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Consistent Dendrochronological Response of the Dioecious *Salix arctica* to Variation in Local Snow Precipitation across Gender and Vegetation Types

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Abstract

Dendroclimatological reconstructions may be influenced by intraspecific variation in radial growth caused by plant gender and ecotypic differentiation. We examined the growth response of the High Arctic *Salix arctica* to interannual variation in snow precipitation in Zackenberg, NE Greenland. Tree ring examinations revealed a consistent response of annual radial growth in this dwarf shrub to variation in the amount of snow precipitation across gender and across three distinct vegetation types. Annual growth, however, differed between vegetation types. These results are discussed with respect to an improved understanding of the factors limiting the growth of *S. arctica*, which can be used for future reconstructions of climatic conditions, especially in remote High Arctic regions.

Introduction

The analysis of tree ring records and climatic covariates is an important tool for identifying limiting factors of plant growth and for the reconstruction of climate change (Schweingruber, 1996). Numerous investigations have documented the climatic constraints for a large number of tree species from all over the world (e.g. Esper et al., 2002; Oberhuber, 2004; Briffa et al., 2004; Martinelli, 2004). In general, temperature and precipitation control radial growth, and these factors can thus be reconstructed from tree ring data. However, besides climatic variables, local abiotic and biotic factors, like snow depth and grazing, affect plant growth and, thus, tree ring formation which may interfere with the detection of general climatic patterns (e.g. Eckstein et al., 1991; Tolvanen et al., 2002; Carrer and Urbinati, 2004). Also, ecotypic differentiation (*sensu* Turesson, 1922) between contrasting vegetation types may determine the responsiveness of individuals towards environmental variation (see Fetcher and Shaver, 1990), which in turn may affect tree ring formation differently across vegetation types. Thus, disentangling the relative effects of climate and local factors is crucial before dendroclimatological models can be used for reconstructing past climatic conditions and for predicting future trends (Schweingruber, 1996).

Reconstruction of historical climate and prediction of future climatic conditions are particularly important for the High Arctic, where climate changes are most pronounced (ACIA, 2005), with concomitant marked perturbations to the ecosystem (Post et al., 2009). Dendroclimatological methods emerge as an important tool for climate change research in the High Arctic, since few direct long-term climatic records are available from this biome. To investigate the importance of local snow precipitation and vegetation type effects on radial growth in the High Arctic, we chose a woody species with a highly northern distribution, the Arctic willow (*Salix arctica* (Pall.) L., Salicaceae), which is widely distributed in Arctic regions (Loren, 2003). In the High Arctic, it grows as a prostrate shrub with a reported maximal age of 110 years (Schmidt et al., 2006). *Salix arctica* is a semi-ring-porous species with widely spaced pores, and is, because of its well-defined growth rings (Schweingruber, 1996), suitable for dendroclimatological studies. Growth rates of *S. arctica* are very low, and stem diameter in samples from NE Greenland was 0.4–1.2 cm, with a mean growth rate of 0.12 mm yr^{-1} in a related study (Schmidt et al., 2006).

Despite the special problems associated with missing or discontinuous rings (Woodcock and Bradley, 1994), *Salix arctica* represents a promising source for dendroclimatological reconstruction (Wilson, 1964; Savile, 1979; Woodcock and Bradley, 1994; Schmidt et al., 2006). In years with extensive snow cover, more narrow tree rings are formed, which makes it possible to reconstruct snow cover for much longer periods than provided by direct climatological observations (Schmidt et al., 2006). Recent analyses suggest that it is indeed possible to use *S. arctica* radial growth to generate proxy climate data and, hence, to reconstruct past snow regimes in the Zackenberg valley for about 100 years (Schmidt et al., 2006).

Schmidt et al. (2006), however, did not examine the potential effect of local conditions such as the vegetation type in which the individual was sampled. Indeed, a potential complication in using *S. arctica* for dendroclimatological studies occurs because the species is dioecious and can be found in a variety of vegetation types. Individuals living in contrasting vegetation types may experience climatic variation differently (Jones et al., 1999), especially in the Arctic where snow cover is unevenly distributed (e.g. Cappelen et al., 2001). Additionally, in dioecious plants, such as *S. arctica*, marked intergender differences in the response to climatic conditions may exist (Jones et al., 1999). Vegetation type

TABLE 1

Populations of *Salix arctica* and soil characteristics in three dominant vegetation types within the Zackenberg valley, NE Greenland (means ± SD; ANOVA; ***, $P < 0.001$; **, $P < 0.01$; ns, $P > 0.05$). Different superscript letters indicate significant differences within rows (Tukey-Kramer test; $P < 0.05$). Soil data were recorded in seven plots; nutrient availability was measured with exchange resins.

	Ablation plateau	*Cassiope* heath	*Salix* snowbed	F statistics
(a) Salix arctica populations				
Plant density (m^{-2})	2.2 ± 2.0^a	22.9 ± 5.4^b	26.4 ± 6.7^b	98.6***
Female:Male	57:43	48:52	60:40	—
(b) Snow depth (cm)#				
Spring 2005	0##	61 ± 29	73 ± 31	—
(c) Soil water (%vol)				
Early summer	4.0 ± 1.7^a	40.9 ± 11.7^b	34.4 ± 7.8^c	253.7***
Late summer	6.1 ± 2.2^a	32.2 ± 10.5^b	21.8 ± 5.6^c	95.0***
(d) Soil nutrient quantities (μg 10 cm^{-2} 43 $days^{-1}$)				
NO_3-N	20.66 ± 4.98^a	4.63 ± 0.70^b	4.27 ± 0.62^b	65.3***
NH_4^+-N	4.77 ± 1.26	5.09 ± 3.03	4.31 ± 1.52	0.3^{ns}
PO_4^{3-}	0.94 ± 0.30	0.33 ± 0.06	1.21 ± 1.52	1.9^{ns}
K^+	30.6 ± 10.7	32.5 ± 9.4	28.5 ± 15.8	0.2^{ns}
Ca^{2+}	1400 ± 263^a	757 ± 347^b	1103 ± 286^a	8.0**
Mg^{2+}	334 ± 53^a	247 ± 121^{ab}	458 ± 131^{ac}	6.8**
S^{2-}	93.8 ± 7.8^a	81.5 ± 2.3^a	192.8 ± 86.6^b	10.3**
Fe^{3+}	5.69 ± 0.95^a	4.57 ± 0.98^{ac}	18.26 ± 11.56^{bd}	9.0**

Manual measurements along approximately 10 km transects conducted in June 2005.
The ablation plateau was snow-free at the beginning of the field season, 1 June 2005.

and gender are, thus, potentially important variables for the description of growth patterns of *S. arctica* in relation to climate.

The overall objectives of this study are to improve our understanding of the local conditions affecting the growth patterns of *S. arctica*, and thus to explore the potential of the species for climate reconstructions in the High Arctic. We examine the effects of local annual snow precipitation on the interannual variation in radial growth of *S. arctica*. This effect is compared with the potential influence of plant gender and vegetation type. The design of the study allows us to test the effects of the three individual factors and potential interactions simultaneously.

The following specific hypotheses were tested: (1) Snow precipitation is a limiting factor for radial growth in the High Arctic *S. arctica*. (2) (a) Plant gender affects radial growth due to intraspecific variation in resource allocation, and (b) the responsiveness of genders toward environmental variation differs. (3) (a) Vegetation types affect radial growth due to differences in the availability of soil and nutrients, and (b) vegetation type-specific ecotypes differ in their responsiveness towards interannual variation in snow precipitation.

Materials and Methods

STUDY SITE AND VEGETATION TYPE CHARACTERISTICS

The study was conducted in the Zackenberg valley in NE Greenland (74°28′N, 21°33′W) at Zackenberg Ecological Research Operations (ZERO), established in 1996 to gain detailed long-term data on the structure and functioning of a High Arctic ecosystem in relation to changes in global as well as local climate (Meltofte et al., 2008). *Salix arctica* plants were sampled in the valley bottom (30–40 m a.s.l.), where three major vegetation types are found: *S. arctica* snowbed, *Cassiope tetragona* heath, and wind-exposed ablation plateau with sparse vegetation. The vegetation types represent three levels of spring snow cover: (1) thick cover in *Salix* snowbed, (2) intermediate accumulation in *Cassiope* heath, and (3) thin or only sporadic snow cover on the ablation plateau. Estimates of snow depth were measured along transects within the *Salix* snowbed and *Cassiope* heath in spring 2005 (Table 1). Snow cover is a key factor explaining variation in soil moisture, nutrients, and length of the vegetation period (Meltofte et al., 2008).

Within each vegetation type, we established seven plots around randomly chosen *S. arctica* plants. Minimum distance between plots was approximately 50 m. To characterize the growth conditions for *S. arctica* at each plot in the three vegetation types we measured soil moisture and nutrient availability. Nutrient supply rates were estimated using *in situ* burials of PRS^{TM}-probes (Western Ag Innovations, Canada); probes were buried on 29 June 2005 and recovered on 11 August 2005, after 43 days of exposure. Two cation and two anion probes were placed ca. 50 cm from labeled *S. arctica* individuals. Upon recovery, probes were processed by Western Ag Innovations following standard procedures (http://www.westernag.ca). The following estimates of nutrient availability were obtained: total N, NO_3-N, NH_4-N, Ca, Mg, K, P, Fe, Mn, Cu, Zn, B, S, and Al. Data on Mg from one plot in a *Salix* snowbed was excluded, as this had a factor 15 higher level than other measurements from the same vegetation type.

The three vegetation types differed markedly with respect to nutrient availability (Table 1). NO_3-N was about five times higher in the ablation plateau compared with *Cassiope* heath and *Salix* snowbed, while no difference was observed in NH_4-N, P, and K. The availability of P was extremely low in all three vegetation types. Base availabilities (Ca, Mg) were significantly lower in the *Cassiope* heath, whereas sulfur and iron concentrations were highest in the *Salix* snowbed. No differences were observed for Al^{2+} (14.3–17.3), Mn^{3+} (0.35–3.41), Cu^{2+} (0.24–1.64), Zn^{2+} (0.45–0.57), and B^{3+} (1.15–1.53; all measured as μg 10 cm^{-2} 43 $days^{-1}$).

Soil moisture was recorded in the uppermost 5 cm using a ThetaProbe ML2X sensor (Delta-T Devices Ltd.). Ten moisture

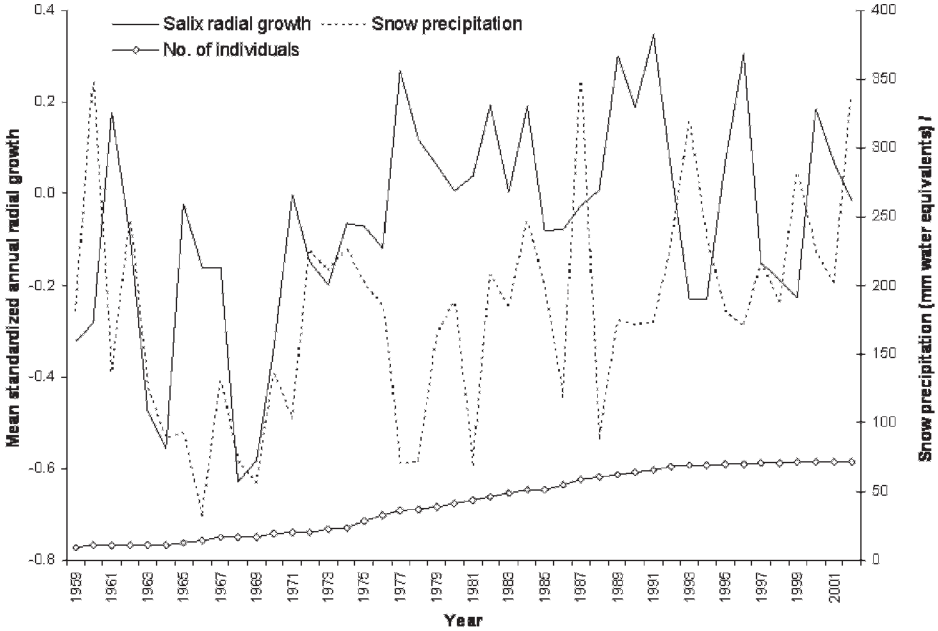

FIGURE 1. **Mean standardized annual radial growth of the dwarf shrub *Salix arctica* and annual snow precipitation in the Zackenberg valley, NE Greenland, 1959 – 2002, along with the number of *S. arctica* individuals examined per year.**

records were taken at each plot when the nutrient probes were established and again on recovery. The vegetation types differed significantly in soil moisture (Table 1). Soil moisture was about 5–10 times higher in the *Cassiope* heath compared with the ablation plateau, while the *Salix* snowbed showed intermediate values. The latter was unexpected as the *Salix* snowbed in general has higher levels of soil moisture than the two other vegetation types (see Elberling et al., 2008).

SAMPLING OF SALIX ARCTICA *AND TREE RING ANALYSIS*

In July 2003, we randomly collected 24 stem samples (12 male and 12 female plants) within *Salix* snowbed, *Cassiope* heath, and ablation plateau, respectively (72 in total). Plant gender was determined based on the presence of catkins or fruit bodies. The stem samples were taken 1–2 cm above the shoot basis, dried at 20°C, and stored in paper bags until processing.

Salix arctica presents several problems for obtaining reliably cross-dated ring-width series because of formation of eccentric pith, and missing and discontinuous rings (C. Baittinger, personal observation; Woodcock and Bradley, 1994). Partial rings are frequent in the areas of the shorter radii but can occur in all parts of a sample. Due to the extremely low radial growth of *S. arctica*, a special approach of microscopic examination was necessary to delineate and measure the annual rings (Schmidt et al., 2006). Samples were cut with a sliding microtome, taking 20-μm-thick cross sections from 1–3 different parts of the stem sample. Microsections were stained with standard solutions (1% safranin), preserved with Aquamount (Gurr®), and digitally scanned (Nikon Super CoolScan 8000 ED, 4000 dpi). After treating the images in standard programs (Adobe Photoshop), they were enlarged and printed on glossy paper. On each sample 2–7 radii were analyzed using a tree ring measuring-stage connected to a PC, and the computer-program DENDRO (Tyers, 1999). Estimates of radial growth in 2003 were excluded from the analysis due to incomplete annual growth. Mean length of the individual radii was 23.1 years (SD = 10.3; range 4–44 years).

To enable proper cross-dating, radii were compared within individuals to localize missing rings and to evaluate the quality of the sample. Rings that were absent from the selected radius but present elsewhere in the microsection were inserted in the tree ring curves. Cross sections from different parts of the stem sample were employed to detect missing rings (Kolishchuk, 1990; Woodcock and Bradley, 1994; Bär et al., 2006).

SALIX ARCTICA *POPULATION CHARACTERISTICS*

Around each individual sampled for tree ring analysis in summer 2003, we estimated the density of other *S. arctica* plants within a radius of 2 m. The density was about 10 times lower in the ablation plateau (2.2 individuals m^{-2}) than in the two other vegetation types (Table 1).

Additionally, we estimated the gender ratio of *S. arctica* by walking a minimum of three transects (50–200 m) within each of the three vegetation types, noting the gender of the nearest *S. arctica* for each 10 m. No significant differences in gender ratio was found among the vegetation types ($\chi^2 < 0.22$, df = 1, $P > 0.64$; Table 1).

LOCAL CLIMATE DATA AND STATISTICAL ANALYSIS

Following the analytical approach we previously used for the analysis of *Salix arctica* radial growth (Schmidt et al., 2006), we analyzed the effects of gender, vegetation type, the amount of local snow precipitation, and all interactions on the standardized (mean = 0, SD = 1), log-transformed annual radial growth in a mixed first-order autoregressive model with individual and radius as random factors, and radius nested within individual. Year was also regarded as random to account for random between-year variation; gender and vegetation type were fixed factors. Model reduction was conducted by successively removing the non-significant ($P > 0.05$) model variables; as post hoc test, we used Tukey-Kramer ($P < 0.05$). Annual estimates of solid snow precipitation in the Zackenberg valley from 1958 to 2002, reconstructed from downscaled NCEP/NCAR data sets and expressed as mm water equivalents, were obtained from Hansen et al. (2008).

Data describing the three vegetation types were log-transformed prior to analyses. Differences in soil moisture and nutrients

TABLE 2

Mean annual radial growth of female and male *Salix arctica* individuals in three High Arctic vegetation types. For the specific vegetation types, different superscript letters indicate significant differences (means ± SD; Tukey-Kramer test; $P < 0.05$).

	All vegetation types	Ablation plateau	*Cassiope* heath	*Salix* snowbed
All plants (mm)	0.11 ± 0.09	0.14 ± 0.11[a]	0.10 ± 0.08[b]	0.11 ± 0.08[b]
Female growth (mm)	0.11 ± 0.08	0.11 ± 0.09	0.10 ± 0.07	0.11 ± 0.09
Male growth (mm)	0.12 ± 0.09	0.17 ± 0.12	0.11 ± 0.08	0.11 ± 0.08

were analyzed in General Linear Models. Deviations from unity in gender ratio were analyzed in a 2 × 2 contingency table. All analyses were conducted in SAS 8 (SAS Institute Inc., 2000).

Results

The radial growth of *S. arctica* in the Zackenberg valley exhibited marked year-to-year fluctuations (Fig. 1), a pattern that can be attributed to interannual variation in snow precipitation since radial growth decreased with increasing amount of snow precipitation ($F_{1,67} = 5.99$, $P = 0.017$). Moreover, the radial growth response to snow precipitation was similar in both genders and in all three vegetation types ($P > 0.141$ for all interaction terms). Thus, snow precipitation was a limiting factor for the radial growth in *S. arctica*, but the responsiveness towards the interannual variation in snow precipitation did not differ between genders or vegetation types. Annual radial growth *per se*, however, differed among vegetation types ($F_{2,65.5} = 7.35$, $P = 0.001$; Table 2), and individuals in the ablation plateau showed significantly higher annual radial growth compared to individuals in the *Cassiope* heath and in the *Salix* snowbed ($P = 0.002$ and $P = 0.013$, respectively; Table 2). Radial growth in the *Cassiope* heath and the *Salix* snowbed showed no difference ($P = 0.772$; Table 2). Gender did not affect annual radial growth ($P = 0.260$; Table 2).

Discussion

The radial growth of *Salix arctica* in High Arctic NE Greenland responded significantly to the interannual variation in local snow precipitation, supporting Hypothesis 1. The results of this study hence confirm the findings of Schmidt et al. (2006), who reported radial growth of *S. arctica* in the Zackenberg valley to be limited by the extent of spring snow cover rather than temperature. Here we can add to this knowledge that the response to interannual variation in snow precipitation is consistent across three distinct vegetation types, dominating the Zackenberg valley, as well as across gender. There are no indications of ecotypic differentiation in the response towards interannual variation in snow precipitation across the vegetation types examined here, despite the large differences in long-term average snow accumulation and hence exposure to freeze-thaw events etc., and despite the fact that *S. arctica* individuals exhibit considerable genetic and phenotypic variation (Steltzer et al., 2008), which otherwise would allow for ecotypic differentiation in the responsiveness towards interannual variation in e.g. snow precipitation.

Similarly, we found no indications of a gender-specific growth response to the interannual variation in snow precipitation. Individuals of *S. arctica* exhibit a consistent negative response towards the amount of snow precipitation, irrespective of gender and vegetation type. Neither hypothesis 2b nor 3b could therefore be supported. The lack of skewed gender ratio (Crawford and Balfour, 1990; Klein et al., 1998) or gender segregation among vegetation types (Dawson and Bliss, 1989b) in the Zackenberg valley may also be explained by the consistent response across individuals. Also, no difference in radial growth was observed between plant genders, and hypothesis 2a was therefore rejected. This contradicts previous findings of a gender-specific pattern in e.g. physiology and growth in *S. arctica* (Dawson and Bliss, 1989a, 1989b; Jones et al., 1999). However, in the closely related *Salix lanata*, Forbes et al. (2010) also reported a common pattern in radial growth across genders. Hence, the intersexual differences observed in other studies on the leaf or shoot level, apparently are not reflected in the more coarse patterns of radial growth.

The three vegetation types examined here showed marked differences in availability of soil moisture and nutrients, and also in the density of *S. arctica*. And while the growth response to interannual variation in snow precipitation did not differ among vegetation types, vegetation type *per se* was important for annual radial growth. The ablation plateau had low availability of water, but has also a long growing season due to the limited snow cover, and was, at least locally, rich in nutrients, which resulted in high annual radial growth there. Hence, though having generally suboptimal conditions, the ablation plateau may locally provide more favorable growing conditions compared to the *Cassiope* heath and the *Salix* snowbed. Hypothesis 3a was hence supported.

Conclusion

The tree ring examinations conducted in the present study confirm the negative impact of snow on *S. arctica* radial growth previously reported (Schmidt et al., 2006). Moreover, the response to interannual variation in snow precipitation was consistent across both genders and across three distinct, dominant vegetation types in the High Arctic. Hence, we found no indications of differentiation in response across the three vegetation types examined. Vegetation type *per se*, however, influenced annual radial growth. The consistent linkage between radial growth and snow significantly improves the use of *S. arctica* dendrochronology in future reconstructions of climatic conditions.

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