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Büntgen, U., Bolze, N., Hellmann, L., Sittler, B., Frauenberger, B., Piermattei, A., ... Krusic, P. J. (2018). Long-term recruitment dynamics of arctic dwarf shrub communities in coastal east Greenland. *Dendrochronologia*, 50, 70–80.

<https://doi.org/10.1016/j.dendro.2018.05.005>

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Long-term recruitment dynamics of Arctic dwarf shrub communities in coastal east Greenland

Running head: The pulse of Arctic shrub recruitment

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ABSTRACT

Warming-induced biological and ecological responses have been reported from high-northern latitude sites, where changes in dwarf shrub communities translate into complex vegetation-

climate feedbacks. Most of the available Arctic tree-ring evidence is, however, restricted to a limited number of species and locations. A combination of wood anatomical and ‘dendro’-ecological techniques provides insights into past growth rates, recruitment dynamics and even community assemblages of Arctic vegetation. Here, we use thin sectioning and ring counting of 1432 dwarf shrub samples from eight species and two tundra regions in coastal east Greenland to assess community recruitment history and its relation to climate. Site and species-specific annual stem increments, as well as estimated plant ages, range from 0.013-0.720 mm and from 4-204 years, respectively. The mean ring width is 0.086 mm, with a mean age of 50 years. Decadal-scale recruitment dynamics of the studied vegetation cover respond to Greenlandic summer temperature variations back to the late 19th century ($r = 0.7$; 1881-2000).

Keywords: Arctic greening; community ecology; dwarf shrubs; East Greenland; global warming; tundra ecosystems; vegetation dynamics

Introduction

Over the past decades, air temperatures in the Arctic increased almost twice as fast as the global mean (ACIA 2004), and state-of-the-art climate model simulations project a continuation of this trend (IPCC 2014). Among the most significant effects of a warmer (and greener) Arctic (Bonan et al. 1995; Chapin et al. 2000; Przybylak 2003) are permafrost thawing and ice melting (IPCC 2014). A reduction in both snow cover and sea ice increases the exposure of ‘dark’ land and ocean cover that translates into lower albedo and/or less reflectivity through a higher absorption of solar radiation (Serreze & Francis 2006). Thus, surface temperatures will continue to rise and enhance snow and ice melt (Pearson et al. 2013).

For a multitude of Arctic organisms, climate-induced and habitat-driven responses have been reported across various spatiotemporal scales (ACIA 2004; Post et al. 2009). These include, changes in nutrient availability and corresponding range shifts towards higher latitudes and elevations, as well as enhanced vegetation growth (Jia et al. 2009; Blok et al. 2010, 2011; Myers-Smith et al. 2011; Elmendorf et al. 2012a, b; Epstein et al. 2012; Büntgen et al. 2015). Vegetation dynamics, in turn, influence a wide range of ecosystem processes like energy, nutrient and moisture fluxes within and between terrestrial, aquatic and marine ecosystems (Liston et al. 2002; Myers-Smith et al. 2011).

Low average temperatures and reduced precipitation totals, together with short growing seasons, are characteristic for most of the Arctic vegetation zone where plant growth is often suppressed (Billings 1973; Overpeck et al. 1997; Przybylak 2003). Consequently, well-adapted, high-northern tundra vegetation is sensitive to even small climatic changes (Molau 1993; Chapin et al. 1995; Wielgolaski 1997; Henry & Molau 1997; Hobbie & Chapin 1998; Walker et al. 2006; Elmendorf et al. 2012a). Although many perennial shrub and dwarf shrub tundra species exhibit distinct annual growth rings (Kanngiesser 1907; Molisch 1938; Schweingruber & Poschlod 2005; Schweingruber et al. 2013; Myers-Smith et al. 2015a, b), our understanding of past vegetation dynamics in the Arctic is limited. Our knowledge gap is mainly driven by a lack of high-resolution, spatial and temporal data, as well as the exceptional costs and physical demands associated with research at the polar limits of plant growth. An updated overview of published Arctic shrub and dwarf shrub articles is shown in **Figure 1**.

Here, we use thin sectioning and ring counting to examine historical changes in the growth level and age structure of eight major dwarf shrub species from two regions in coastal east Greenland. The first is a new collection on Traill Island in 2014 (this study) and the other is an extant collection, approximately 250 km south of Traill, made in 2012 at Scoresbysund

(Büntgen et al. 2015). We combine the wood anatomical and ‘dendro’-ecological information from both regions to reconstruct site- and species-specific population dynamics of Arctic dwarf shrubs back to the late 19th century. With the combined dataset of 1432 samples, we address the: 1) turnover rate and productivity level of east Greenland’s dwarf shrub vegetation, 2) temperature dependency of historical recruitment pulses, and 3) suitability of simple ring counts to estimate community-wide vegetation dynamics at decadal resolution.

Material and Methods

Study area and sampling design

The Traill Island study is located within the lower reaches of the Karupelv Valley in coastal east Greenland around 72°35’ N and 23°18’ W (**Fig. 1**). This area, at the southern end of the north-east Greenland National Park, along the King Oscar Fjord, is a post-glacial outwash plain bound by mountainous slopes and upland plateaus over 1000 m above sea level (Worsley & Gurney 1996). The valley consists of undifferentiated, superficial quaternary deposits, with patterned grounds, solifluction lobes, raised beaches and thaw slumps. The harsh, High-Arctic climate conditions restrict the vegetation period to approximately two months a year, during which rainfall is rare and the average July-August temperature mean is 5-6° C (Nuna-Tek 1989; Rau 1995). Annual precipitation totals of approximately 320-400 mm, and annual temperature means close to -10° C result in continuous snow cover from early-September until the end of June (Washburn 1967), with maximal snow depths in early spring. *Salix arctica* is the most abundant species followed by *Cassiope tetragona* and *Dryas octopetala*. The sampling sites on Traill are characterized by a discontinuous polar semi-desert vegetation (Born & Böcher 2001), including dwarf shrub heath, herb slopes, moss-sedge meadows, snow patches, organic crusts, fell field, and tundra hummock. Basalt rock

outcrops, alluvial fens and gravel deposits are often free of vegetation cover. In July 2014, when sampling took place, all Traill plots were completely snow-free.

Between July 12-24th, 2014, 875 dwarf shrub samples, of the ten most abundant deciduous and evergreen Arctic tundra species (*Arctous* (*Arctostaphylos*) *alpina*, *Betula nana*, *Cassiope hypnoides* (now also named *Harrimanella hypnoides*), *Cassiope tetragona*, *Dryas octopetala*, *Empetrum nigrum*, *Rhododendron lapponicum*, *Salix arctica*, *Salix herbacea* and *Vaccinium uliginosum*), were collected from 19 plots on Traill Island. Individual plot sizes were defined by the abundance of prevailing species and site-specific characteristics of vegetation density (Büntgen et al. 2015). The 19 plots are randomly distributed across different geographical aspects between 6 and 480 m above sea level, and all within 6 km of each other. The within plot sampling concentrated on collecting the widest possible range of plant sizes. To determine the maximum number of annual growth rings, and thus absolute plant ages, both the continuous below- and aboveground root and stem system of each specimen was excavated (Büntgen et al. 2015). Sealed in plastic bags, each sample was carefully labelled and preserved in a 50 % aqueous alcohol solution.

Sample preparation and data compilation

At the Swiss Federal Research Institute WSL in Birmensdorf, thin sections of 10-25 µm were cut with a sliding microtome (Gärtner & Nievergelt 2010) from the oldest part of the stem, the so-called root collar (Schweingruber et al. 2013). A combination of water and pure alcohol is used to moisten the cross-sectional surface, and a drop of glycerol to prevent the thin sections from drying out. Each sample is bleached for five minutes with Eau de Javel (sodium hypochlorite and potassium hypochlorite), then double stained with a 1:1 Safranin and Astra-Blue solution that colours lignified structures red and non-lignified material blue (Gärtner & Schweingruber 2013). Surplus stain is removed with ethanol to further dehydrate the thin

sections, which are finally embedded in Canada balsam under a permanent cover glass and dried for 12-24 hours at 60° C (Gärtner & Schweingruber 2013).

From each thin section, the longest xylem radius is measured, the consecutive number of rings counted, and the corresponding bark thickness recorded (Büntgen et al. 2015). Plant ages are estimated since accurate cross-dating of many samples was not possible. However, with massive replication, simple ring counting can still provide useful information for the reconstruction of community-wide vegetation dynamics (Büntgen et al. 2015; Myers-Smith et al. 2015a).

Despite the advantage of having micro-sections, the annual growth rings of *Salix herbacea* and *Cassiope hypnoides* (also called *Harrimanella hypnoides*) are difficult to identify. Data from these two species are thus excluded from further analyses. The final dataset from Traill includes 619 samples from eight species: *Arctous alpina*, *Betula nana*, *Cassiope tetragona*, *Dryas octopetala*, *Empetrum nigrum*, *Rhododendron lapponicum*, *Salix arctica* and *Vaccinium uliginosum*. This new dataset was visually and statistically compared against a subset of data presented in Büntgen et al. (2015). The existing dataset from Scoresbysund incorporates information on ring counts and wood anatomical features from ten Arctic dwarf shrub species. To make the Scoresbysund dataset comparable to the new collection from Traill, all *Cassiope hypnoides* and *Salix herbacea* measurements are removed, reducing the Scoresbysund dataset to 813 dwarf shrub samples from the Ittoqqortoormiit region (70°27' N and 21°58' W). Separated by approximately 250 km, the more northern Traill plots represent the High-Arctic tundra biome, whereas Scoresbysund reflects a slightly more oceanic assemblage at the transition of the Low-Arctic zone. Although following the same protocol, the sampling in Scoresbysund (14-19th July 2012) and Traill (12-24th July 2014), as well as the subsequent sample preparation and analyses were performed by different teams of researchers.

Homogenized temperature measurements from five meteorological stations of the Danish Meteorological Institute (DMI; www.dmi.dk) were used for comparison against historical estimates of shrub recruitment (**Fig. 1**). Monthly resolved mean temperature series were created from long observations in the coastal northwest Greenland settlement of Pituffik (Thule Air Base; 76°31'N and 68°51'W) that cover 1948-2011, as well as from measurements on the small island of Mittarfik Upernavik in west Greenland (72°47'N and 56°07'W), from the nearby mainland station in Mittarfik Ilulissat (Jakobshavn Airport; 69°14'N and 51°03'W), from Nuuk in the southwest (Gothåb; 64°11'N and 51°40'W), and from the most southern station in Ivittut (Kangilinnguit; 61°12'N and 48°10'W), with all of them reaching back to 1873. The herein applied proxy/target comparison over a fairly unusual long-distance was indeed necessary due to the lack of suitable instrumental measurements along Greenland's east coast (Box 2002; Büntgen et al. 2015). In fact, the most critical aspect of choosing meteorological records was the total length of continuous, monthly resolved measurements. Due to the likelihood of smearing effects from spatial data interpolation, gridded indices were not considered. The individual summer and annual mean temperature readings, herein selected from the five stations along the west coast of Greenland (**Fig. 1**), share a reasonably strong common signal during their period of overlap. All time-series were transformed into anomalies relative to the 1981-2010 climatological mean. The average cross-correlation coefficients, of the normalized station data, calculated over the period 1948-2011, during summer (June-August), the warm season (April-September), winter (December-February), and annually (January-December), are 0.67, 0.67, 0.88 and 0.84, respectively. Recognizing the distance separating our sampling sites on the east coast from the instrumental stations along the west coast (see discussion), this compromise is one way to examine temporal characteristics in the relationship between temperature variability and the intensity of shrub recruitment (Büntgen et al. 2015).

Decadal-scale changes in annual and summer temperature anomalies are compared with wavelength-dependent estimates of dwarf shrub recruitment dynamics back to the late 19th century. Using a recent version of the ARSTAN/DPL software (Cook & Krusic 2005), all proxy (shrub recruitment) and target (temperature) were band-pass filtered using cubic smoothing splines with 50 % frequency cut-off at 10 and 15 years (Büntgen et al. 2006). Exclusion of the highest (year-to-year) and lowest (multi-decadal to centennial) frequencies is necessary due to the fact that much of the year-to-year recruitment variability is prone to dating uncertainty, and that the overall long-term decline in recruitment back in time, as well as the most recent recruitment depression, are possibly affected by the sampling design. After testing our data for normal distribution, moving, as well as split period and lagged, Pearson's correlation coefficients were applied to investigate different effects of methodological uncertainty, biological memory, and the temporal stability of the relationship between growth and climate.

Results

The mean age of all samples from Traill is 32 years, with clear differences attributable to species (**Fig. 2a**). The youngest (four years) and oldest (125 years) individuals from Traill are represented by *Salix arctica*. A total of 183 samples have ages up to 60 years, and 273 plants are between 21 and 40 years old. A total of 582 samples, from seven out of eight species, reveal ages up to 60 years, and 27 plants from six species are between 61 and 80 years old. Ten samples of *Dryas octopetala*, *Rhododendron lapponicum* and *Salix arctica* are over 81 years, and three individuals from Traill were found to be over 100 years old (**Fig. 2a**). The average ring width of all dwarf shrub species from Traill is 0.11 mm (**Fig. 2b**), but individual plants can vary from 0.022-0.700 mm. *Cassiope tetragona* often reveals ring widths <0.05

mm, whereas *Salix arctica* and *Betula nana* exhibit highest average ring widths (**Fig. 2b**).

Sample replication is highly variable between species and regions (**Fig. 2c**).

Specimens previously collected in Scoresbysund are generally older than the new material from Traill (**Fig. 2a**). When calculated over all samples and species, the mean age of the Scoresbysund samples is 62 years. Plant ages of more than 100 years are reported for 84 individuals, including *Betula nana*, *Rhododendron lapponicum* and *Salix arctica*. About one third (30.3 %) of all samples reached ages between 41 and 60 years. The average annual xylem diameter increments of the Traill and Scoresbysund samples are 0.084 and 0.066 mm, respectively. *Betula nana* and *Salix arctica* show the highest average growth rates in both regions (**Fig. 2b**), whereas the minimum is found in *Cassiope tetragona*. The bark thickness of the Traill samples is on average 1.0 mm thinner than in Scoresbysund (**Fig. 3**). Total bark thickness, maximum xylem radius and average ring width in all samples from Traill as well as Scoresbysund are positively associated (**Fig. 3**).

After merging the two datasets from Traill and Scoresbysund, the average ring width of all 1432 samples ranges from 0.012-0.700 mm, with a mean of 0.086 mm (**Fig. 4**). Divided into eleven equally wide ring width classes, the class from 0.051-0.100 mm is the best replicated, representing 39.3 % of all samples (**Fig. 4a**). Approximately one third of the samples are included in the narrowest ring width class (0.00-0.05 mm). *Cassiope tetragona* and *Dryas octopetala* form the smallest growth rings. *Betula nana* and *Salix arctica* produce higher than average ring widths, often ranging between 0.251 and 0.700 mm. The average radial stem increment of all samples is 0.074 mm/year. The lowest annual stem growth is found in *Dryas octopetala*, and *Salix arctica* exhibits the highest radial stem increment per year. A total of 94 % of all sampled plants are younger than 100 years (**Fig. 4b**). Divided into three 20-year age classes, the 21-40-year age class includes 34.3 % of all dwarf shrub samples, dominated by *Salix arctica*. A total of 23.9 % of all individuals have ages between 41 and 60 years. The

remaining 6 % are between 101 and 204 years old. The number of counted rings is negatively related with the average annual ring width (**Fig. 4c**). Growth rings in young plants are generally wider than in old plants.

The overall, long-term trends in recruitment history at Traill and Scoresbysund are similar (**Fig. 5a**). Rather low values are found during the first half of the 20th century and during the past decade, with higher values in between. Nevertheless, the degree of year-to-year coherency at both sites is not stable over time (**Fig. 5b**). The decadal-scale (10-15-year band-pass filtered) temperature variability, back to the late 19th century, is found to be similar ($r = 0.96$) for annual and summer means (**Fig. 6a**). However, some discrepancy, between the annual and summer means, exist from the 1940s to the 1960s, and again since the 1990s. Comparison against the band-pass filtered recruitment data suggests that mid-frequency summer temperature variability is significantly positively correlated ($r = 0.41-0.83$) with Arctic vegetation dynamics back to the 1880s (**Fig. 6b**). That is, recruitment pulses either coincide or follow warm summers. More specifically, there is a tendency towards increasing lags back in time, with overall smaller lags found in the Scoresbysund recruitment history. The decadal-scale temperature dependency of the mid-frequency shrub recruitment is generally higher in the Traill data compared to those from Scoresbysund, and further increases when averaging both datasets (**Fig. 6b**).

Discussion

Sampling strategy and growth characteristics

The recruitment history of Traill's dwarf shrub community is different than that at Scoresbysund. To begin explaining this discrepancy, we cannot ignore the possibility that some of the difference is due to the methodological challenges in both the collection of samples in the field (Bär et al. 2006; Myers-Smith et al. 2015a), as well as the precise

physiological aging of Arctic dwarf shrubs. Though the intent of sampling on Traill was to closely replicate that performed at Scoresbysund, it should be noted that different researchers carried out both the field and laboratory work. However, little to no uncertainty is expected to originate from the microscopic identification of the root collar (Schweingruber & Poschlod 2005; Schweingruber & Büntgen 2013). Moreover, ring counts can only provide a minimum estimate of plant age and usually underestimate the true age (Myers-Smith et al. 2015a). Past recruitment activity is further underestimated by the omission of dead specimens that are not collected during fieldwork (Büntgen et al. 2014, 2015). The overall younger samples from Traill might be related to the fact that the distribution of prevailing dwarf shrub sizes at both sites is not the same. Moreover, both areas are characterized by different site conditions, and may represent different stages of natural recruitment cycles, or even Arctic ecosystem succession.

Sparse plant cover, with a low vertical structure, characterizes high-northern vegetation zones. Only a few well-adapted plants can stand the harsh temperatures and extreme environmental conditions in this barren landscape (Körner 2003). An important plant adaptation to Arctic conditions is the prostrate growth form, and creeping stand structure (Wielgolaski & Karlsen 2006). At the level of individual plants, juvenile growth often takes place on multiple shoots in horizontal instead of vertical direction (de Witte & Stöcklin 2010). This early growth habit makes detection of that part of the stem with the greatest age – the root collar – difficult to identify (Dahlgren et al. 2016).

In Arctic regions, high winds persist throughout most of the year and small plants therefore often become abraded or covered by soil particles (Fitter & Hay 1987). The transformation of root to stem occurs after a certain time of exposure (Schweingruber 2007). Moreover, many shrub species, such as *Arctous alpina*, *Dryas octopetala*, *Empetrum nigrum* and *Salix arctica* reproduce vegetatively (de Witte & Stöcklin 2010). If the main root and basal stem are

replaced by adventitious shoots, these parts are often difficult to distinguish, and hence complicate the counting of the maximum number of rings that is necessary to define plant age. Thus, cutting at different stem heights leads to varying outcomes in the number of growth rings, measured ring widths, and portion of missing rings (Büntgen & Schweingruber 2010; Myers-Smith et al. 2015a).

Recruitment pulses and temperature changes

Our study demonstrates there exists a relationship between decadal-scale summer temperature and the mid-frequency recruitment rate of eight Arctic shrub species with lags varying from one to nine years, and an increasing tendency back in time. A short growing season, low temperature, high desiccation, and low nutrient supply are the main limiting factors of plant life in the Arctic. The combination of a harsh climate and environment often result in reduced growth and high longevity. More than 50 % of Arctic and alpine plants are able to complete their life cycle through vegetative reproduction (Körner 2003). *Dryas octopetala*, *Empetrum nigrum*, *Salix arctica* and *Vaccinium uliginosum* do not depend on energy and nutrient consuming seed production and colonize nutrient-limited and highly heterogeneous habitats by vegetative sprouting (Lambers et al. 2008). The subsequent ecological effect is the development of genetically-uniform plant populations. In one respect, slow growth and persistence of clonal plant populations are expected to buffer the potential impact of environmental change and thus enhance community stability and ecosystem resilience (Grime 2006).

Since summer temperatures have increased over the past decades, shrubs show enhanced growth rates in many, though not all, Arctic regions (Forbes et al. 2010; Hallinger et al. 2010; Schmidt et al. 2010; Blok et al. 2011; Myers-Smith et al. 2011, 2015b). Our time-series and correlation analyses suggest that the estimated dwarf shrub recruitment is predominantly

driven by changes in growing season temperature (June-August). The break of dormant buds in deciduous Arctic shrubs is mainly controlled by summer air temperature (Pop et al. 2000; Lambers et al. 2008), occurring earlier in deciduous than in evergreen species (Billings & Mooney 1968). Fast growing and early flowering deciduous shrubs like *Betula nana* benefit from producing photosynthetic tissue early in the growing season (Molau et al. 2005). Recruitment rates, plant ages, and sample replication differed between the investigated species and regions. In our data, we find some years were climatically more favourable for growth for some species but caused a recruitment delay in others. The more extreme environmental conditions are, the lower is the biological competition (i.e. evolutionary theory; Heide 1985).

We observed distinctly younger shrubs at Traill compared to Scoresbysund. At the same time, the observed delay in recruitment following warm summers was generally shorter on Traill. Our result suggests a considerable recruitment intensity at Traill in response to recent warming. This is well in line with results of other studies, which reported temperature-mediated expansion of Arctic shrubs to high latitudes (Post et al. 2009; Forbes et al. 2010; Fraser et al. 2014; Büntgen et al. 2015; Myers-Smith et al. 2015b). In using the same temperature station data from the west coast of Greenland for the comparison with shrub recruitment in both regions, we are unable to resolve the effect of local climatic conditions at both study sites. Nevertheless, recruitment lags, growth rates and anatomical features indicate less extreme conditions at Traill compared to Scoresbysund, and/or more competition under generally warmer conditions (Bär et al. 2006).

Though the Traill samples' mean average ring widths and xylem diameter growths are higher than those in Scoresbysund, their average ages and bark thickness are also lower. These results may be reflective of a sampling bias (Büntgen et al. 2015). Twigs and branches have thinner bark than stems (Schweingruber 2007). Though we know 15.6 % of the Traill samples

are roots, it is unknown what percentages are stem and branch material. Slower growing individuals of *Cassiope tetragona* and *Rhododendron lapponicum*, characterized by smaller growth rings, formed thicker stem bark than faster growing individuals. It is unknown whether stem secondary growth is a response to different environmental conditions at both study sites. The correlation between thicker bark and smaller rings can be explained by the potential of bark to stiffen the young shrub stems in order to provide support against wind and snow (Niklas 1999). Additionally, the age- and species-specific allocation to bark may be in response to protecting the xylem from cold temperature extremes.

Details into herbivory, as an influencing factor for shrub recruitment, abundance, seed production, and transport are insufficient (Myers-Smith et al. 2011). The northern collared lemming (*Dicrostonyx groenlandicus*), Arctic hare (*Lepus arcticus*) and muskoxen (*Ovibos moschatus*) are frequent herbivores in east Greenland (Thing et al. 1987; Dalerum & Angerbjörn 2000; Vowles et al. 2017). Shrub communities are certainly affected by these herbivores. Data from a monitoring program in northeast Greenland revealed reduced growth and reproduction of *Salix arctica* caused by muskoxen (Aastrup 2003; Forchhammer 2003). Similarly, collared lemmings that spend the winter under the thick snow cover, can reduce the abundance of *Dryas octopetala* (Berg et al. 2008; Weijers et al. 2017). As damage due to herbivory is not possible to discern, the impact of grazing on the age structure of our samples (*Dryas octopetala* and *Salix arctica*) is unknown.

Meteorological observations and ecological responses

The extent network of meteorological stations at higher northern-latitudes, especially in north and east Greenland, is limited in space and length of recording. The quality and quantity of existing records is admittedly insufficient for assessing growth-climate relationships (Overland et al. 2004).

Most climate stations on Greenland are located in the populated southern parts and along the west coast of the island (Cappelen et al. 2016). Different periods of instrumental coverage in the Arctic make it difficult to compare these data to each other (Przybylak 2000; Box 2002). With the exception of the Tasiilaq station (Ammassalik; 65°36'N and 37°37'W), most instrumental temperature readings on Greenland's east coast, including Scoresbysund (Ittoqqortoormiit; 70°29'N and 21°57'W) and Aputiteeq (66°01'N and 35°52'W), do not cover the entire 20th century (Box 2002). However, temperature measurements from Tasiilaq were not coherent enough to be implemented in our target network (Büntgen et al. 2015). Although based on 1432 individual shrubs, several data-related and methodological-induced uncertainties cannot be ignored. Cross-dating was impossible for all samples due to the overall number of extremely narrow and missing rings, as well as the high degree of variation in secondary growth forms (Buchwal et al. 2013; Schweingruber et al. 2013). The obtained plant ages are therefore only minimum estimates (Schweingruber & Büntgen 2013). Moreover, the declining sample size back in time parallels differences in species composition, which further affects any direct assessment of year-to-year recruitment-temperature dependency. Additional ambiguity may result from overlooking the very youngest and smallest shrub individuals during sampling. This fact alone could explain the lack of modern recruitment since around the mid 1990s when temperatures actually increased most (Büntgen et al. 2015). In addition, the observed temporal offset between warmer temperatures and recruitment pulses might be partly related to inconsistency in the instrumental temperature measurements themselves. A possible bias in seasonal station readings is indicated by a significant decline in the coherency between the annual and summer temperature means.

Conclusions

Following a long tradition of dendrochronological research in Greenland (Kraus 1873; Good 1927; Molisch 1938; Parsons et al. 1994; Büntgen et al. 2015; Young et al. 2016; Buras et al. 2017; Weijers et al. 2017; Gamm et al. 2018), this study – at the interface of wood anatomy and ‘dendro’-ecology – provides another independent line of evidence for low cambial activity and high species longevity in dwarf shrubs at two sites in coastal east Greenland. Moreover, we confirm significant agreement between decadal-scale summer temperature variability and lagged, mid-frequency recruitment intensity. Although implying low turnover rates and an overall stable composition of Arctic dwarf shrub communities, warming-induced recruitment pulses also suggest the ability of tundra vegetation to respond within a couple of years to abiotic factors, including environmental and climatic changes.

Long-term estimates of historical changes in community-wide biomass production and carbon allocation within and among different plant species are especially important for the vast circumpolar tundra biome, for which such information is still limited. To further enhance our understanding of the response of shrub and dwarf shrub cover to climate change, future research should consider massively replicated sampling designs at the stand and even landscape level, including all age classes and species. Additionally, the importance of microsite climate conditions should not be underestimated since local soil conditions indirectly mediate the recruitment and growth response to rising air temperatures (Myers-Smith et al. 2011). The expected insight will be beneficial for a wide range of timely aspects in functional ecology and biogeography, as well as ecosystem modelling, well beyond the geographical limits of forest growth.

Acknowledgements

Ulf Büntgen received funding from the Ministry of Education, Youth and Sports of Czech Republic within the National Sustainability Program I (NPU I grant number LO1415), Lena

Hellmann received funding from the SNF (Project number P2BEP2_168645). The Eva Mayr-Stihl Foundation kindly supported fieldwork. The Greenland Home Rule issued access permits to the North Greenland National Park, and Benoit Sittler received support from the Groupe de Recherche en Ecologie Arctique (F). Two anonymous referees kindly commented on earlier manuscript versions.

Author contributions

UB initiated and coordinated the study. All authors either provided data, methods and/or intellectual input. NB, UB, PJK and LH wrote the paper with input from all others.

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Figures 1-6

Fig. 1. Arctic dwarf shrub studies with the various symbols and shadings indicating different observational methods (RW: ring width, WA: wood anatomy). Varia refers to correlation coefficients between ring width and temperature variations, leaf chemistry and imaging records. The green and blue dots show our study sites in Traill and Scoresbysund (Büntgen et al. 2015; this study), respectively. Numbers at each location enable references to be associated: 1 = Sturm et al. 2001; 2 = Tape et al. 2012; 3 = Tape et al. 2006; 4 = Dial et al. 2007; 5 = Forbes et al. 2010; 6 = Frost et al. 2013; 7 = Frost and Epstein 2014; 8 = Blok et al.

2011; 9 = Weijers et al. 2010; 10 = Rozema et al. 2009 ; 11 = Hallinger et al. 2010; 12 = Hallinger and Wilmking 2011; 13 = Wilson and Nilsson 2009; 14 = Ravolainen et al. 2011; 15 = Hollesen et al. 2015; 16 = Jørgensen et al. 2013; 17 = Young et al. 2016; 18 = Daniëls et al. 2011; 19 = Büntgen et al. 2015; 20 = This Study; 21 = Myers-Smith et al. 2011b; 22 = Lantz et al. 2010; 23 = Mackay and Burn 2011; 24 = Fraser et al. 2014; 25 = Danby and Hik 2007; 26 = Myers-Smith 2011; 27 = Tremblay 2010; 28 = Tremblay et al. 2012; 29 = Ropars and Boudreau 2011; 30 = Upshall 2011; 31 = Hudson and Henry 2009; 32 = Hill and Henry 2011; 33 = Buras et al. 2017; 34 = Ackerman et al. 2017; 35 = Buchwal et al. 2013; 36 = Buchwal et al. 2015; 37 = Schmidt et al. 2006; 38 = Schmidt et al. 2010; 39 = Boulanger-Lapointe et al. 2014; 40 = Jørgensen et al. 2015; 41 = Rayback and Henry 2005; 42 = Rayback and Henry 2006; 43 = Rayback et al. 2012; 44 = Rayback et al. 2011; 45 = Weijers et al. 2012; 46 = Weijers et al. 2017; 47 = Havström et al. 1993; 48 = Parsons et al. 1994; 49 = Michelsen et al. 1996; 50 = Bokhorst et al. 2008; 51 = Baddeley et al. 1994; 52 = Press et al. 1998a; 53 = Hartley et al. 1999; 54 = Wookey et al. 1993; 55 = Johanson et al. 1995; 56 = Shevtsova et al. 1995; 57 = Richardson et al. 2002; 58 = Phoenix et al. 2001; 59 = Lantz et al. 2010; 60 = Zvereva and Kozlov 2004; 61 = Shevtsova et al. 1997; 62 = Weijers et al. 2013; 63 = Schmidt et al. 1999; 64 = Blok et al. 2015; 65 = Preece et al. 2012; 66 = Nams et al. 1987; 67 = Jones et al. 1997; 68 = Karlsson 1985; 69 = Johnstone 1995; 70 = Karlsson 1985; 71 = Starr and Oberbauer 2003; 72 = Press et al. 1998b; 73 = Havström et al. 1995; 74 = Gough et al. 2002; 75 = Pop et al. 2000; 76 = Tolvanen and Henry 2001; 77 = Berner et al. 2015; 78 = Berner et al. 2018; 79 = Gamm et al. 2018). Background shading shows the mean June-August summer temperature trend (°C) from 1961-2010 based on gridded GISTEMP data (Hansen et al. 2010). The five instrumental stations in Pituffik, Mittarfik Upernavik, Mittarfik Ilulissat, Nuuk and Ivittut, from which temperatures were used for comparison are indicated by blue stars.

Fig. 2. Species-specific differences in (A) plant age, (B) ring width (mm) and (C) sample replication of the 813 and 619 dwarf shrubs from Scoresbysund and Traill (blue and green), respectively. Data are further separated into root (r) and shoot (s) discs (%), and the red asterisks indicate statistically significant differences. The inset pictures are *Betula nana* root (left; without pith) and shoot (right; with pith) thin sections (100 x). The eight different Arctic dwarf shrub species (*Arctous alpina*, *Betula nana*, *Cassiope tetragona*, *Dryas octopetala*, *Empetrum nigrum*, *Rhododendron lapponicum*, *Salix arctica* and *Vaccinium uliginosum*) are abbreviated by Aa, Bn, Ct, Do, En, Rl, Sa and Vu, respectively.

Fig. 3. Relationships between average ring width, total bark thickness and maximum xylem radius within and between the 813 and 619 Arctic dwarf shrub samples from Scoresbysund and Traill (blue and green), respectively (see Figure 2 for details).

Fig. 4. Species-specific differences in (A) average ring width (mm) and (B) estimated plant age (years) of the newly combined Scoresbysund-Traill dataset that includes root/shoot collar samples of 1432 individual Arctic dwarf shrubs representing eight species (see Schweingruber et al. 2013 and Büntgen et al. 2015 for details). (C) The significantly negative relationship between average measured ring width (mm) and estimated plant age (years) (p = significance of the regression slope, and r = Pearson's correlation coefficient).

Fig. 5. (A) Recruitment dynamics of eight Arctic dwarf shrub species from Scoresbysund (blue; $n = 813$) and Traill (green; $n = 619$), as well as the combined dataset (black; $n = 1432$). (B) Non-centred 31-year moving correlation coefficients between the two site's recruitment records from coastal east Greenland.

Fig. 6. (A) Annual (January-December) and summer (June-August) temperature means (orange and red) after 10-15-year band-pass filtering. (B) Comparison between the decadal-scale summer temperature changes (red) and Arctic dwarf shrub recruitment dynamics. Data from Scoresbysund (blue; $n = 813$) and Traill (green; $n = 619$), as well as their mean (black; $n = 1432$) have been 10-15-year band-pass filtered and consecutively lagged between one and nine years depending on their best fit with decadal-scale JJA temperature variations calculated over three 40-year intervals (2000-1961, 1960-1921, 1920-1880). The horizontal grey shadings show the correlation coefficients of the time-series from Scoresbysund and Traill (blue and green) after lagging, as well as their mean (black) calculated against JJA temperatures over the three different intervals. All individual time-series were normalized to have a mean of zero and a standard deviation of one (i.e. data are expressed as z-scores).