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Reconstructing Century-long Snow Regimes Using Estimates of High Arctic *Salix arctica* Radial Growth

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Abstract

Using a combination of microscopic examination and electronic scanning and printing, we analyzed the impacts of early spring snow cover extent and temperature during the growing season on the annual radial growth in arctic willow (*Salix arctica* Pallas) in the Zackenberg valley, High Arctic Northeast Greenland. So far, only little dendroclimatological research has been conducted on *Salix arctica*, and the species constitutes a yet-untapped resource for climate reconstruction in the Arctic. We obtained reliable annual radial growth measurements from a total of 43 *Salix arctica* stem samples and analyzed these in a mixed model to determine the limiting climatic factors. We found that early spring snow cover extent impacted the annual growth significantly, whereas variable temperature regimes seemed unimportant. Following the building of a site chronology for the Zackenberg valley, the early spring snow cover extent during the last century was reconstructed.

Introduction

Climate change is expected to be most pronounced in the Arctic regions of the world (ACIA, 2004), and compared to the global average, temperature is already rising at a faster rate in large parts of the Arctic (Chapman and Walsh, 2002). At the higher latitudes, precipitation has generally increased, while the snow season generally has declined (Serreze et al., 2000; ACIA, 2004). Future temperature scenarios predict terrestrial annual average temperature increases of about 3–5°C, with even more drastic increases during winter (4–7°C; ACIA, 2004). Also, precipitation, especially during autumn and winter, is expected to continue to increase significantly (ACIA, 2004).

Knowledge of past climatic conditions is essential to the understanding of present and future climate. Only a very limited number of long-term time series on the climatic conditions in High Arctic Greenland exists, and especially information on the more local climatic conditions is needed. Specifically, upon the erection of the large-scale monitoring program at Zackenberg Ecological Research Operations (ZERO; see, e.g., Rasch and Caning, 2003) in Northeast Greenland, detailed knowledge on the past climatic conditions in the valley is important for the understanding of the patterns and processes of this High Arctic ecosystem.

Dendroclimatology, that is, the analysis of tree-ring records and climatic covariates, is an important tool for the identification of the limiting factors for plant growth, and, hence, for the reconstruction of past climatic conditions. Numerous investigations have documented the limiting climatic factors for a large number of tree species from all over the world. For example, temperature and precipitation often affect tree radial growth (Linderholm et al., 2003; Takahashi et al., 2003; Mäkinen et al., 2003; Oberhuber, 2004). Consequently, dendroclimatology has enabled the reconstruction of past events and climatic conditions, such as temperature regimes (e.g., Esper et al., 2002), snow depths, and

extreme snow events (e.g., Bégin and Boivin, 2001). Also, large-scale climatic phenomena integrating several climatic variables, such as the North Atlantic Oscillation (Hurrell, 1995), may also be correlated with tree-ring growth (Linderholm et al., 2003; Mäkinen et al., 2003). However, the response of radial growth to climatic variability may also be age-dependent (Carrer and Urbinati, 2004), and the reconstruction of past climate needs to integrate this variability (Szeicz and MacDonald, 1994) along with any potential auto-covariation in growth. Finally, site specific conditions, such as elevation, may alter the response to climatic variability (Tardif et al., 2003; Oberhuber, 2004).

Although the potential of arctic willow (*Salix arctica* Pallas) as provider of useful information for dendroclimatological reconstruction was recognized several years ago (Savile, 1979; Woodcock and Bradley, 1994), little research has been conducted since then, and the species constitutes a yet-untapped resource for climate reconstruction in the Arctic. In the present study, we use a novel approach of microscopic examination and digital scanning and printing to examine the impacts of early spring snow cover extent and temperature during the growing season on the annual radial growth in *Salix arctica* in High Arctic Northeast Greenland, thereby allowing the reconstruction of past climatic conditions.

Material and Methods

THE SPECIES

The arctic willow *Salix arctica* is one of the most northerly occurring plants (Woodcock and Bradley, 1994) and has a wide geographic distribution, occurring on Greenland, Asia, North America, and sporadically in northern Europe. In the High Arctic, it forms a prostrate shrub (Beschel and Webb, 1963), and is one of few tree-like woody plants in High Arctic Greenland (Fig. 1). *Salix arctica* is



FIGURE 1. Female arctic willow (*Salix arctica*) individual on an abrasion plateau, Zackenberg, Northeast Greenland. Photo by Niels M. Schmidt.

a semi-ring-porous tree species with well-defined growth rings, whose boundaries are delimited by one or more rows of cells that are rectangular in cross section (Schweingruber, 1990). This species, however, also presents a number of problems for obtaining reliably cross-dated ring-width series because of formation of eccentric pith, and missing and discontinuous rings (Beschel and Webb, 1963; Woodcock and Bradley, 1994).

SITE DESCRIPTION

Collection of *Salix arctica* stem samples was carried out in the Zackenberg valley, Northeast Greenland (74°28'N, 21°33'W; Fig. 2). The valley is situated in the High Arctic, and annual mean temperature is around -10°C, and around 1°C during the growing season, May through August. Average annual precipitation is about 180 mm. Generally, snow cover is extensive in the valley from October–November until late June.

The valley lowland consists of a mosaic of habitat types but is dominated by *Cassiope* heath, *Dryas* heath, *Salix* snowbeds, fen areas, and abrasion plateaus (Bay, 1998). *Salix arctica* is found in most habitat types, but is most abundant in snowbeds, *Cassiope* heaths, and fen areas. On the abrasion plateaus, *Salix arctica* is often almost the only plant species.

SAMPLE COLLECTION AND PREPARATION

Fifty *Salix arctica* stems were sampled in the valley lowland. Stems were cut just above the root collar, and in order to obtain the

longest time series possible we sampled the largest and oldest willow stems in the valley lowland. Samples were taken with an inter-individual distance of at least 25 m. Upon collection, samples were oven-dried (20°C) and stored individually in small paper bags until processing. All stems were sampled in August 2001 after the end of the growing season (see Rasch and Caning, 2003).

The diameter of the xylem of the stems ranged from 0.4 cm in the smallest specimen to 1.2 cm in the largest. Due to the extremely low growth rates, microscopic examination of the specimen was necessary. Stem samples were boiled in water prior to sectioning with a sliding microtome. From one to three different locations on each stem 20 µm microsections were taken and stained with 1% safranin. Hereafter, microsections were mounted in slide frames and digitally scanned (Nikon Super CoolScan 8000 ED, 4000 dpi). After treating the images in standard programs (Paint Shop and Adobe Photoshop), images were enlarged and printed (HP Deskjet 890, 600 × 600 dpi) on glossy A4 paper (HP Superior Paper 180). Though somewhat similar to the method applied by Woodcock and Bradley (1994), who projected segments of the circular section onto paper and traced the growth-ring boundaries, our approach is much less time consuming.

On each microsection at least two but as many as seven radii were measured using a tree-ring measuring-stage connected to a PC, and the computer program DENDRO (Tyers, 1999). As mentioned above, *Salix arctica* presents a number of problems for obtaining reliably cross-dated radial growth series due to the difficulties with missing or partial rings, particularly in the areas of the shorter radii. The individual radii were therefore checked carefully and compared visually on the

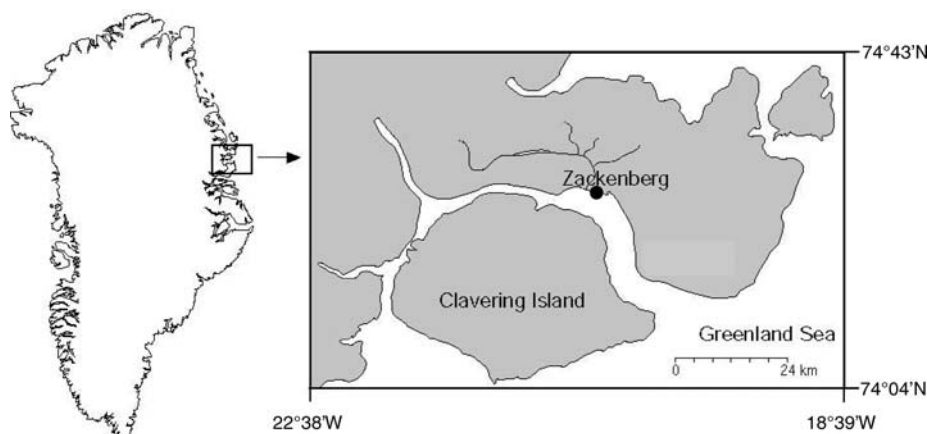


FIGURE 2. Map showing the location of the *Salix arctica* stem collection in High Arctic Northeast Greenland.

monitor and, when necessary, printed and examined on a lightboard to locate missing and discontinuous rings. Printed microsections were examined carefully to characterize the structures of the wood, especially at the tree-ring boundary. Rings that were absent from the selected radius but present elsewhere in the microsection were inserted in the curve as missing values.

Hereafter the radii from each individual were used to build the individual tree-ring curve, the average growth-curve for the individual (Table 1). As for the radii, we also attempted to cross-date the individuals using *t*-values (Baillie and Pilcher, 1973; Rinn, 1989) and visual comparisons of the tree-ring series. One individual with one radius only and six individuals that did not crossdate were rejected, leaving a total of 43 individuals for the following analyses.

DATA ANALYSES

In order to determine the climatic parameters limiting the annual growth in *Salix arctica*, we analyzed the log_e-transformed estimates of annual radial growth in first-order autoregressive mixed models with the local climate covariates. Specifically, each model contained the annual radial growth as response variable, early spring snow cover extent (mean percentage coverage below 600 m a.s.l. in the valley on 10 June) in the years 1995 through 2001 (obtained from Rasch and Canning, 2003), and one of the following temperature variables as predictors: mean local air temperature in (1) May through August, (2) June through August, (3) May, (4) June, (5) July, or (6) August—i.e., the period embracing the growing season in the Zackenberg valley (Rasch and Canning, 2003). Temperature data for the years 1958 to 1975 were available from Daneborg Weather Station approximately 25 km east of Zackenberg (Cappelen et al., 2001) and again from 1982 to 2001. In all models, the interaction between snow cover extent and temperature was also included. Individual and radii were regarded as random, and radii nested within individual. Analyses were run in SAS 8.02 using the PROC MIXED procedure with restricted maximum-likelihood estimation of regression coefficients (SAS Institute Inc., 2000). Model reduction was conducted using log-likelihood ratio tests (Littel et al., 1996).

We reconstructed the past local climatic conditions in the Zackenberg valley by first constructing a site chronology from the standardized individual radial growth curves (mean = 0, SD = 1 within radii), and removed the first-order autocorrelation from the site chronology. The climatic variables mentioned above were then used as predictands in models with the site chronology residual growth as predictor. Statistically significant regression coefficients were used to reconstruct the past climate.

Results

The diameter of the xylem of the stems ranged from 0.4 cm in the smallest stem to 1.2 cm in the largest. The stem with the lowest number of annual rings showed 16 annual rings from the pith (center) to the bark, whereas 94 rings were measured in the stem with the highest number of annual rings, though this specimen was at least 110 years old. The average annual radial growth was 0.12 mm ± 0.09 (mean ± SD; range 0.061 to 1.06 mm). When the annual radial growth of each radius was plotted against year, no age trend was visible in the radii, probably mainly because of the very limited annual growth of this species, which made the early years of growth impossible to separate. Hence, no age detrending was conducted. The temporal dynamics of the mean standardized *Salix arctica* radial growth is shown in Figure 3.

In all mixed models, the first-order autoregressive error structure was significant ($G > 7.5$, $df = 2$, $P < 0.024$). Also, the effect of the random factor individual was significant ($G > 32.9$, $df = 1$, $P < 0.0001$), while the effect of radii was not ($G > 0.2$, $df = 1$, $P <$

TABLE 1

Standard dendrochronological statistics for the tree-ring curves for the 43 *Salix arctica* individuals used in the present study. Two to seven radii were used to build each individual tree-ring curve. Length is the number of years analyzed. Mean sensitivity indicates the mean percentage change from each measured yearly value to the next (Douglas, 1928). AR is the first-order autocorrelation coefficients (Fritts, 1976).

Individual	Length (yr)	Mean growth (mm)	SD (mm)	Mean sensitivity	AR
G2210119	74	0.1028	0.0664	0.54	0.32
G2210129	74	0.1078	0.0655	0.61	0.30
G2210139	32	0.1416	0.0810	0.58	0.27
G2210239	43	0.0916	0.0462	0.52	-0.11
G2310219	30	0.0810	0.0284	0.36	0.18
G2310319	62	0.1431	0.0755	0.56	0.19
G2310329	56	0.1618	0.1186	0.52	0.41
G2310619	75	0.0884	0.0584	0.53	0.21
G2310712	94	0.1118	0.0609	0.49	0.28
G2310819	36	0.1103	0.1216	0.53	0.39
G2410119	17	0.2171	0.0973	0.57	-0.04
G2410319	25	0.1096	0.0575	0.49	0.35
G2410519	22	0.0900	0.0592	0.53	0.45
G2410619	23	0.1035	0.0528	0.41	0.38
G2411009	31	0.1042	0.0518	0.39	0.31
G2411219	53	0.0789	0.0431	0.55	-0.01
G2610119	17	0.0976	0.0638	0.71	0.17
G2610319	28	0.1489	0.0861	0.53	0.15
G2610619	17	0.1259	0.0961	0.45	0.39
G2610719	35	0.0837	0.0649	0.74	0.21
G2610919	32	0.2563	0.1695	0.57	0.37
G2612019	22	0.1141	0.0882	0.55	0.50
G2612219	36	0.0753	0.0474	0.56	0.25
G2612419	38	0.0811	0.0422	0.5	0.18
G2612519	32	0.0881	0.0606	0.43	0.73
G2710129	53	0.0691	0.0557	0.45	0.56
G2711019	16	0.1325	0.0867	0.43	0.25
G2711219	29	0.0724	0.0440	0.63	0.05
G2711319	33	0.0800	0.0511	0.57	0.12
G2711419	31	0.0706	0.0363	0.39	0.40
G2712019	31	0.1135	0.0694	0.64	0.16
G2712119	31	0.1248	0.0878	0.65	-0.01
G2810419	21	0.1157	0.0817	0.68	0.47
G2811219	25	0.2208	0.1608	0.72	0.04
G2811919	22	0.1073	0.0721	0.77	-0.20
G2812019	25	0.2048	0.1191	0.36	0.57
G3010319	30	0.0777	0.0395	0.53	0.14
G3010619	24	0.1154	0.0723	0.53	0.40
G3010919	23	0.0939	0.0460	0.46	0.37
G3011219	26	0.1500	0.0880	0.59	0.33
G3011319	20	0.2910	0.1899	0.47	0.53
G3011819	45	0.1033	0.0619	0.55	0.24
G3012109	41	0.0793	0.0494	0.49	0.30
Grand mean	34	0.1247	0.0875	0.55	0.25

0.6547), and therefore omitted from the analyses. Radial growth, hence, varied across individuals, but not within individuals.

In the mixed models, only the early spring snow cover in the valley had a significant impact on *Salix arctica* radial growth ($P < 0.0001$), and in years with limited snow cover *Salix arctica* tree-ring width was larger than in years with extensive snow cover. In contrast to this, neither temperature in May, June, July, and August, nor temperature in May through August, nor in June through August had a significant influence on the radial growth (Table 2). There was, however, indications of a positive effect of the mean temperature in the growing season on the radial growth, but the relationship was

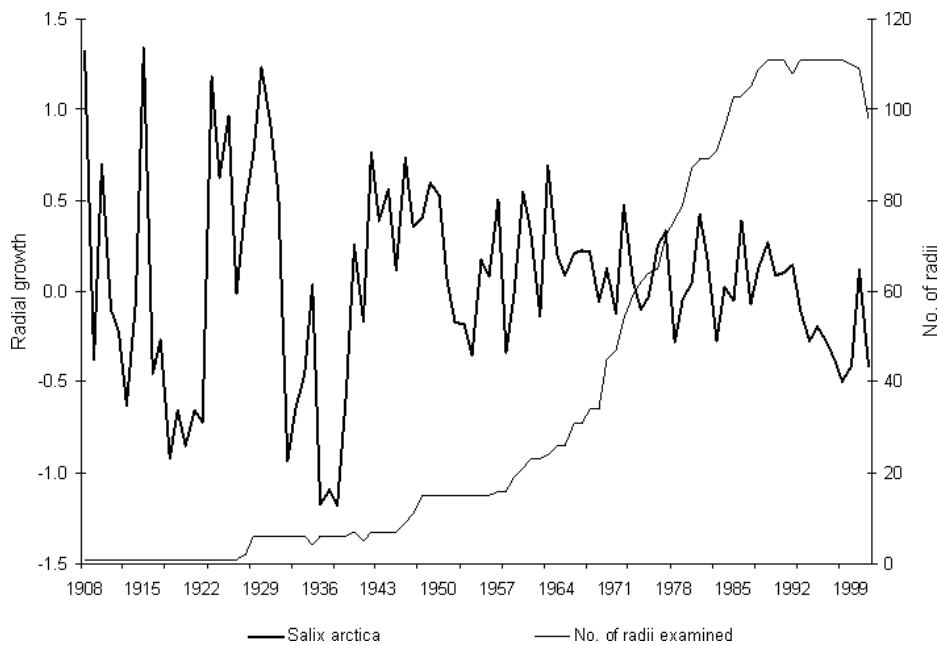


FIGURE 3. Standardized mean annual radial growth of 43 *Salix arctica* sampled in the Zackenberg valley, Northeast Greenland. Also given is the number of radii examined from each year. Linear regression indicates a decrease in annual radial growth from around 1960 onward ($R^2 = 0.33$, $F_{1,40} = 19.30$, $P < 0.0001$), whereas no trend was visible when looking at the entire period ($R^2 = 0.00$, $F_{1,92} = 0.22$, $P = 0.640$).

insignificant (Table 2). All interactions between snow cover extent and temperature regimes were insignificant ($P > 0.05$).

In the site chronology, the residual standardized mean annual radial growth of *Salix arctica* was significantly correlated with local snow cover ($R^2 = 0.66$, $F_{1,5} = 9.82$, $P = 0.0259$; Fig. 4, insert), and the early spring snow cover reconstructed from this relationship in the years 1908 through 2001 is shown in Figure 4. As in the mixed models, temperature regimes were not significantly correlated with the site chronology residual growth ($R^2 < 0.05$, $F_{1,5} < 2.05$, $P > 0.1613$).

Discussion

The *Salix arctica* chronology constructed in this study represents the first retrospective index of the extent of early spring snow cover in High Arctic Greenland, covering almost a century. The extreme conditions in this harsh environment are reflected in the extremely small mean annual radial growth (0.12 mm), which is smaller than the mean annual growth reported from Sabine Island close to Zackenberg (0.24 mm; Kraus, 1874, cited in Wilson, 1964), but larger than the 0.07 mm reported for *Salix arctica* from more northerly sites (75°N, Wilson,

1964; 82°N, Woodcock and Bradley, 1994). Our methodology of microscopic examination and digitizing of microsections, which is a refined version of the method applied by Woodcock and Bradley (1994), allowed us in a precise and less time-consuming manner to examine an otherwise problematic species with such a low annual radial growth and several missing and partial rings.

Trees living under extreme conditions are likely to exhibit a strong response to climatic variability (Fritts, 1976; Mäkinen et al., 2003). At lower latitudes, temperature is often one of the most important factors limiting the annual tree-ring growth (e.g., Mäkinen et al., 2000; Tardif et al., 2003). In the present study, however, temperature seemed unimportant for the radial growth, whereas snow cover extent had a marked effect on radial growth. This result is particularly noteworthy given the relatively long temperature time series and the short snow cover time series used in our analyses. However, the short time series on snow cover also warrants that there may be large uncertainties associated with the reconstructed snow cover. Unlike temperature and precipitation, terrestrial snow cover defines the time window for primary productivity sharply, especially in the Arctic with its pronounced seasonality. Extensive snow cover delays the onset of the growing season (Vaganov et al., 1999; Bamzai, 2003; Kiryanov et al., 2003), which is directly traceable in reduced radial growth in *Salix arctica*, and, hence, probably also in a number of plant species in the Zackenberg valley. Mäkinen et al. (2000) also reported a negative correlation between subarctic spruce tree-ring width and early spring precipitation, which often falls as snow, thereby delaying the onset of the growing season. Vaganov et al. (1999) suggested that the increased precipitation in subarctic regions has reduced the temperature sensitivity of tree-ring growth due to the delay in snow melt.

There are indications of a general decrease in snow cover extent in the Arctic (Serreze et al., 2000; Bamzai, 2003), which, through its impact on primary productivity, is likely to have a cascading effect up through the Arctic ecosystem. Our analyses, however, suggest that the early spring snow cover extent in the Zackenberg valley is increasing (Fig. 4), while the mean annual tree-ring growth is decreasing correspondingly (Fig. 3). The relationship is most pronounced from the 1960s onwards, where the replication of the *Salix arctica* site chronology is best (Fig. 3). Thus, the local climate in the Zackenberg valley may become increasingly maritime with more winter precipitation (see Vibe, 1967) and hence less continental, which may be

TABLE 2

Summarized results from the linear mixed model analyses with *Salix arctica* radial growth as response variable and temperature regimes during the growing season in the Zackenberg valley, Northeast Greenland, as predictor variables. Covariate regression estimates (*b*) are given with standard error of mean (SE) and associated *F* and *P* values. Estimation of *b*'s were performed in separate models.

Predictor covariate	<i>b</i>	SE	<i>F</i> value	<i>P</i> value
Temperature May through August	0.08549	[0.05185]	1.65	0.1000
Temperature June through August	0.05267	[0.04099]	1.28	0.1998
Temperature May	0.02944	[0.03037]	0.97	0.3326
Temperature June	0.01922	[0.05476]	0.35	0.7258
Temperature July	0.02581	[0.01776]	1.45	0.1468
Temperature August	0.00192	[0.01885]	0.10	0.9189

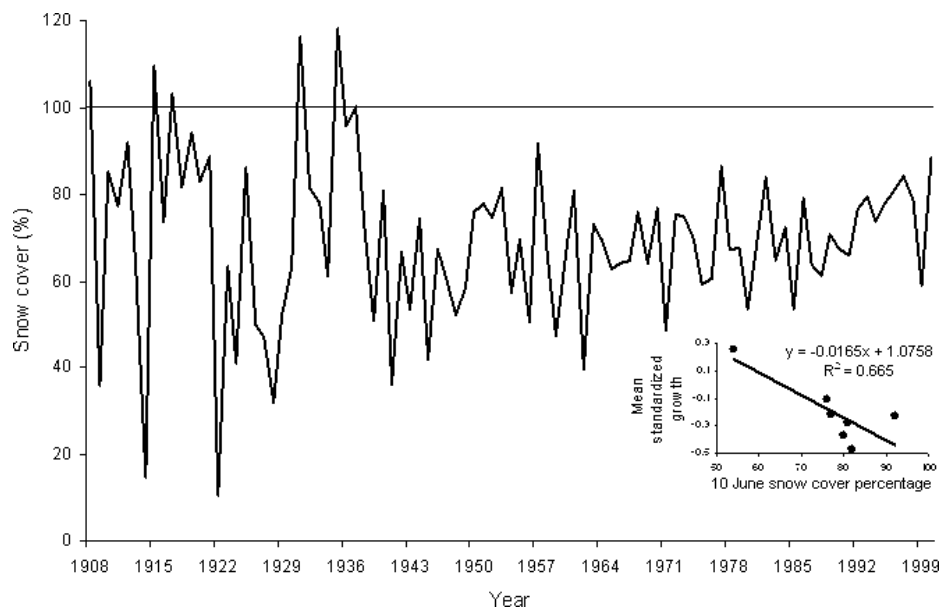


FIGURE 4. Reconstructed snow cover in the Zackenberg valley, Northeast Greenland, 1908–2001. Snow cover is expressed as the percentage of snow covered land in the valley lowland in early spring (10 June). Linear regression indicates an increase in early spring snow cover extent from around 1960 onwards ($R^2 = 0.15$, $F_{1,40} = 6.96$, $P = 0.012$), whereas no trend was visible when looking at the entire period ($R^2 = 0.00$, $F_{1,92} = 0.01$, $P = 0.925$). Insert shows the linear correlation between the residual standardized mean *Salix arctica* radial growth and snow cover extent in the valley.

linked to the reduction in sea-ice formation in the Greenland Sea (Hinkler, 2005). In particular, changes in the amount of snow and its extension is likely to have a marked impact on the entire Arctic ecosystem (Petersen et al., 2001).

In many dendroclimatological studies, autocorrelation is removed just prior to the investigation of climatic influence (e.g., Linderholm et al., 2003). In the present study, however, we incorporate the autoregressive structure and climate covariates into a common model when determining the limiting climatic factors, thereby enabling simultaneous estimates of impacts, and hence biological relevance, of both climate and previous year's growth. The significant autoregressive error structure in our study suggests that present year's radial growth is negatively affected by the growth in the previous year. Hence, years with unfavorable conditions and concomitant small radial growth resulted in low radial growth the following year. Besides extensive spring snow cover, unfavorable conditions may include grazing by herbivores; for example, Maschinski (2001) reported *Salix arizonica* (Dorn) to be unable to fully compensate from the negative effects of grazing within a year. In the Zackenberg valley, musk oxen (*Ovibos moschatus* Zimmermann) and collared lemmings (*Dicrostonyx groenlandicus* Traill) are the most common herbivores (see Rasch and Caning, 2003). In High Arctic Greenland both species feed on *Salix arctica* (Klein and Bay, 1991) and are, hence, likely to affect its radial growth and other life-history traits. We know that variation in *Salix arctica* phenology affects the behavior of musk oxen in the valley (Forchhammer et al., 2005), but to what extent grazing by herbivores affects the annual growth in *Salix arctica* in the Zackenberg valley is currently unknown. However, some of the variation in radial growth not accounted for by our model parameters may indeed be attributable to grazing herbivores.

Acknowledgments

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References Cited

- ACIA, 2004: *Impacts of a warming Arctic: Arctic Climate Impact Assessment*. Cambridge: Cambridge University Press, 139 pp.
- Baillie, M. G. L., and Pilcher, J. R., 1973: A simple cross-dating program for tree-ring research. *Tree-ring Bulletin*, 33: 7–14.
- Bamzai, A. S., 2003: Relationships between snow cover variability and Arctic Oscillation index on a hierarchy of time scales. *International Journal of Climatology*, 23: 131–142.
- Bay, C., 1998: Vegetation mapping of the Zackenberg valley, Northeast Greenland. Copenhagen: Danish Polar Center and University of Copenhagen, 29 pp.
- Bégin, Y., and Boivin, S., 2001: Tree-ring dating of past snow regimes. In Jones, H. G., Pomeroy, J. W., Walker, D. A., and Hoham, R. W. (eds.), *Snow ecology—an interdisciplinary examination of snow-covered ecosystems*. Cambridge, UK: Cambridge University Press, 325–346.
- Beschel, R. E., and Webb, D., 1963: Growth ring studies on arctic willows. Axel Heiberg Research Reports: Preliminary Report 1961–1962, 189–198.
- Cappelen, J., Jørgensen, B. V., Laursen, E. V., Stannius, L. S., and Thomsen, R. S., 2001: The observed climate of Greenland, 1958–99—with climatological standard normals, 1961–90. 00–18. Copenhagen: Danish Meteorological Institute, 152 pp.
- Carré, M., and Urbinati, C., 2004: Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. *Ecology*, 85: 730–740.
- Chapman, W. L., and Walsh, J. E., 2002: Recent variations in sea ice and air temperature in high latitudes. *Bulletin of the American Meteorological Society*, 74: 33–48.
- Douglas, A. E., 1928: *Climate Cycles and Tree Growth II: A Study of the Annual Rings of Trees in Relation to Climate and Solar Activity*. Washington, D.C.: Carnegie Institution.
- Esper, J., Cook, E. R., and Schweingruber, F. H., 2002: Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability. *Science*, 295: 2250–2253.
- Forchhammer, M. C., Post, E., Berg, T. B., Høye, T. T., and Schmidt, N. M., 2005: Local-scale and short-term herbivore-plant spatial dynamics reflect influences of large-scale climate. *Ecology*, 86: 2644–2651.
- Fritts, H. C., 1976: *Tree rings and climate*. London: Academic Press, 567 pp.
- Hinkler, J., 2005: *From digital cameras to large scale sea-ice dynamics—a snow-ecosystem perspective*. Ph.D. thesis, University of Copenhagen, Denmark.

- Hurrell, J. W., 1995: Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science*, 269: 676–679.
- Kirdyanov, A., Hughes, M., Vaganov, E., Schweingruber, F., and Silkin, P., 2003: The importance of early summer temperature and date of snow melt for three growth in the Siberian Subarctic. *Trees—Structure and Function*, 17: 61–69.
- Klein, D. R., and Bay, C., 1991: Diet selection by vertebrate herbivores in the High Arctic of Greenland. *Holarctic Ecology*, 14: 152–155.
- Linderholm, H. W., Solberg, B. Ø., and Lindholm, M., 2003: Tree-ring records from central Fennoscandia: the relationship between tree growth and climate along a west-east transect. *The Holocene*, 13: 887–895.
- Littel, R. C., Milliken, G. A., Stroup, W. W., and Wolfinger, R. D., 1996: *SAS Systems for Mixed Models*. Cary, NC, U.S.A.: SAS Institute Inc., 633 pp.
- Mäkinen, H., Nöjd, P., and Mielikäinen, K., 2000: Climatic signal in annual growth variation of Norway spruce (*Picea abies*) along a transect from central Finland to the Arctic timberline. *Canadian Journal of Forest Research*, 30: 769–777.
- Mäkinen, H., Nöjd, P., Kahle, H.-P., Neumann, U., Tveite, B., Mielikäinen, K., Röhle, H., and Spiecker, H., 2003: Large-scale climatic variability and radial increment variation of *Picea abies* (L.) Karst. in central and northern Europe. *Trees—Structure and Function*, 17: 173–184.
- Maschinski, J., 2001: Impacts of ungulate herbivores on a rare willow at the southern edge of its range. *Biological Conservation*, 101: 119–130.
- Oberhuber, W., 2004: Influence of climate on radial growth of *Pinus cembra* within the alpine timberline ecotone. *Tree Physiology*, 24: 291–301.
- Petersen, H., Meltofte, H., Rysgaard, S., Rasch, M., Jonasson, S., Christensen, S. R., Friborg, T., Sjøgaard, H., and Pedersen, S. A., 2001: The Arctic. In Jørgensen, A. M. K., Fenger, J., and Halsnæs, K. (eds.), *Climate Change Research—Danish Contributions*. Copenhagen: Danish Climate Center, DMI, 303–330.
- Rasch, M., and Caning, K., 2003: Zackenberg Ecological Research Operations. 8th annual report, 2002. Copenhagen: Danish Polar Center, 80 pp.
- Rinn, F., 1989: *TSAP Version 3.0 Reference Manual*. Heidelberg, Germany: Frank Rinn.
- SAS Institute Inc., 2000: *The SAS system for Windows, version 8e*. Cary, NC, U.S.A.: SAS Institute Inc.
- Savile, D. B. O., 1979: Ring counts in *Salix arctica* from northern Ellesmere Island. *Canadian Field-Naturalist*, 93: 81–82.
- Schweingruber, F. H., 1990: *Anatomie europäischer Hölzer—ein Atlas zur Bestimmung europäischer Baum-, Strauch- und Zwergstrauchhölzer*. Stuttgart: Haupt, 800 pp.
- Serreze, M. C., Walsh, J. E., Chapin, F. S. I., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W. C., Morison, J., Zhang, T., and Barry, R. G., 2000: Observational evidence of recent change in the northern high-latitude environment. *Climatic Change*, 46: 159–207.
- Szeicz, J. M., and MacDonald, G. M., 1994: Age-dependent tree-ring growth responses of subarctic white spruce to climate. *Canadian Journal of Forest Research*, 24: 120–132.
- Takahashi, K., Azuma, H., and Yasue, K., 2003: Effects of climate on the radial growth of three species in the upper and lower distribution limits of an altitudinal ecotone on Mount Norikura, central Japan. *Ecological Research*, 18: 549–558.
- Tardif, J., Camarero, J. J., Ribas, M., and Gutiérrez, E., 2003: Spatiotemporal variability in tree growth in the central Pyrenees: Climatic and site influences. *Ecological Monographs*, 73: 241–257.
- Tyers, I., 1999: *DENDRO for Windows Program guide*. ARCUS report 500. Sheffield: University of Sheffield.
- Vaganov, E. A., Hughes, M. K., Kirdyanov, A. V., Schweingruber, F. H., and Silkin, P. P., 1999: Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature*, 400: 149–151.
- Vibe, C., 1967: Arctic animals in relation to climatic fluctuations. *Meddelelser om Grønland*, 170: 1–227.
- Wilson, J. W., 1964: Annual growth of *Salix arctica* in the High-Arctic. *Annals of Botany*, 28: 71–76.
- Woodcock, H., and Bradley, R. S., 1994: *Salix arctica* (Pall.): Its potential for dendroclimatological studies in the High Arctic. *Dendrochronologia*, 12: 11–22.

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