth series from the same shrub over all shrubs; *rbar.bt*, mean interseries correlation between all series from different shrubs

Study species Sampling location Geographic coordinates	*Salix arctica* Pall. Northern Greenland, Peary Land 82° N; 32–33° W		*Salix polaris* Wahlenb. Central Spitsbergen 78° N; 16° E	
Chronology timespan	(1925–2014)		(1941–2010)	
# shrubs/# cross sections	10/24		10/117	
# radii measured	77		420	
Mean shrub age (± sd) [yrs]	58 (25)		48 (9)	
Max shrub age [yrs]	90		70	
Total % missing rings	5.3		6.4	
Timespan >3 shrubs	(1931–2014)		(1957–2010)	
EPS > 0.85 [yr]	1967		1945	
	(1960–2010)			
mean ring width (± sd) [mm]	0.122 (0.037)		0.056 (0.020)	
max ring width [mm]	0.234		0.111	
	(1960–2010)			
	raw	RWI	raw	RWI
MS	0.581	0.578	0.652	0.653
Gini	0.306	0.289	0.329	0.303
AR (1)	0.282	0.246	0.143	0.071
r	0.417	0.398	0.488	0.453
rbar.tot	0.224	0.186	0.309	0.257
rbar.wt	0.51	0.389	0.611	0.566
rbar.bt	0.193	0.164	0.268	0.216
snr	2.784	2.475	5.828	4.534
EPS	0.736	0.712	0.854	0.819

relationship analyses for both willow species were performed only with air temperature data and AO/NAO indices, as precipitation records from Peary Land are neither representative for our site, nor available for the entire study period.

To test climate sensitivity of both species while accounting for potential variation in growing season lengths between the study sites and influence of climate during and outside of the growing season, various temporal scales and climate-growth relationship analyses were performed. Following common procedures in dendroclimatology, we primarily calculated Pearson's correlation coefficients to investigate relations between radial growth of each willow shrub species and monthly climate. Specifically, correlations with air temperature and AO/NAO indices were computed on monthly, i.e., from previous June to September of the year of growth, and seasonal basis, i.e., using a combination of two to three following months for which the highest monthly correlation was revealed. These analyses enable the comparison with earlier dendrochronological studies. To all correlations performed, *p* values were adjusted for multiple comparisons using the false discovery rate

(Benjamini and Hochberg 1995) and Bonferoni (Bland and Altman 1995) corrections. In the main text, the results of the first method are reported. Complete comparisons between raw and adjusted *p* values (two methods), together with additional bootstrapped correlation analyses performed between the chronologies and summer temperature as well as AO/NAO indices, are presented in the Supplementary Materials (Suppl. Table 7–9; Suppl. Fig. S10-S16). Also, linear mixed effect (LME) modeling was performed to account for potential site-based variability of shrubs' climate sensitivity. The full methods and results of LME modeling are shown in the Supplementary Materials (Suppl. Table 1–6).

To account for variations in temperatures over shorter time-scales, and therefore differences in lengths of growing seasons at both study areas, moving correlations were calculated between average 10-days mean air temperatures offset by 1-day and standardized chronologies of both *Salix* species. For these analyses homogenized daily temperature data (see below) were used for the common period 1976–2010. Also relationships between growth rings and summer temperature (at
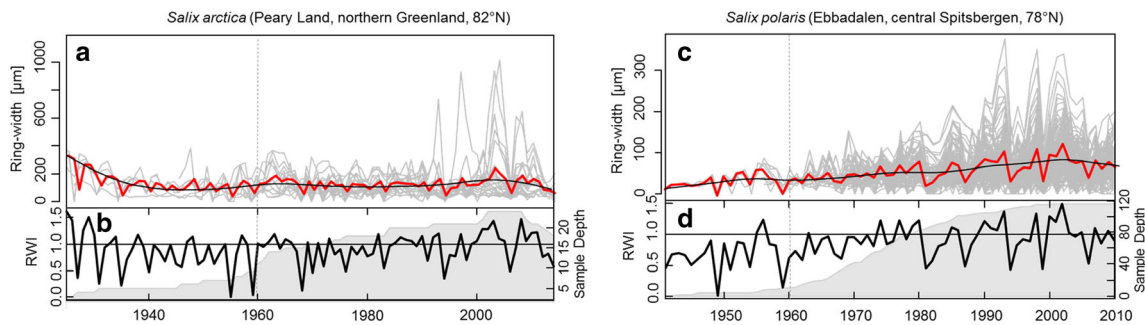
Fig. 2 The High Arctic dwarf shrub chronologies: **a** raw (red) and **b** standardized (black) *Salix arctica* Pall. ring-width chronology from Northern Greenland (Peary Land, 82°N); **c** raw (red) and **d** standardized (black) *Salix polaris* Wahlenb. ring-width chronology from central Spitsbergen, Svalbard (Petuniabukta, 78°N); RWI: ring-width index after regional curve standardization (RCS). Sample depth refers to total number of cross-sections. The vertical dashed lines in both graphs mark the onset of the common period, i.e., 1960, used in the climate-growth relationship analyses

monthly and seasonal resolution) of both species were tested over two periods, i.e., an early (1960–1985) and a recent (1986–2010) period. This was done by fitting a linear model and conducting a regression analysis between standardized mean annual growth (RWI) and mean monthly (July, August) and seasonal (July–August) temperature, respectively, for each studied species. This comparison of climate sensitivity of shrub growth across two periods was performed to evaluate trends in growth responses as a function of changing temperature. Additionally, temporal trends in temperature were assessed by fitting linear models.

Climate data

Mean monthly temperature data for Peary Land, northern Greenland, were obtained from CRUTEM4 gridded land-surface air temperature dataset (Jones et al. 2012; Osborn and Jones 2014) and based mainly on records obtained from Station Nord climatic station (81° 43′ N, 17° 47′ W) for the period 1960–2008, supplemented for last 2 years by data obtained from Danish Meteorological Institute (DMI 2018). Nevertheless, the following data gaps have been identified for our final temperature dataset: June1972–September 1975, February 1976, January–March and May 1977, January–November 1981, April–June 2007, February–March 2009. Mean monthly temperatures from Svalbard Airport (78° 15′ N 15° 28′ E) were obtained for the period 1960–2001 through the package "nordklimdata1" in R (08/01 KLIMA, 2001) and supplemented with DNMI (2018) data for the same station up to year 2010.

For running correlations with mean daily air temperatures, the following climate station data were used from period 1976–2010: Station Nord for Peary Land, Northern Greenland (source: DMI 2018; 04310 Station Nord for period 1976–2006 and 04312 Station Nord AWS for period 2007–2010), and homogenized Svalbard Lufthavn data from central Spitsbergen (source: DNMI 2018).

Monthly Arctic Oscillation (AO) and North Atlantic Oscillation (NAO) index values were obtained from Climate Prediction Center (CPC), a part of National Oceanic and Atmospheric Administration's (NOAA) National Weather Service (CPC 2016, www.cpc.ncep.noaa.gov).

Results

Air temperature characteristics and trends

Table 2 and Fig. 1c, d summarize the results of climate data, mainly temperature, from the two sites. Linear regression analyses over 1960–2010 revealed that two strongest positive trends in mean monthly temperature were recorded in Peary Land for April (0.08 °C year^{-1}, $p = 0.003$) and November (0.07 °C year^{-1}, $p = 0.005$), whereas for central Spitsbergen for February (0.15 °C year^{-1}, $p < 0.001$) and January (0.13 °C year^{-1}, $p = 0.007$). The trend in mean annual temperature, although not statistically different, was higher for central Spitsbergen (0.08 °C year^{-1}, $p < 0.001$, df = 49) than for Peary Land (0.05 °C year^{-1}, $p < 0.001$, df = 40). Seasonal temperature trends both for winter (pDJF) and summer (JulAug) were higher for central Spitsbergen (0.12 °C year^{-1}, $p < 0.001$ and 0.03 °C year^{-1}, $p < 0.001$ respectively) than for Peary Land (0.04 °C year^{-1}, $p = 0.008$ and 0.03 °C year^{-1}, $p = 0.031$ respectively) (Fig. 1c, d). In Peary Land, the strongest positive trend in summer air temperature was observed for July ($r^2 = 0.129$, $p < 0.05$, slope = 0.035, df = 44), whereas in central Spitsbergen for July ($r^2 = 0.256$, p < 0.001, slope = 0.034, df = 49) and August ($r^2 = 0.253$, $p < 0.001$, slope = 0.031, df = 49). Also, for central Spitsbergen considerable increase of a positive trend in August temperature was observed in the recent period, i.e., from 1986 to 2010 ($r^2 = 0.254$, $p < 0.05$, slope = 0.053, df = 23). Trends estimated for summer months temperature were not significant for Peary Land over that period (i.e., for June: $p = 0.402$; for July: $p = 0.082$; for August: $p = 0.856$).

Table 2 Comparison between climate variables of Northern Greenland (Peary Land, 82°N) and central Spitsbergen, Svalbard (78° N). TEMP: temperature data (°C) were computed over the common period 1960–2010. See "Material and Methods" for temperature data sources; PRECIP: precipitation data source: * after Bennike (1987); ** measured over the period 1976–2010 at the Svalbard Airport weather station, DNMI (2018); *sd* standard deviation

Climate variable		Northern Greenland (82°N) Peary Land	Svalbard (78°N) Central Spitsbergen
Mean annual TEMP		− 16.2	− 5.8
	sd	1.1	1.8
Mean annual PRECIP [mm]		< 100*	184**
Mean TEMP for the coldest month (Feb)		− 30.1	− 15
	sd	2.9	4.2
Mean winter TEMP (prev. Dec to current Feb)		− 29.1	− 13.7
	sd	1.7	3.6
Mean TEMP for the warmest month (Jul)		3.7	6.2
	sd	1.5	1
Mean summer TEMP (JulAug)		3	5.7
	sd	1.3	0.9
Max mean TEMP for JulAug (year)		6.6 (2003)	7.6 (1998)
Min mean TEMP for JulAug (year)		0.4 (1970, 1982)	3.8 (1962)
Max mean TEMP for Jul		8 (2003)	8.3 (1998)

Shrub species chronologies and growth ring patterns

Growth ring measurements and successful cross-dating of ten shrubs per High Arctic site resulted in two willow shrub ring-width chronologies (Fig. 2). The *S. arctica* chronology from Peary Land covered 90 years (1925–2014), whereas the *S. polaris* chronology from central Spitsbergen was 70 years long (1941–2010). Mean age of *S. arctica* individuals was 58 years (max = 90, sd = 25), whereas mean age of *S. polaris* was 48 years (max = 70, sd = 9). The *S. polaris* chronology was represented by higher mean sensitivity and mean inter-series correlation, but lower first-order autocorrelation than *S. arctica* (Table 1).

Among 1187 growth rings measured in *S. arctica* and 4289 rings analyzed in *S. polaris* there were in total 5.3% (i.e., 64 rings) and 6.4% (i.e., 275 rings) missing rings detected respectively, which represents locally missing rings (i.e., missing in some part of the shrub) together with completely missing rings (i.e., missing entirely in a shrub individual) (Table 2). Despite different amounts of cross-sections per species and different ages of the willow shrubs analyzed, the total number of completely missing rings, i.e., rings that were not detected in a particular shrub but found in another shrub, was similar between the species. The number of missing rings equalled 2.1% (i.e., 12 rings) and 1.9% (i.e., 9 rings) for *S. arctica* and *S. polaris*, respectively (Suppl. Table 1). Continuously missing outer rings (CMOR) were not observed in *S. polaris*, but were detected in four (i.e., 17%) *S. arctica* cross-sections. A maximum of six consecutive CMOR were detected in a single *S. arctica* shrub.

Mean annual radial growth over the 1960–2010 period measured 0.122 mm (sd = 0.04) for *S. arctica* (Greenland) and 0.056 mm (sd = 0.02) for *S. polaris* (Svalbard). Maximum mean annual ring width was registered for *S. arctica* chronology in 2003 (0.234 mm) and for *S. polaris* chronology in 2002 (0.111 mm).

Temperature-dependent growth

Both willow species from the two High Arctic sites revealed a significant summer temperature signal over the 50-year study period (1960–2010) (Fig. 3a, b, Suppl. Table 7). The raw *S. arctica* ring-widths from Peary Land were found to correlate with mean July ($r = 0.397$, $p = 0.016$) and July–August (JULAUG) air temperature ($r = 0.424$, $p = 0.016$), whereas the correlations between the standardized *S. arctica* chronology and both July and July–August were nearly significant ($p = 0.054$). Standardized *S. polaris* radial growth at our site in central Spitsbergen was found to be strongly correlated with mean July ($r = 0.486$, $p = 0.002$), August ($r = 0.502$, $p = 0.001$), and mean July–August temperature ($r = 0.550$, $p < 0.001$). Additionally, the raw *S. polaris* chronology revealed a positive correlation with previous September air temperature ($r = 0.305$, $p = 0.017$) and current June temperature ($p = 0.006$). Summer temperature signal was additionally observed in both species with bootstrapped confidence intervals computed for correlation coefficients (Suppl. Fig. S11–S12).

Growth increase for *S. polaris* estimated between a recent (1986–2010) and an early (1960–1985) period equalled 23.1 μm for raw tree ring widths (33.6%) and 0.113 for
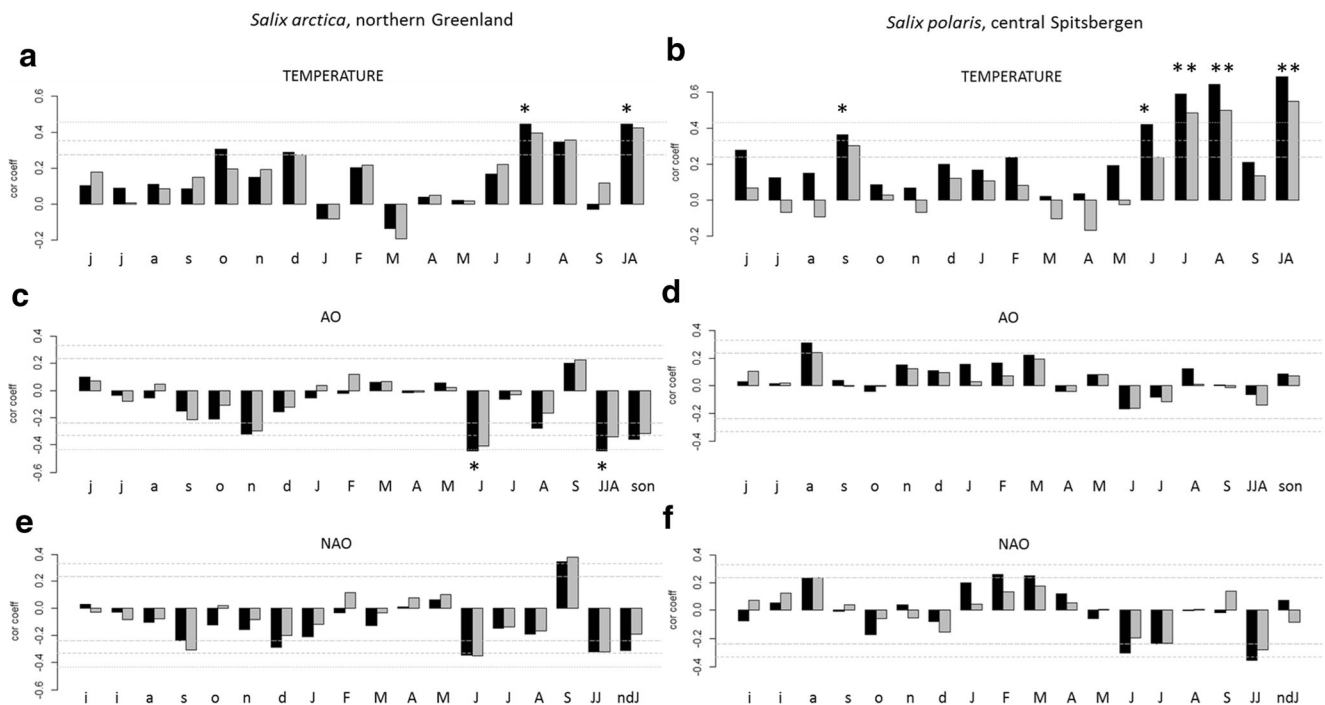
Fig. 3 Pearson's correlation coefficients between raw (black) and RCS standardized (gray) growth rings chronologies of *Salix arctica* (**a**, **c**, **e**) from Peary Land (82° N), Northern Greenland and *Salix polaris* (**b**, **d**, **f**) from central Spitsbergen, Svalbard (78° N), and monthly and seasonal temperatures (**a**, **b**), AO indices (**c**, **d**), and NAO indices (**e**, **f**). Correlations were computed over the common period 1960–2010. Significance levels are marked with dashed lines (raw *p*-values: $p < 0.05$, $p < 0.01$, $p < 0.001$, respectively) and asterisks indicate significant correlation coefficients obtained with p-values adjusted for the false discovery rate. Lowercase letters represent previous year months, uppercase letters current year months. JJ: current June and July; JJA: current June–August; ndJ: previous November-current January; son: previous September–November). See Material & Methods for climatic data sources. Degrees of freedom (df) differs between A (df = 44) and B (df = 49), due to gaps in the Greenland temperature record

detrended RWI (11.6%), whereas for *S. arctica* it was 11.2 μm (8.7%) and 0.153 (14.9%), respectively. In addition, linear regression analyses revealed a positive linear trend in annual growth of the two willow shrub species in relation to summer temperature at both High Arctic locations. Stronger positive relationships between *Salix* growth and summer temperature were found in the recent period, i.e., 1986–2010, as compared to the early period (i.e., 1960–1985) at both locations (Fig. 4; Suppl. Fig. S2 and S5). Linear mixed effect (LME) modeling (Suppl. Mat.) confirmed the results obtained using more traditional dendrochronological methods and indicated that the detected summer temperature-growth relationships at both sites and both species were largely consistent when accounting for variability across sites and years (Suppl. Table 2–3).

The correlation analysis with moving 10-day-windows of mean air temperatures and standardized *Salix* ring-width growth revealed that among temperature variables *S. arctica* (Peary Land) secondary growth was mainly influenced by temperatures during the beginning of July, whereas secondary growth of *S. polaris* (central Spitsbergen) was mainly influenced by August temperatures (Fig. 5a). The highest correlations with 10-day mean air temperature for *S. arctica* was with mean temperatures between 1st and 10th of July ($r = 0.62$,

$p < 0.05$) and between 10th and 20th of August for *S. polaris* at ($r = 0.64$, $p < 0.01$).

AO/NAO indices versus growth

We found significant correlations (Fig. 3c–f, Suppl. Fig. S6, Suppl. Table 8) between radial growth of *S. arctica* dwarf shrubs and regional atmospheric circulation pattern reflected in monthly and seasonal AO indices over a half century-long period (1960–2010). Specifically, both species demonstrated reduced growth with positive AO and/or NAO summer indices. The raw *S. arctica* chronology from Peary Land was negatively correlated with June–July-August (JJA) AO index ($r = -0.341$, $p = 0.011$). In addition, the correlation between autumn AO index of the previous year (i.e., September–October-November, son) and raw *S. arctica* growth at our site in Northern Greenland was nearly significant ($r = -0.318$, $p = 0.058$). Correction of *p* values according to the false discovery rate suggested no further significant relationships between *Salix* growth and AO/NAO indices. However, correlation coefficients with bootstrapped confidence intervals suggest significant correlations between the standardized *S. arctica* chronology and previous November and current

Salix arctica, Peary Land   Salix polaris, central Spitsbergen
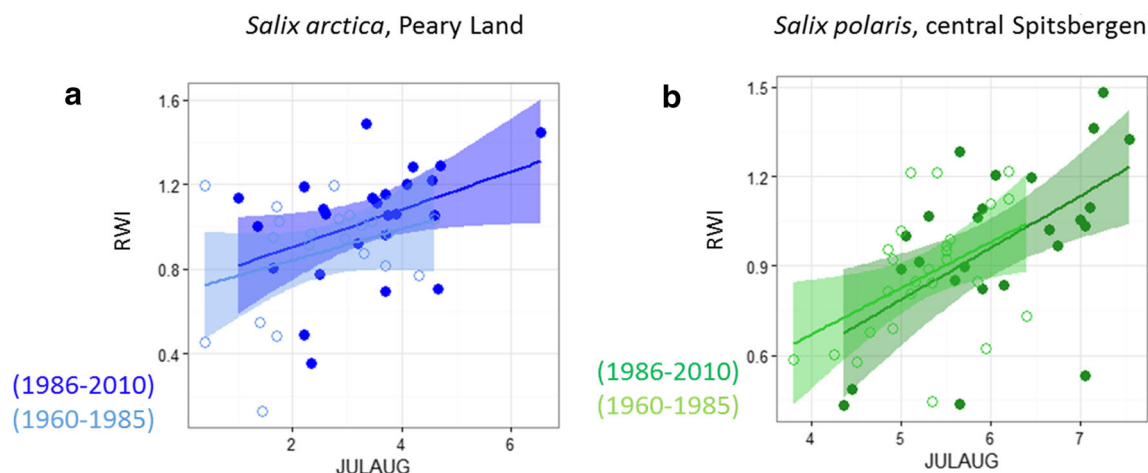
Fig. 4 Linear regression analyses of *Salix* spp. ring-width index (RWI, standardized chronologies) to summer air temperature for two periods: (1960–1985)—open circles; (1986–2010)—filled circles. *Salix arctica* chronology (blue) from Peary Land (82° N), Northern Greenland; **b** *Salix polaris* chronology (green) from central Spitsbergen (78° N); Climatic data source: see Fig. 2 caption

June AO index, as well previous September, current June and current September NAO index (Suppl. Fig. S13-S14). Furthermore, bootstrapped confidence intervals suggest significant correlation coefficients between the standardized *S. polaris* chronology and previous August NAO index (Suppl. Fig. S16).

Discussion

Temperature sensitivity of two willow shrub species from two distinct High Arctic sites

Despite differences in site-specific conditions and regional climate, the two willow shrub species studied, each from another remote High Arctic location, were characterized by summer temperature sensitivity recorded in their ring-width chronologies spanning a half-century (1960–2010). This significant summer temperature signal found for both species is in line with observations for non-dwarf *Salix* spp. shrubs from other Arctic sites, such as: *Salix pulchra* in Northeastern Siberia (70° N) (Blok et al. 2011) and in Southwest Yukon Territory (61° N) (Weijers et al. 2018), *Salix lanata* in Northwest Russian Arctic (68° N) (Forbes et al. 2010), and *Salix glauca* in Western Greenland (67° N) (Young et al. 2016). Correspondingly, summer temperature signals were found in the evergreen dwarf shrub *Cassiope tetragona* in the Canadian High Arctic (Johnstone and Henry 1997; Rayback et al. 2012) and Northern Peary Land, Greenland (Weijers et al. 2017), approx. 130 km from our *S. arctica* study site in northern Greenland, as well as in central Spitsbergen, Svalbard (Weijers et al. 2010), approx. 65 km from our *S. polaris* study site. Additionally, the correlations with daily temperatures performed (Fig. 5) detailed the summer temperature sensitivity of both species obtained using monthly values. The results highlight that peak correlations between *S. arctica*

(Northern Greenland) and temperature emerge much earlier in the growing season than it was noted for *S. polaris* (Spitsbergen). This difference is most likely linked to contrasting length of the growing season at two study sites (Fig. 5b, c), favoring growth of *S. polaris* shrubs from Spitsbergen during much warmer August in this part of the High Arctic.

As expected, air temperature is an important environmental parameter explaining radial growth at both sites, but relatively low correlation coefficients suggest that other factors, besides air temperature, may also be important for the growth of willow dwarf shrubs in the High Arctic. As indicated in previous studies conducted on shrubs in the Low Arctic, snow cover (Hallinger et al. 2010) and soil moisture (Myers-Smith et al. 2015; Ackerman et al. 2017) could be potential drivers for favorable *Salix* spp. growth. However, verification of such relationships is hampered by lack of other-than-temperature climate data in situ from High Arctic locations, where wind-drifted snow cover is challenging to measure (cf. Haas et al. 2017).

In contrast, Schmidt et al. (2006) found no correlation between *S. arctica* ring growth and summer temperature in Zackenberg in Eastern Greenland (74°N), but a negative correlation with early spring snow cover instead. Similarly, Owczarek and Opała (2016) found no correlation between *S. polaris* growth and summer temperature in Southwestern Spitsbergen and Zalatan and Gajewski (2006) found no temperature signal in *Salix alaxensis* at Victoria Island in the Western Canadian Arctic (71° N). This further indicates that other potentially more local and micro-site conditions such as topography (cf. Ropars et al. 2015) counter the effects of temperature and therefore might limit upscaling of shrub growth sensitivity from plot to regional scales. Hence, the incoherence in various shrubs species growth responses to summer temperature requires further investigations, most likely at the regional level, to assess both species-specific and site-specific growth relations to various climatic regimes in the Arctic.
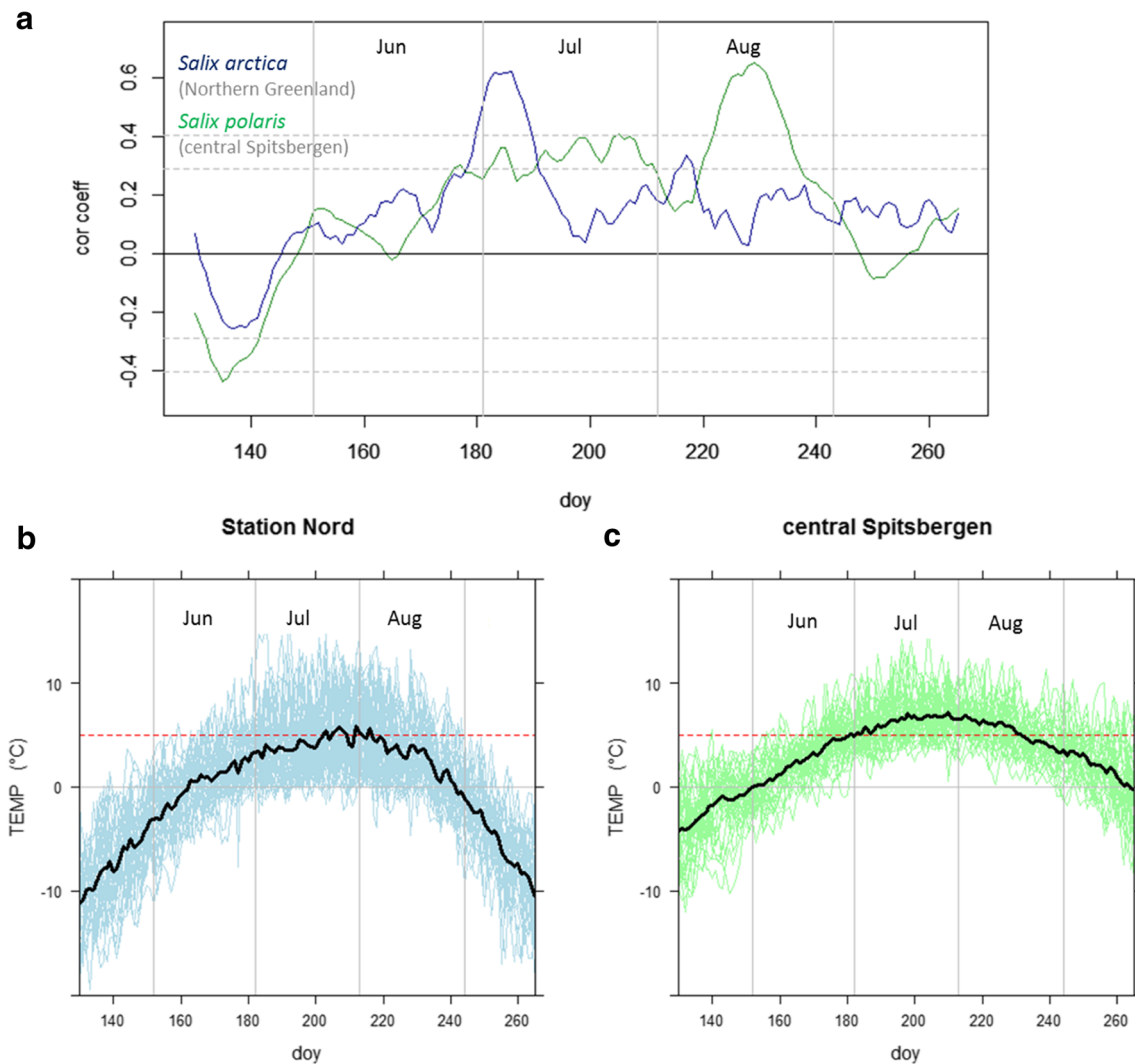
Fig. 5 **a** Moving correlations between the standardized *Salix arctica* (Northern Greenland; blue line) and *Salix polaris* (Spitsbergen; green line) chronologies and 10-day mean temperatures (offset: 1 day) over the period 1976–2010. The horizontal dashed lines indicate significance levels ($p < 0.05$ and $p < 0.01$). **b, c** Mean daily air temperatures (black lines) during the growing season over the period 1976–2010 at **b** Station Nord, Northern Greenland (blue lines represent mean daily temperatures for each year), and **c** Svalbard Airport, Spitsbergen (green lines represent mean daily temperatures for each year). Dashed red lines represent 5 °C, a common thermal threshold for cambial activity; doy - day of year. See "Material and Methods" for temperature data sources

AO/NAO indices signature in willow shrubs' chronologies

Specific relationships revealed between seasonal and monthly atmospheric oscillation indices and shrub annual growth, especially for *S. arctica*, indicate that AO/NAO indices serve as a potential measure of climatic conditions important for dwarf willow shrubs growth in the High Arctic. Since both AO/NAO indices and temperature are only weakly correlated (Suppl. Fig. S3), such relationships may suggest that not only local air temperature but also regional climatic patterns captured in monthly or seasonal AO/NAO indices may be relevant for scaling shrub radial growth over a regional scale. Variation in precipitation, rain-on-snow events, and cloudiness, are most likely strongly related to pressure differences and thus exhibited

in seasonal AO/NAO indices (Putkonen and Roe 2003; Hurrel et al. 2003). Thus, the specific relationships found between shrubs' growth and AO/NAO indices can be an important predictor of plant growth in remote high arctic areas which lack long-term climatic records (see Weijers et al. 2017).

The strongest pairwise correlation between AO/NAO indices and study sites temperatures was in this study found for negative NAO index and Station Nord (Northern Greenland) in June ($r^2 = 0.218$, df = 43, $p = 0.002$) (Suppl. Fig. S3). This relationship can be explained by the link between negative NAO index and warm weather associated with a high pressure system, which peaks in June in this section of the Arctic (Overland et al. 2012). This may further justify the negative June NAO signature found in *S. arctica* chronology (Fig. 3e). However, considering the overall relatively weak correlations between both study site monthly

temperatures and regional AO/NAO indices (Suppl. Fig. S3) the significant seasonal relationship revealed between both shrub species and regional climate (reflected in both indices) remains somehow puzzling. One way of a possible inference could link a negative phase of AO/NAO indices with a reduction in cloudiness (Hofer et al. 2017; Lim et al. 2016) and therefore with drier and more favorable for dwarf shrubs growth conditions during short arctic growing season.

Only a few studies have revealed AO/NAO indices fingerprints in Arctic shrub growth, exclusively with *Cassiope tetragona* (Aanes et al. 2002; Welker et al. 2005; Weijers et al. 2017). Specifically, the latter study conducted in Northern Greenland (Johannes V. Jensen Land, Northern Peary Land) revealed that growth of that species was significantly correlated with June NAO and previous October AO. This is in line with the correlations obtained for *S. arctica* and AO/NAO indices in this study. Whereas in Svalbard, a negative correlation with summer AO (June–September) index was revealed for *Cassiope tetragona* growth from Spitsbergen (Aanes et al. 2002) and no correlation with NAO index. In contrast, our study on *S. polaris* from a nearby location showed no correlation with AO summer index but a negative correlation with NAO June–July index instead. This suggests species-specific responses to climate reflected by AO/NAO indices for the Svalbard region, despite high correspondence between those two indices (Suppl. Fig. S4).

The correlation found between a negative AO index during the dormant period (previous September - previous November, son) and *S. arctica* growth in Northern Greenland suggests that willow shrub growth might be related to variations in seasonal snow cover, as snow cover at higher latitudes is positively coupled with a negative AO phase (Bamzai 2003; Saito and Cohen 2003; Allen and Zender 2011). This might indicate that growth of *S. arctica* in one of the northernmost High Arctic site relies on snow cover, which can be explained by the importance of meltwater during the growing season and snow cover insulation during dormancy. Positive relationship between enhanced snow cover and *S. arctica* growth was found in other High Arctic located in North-Western Greenland (Leffler and Welker 2013), as well for *Cassiope tetragona* in Svalbard (Blok et al. 2015). We conclude that further exploration is required to gain understanding of these arctic teleconnections, i.e., importance of AO/NAO signatures in the High Arctic dwarf shrubs. The results from two sites in this study are important as these sites represent contrasting environmental conditions across the High Arctic, but current exploration is hampered by a lack of high resolution in situ data (including dormant period) such as precipitation or snow depths at multiple sites across the High Arctic.

Chronology quality

Although we analyzed plants, which were sampled across different habitat types, we obtained relatively high, for dwarf

shrub series, inter-series correlation coefficients (*r*) and a consistent summer temperature signal for both species. Yet, the *S. arctica* chronology was represented by overall lower descriptive statistic values (Table 1), such as a lower inter-series correlation between shrubs (rbar.bt) and EPS, which most likely resulted from both lower sample depth per study plot and relatively higher distance between the sampling plots than applied for *S. polaris* shrubs in central Spitsbergen. Inter-series correlation between individual *S. arctica* shrubs is likely to increase when a higher number of shrubs is sampled per study.

Missing rings are a common phenomenon in arctic shrubs and might prevent successful cross-dating of shrubs growing under harsh conditions (Woodcock and Bradley 1994; Zalatan and Gajewski 2006). The relative low number of shrubs studied from both sites in our study might potentially increase the risk of not detecting missing rings. However, we believe that missing rings were successfully detected through the application of serial sectioning. The inclusion of shrubs in our study from different micro-sites, both in terms of geographical location and environmental settings, most likely increased the chance of missing rings detection, which occurrence might be highly site-specific. In addition, the significant relations with summer temperatures obtained in our study strengthens the notion that the elimination of missing rings for our study period has been fulfilled. Our study thus reaffirms that i) only a careful study of annual growth rings performed on dyed and complete thin-sections, followed by ii) thorough cross-dating within and between the shrubs, enables reliable, i.e. calendar dating of High Arctic willow shrub rings and construction of ring-width chronologies.

Summary and perspectives

This study presents the first comparison of willow dwarf shrubs radial growth chronologies from two remote High Arctic sites. Despite the differences in local climates, both studied species, i.e., the northernmost *S. arctica* ring width chronology constructed for Peary Land in Northern Greenland (82°N) and *S. polaris* from central Svalbard (78°N), showed similarity and consistency in growth responses to summer temperatures. Moreover, both species highlighted significant relationships with large-scale atmospheric circulation patterns, such as AO/NAO indices at both locations.

Through the application of shrub sampling across a relatively large area, supplemented by serial sectioning and careful detection of locally and completely missing rings, we were able to successfully cross-date relatively old shrubs from different micro-sites in two contrasting sites in the High Arctic. We suggest that extension of the chronology lengths and associated climatic signals is possible through a more extensive sampling campaign in the northernmost polar deserts, which are lacking high resolution in situ climate data. This is

especially true for *S. arctica* shrubs from Northern Greenland, which, despite more extreme climatic conditions, expressed more advanced ages than shrubs from central Spitsbergen.

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