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A WARMER AND GREENER COLD WORLD: SUMMER WARMING INCREASES SHRUB GROWTH IN THE ALPINE AND HIGH ARCTIC TUNDRA

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With 5 figures, 2 tables and appendix

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Summary: The Arctic and alpine biome is rapidly warming, which might be causing an encroachment of relatively tall woody shrub vegetation into tundra ecosystems, which will probably result in an overall positive feedback to climate warming. This encroachment is, however, believed to remain limited to the relatively warm parts of the biome, where taller shrubs may displace shorter species. Still, climate sensitivity of shrub growth strongly differs between species and sites and High Arctic dwarf shrub species may respond rapidly to increasing temperatures in absence of taller species. In addition, it remains largely unknown whether shrubs from different functional groups from the same sites respond similarly to climate drivers. In the present study we examined the climate-growth relationships of six different site-species combinations: one evergreen and one deciduous shrub species at two alpine sites, and one evergreen dwarf shrub species at two High Arctic sites. We compared linear mixed models for each combination, explaining existing shrub growth data with site-specific interpolated monthly and seasonal climate data from the gridded meteorological dataset CRU TS4.00. Shrub growth rates were found to be sensitive to summer climate for all species at all sites. Continued and projected warming is thus likely to stimulate a further encroachment of shrubs in these systems, at least through a densification of existing stands. Dwarf shrub growth strongly responded to the recent warming at both High Arctic sites, contrasting with previous work suggesting that shrub expansion might remain limited to warmer tundra regions. At the alpine sites, growth of evergreen shrubs was found to be more dependent on summer climate than growth of deciduous shrubs, perhaps because these evergreen species are less prone to herbivory. However, biome-wide generalizations at the functional group level may be difficult to interpolate to the species level. Micro-site conditions, such as the determination of growing season length and winter soil temperatures, and influence on growing season soil moisture by snow depth, may determine the strength of the climate-growth relationships found.

Zusammenfassung: Gegenwärtig ist eine rapide klimatische Erwärmung im arktisch-alpinen Biom zu beobachten, welche mit einer Ausbreitung von relativ hochwüchsiger verholzender Gebüschvegetation in die Tundraökosystemen in Verbindung steht und durch positive Rückkopplungen zu einer Verstärkung des Temperaturtrends beitragen könnte. Es wird allgemein angenommen, dass die Verbuschung auf relativ warme Standorte beschränkt bleiben wird. Hinsichtlich der Klimasensitivität sind jedoch regionale Unterschiede zu erwarten, und es ist weitgehend unbekannt, ob Zwergsträucher unterschiedlicher funktionaler Gruppen unter gleichen standörtlichen Bedingungen ähnlich auf Klimaveränderungen reagieren. In der vorliegenden Studie testen wir die Klima-Wachstums-Beziehungen von sechs verschiedenen Standort-Pflanzenarten-Kombinationen. Dazu wurden je eine immergrüne und eine laubwerfende Pflanzenart an zwei alpinen Standorten sowie je eine immergrüne Pflanzenart an zwei hocharktischen Standorten ausgewählt. Das Wachstumsverhalten wurde auf Basis von Strauchwachstumsdaten in Verbindung mit standortspezifisch interpolierten Klimadaten des aktuellen CRU TS4.00 Gitternetzes analysiert. Das Strauchwachstum aller untersuchten Pflanzenarten an sämtlichen Standorten reagierte sensitiv auf die sommerlichen Klimabedingungen. Es ist deshalb wahrscheinlich, dass eine künftig anhaltende Erwärmung die weitere Verbuschung in den arktisch-alpinen Ökosystemen stimulieren wird; zumindest ist von einer Verdichtung bestehender Buschbestände auszugehen. Da das Zwergstrauchwachstum an den hocharktischen Standorten stark auf die rezente Erwärmung reagierte, ist gegenüber bisherigen Annahmen zu erwarten, dass die künftige Verbuschung nicht auf die wärmeren Tundraregionen beschränkt bleiben wird. Das Strauchwachstum der immergrünen Arten an den alpinen Standorten zeigte eine stärkere Abhängigkeit von den klimatischen Sommerbedingungen als das der laubwerfenden Sträucher. Dies könnte daran liegen, dass einige immergrüne Arten weniger anfällig gegenüber Verbiss sind. Biom-übergreifende Generalisierungen auf Ebene der funktionellen Pflanzengruppen sind jedoch nicht ohne Weiteres auf die Ebene der Pflanzenarten zu übertragen. Die Ausprägung der Klima-Wachstums-Verhältnisse ist vermutlich an die mikrotopographisch determinierten Standortbedingungen, wie die Dauer der Wachstumsperiode, die winterlichen Bodentemperaturen, die sommerliche Bodenfeuchte und die Schneebedeckungsverhältnisse, gekoppelt.

Keywords: Arctic-alpine ecosystems, Arctic greening, climate change, dendrochronology, ecology, shrub expansion

1 Introduction

The Arctic is warming faster than other regions of the globe (BINDOFF et al. 2013) and northern high latitudes are among the regions of the world for which the greatest warming is projected this century (KIRTMAN et al. 2013) and beyond (COLLINS et al. 2013). In addition, recent evidence indicates that the rate of temperature change is also amplified with elevation (PEPIN et al. 2015). As a result of this warming, the Arctic-alpine and boreal vegetation zones are anticipated to shift both northwards and into higher elevations in the northern hemisphere (SETTELE et al. 2014). Moreover, an increase in vegetation productivity has already been observed in many Arctic and alpine tundra regions through the use of remotely sensed proxies (GOETZ et al. 2011; EPSTEIN et al. 2012; MCMANUS et al. 2012), although different satellite proxies partly differ in their outcome (GUAY et al. 2014) and the greening trend may have recently turned into browning in some parts of the Arctic (PHOENIX and BJERKE 2016), perhaps related to frost damage after winter warming events (BOKHORST et al. 2009). The observed increase in productivity has been attributed to an encroachment of woody vegetation into the tundra (FORBES et al. 2010; MACIAS-FAURIA et al. 2012). Repeat vegetation surveys suggest that shrub cover, especially that of tall deciduous shrubs, has increased in response to ambient warming throughout the tundra biome (ELMENDORF et al. 2012b). This observation is furthermore supported by shrub cover increases in response to experimental warming across tundra sites (WALKER et al. 2006; ELMENDORF et al. 2012a). Increases in shrub, and sometimes graminoid, cover in response to ambient or experimental warming, are often observed together with a decline in cover of lower statured plant functional groups such as mosses and lichens (WALKER et al. 2006; ELMENDORF et al. 2012a; 2012b). The recent increase in shrub abundance in tundra regions in response to climate warming is most likely not a new phenomenon, as evidence from pollen records has shown a greater shrub abundance during warm periods in the Late Quaternary in the North-American (HU et al. 2002; HIGUERA et al. 2008), and Siberian (VELICHKO et al. 1997) tundra.

Coupled climate-vegetation modelling has suggested a possible increase of over fifty percent of woody cover in the Arctic by mid-century, which will likely result in an overall positive feedback to climate warming (PEARSON et al. 2013). Such positive feedbacks to warming caused by shrub en-

croachment include a reduction in albedo as a result of darker canopies and dark branches protruding through a melting spring snowpack (CHAPIN et al. 2005; BONFILS et al. 2012; PEARSON et al. 2013). Moreover, an increase in shrub cover and height could result in locally increased snow catchment and warmer winter soils with greater microbial activity, which in turn may lead to greater nitrogen availability and potentially a further increase in shrub growth during the following growing season (STURM et al. 2005; BLOK et al. 2015). Positive feedbacks are, on the other hand, partly offset by negative feedbacks. Microbial activity, for example, may be reduced in summer because of cooler soils due to greater shading under a denser shrub cover (BLOK et al. 2010). In addition, increased shrub growth increases the carbon stock in standing biomass. FORMICA et al. (2014), for example, observed a strong increase in shrub cover at an alpine tundra site in the Rocky Mountains of Colorado over the past decades, which significantly increased the amount of carbon in the standing biomass. Overall, a large-scale increase in shrub cover will alter tundra ecosystem structure and could influence carbon and nutrient cycling, energy fluxes, regional climate, soil-atmosphere water exchange, and species interactions (see MYERS-SMITH et al. 2011 for a review).

Although, in general, an increase in shrub cover is projected for tundra ecosystems, the potential of shrubs to increase in response to climate warming depends on specific site conditions and varies between species. A biome-wide dendroecological synthesis study on climate sensitivity of shrub growth found heterogeneous growth responses to climate throughout the Arctic-alpine tundra (MYERS-SMITH et al. 2015a). Although MYERS-SMITH et al. (2015a) reported high overall climate sensitivity of shrubs, less than half of the genus-by-site combinations studied showed a positive response to summer temperature, and a significant fraction (17%) showed negative relationships with summer temperature. MYERS-SMITH et al. (2015a) furthermore concluded that the growth sensitivity of shrubs to climate is highest at the boundary between the Low and High Arctic, at sites with greater soil moisture, for shrubs growing at their northern or upper elevational range limits, and greater for taller than lower-statured species. In addition, shrub encroachment is believed to remain limited to the relatively warm parts of the biome, as a positive effect of ambient and experimental warming has mainly been observed on the abundance of taller deciduous shrubs in the Low Arctic (ELMENDORF et al. 2012a; 2012b).

Still, evergreen dwarf shrub species have been observed to be sensitive to summer temperatures at some Arctic and alpine sites (BÄR et al. 2008; BUIZER et al. 2012; WEIJERS et al. 2012) and have been shown to increase their leaf size and height in response to experimental warming (HUDSON et al. 2011) and cover in response to ambient warming (HUDSON and HENRY 2009) on Ellesmere Island in High Arctic Canada. High Arctic dwarf shrub species may thus respond rapidly to increasing temperatures in absence of taller species. In addition, it remains largely unknown whether shrubs from different functional groups from the same sites respond similarly to climate drivers, as growth responses of shrub species with different traits and habitats are seldom compared in the same plant communities.

Here, climate-growth relationships are studied for six site-species combinations in a re-analysis using the shrub growth datasets from previous studies and site-specific interpolated climate data from the gridded meteorological dataset CRU TS4.00 (HARRIS et al. 2014; CRU et al. 2017). The growth data consists of either annual shoot length increment or annual ring-width series from four different shrub species, which all have a (near) circumarctic distribution and are commonly found in the tundra biome: the deciduous species *Betula nana* and *Salix pulchra*, and the evergreen species *Cassiope tetragona* and *Empetrum nigrum* ssp. *hermaphroditum*. Shrub growth responses were studied at four different sites using linear mixed models over the period 1950–2012, with exact period lengths depending on shrub age and sampling date. Two sites were located in the High Arctic and two in alpine regions. At each alpine site, one deciduous and one evergreen species were studied.

The aims of this study were to identify the climatic drivers of shrub growth at the different sites and for the different species, using identical statistical methods and monthly data from a single gridded climate dataset, and to compare the strength of the climate-growth relationships between the six site-species combinations. Based on the previous climate-growth analyses using parts of this shrub growth dataset (BLOK et al. 2015; MYERS-SMITH and HIK 2018; WEIJERS et al. 2017; 2018), we expected shrub growth to be driven by summer climate at all sites. Moreover, we hypothesized stronger links between climate and growth at the High Arctic sites, which experience cold summers, in comparison to the alpine sites, which are relatively warm during summer.

2 Material and Methods

2.1 Study sites

Shrub growth was studied at four different tundra sites, one alpine and one High Arctic site in North America as well as in Europe (Fig. 1). The main environmental characteristics of the sites are given in table 1. The species studied were chosen for their (near) circumarctic distribution and their (co-) dominance at the study sites (Tab. 1).

The first site is located in the alpine tundra on the slopes of the Pika valley in the Kluane Region of the Yukon Territory in northwest Canada. Here, the deciduous tall shrub *Salix pulchra* was sampled late August 2007 (see MYERS-SMITH and HIK 2018 for more details), and the evergreen dwarf shrub *Cassiope tetragona* at the end of the growing season of 2010 (see WEIJERS et al. 2018 for more details). *Cassiope tetragona* (L.) D. Don. (Ericaceae), or Arctic bell heather, is a multi-branched, clonal, hemi-prostrate, evergreen dwarf shrub with a circumarctic distribution (EIDSESEN et al. 2007; WEIJERS et al. 2017). At this site it is dominant in late snow beds. *Salix pulchra* Cham. (Salicaceae) is a canopy-forming deciduous shrub commonly found in the Siberian and northwest North American tundra (CYSIP 2017). It is the most abundant *Salix* species in Pika valley.

The second site is located in the sparsely vegetated polar desert in High Arctic Johannes V. Jensen Land, North Peary Land, Greenland, which is the world's northernmost landmass (Fig. 1). This site is located approx. 756 km from the geographic North Pole. At this site *C. tetragona* shrubs (Fig. 2a) were sampled in July, 2013 (see WEIJERS et al. 2017 for details).

The third site, Vole, is a near-treeline lichen heath ridge site (Fig. 1, Fig. 2b) located in the low alpine belt of the Central Norwegian Scandes mountain range. Here, the deciduous dwarf shrub *Betula nana* (L.) (Betulaceae) and the evergreen species *Empetrum nigrum* (L.) ssp. *hermaphroditum* (Hagerup) Böcher (Ericaceae) grow intertwined in direct competition for light and resources. The species were sampled at the end of the growing season of 2012 and at the start of the growing season in 2013. Both species are common throughout the southern Arctic and northern parts of the boreal zone and have a circumpolar distribution (GROOT et al. 1997; TYBIRK et al. 2000). *E. hermaphroditum* is a shade-tolerant species (CAMPIOLI et al. 2012a) and it is also an important constituent of the understorey vegetation in the boreal forest of Scandinavia, north-western Russia, and the Baltic states (TYBIRK et al. 2000).

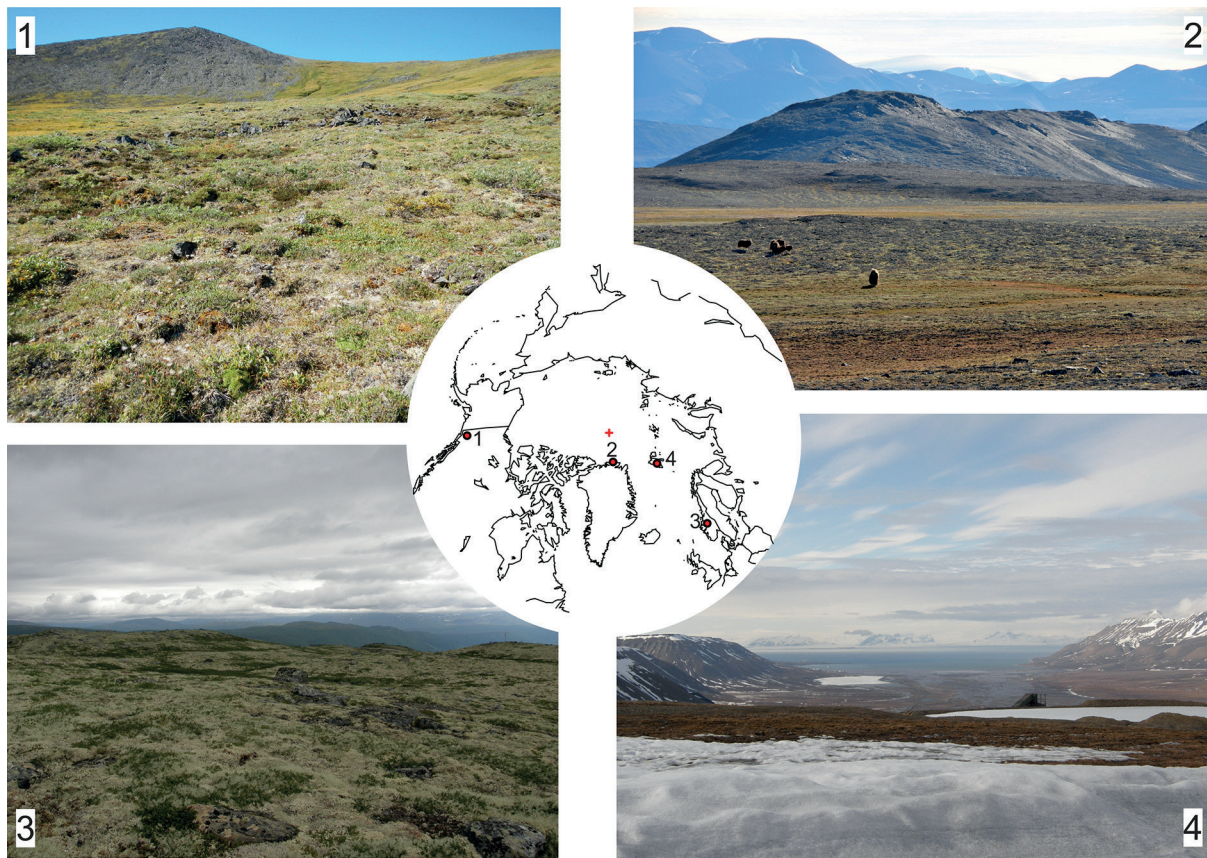


Fig. 1: Locations of the study sites indicated with numbers and red circles on the map. The red cross designates the geographic North Pole. 1. Alpine tundra in the Pika valley, Kluane Region, Yukon Territory, Canada. Photo by Isla Myers-Smith, 2013. 2. High Arctic polar desert in Johannes V. Jensen Land, Greenland. Photo by Jørgen Bojesen-Koefoed, 2013. 3. Alpine lichen heath at Vole, Vågåmo, Oppland, Norway. 4. View into Adventdalen, Spitsbergen, Svalbard.

The fourth site is located in the tundra in the Adventdalen valley (Fig. 1) on the island Spitsbergen, which is part of the High Arctic Svalbard archipelago. From this site *C. tetragona* individuals (Fig. 2c) were harvested from control plots of a snow manipulation experiment early July 2012 (see BLOK et al. 2015 for details).

To prevent repeated sampling of the same genet, several meters distances were kept between sampling locations at all sites.

2.2 Climate

Mean monthly temperatures and mean monthly precipitation sums (1901-2015) were extracted for each site from a single monthly gridded meteorological dataset CRU TS4.00 (HARRIS et al. 2014; CRU et al. 2017) for the four grids ($0.5^\circ \times 0.5^\circ$) with centres nearest to the sites for the comparison of climate sensitivity of shrub

growth. This way the effect of different weather station density in the different study regions on the observed climate sensitivity of shrubs was minimized. The CRU TS4.00 dataset contains a lower amount of repeated site mean values, used to fill in gaps, than previous versions. This is especially relevant for the study site in J.V. Jensen Land, North Greenland, for which the precipitation data in previous version solely consisted of repeated mean values (cf. WEIJERS et al. 2017). In addition, monthly climate data were obtained for each site from either the nearest weather station or a different modelled gridded dataset (see Tab. 1 for details) for a validation of the CRU data (see below).

The gridded climate data from the CRU TS4.00 dataset at the grid points nearest to the four study sites are summarized in Fig. 3 and shown in Fig. A1. Vole is the warmest site with a mean annual temperature just above 0°C . The difference in temperature between both alpine sites (Vole in

Tab. 1: Environmental characteristics of the four research sites. Mean values were calculated over the 30-year period 1981-2010, except: ¹1973-2002, and ²1994-2012.

	Pika	Johannes V. Jensen Land	Vole	Adventdalen
Latitude	61.22 °N	83.20 °N	61.90 °N	78.17 °N
Longitude	138.28 °W	33.22 °W	9.14 °E	16.27 °E
Elevation (m a.s.l.)	1755	538	1100	108
Mean July temperature CRU TS4.00 (°C)	10.3	-2.1	11.0	3.9
Mean July temperature (°C) nearest weather station or modelled	9.29	5.4 ¹	10.5 ²	6.45
Mean annual temperature (°C) CRU TS4.00	-5.01	-21.57	0.19	-8.47
Mean annual temperature (°C) nearest weather station or modelled	-4.34	-15.24 ¹	-0.17 ²	-5.1
Mean precipitation sum (mm) CRU TS4.00	301	49	604	590
Mean precipitation sum (mm) nearest weather station or modelled	502	254	439	187
Nearest weather station or model	Climate WNA v5.40 (WANG et al. 2017) 61.22 °N 138.28 °W 1755 m	Precipitation: Station Nord 81.60 °N 16.67 °W 13 m (LAWRIMORE et al. 2011; NOAA 2016). Temperature: Kap Moltke, Greenland (Peary Land Foundation; see WEIJERS et al. (2017)) 82.15 °N 29.95 °W 4 m	Precipitation: seNorge.no (SENORGE.NO 2017) 61.90 °N 9.15 °E 1099 m; Temperature: on-site microclimate station 61.90 °N 9.14 °E 1100 m	Svalbard Airport, Spitsbergen (DNMI 2016) 78.25 °N, 15.50 °E 28 m
Vegetation	Alpine Shrub Tundra dominated by <i>Salix</i> species; <i>Cassiope tetragona</i> dominant in late snow beds	Sparsely vegetated Polar Desert dominated by <i>Cassiope tetragona</i> , <i>Salix arctica</i> , and <i>Dryas integrifolia</i>	Alpine Lichen Heath, with <i>Betula nana</i> and <i>Empetrum nigrum</i> ssp. <i>bermaphroditum</i> as the dominant dwarf shrub species (LÖFFLER 2003)	Dry tundra heath dominated by <i>Cassiope tetragona</i> , and moist tundra meadow dominated by <i>Salix polaris</i>
Shrub species studied (No. of shrubs)	<i>Cassiope tetragona</i> (16) and <i>Salix pulchra</i> (17)	<i>Cassiope tetragona</i> (30)	<i>Betula nana</i> (13) and <i>Empetrum nigrum</i> ssp. <i>bermaphroditum</i> (17)	<i>Cassiope tetragona</i> (18)

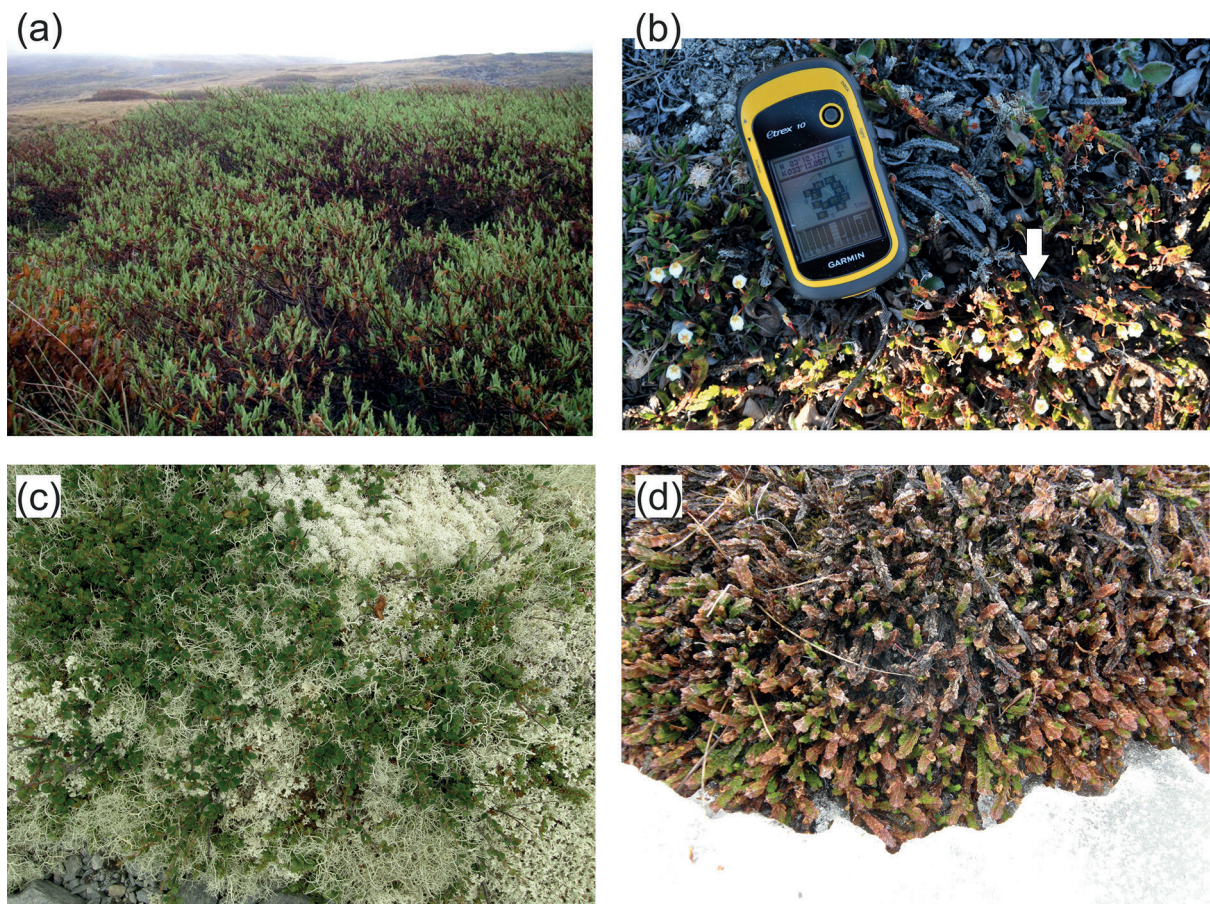


Fig. 2: Tall *Salix pulchra* shrubs growing in the Kluane Region, Yukon Territory, Canada. Photo by Isla Myers-Smith (a). *Cassiope tetragona* flowering in the polar desert late July in Johannes V. Jensen Land, Greenland. The arrow points towards several *C. tetragona* branches. *Dryas octopetala* and *Salix arctica* are also present. Photo by Jørgen Bojesen-Koefoed, 2013 (b). Lichen heath at Vole, Vågåmo, Oppland, Norway. *Betula nana* (broad leaves) and *Empetrum nigrum* ssp. *hermaphroditum* are growing intertwined, covered with lichens (c). *Cassiope tetragona* during snowmelt early June in Adventdalen, Spitsbergen, Svalbard (d).

Norway and Pika in Canada) are greatest in winter, with mean temperatures below -20°C in the coldest month, January, at Pika, and above -10°C in Vole. According to the CRU dataset, Vole receives more precipitation annually than Pika. However, gridded climate datasets specifically modelled for these sites suggest similar amounts of annual precipitation for both sites (Tab. 1).

Johannes V. Jensen Land is the most extreme site with the coldest monthly temperatures (-21.57°C annual mean) and lowest monthly precipitation sums (49 mm annual sum). The year-round below-zero mean monthly temperatures at Johannes V. Jensen Land suggested by the CRU may be a result of the elevation at the grid point centre (approx. 833 m), which is higher than the study site (538 m a.s.l.). The other High Arctic study site, Adventdalen, is both warmer and wetter according to the CRU dataset. The precipita-

tion sums as estimated for Adventdalen by the CRU model are, however, much higher than those measured at the Svalbard Airport weather station (Tab. 1; Fig. A1b).

Despite discrepancies in amounts, monthly precipitation sums of the CRU TS4.00 dataset and those from different interpolation models or those measured at the nearest weather station are correlated at all sites for all months, except for August at Adventdalen, Svalbard, and the months for which no precipitation is estimated throughout the record at Johannes V. Jensen Land (January, May, October, and December). Mean monthly temperatures between the CRU and local datasets are correlated at all sites in all months, except in November at Johannes V. Jensen Land (cf. Fig. A1a). Interannual variation in the monthly CRU series is thus likely similar to that at the study sites.

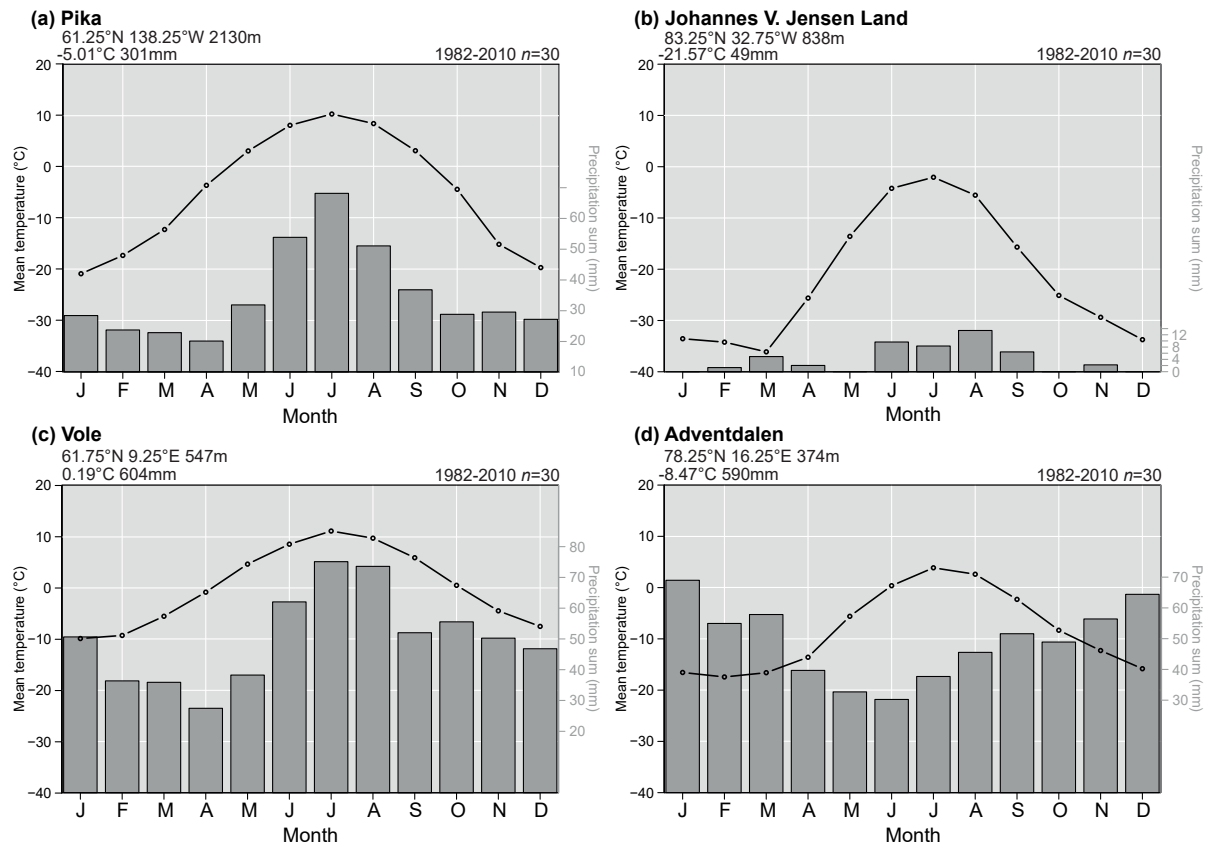


Fig. 3: Mean monthly temperatures ($^{\circ}\text{C}$; lines) and mean monthly precipitation sums (mm; bars) for the grid points nearest to the study sites from the CRU TS4.00 dataset (Harris et al. 2014). (a) Pika valley, Kluane Region, Yukon Territory, Canada; (b) Johannes V. Jensen Land, Greenland; (c) Vole, Vågåmo, Oppland, Norway; (d) Adventdalen, Spitsbergen, Svalbard. Coordinates (decimal degrees) of the midpoint of each grid are given below the site names, followed by the elevation (m a.s.l.) of the midpoint. Directly above the left-hand corner of each panel, the related mean annual temperature ($^{\circ}\text{C}$) and mean annual precipitation sum (mm) are given. Periods over which the monthly means were calculated are given directly above the upper right corner of each panel, followed by the number of years included in the calculation of the means (n).

2.3 Annual shrub ring-width measurement

Annual growth of the *Betula nana*, *Empetrum nigrum* ssp. *hermaphroditum* and *Salix pulchra* individuals was quantified as annual radial ring width.

As *B. nana* (MEINARDUS et al. 2011; HOLLESEN et al. 2015) and *E. hermaphroditum* (BÄR et al. 2006; 2007) exhibit high intra-plant growth variability, serial sectioning (KOLISHCHUK 1990) was applied on the shrub samples from these species. Thin cross-sections of $\sim 5\text{--}10\ \mu\text{m}$ were cut at regular intervals along the main stem(s), starting at the base, (BÄR et al. 2006; 2007; BUCHWAL et al. 2013) with a sledge microtome (GSL-1; GÄRTNER et al. 2014), and stained with a mixture of Safranin and Astrablue. This enabled differentiation between lignified (Safranin) and non-lignified (Astrablue) cell walls. Thin sections were then dehydrated with alcohol and fixed on slides in Canada Balsam and dried at

$60\ ^{\circ}\text{C}$ in an oven for at least 24 h (GÄRTNER and SCHWEINGRUBER 2013). Consequently, high-resolution digital images of overlapping parts of the thin section were taken at $80\times$ magnification and stitched together in the programme Autopano 4 (Fig. 4a and b). Ring widths were measured in ImageJ (RASBAND 2016) with a resolution of $1\ \mu\text{m}$ along multiple (2–11, mostly 4) radii, to account for wedging rings and lobed growth. The radii of cross-sections were cross-dated visually by following the rings on the stitched photographs, through counting of the rings and, often, through colouring the ring boundaries in ImageJ. This way, wedging rings were identified. Consequently, the radii were averaged per cross-section. In a next step, cross-sections of shrub individuals were visually cross-dated in MS Excel 2013 using similarities in growth patterns between ring-width series. This way, locally missing rings were identified and ring-

width series corrected. Mean cross-section series were then averaged per shrub into individual shrub chronologies.

The upright growth form of *S. pulchra* results in a more regular and generally concentric formation of rings in comparison to the hemi-prostrate species *B. nana* and *E. hermaphroditum* (Fig. 3). Serial sectioning was therefore unnecessary and was not applied on samples of this species. For annual radial growth measurements of *S. pulchra*, thin sections of the shrub stems were cut from 3-5 cm long stem discs taken just above the stem-root boundary (see MYERS-SMITH and HIK 2018). Sections were not stained, as staining obscured the visibility of ring boundaries. Thin sections were then mounted on glass slides and digital images of the slides were taken with a microscope mounted digital camera (Fig. 4c; MYERS-SMITH et al. 2015b). Ring widths were measured along four radii with a resolution of 1 μm in either WinDendro (Regent Instruments, Inc., Quebec, Canada) or ImageJ (RASBAND 2016). Locally missing (wedging) rings were accounted for during visual crossdating

conducted on the raw ring width measurements using marker rings such as those of 2004 (wide rings) and 2001 (narrow rings). The radii were then averaged per cross-section to form shrub chronologies for each individual. The first five growth rings were removed from each mean *S. pulchra* shrub series to account for irregular growth during early life.

2.4 Annual shoot length measurement

Annual growth of *Cassiope tetragona* individuals was quantified as annual shoot length increment. Annual shoot length was measured as distances between *wintermarksepta* (WMS), which are dark bands of meristem tissue; clearly visible within the white piths in lateral cross-sections of *C. tetragona* stems (Fig. 4d). WMS coincide with lows in leaf lengths, which grow in four rows along its stems, and demarcate annual shoot length growth (ROZEMA et al. 2009; WEIJERS et al. 2010; 2012; 2013b; 2017; MYERS-SMITH et al. 2015a). WMS distances were measured

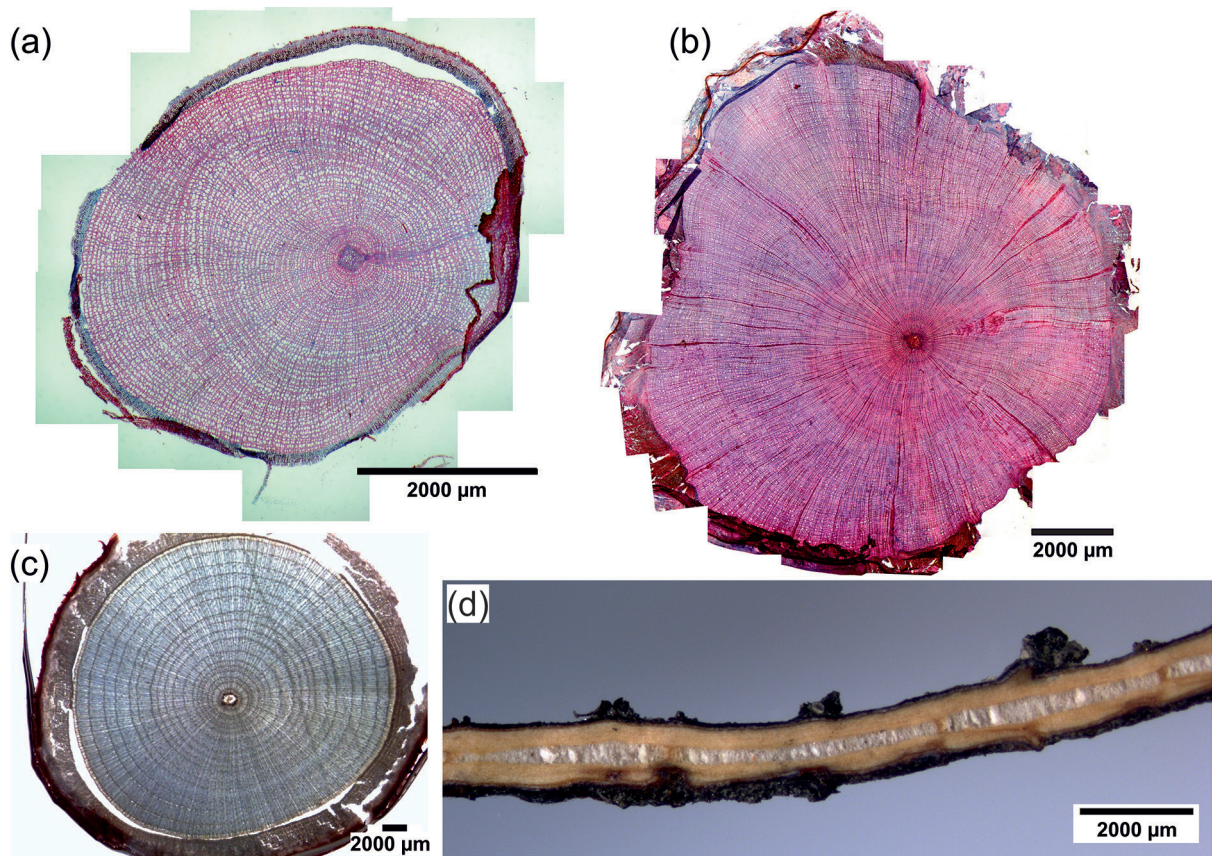


Fig. 4: Annual radial growth rings in cross-sections of *Empetrum nigrum* ssp. *hermaphroditum* (a), *Betula nana* (b), and *Salix pulchra* (c); Annual shoot length increments as demarcated by *wintermarksepta* (WMS) in a lateral section of a *Cassiope tetragona* stem (d).

under a stereo microscope with 0.1 mm precision. Annual shoot length was measured for multiple branches per shrub for the *C. tetragona* samples from Pika (354 branches, 9–45 per plant; see WEIJERS et al. 2018 for details) and from Johannes V. Jensen Land (158 branches, 1–14 per sample; see WEIJERS et al. 2017). For these sites, individual branch chronologies were visually cross-dated using the known dates of harvest, similarities in growth patterns within and between shrubs, and the presence of positive pointer years. Branch series were first cross-dated with series of the same shrub, and finally with those from other *C. tetragona* shrubs of the same site. For graphical explanations of the cross-dating process of *C. tetragona* shoot length chronologies, see WEIJERS et al. (2010; 2013b). Branch chronologies were then averaged per shrub to form individual shrub series. Growth of the *C. tetragona* samples from Adventdalen, Svalbard, was measured on single branches from 18 individuals.

2.5 Climate-growth analysis

Linear mixed model analyses were used to test relationships between monthly and seasonal mean temperatures and mean precipitation sums on the one hand and shrub growth on the other at the four study sites. Climate-growth models were compared over the period 1950–2012, with exact period lengths depending on individual shrub series length and sampling date. Growth-ring or shoot length data from the years of harvest were not included in the models, as growth was (possibly) not completed at the times of harvest. The period before 1950 was excluded from the analyses, as monthly climate data of the CRU TS4.00 dataset for the High Arctic sites contained many repeated values prior to 1950, especially the precipitation data for Northern Greenland; A result of a lack of measurements in these remote areas before 1950. The mixed model analyses were executed with the R-package nlme (PINHEIRO et al. 2017) in R version 3.4.1 (R CORE TEAM 2017). Maximum likelihood estimation was used for model comparison and restricted maximum likelihood estimation for slope estimates (CRAWLEY 2007). The ring-width and shoot length data as well as the climate data were normalized per shrub and site, respectively, through subtraction of the mean, followed by a division by the standard deviation, before the analyses. The models contained either annual ring-widths or shoot lengths of individual shrubs as the response variable and

climate variables as fixed effects. Random intercepts were included in the models for year next to an autocorrelation structure (AR1, autoregressive process of order one). For each mixed model conditional pseudo- R^2 values were calculated with the `r.squaredGLMM` function of the MuMIn package (NAKAGAWA and SCHIELZETH 2013).

Climate-growth models included temperature means and precipitation sums from 17 individual months (previous June to current October), the four seasons, and early (June–July) and late (July–August) summer as fixed effects. Winter was defined as November–March, spring as April–May, summer as June–August, early summer as June–July, late summer as July–August, and autumn as September–October. For each site-species combination (6 in total), 46 climate-growth models and a null model were compared, except for *C. tetragona* from Johannes V. Jensen Land, Greenland (41 climate models), as for this site precipitation sums for January, May, (previous) October, and December were excluded, as those consist of a repetition of zeros (Fig. 3b and Fig. A1b). First, climate-growth models, which performed better than the respective null model were selected using the Akaike Information Criterion ($\Delta\text{AIC}>2$). Thereafter, Akaike weights, a relative weight of evidence for each model (JOHNSON and OMLAND 2004), were calculated for model comparison.

In total, three separate statistics were calculated to qualify the strength of the relationships between shrub growth and climate at the four sites for the selected models, similar as in the biome-wide synthesis on climate sensitivity of tundra shrub growth by MYERS-SMITH et al. (2015a). These statistics consisted of the difference in AIC value between the selected climate models and a null model, the pseudo- R^2 -value for the models, and the slope of the models, disregarding the sign.

We calculated site chronologies for graphical representation of growth variability over time for each site-species combination (Fig. A2). Site chronologies were constructed using bi-weighted robust means after standardization of growth series with a horizontal line through the mean at the branch (shoot lengths) or cross-section (ring-widths) level. Furthermore, we calculated the main interseries correlation coefficient (\bar{r}) and the expressed population signal (EPS; WIGLEY et al. 1984) for each site chronology. Standardization, chronology construction, and calculation of chronology statistics were executed with the package `dplR` v1.6.6 (BUNN 2008) in R version 3.4.1 (R CORE TEAM 2017).

3 Results

The variability of growth for all species at all sites was best explained by summer climate, with most support for early summer (June-July) and July temperature models (Tab. 2). Late summer (July-August) temperatures were found to be less important for growth, with only little support (low Akaike weights) for late summer temperature models for three site-species combinations: *C. tetragona* at both High Arctic sites and *E. hermaphroditum* at the alpine site (Vole) in Norway (Tab. 2). All temperature models with mean temperatures of summer months, for which at least some evidence was found, had positive slopes. Hence, shrub growth of all species benefits from relatively warm summer weather at the studied sites. The only site-species combination for which no positive link between summer temperature and growth was found was *B. nana* at Vole in Norway. Growth of this species was found to be negatively associated with summer precipitation at this site (Tab. 2). There was also some support for summer precipitation models with negative slopes for *S. pulchra* from the Pika valley in the Yukon Territory, Canada (Akaike weight of 0.01) and for *C. tetragona* from Johannes V. Jensen Land, northern Greenland (Akaike weight of 0.04; Tab. 2). In figure A3 the variability in growth and the climate parameter from each best climate-growth model are plotted as time-series, separately for each site-species combination.

In addition to summer climate sensitivity, there was some indication for a negative influence of winter and February temperatures on *B. nana* growth (Akaike weights of 0.06), and a negative influence of spring temperatures (Akaike weight of 0.06) as well as a positive influence of September precipitation (Akaike weight of 0.08) on *E. hermaphroditum* growth at the alpine site Vole, Vågåmo, Oppland, Norway. In addition, there was some support for a positive influence of May temperatures (Akaike weight of 0.01) on *C. tetragona* growth in Adventdalen on Spitsbergen, Svalbard (Tab. 2).

The R^2 -values and, to a lesser extent, the absolute slope values of the best climate model for each of the six site-species combinations studied suggest that the growth response to summer climate is stronger at high latitude sites than at alpine sites at lower latitudes (Fig. 5 and Tab. 2). The Δ AIC-values at the alpine site in the Pika valley in the Yukon, Canada, however, are intermediate (*S. pulchra*) or higher (*C. tetragona*) than those at the High Arctic sites.

4 Discussion

Our findings substantiate the notion that shrub growth in tundra ecosystems is generally limited by temperature across the biome, but not uniformly so. Climate-growth relationships in shrub species have previously been shown to be heterogeneous throughout the biome, with positive relationships found between summer temperatures and shrub growth for 46% of the 46 genus-site combinations studied in MYERS-SMITH et al. (2015a). MYERS-SMITH et al. (2015a) furthermore found greater climate sensitivity of shrubs growing near their northern latitudinal or elevational range limits. Our results, including one site-species combination included in MYERS-SMITH et al. (2015a), i.e. Pika *Salix* species, and five additional site-species combinations not included in the previous study, support this finding with stronger relationships between shrub growth and summer climate at both High Arctic sites and at the Yukon alpine site, Pika, which contained tall-shrubline *S. pulchra* shrubs (see MYERS-SMITH and HIK 2018). Only *C. tetragona* from Pika may not fit this pattern, given its high Δ AIC-value as this site. However, at Pika, *C. tetragona* grows pre-dominantly at locations with long lasting snow cover, and hence early growing season temperatures may be crucial there in determining growing season length (WEIJERS et al. 2018).

Our findings somewhat contrast with those of ELMENDORF et al. (2012a), who found deciduous, tall and low statured shrubs to show the strongest positive response to experimental warming at 61 tundra sites across the tundra biome. Dwarf shrub cover, on the other hand, was found to decrease. In addition, the response of shrub abundance to long-term experimental warming was found to be greatest at relatively warm sites. In a different synthesis study of tundra vegetation change in response to ambient warming at 46 sites across the tundra biome, tall and low-statured but not dwarf or evergreen shrubs were found to increase in abundance with summer climate warming (ELMENDORF et al. 2012b). In contrast, we found a strong positive growth response of *C. tetragona*, an evergreen dwarf shrub, to warm summer temperatures in the cold High Arctic, as well as in the much warmer alpine tundra at the Pika valley in the Yukon, Canada. This discrepancy may be due to the fact that in both synthesis studies, changes were examined at the growth-form rather than at the species level (ELMENDORF et al. 2012a; 2012b). Moreover, in both studies High Arctic sites were underrepresented (cf. WEIJERS et al. 2017), as were specific ecotopes such as late snow-beds. Biome-

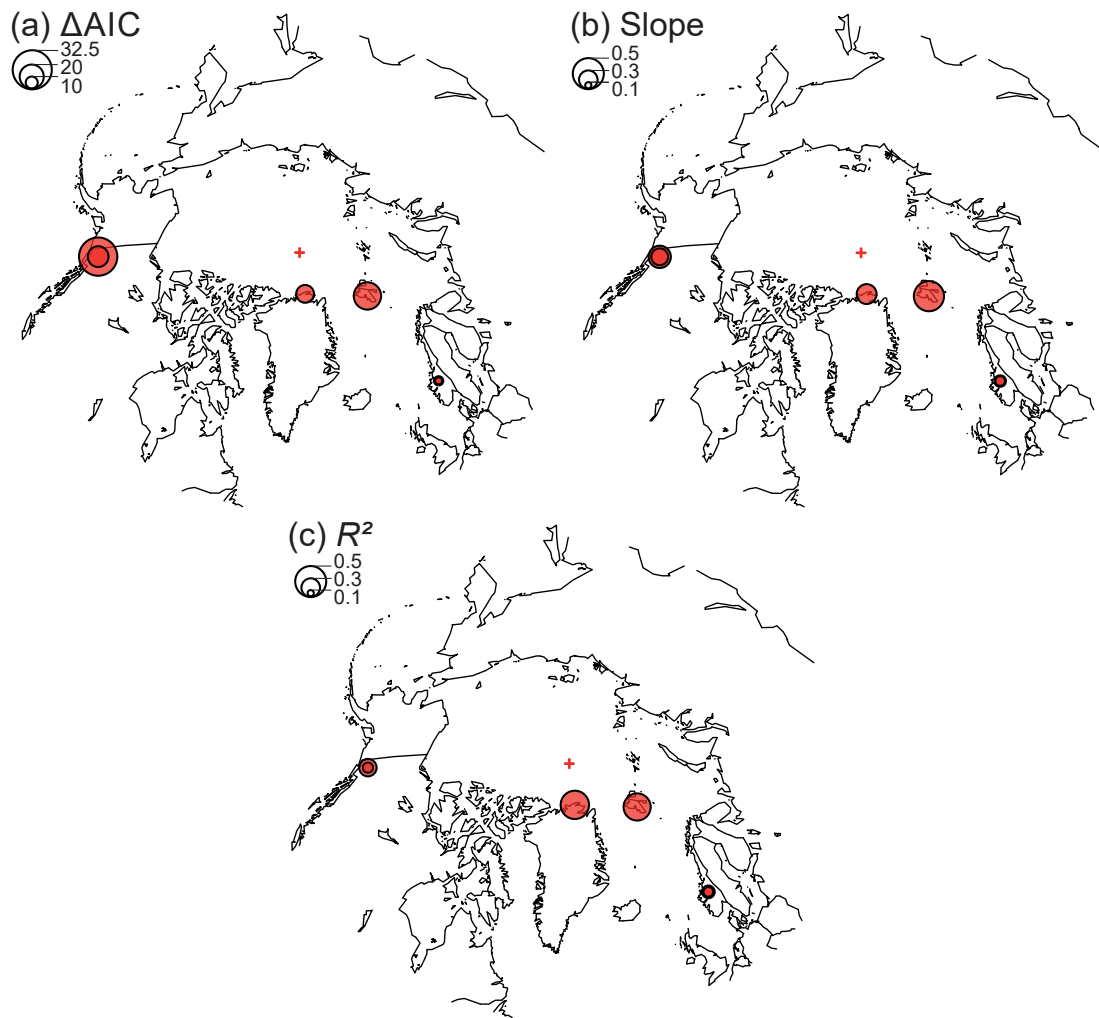


Fig. 5: Strength of the relationships between annual shrub growth and climate for the best climate models for each of the six site-species combinations as indicated by ΔAIC (a), absolute slope of the best model (b), and R^2 (c). The sizes of the circles show the strength of the relationships, as indicated by each of the three statistics (see legends). The red cross in each panel indicates the geographic North Pole.

wide generalizations about directions of change at the functional group level may not well represent species level responses. Furthermore, generalized biome-level findings may be less applicable to sites where species distribution is strongly linked to the fine-scale redistribution of snow in winter by wind according to micro-topography, i.e. downslope snow accumulation on lee-sides of slopes and in depressions, and related variations in soil moisture content during summer (WEIJERS et al. 2017).

Based on their observations, ELMENDORF et al. (2012a) suggest that High Arctic tundra will remain resistant to shrub expansion over the next few decades. Also, some of the *C. tetragona* chronologies from the eastern Canadian Arctic in the study by MYERS-SMITH et al. (2015a), all ending in the 1990s,

did not cover the most recent and strongest High Arctic warming phase, and exhibited low or no sensitivity to summer temperature. Our findings, however, indicate that growth of dwarf shrubs species, such as *C. tetragona*, will likely continue to increase under projected future warming in the High Arctic and an expansion of shrub cover through a densification of existing stands (MYERS-SMITH et al. 2011) is thus likely (cf. WEIJERS et al. 2017). However, shrub recruitment pulses may actually be driven by either increasing summer (BÜNTGEN et al. 2015) or winter temperatures (MYERS-SMITH and HIK 2018), and rising winter temperatures may thus be responsible for the colonization of new areas for some species. In addition, re-colonization of fore-fronts of retreating glaciers by species as *C. tetragona*

Tab. 2: Results of the mixed model analyses with annual shoot lengths (*Cassiope tetragona*) or annual ring widths (other species) included in the models as the response variable and climate variables as fixed effects, calculated over the period 1950–2012. Selected models are models with AIC values of at least 2 lower than the corresponding null model and Akaike weights ≥ 0.01 . Akaike weights are the relative weight of evidence for each model. R²-values are conditional pseudo-R² values. T: mean temperature; P: precipitation sum.

Site	Species	Selected Models	Δ AIC	Akaike weight	Slope \pm SE	R ²
Pika valley, Kluane Region, Yukon Territory, Canada	<i>Cassiope tetragona</i>	Early summer T	31.75	0.96	0.37 \pm 0.06	0.29
		Summer T	25.45	0.04	0.35 \pm 0.06	0.29
	<i>Salix pulchra</i>	July T	17.20	0.57	0.28 \pm 0.06	0.17
		Early summer T	16.49	0.40	0.28 \pm 0.06	0.17
		Summer P	9.88	0.01	-0.25 \pm 0.06	0.15
		Summer T	8.56	0.01	0.22 \pm 0.07	0.17
Johannes V. Jensen Land, Greenland	<i>Cassiope tetragona</i>	July T	14.76	0.79	0.33 \pm 0.08	0.47
		Early summer T	11.47	0.15	0.30 \pm 0.08	0.47
		July P	8.82	0.04	-0.27 \pm 0.08	0.47
		Summer T	5.42	0.01	0.23 \pm 0.08	0.47
Vole, Vågåmo, Oppland, Norway	<i>Betula nana</i>	Summer P	5.93	0.40	-0.16 \pm 0.06	0.16
		Early summer P	5.61	0.34	-0.15 \pm 0.06	0.17
		June P	2.55	0.07	-0.12 \pm 0.06	0.17
		Late summer P	2.45	0.07	-0.12 \pm 0.06	0.17
		Feb T	2.24	0.06	-0.12 \pm 0.06	0.17
		Winter T	2.24	0.06	-0.12 \pm 0.06	0.17
	<i>Empetrum nigrum</i> ssp. <i>bermaphroditum</i>	July T	7.63	0.65	0.19 \pm 0.06	0.21
		Early summer T	3.94	0.10	0.15 \pm 0.06	0.21
		September P	3.42	0.08	0.15 \pm 0.06	0.21
		Spring T	2.92	0.06	-0.14 \pm 0.06	0.21
		Late summer T	2.80	0.06	0.14 \pm 0.06	0.21
		Summer T	2.20	0.04	0.13 \pm 0.06	0.21
Adventdalen, Spitsbergen, Svalbard	<i>Cassiope tetragona</i>	Summer T	22.66	0.57	0.50 \pm 0.09	0.45
		Early summer T	21.84	0.38	0.48 \pm 0.09	0.44
		Late summer T	16.45	0.03	0.46 \pm 0.10	0.46
		May T	14.68	0.01	0.44 \pm 0.10	0.45
		August T	13.20	0.01	0.43 \pm 0.10	0.46
		June T	13.19	0.01	0.39 \pm 0.09	0.44

may very well be possible in the High Arctic, as sometimes intact subfossil individuals of this species are found at such locations (HAVSTRÖM et al. 1995; LOWELL et al. 2013). The expectation of an increase in dwarf shrub cover in the High Arctic is furthermore supported by the fact that biomass and summer temperatures have been found to be related across plant species in High Arctic Svalbard (VAN DER WAL and STIEN 2014). In the Canadian High Arctic, evergreen dwarf shrub cover increased in response to ambient warming (HUDSON and HENRY 2009) and leaf size and plant height of *C. tetragona* also increased in response to long-term experimental warming (HUDSON et al. 2011). Moreover, *C. tetragona* shoot length has been shown to increase in response to experimental summer warming in the High Arctic (HAVSTRÖM et al. 1993; ROZEMA et al. 2009; WEIJERS et al. 2012) and annual shoot length of *C. tetragona* has been used as a proxy for summer

temperatures in High Arctic Canada, Svalbard, and Greenland (RAYBACK and HENRY 2006; WEIJERS et al. 2010; 2013b; 2017).

The potential of shrubs to respond to summer warming may be limited by soil moisture content (MYERS-SMITH et al. 2015a; ACKERMAN et al. 2017). Annual precipitation sums at Johannes V. Jensen Land, Greenland are likely lower than those at Adventdalen, Svalbard. In addition, *C. tetragona* growth response to summer temperature was found to be lower at Johannes V. Jensen Land, Greenland than in Svalbard, with lower slope- and Δ AIC-values for the best summer climate model, which could in part be due to lower soil moisture content or the more extreme growing environment. However, there are no local *in situ* instrumental climate data available for the site in North Greenland, and the interpolated CRU data may be a relatively poor representation of the local climate as they are based on weather sta-

tions in Alert, Ellesmere Island (approx. 405 km distance; see WEIJERS et al. 2017), and Svalbard Airport, Spitsbergen, Svalbard (approx. 986 km distance; cf. Fig. A1). Inclusion of monthly indices of the large-scale climate phenomena North Atlantic Oscillation (NAO) and Arctic Oscillation (AO), which during their negative phase result in clearer skies and relatively warm weather during summer over this part of the Arctic (see OVERLAND et al. 2012), in climate-growth models, resulted in a larger portion of variance in *C. tetragona* growth explained at this site (WEIJERS et al. 2017). Also, soil moisture content likely remains high throughout the growing season at most High Arctic *C. tetragona* sites, because of the low evaporation rates as well as the poor drainage of permafrost soils and meltwater availability from snow patches, as the species' presence in the High Arctic relies on winter snow cover (BAY 1992). In addition, the species was found to increase its stomatal conductance, but not its growth, in response to a doubling of summer precipitation on a relatively dry slope adjacent to Adventdalen, Spitsbergen, Svalbard (WEIJERS et al. 2013a).

Winter and spring precipitation as snow has been found to potentially negatively impact growth of *S. arctica* in north-eastern Greenland (SCHMIDT et al. 2006; 2010) and growth of *C. tetragona* (BLOK et al. 2015) and reproductive success of the vegetation (COOPER et al. 2011) at our site in Adventdalen, Spitsbergen, Svalbard, as deeper snow may shorten the growing season length. However, we did not find evidence for an effect of winter or spring precipitation for any of the site-species combination studied, neither positive nor negative. This may be a consequence of the positive effects of a deeper snow layer, such as protection against frost damage and greater nitrogen availability in the proceeding summer, the latter due to higher microbial activity in warmer winter soils under deeper snow (STURM et al. 2005). BLOK et al. (2015) reported longer *C. tetragona* shoots with higher $\delta^{15}\text{N}$ under experimentally deepened snow conditions, suggesting that soil N-availability increased due to higher nitrogen mineralization in winter soils under deepened snow conditions. HALLINGER et al. (2010) found positive links between snowfall and alpine *Juniper* shrub growth in Subarctic Sweden. Positive and negative effects of snow may thus be evened out, which may explain the lack of correlations found. Another explanation may be the fact that winter snow depth at Arctic-alpine sites is relatively independent of winter precipitation, as excess snow is removed by wind and redistributed according to topography (ERICKSON et al. 2005).

Spring and summer precipitation can be a growth-limiting factor for tundra shrubs at some Arctic and alpine tundra sites (RAYBACK et al. 2010; LIANG et al. 2012; KEUPER et al. 2012; LI et al. 2016), but we did not find a positive influence of spring or summer precipitation for the site-species combinations studied here. However, precipitation is spatially highly variable and Arctic precipitation records are restricted to a few meteorological stations which limits data availability to gridded climate datasets (MYERS-SMITH and MYERS 2018). Still, we did find some support for the September precipitation model, with positive slope, explaining *E. hermaphroditum* growth at the alpine site Vole, Oppland, Norway. Autumn precipitation may be important for growth at the end of the growing season when photosynthesis may become more moisture-limited as a result of lower soil moisture levels.

For all site-species combinations a summer temperature model best explained variation in annual growth, except for *B. nana* at the alpine site Vole, Oppland in Norway, for which a summer precipitation model with a negative slope was the best model. A direct negative influence of summer precipitation is unlikely at this site, as *B. nana* growth was found to increase at a Siberian site with similar summer temperatures in response to a doubling of precipitation to amounts similar to those at Vole (KEUPER et al. 2012). Most likely, cloudy weather associated with summer precipitation reduces photosynthetically active radiation (PAR) and thus photosynthetic productivity and radial growth in *B. nana*, since this shade-intolerant species is sensitive to PAR-reduction (CAMPIOLI et al. 2012b). Additionally, higher amounts of summer precipitation may result in enhanced nitrogen leaching (ÄCKERMANN et al. 2015), which may have a negative influence on *B. nana* growth rates, as growth of this species has been shown to be strongly nitrogen-limited (BRET-HARTE et al. 2001; 2002; MACK et al. 2004). Notably, we also found some evidence for a negative influence of summer precipitation on *S. pulchra* growth at Pika, Yukon Territory (Tab. 2) and a negative influence of July precipitation on *C. tetragona* at Johannes V. Jensen Land in northern Greenland, both potentially also related to PAR-reductions due to related cloudy weather and nitrogen leaching. The negative influence of summer or July precipitation at these sites may also be a consequence of the negative correlation between temperature and precipitation during summer months or July, respectively, in the CRU TS4.00 datasets of these sites.

Deciduous shrubs generally benefit more from climate warming than evergreen shrubs (ELMENDORF et al. 2012a; 2012b; MYERS-SMITH et al. 2015a). Yet, at

both alpine sites, we found a stronger relationship between summer climate and growth for the evergreen shrub species studied. In addition, annual growth of *C. tetragona* has been shown to correspond to greening over a larger region of Yukon-Alaskan alpine tundra, as observed by remotely sensed normalized difference vegetation index (NDVI), than *S. pulchra* (WEIJERS et al. 2018). The weaker response to summer climate of *B. nana* at Vole, Norway, may be explained by higher grazing pressure, as expansion of *B. nana*, and not *E. hermaphroditum* has been shown to be inhibited by herbivory in an enclosure experiment in the Scandinavian mountains (VOWLES et al. 2017). The strong response to summer climate of the evergreen *C. tetragona* at Pika, Canada compared to that of *S. pulchra* from the same site may be best explained by the micro-climatic conditions in the snowbed localities, related to a delayed start of the growing season at such localities or higher soil moisture availability. Herbivory may also offer an explanation, as *C. tetragona* is not grazed upon (MALLIK et al. 2011).

5 Conclusions

Our results confirm that shrub growth rates in Arctic and alpine ecosystems are in general sensitive to summer climate. Continued and projected warming is thus likely to stimulate a further encroachment of shrubs in these systems through a densification of existing stands. Recruitment of new shrub specimens, however, may rely on winter warming for some species and on the distribution of snow for others.

Our findings contrast with the previous notion that shrub expansion may remain limited to the warmer and wetter parts of the tundra biome, given the strong positive growth response to recent warming in the High Arctic polar desert.

Our findings did not concur with previous observations of greater climate sensitivity of tall and low deciduous shrub growth to summer climate when compared to dwarf evergreen shrubs. Moreover, current biome-wide generalizations at the functional group level are difficult to interpolate to the species level, as micro-site conditions, for example the determination of growing season length by snow depth and related soil moisture content may determine the strength of the climate-growth relationships found. Further analyses of shrub growth sensitivity to climate from specific tundra ecotopes, such as snow-beds and different slope positions, thus remain necessary to gain a better understanding of the ongoing restructuring of Arctic-alpine landscapes in response to climate change.

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Appendix

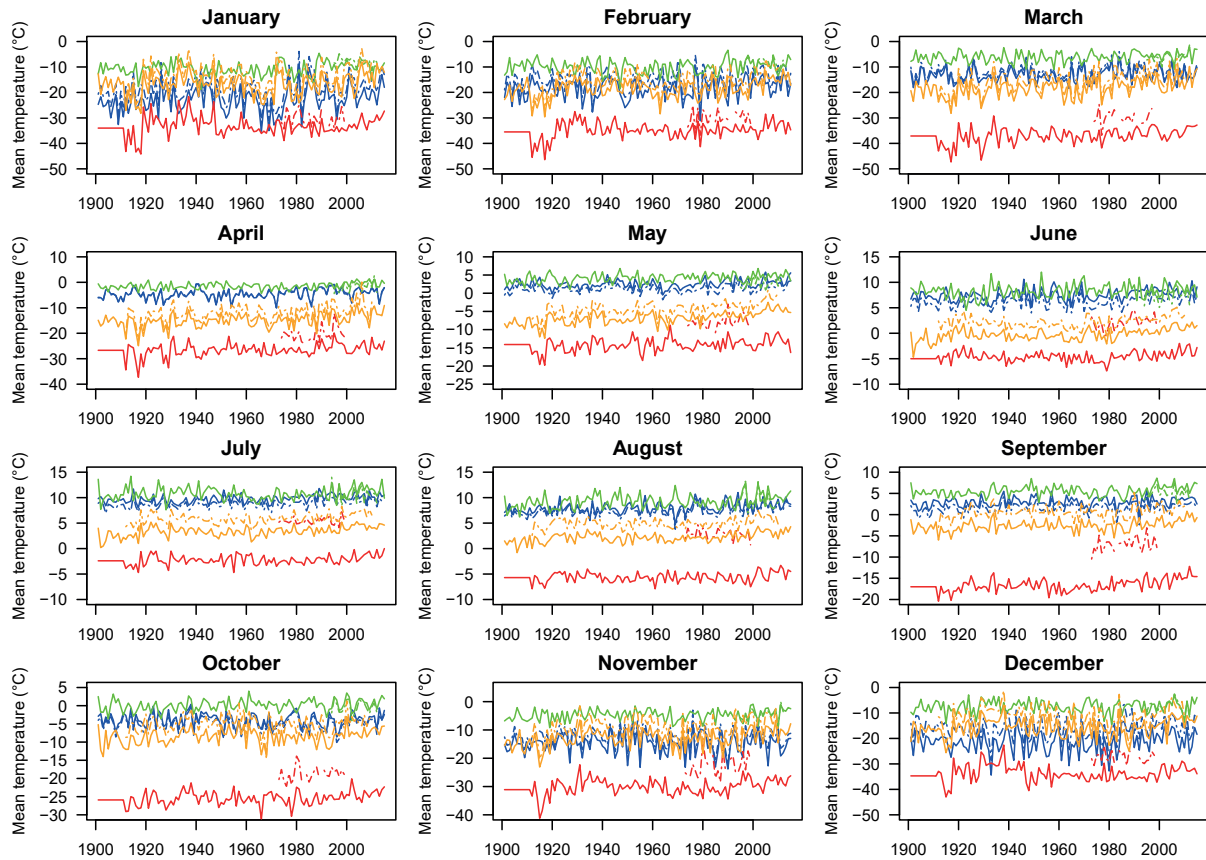


Fig. A1a: Monthly mean temperatures valid for 1. Pika valley, Kluane Region, Yukon Territory, Canada (blue lines); 2. Johannes V. Jensen Land, Greenland (red lines); 3. Vole, Vågåmo, Oppland, Norway (green lines); 4. Adventdalen, Spitsbergen, Svalbard (orange lines). Solid lines represent monthly values from the CRU TS4.00 dataset (HARRIS et al. 2014; CRU et al. 2017) and dashed lines represent monthly values from either the nearest weather station to the respective site or a different gridded modelled dataset. For Pika the dataset used for comparison is the modelled climate data for the point 61.22°N, 138.28°W at 1755 m elevation from Climate WNA v5.40 (WANG et al. 2017); for Johannes V. Jensen Land the temperature data was measured at the Kap Moltke research station in Northern Greenland (Peary Land Foundation, see WEIJERS et al. (2017)); for Vole temperature data from the on-site microclimate station (61.90°N, 9.14 °E; 1100 m a.s.l.); for Adventdalen the homogenized Svalbard Airport (78.25°N, 15.50°E; 28 m a.s.l.) series (DNMI 2016) was used for comparison.

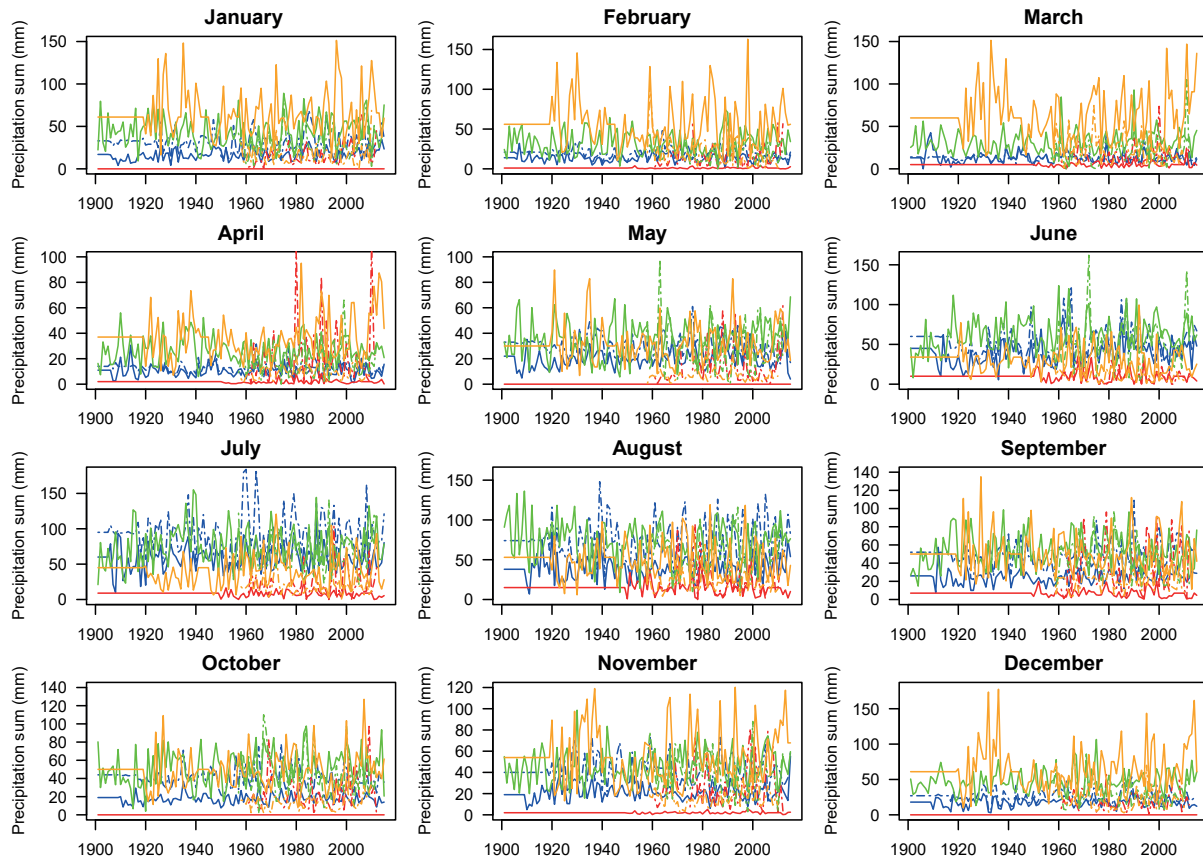


Fig. A1b: Monthly precipitation sums valid for 1. Pika valley, Kluane Region, Yukon Territory, Canada (blue lines); 2. Johannes V. Jensen Land, Greenland (red lines); 3. Vole, Vågåmo, Oppland, Norway (green lines); 4. Adventdalen, Spitsbergen, Svalbard (orange lines). Solid lines represent monthly values from the CRU TS4.00 dataset (HARRIS et al. 2014; CRU et al. 2017) and dashed lines represent monthly values from either the nearest weather station to the respective site or a different gridded modelled dataset. For Pika the dataset used for comparison is the modelled climate data for the point 61.22°N, 138.28°W at 1755 m elevation from Climate WNA v5.40 (WANG et al. 2017); for Johannes V. Jensen Land the precipitation data was measured at Station Nord (81.60°N, 16.67°W; 13 m a.s.l.; NOAA 2016; LAWRIK et al. 2011); for Vole the modelled precipitation data for the point 61.90°N, 9.15°E; 1099 m elevation from the Norwegian Water Resources and Energy Directorate were used (SENORGE.NO 2017); for Adventdalen the homogenized Svalbard Airport (78.25°N, 15.50°E; 28 m a.s.l.) series (DNMI 2016) was used for comparison.

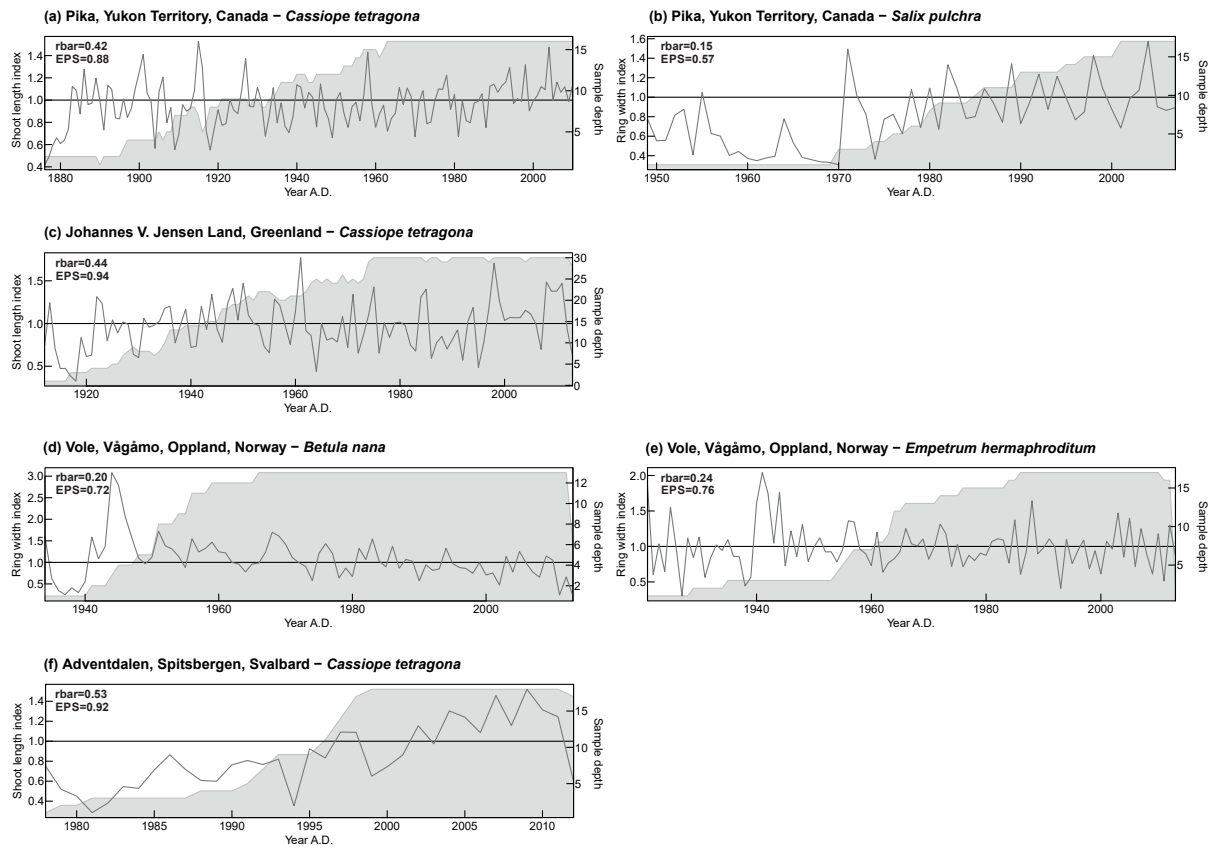


Fig. A2: Mean standardized site chronologies for *Cassiope tetragona* (a) and *Salix pulchra* (b) from the Pika valley, Kluane Region, Yukon Territory, Canada; for *C. tetragona* (c) from Johannes V. Jensen Land, Greenland; for *Betula nana* (d) and *Empetrum nigrum* ssp. *hermaphroditum* (e) from Vole, Vågåmo, Oppland, Norway; and for *C. tetragona* (f) from Adventdalen, Spitsbergen, Svalbard. The mean interseries correlation coefficient (r_{bar}) and expressed population signal (EPS) of each mean chronology are given in the upper-left corner of each panel. Grey areas represent sample size.

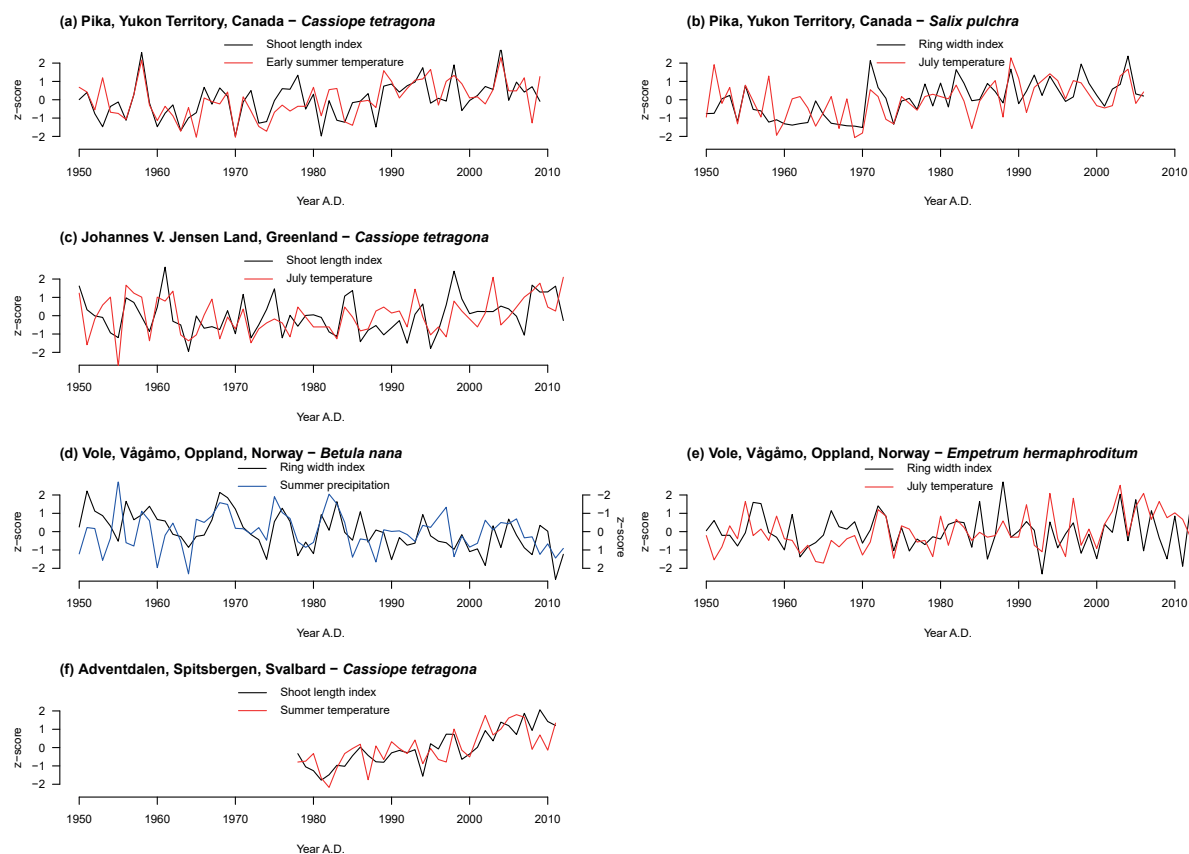


Fig. A3: Standardized (z-scores) site chronologies plotted with the climate parameter (z-scores) from the best climate-growth model for each site-species combination. *Cassiopia tetragona* growth and early summer temperatures (a) and July temperatures and *Salix pulchra* growth (b) at the Pika valley, Klucane Region, Yukon Territory, Canada; *C. tetragona* growth and July temperatures at Johannes V. Jensen Land, Greenland (c); *Betula nana* growth and summer precipitation (d) and *Empetrum nigrum* ssp. *hermaphroditum* growth and July temperatures (e) at Vole, Vågåmo, Oppland, Norway; and *C. tetragona* growth and summer temperatures at Adventdalen, Spitsbergen, Svalbard (f). Note the inverted y-axis for summer precipitation in (d).