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Xylem anatomical trait variability provides insight on the climate-growth relationship of *Betula nana* in western Greenland

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A B S T R A C T

Climate change has been reported to affect shrub growth positively at several sites at high northern latitudes, including several arctic environments. The observed growth rates are, however, not uniform in space and time, and the mechanistic drivers of these patterns remain poorly understood. Here we investigated spatio-temporal interactions between climatic conditions, xylem anatomical traits, and annual growth of 21 *Betula nana* L. individuals from western Greenland for the period 2001–2011. Structural equation modeling showed that summer precipitation and winter temperature are affecting annual growth positively. Furthermore, vessel lumen area and vessel grouping, which are related to water conductivity and hydraulic connectivity of the xylem, respectively, positively influenced annual growth. To optimize growth *B. nana* was thus able to adjust its water transporting system. Annual variation in vessel lumen area seemed to be driven mostly by spring and summer temperatures, whereas annual variation in vessel grouping was driven by winter temperature. Linear models did not reveal a pattern in the spatial variation of xylem anatomical traits across the sampled climatic gradient. However, growth was positively correlated with local variation in insolation. Our results suggest that *B. nana* can adjust its hydraulic capacity to annual fluctuations in climatic conditions in order to optimize its total radial stem growth rate.

Introduction

Temperatures in Greenland are increasing (Stendel et al., 2008), whereas precipitation patterns are showing both positive and negative trends (Mernild et al., 2014). Recent studies have demonstrated that arctic shrubs respond to these changes by faster growth and an increased height and/or larger vegetation cover (Myers-Smith et al., 2011; Campioli et al., 2012), although considerable variation has been detected across climatic and environmental gradients (Elmendorf et al., 2012a, 2012b; Tape et al., 2012), as well as among species (Büntgen et al., 2015;

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Myers-Smith et al., 2015; Young et al., 2016). Climatic conditions in the growing season have been shown to strongly affect growth in arctic shrubs (Myers-Smith et al., 2015), while some studies have highlighted the importance of winter conditions as well (Hollesen et al., 2015). To gain further insight into the mechanisms driving different responses, more detailed and species-specific studies focusing on the plasticity of functional traits are needed (Myers-Smith et al., 2011; Schweingruber et al., 2013). More specifically, a deeper understanding of how hydraulic properties of arctic shrubs respond to climatic changes across space and time, and how these possibly affect inter-annual changes in radial stem growth, is still lacking (cf. Fonti et al., 2010; Gärtner-Roer et al., 2013). Species-specific research in other regions of the world has provided interesting insight into the importance of wood anatomical adaptations. In the Mediterranean region, it has been shown that growth and vessel size depend on climatic conditions, with the widest vessels occurring under warm and dry conditions (Olano et al., 2013); a study from the Rocky Mountains revealed that vessel size increases with water availability (von Arx et al., 2012); and a study from the mangroves suggested that wood anatomical adaptations determine the distribution of dominant woody species (Robert et al., 2009). It is known that arctic species differ in their xylem anatomical adaptations, but the plasticity of these traits has not been well studied. This makes it hard to foresee how these species will react to climate change (Gorsuch et al., 2001). A recent study from western Greenland shows that summer temperature has a positive effect on tracheid size in *Juniperus communis* (Lehejcek et al., 2016), but how this affects growth is still unclear. Understanding the capacity of arctic shrubs to modify water uptake and transport in response to changes in abiotic factors and how this affects growth will undoubtedly influence our predictions of future shrub dynamics across the high northern latitudes (Myers-Smith et al., 2011).

Vessels are responsible for long-distance water transport in plants and thus crucial for their survival and growth (Fonti et al., 2010). Vessel size is expected to affect growth positively because the water transporting capacity of vessels increases with their diameter to the fourth power according to Hagen-Poiseuille's law (Hacke and Sperry, 2001). However, wider vessels are more prone to cavitation due to freezing and drought. In wide vessels air bubbles formed by cavitation are generally larger and dissolve much slower, which enhances the risk that they expand and block the entire vessel (Hacke and Sperry, 2001). Variation in early spring temperatures is critical for the formation of vessels as late frost events or drought can destroy newly formed vessels through cavitation (Fonti et al., 2007, 2010). In Greenland, episodic snowmelt events caused by abrupt temperature increase during foehn winds make this a real threat for the integrity of the water-transport system when the temperature drops again. These freeze-thaw events are suggested to become more frequent due to the warming climate (Pedersen et al., 2015) and in response vessel size could be expected to decrease. On the other hand, Greenland has faced a strong overall warming during the past decades (Hanna et al., 2012), which could induce a selection for wider vessels due to the overall decreased risk of freezing. Vessel width is therefore subject to a safety versus hydraulic efficiency trade-off: selective pressures simultaneously favor adaptation to avoid embolisms and to enhance hydraulic efficiency and thus growth and competitive ability during the short arctic growing season (Tyree et al., 1994; Gorsuch et al., 2001; von Arx et al., 2012). Previous investigations have shown that species adapted to efficient water transport are more affected by sudden freezing events whereas species adapted to freezing seem to have a less efficient water transport system (Langan et al., 1997; Boorse et al., 1998). Another xylem anatomical trait related to hydraulic efficiency is the connectivity among vessels, also referred to as vessel grouping in a cross-sectional view (von Arx et al., 2013). Modeling has suggested a positive effect of hydraulic connectivity on water transport efficiency (Loepfe et al., 2007), which in turn may stimulate growth. At the same time a high degree of vessel connectivity could be an advantage because it increases resilience to cavitation by providing alternative routes for water transport if some vessels are cavitated (Carlquist, 1984, 2009). However, drought-induced cavitation caused by air seeding under extreme xylem tension is thought to spread between connected vessels through the inter-vessel pits (Loepfe et al., 2007), suggesting vessel connectivity may be a disadvantage under dry conditions. Hence, higher xylem connectivity is an advantageous strategy to increase hydraulic efficiency, as the water can by-pass cavitated vessels, but at the same time increases the risk of cavitation under dry conditions. *Betula nana* L. growth has been shown to be positively affected by summer precipitation during warm years in areas where drought stress can occur (Li et al., 2016). This effect could be a possible consequence of an increase in vessel grouping when the risk of drought and thereby air seeding decreases. Future warming and changed precipitation patterns will change the amount of snow and meltwater and lead to changes in water availability. Therefore, a better understanding of how and if plants are able to adapt their hydraulic system to changes in water availability is important.

The overall aim of this paper is to investigate the dynamics of xylem anatomy and radial growth variability in response to temperature fluctuations and

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water constraints in *B. nana* (dwarf birch) in western Greenland. This species is a semi-ring porous deciduous shrub widespread across arctic and alpine environments of Eurasia and North America (Hultén and Fries, 1986). Annual growth rates of *B. nana* have been shown to increase under higher summer and winter temperatures (Bret-Harte et al., 2002; Blok et al., 2011; Zamin and Grogan, 2012; Hollesen et al., 2015; Büntgen et al., 2015). Specifically, we address the following questions in both temporal and spatial contexts: (1) How do xylem anatomical traits respond to annual variations in climatic conditions? and (2) How do inter-annual fluctuations in these traits influence the overall annual growth rates? We use structural equation modeling to disentangle the complex causal and temporal relationships between basal area increments, xylem anatomical traits, and key climatic variables. Multiple linear models are utilized to investigate the relationships in climatic space. In this way, we expect to improve our understanding of the ecophysiological adaptability of arctic shrubs and how they will respond to climate change.

Materials and Methods

Study Area and Shrubs Sampling

The study area is located in the Nuuk Fjord in western Greenland (64.18°N, 51.72°W) in the Low Arctic zone (according to the bioclimatic definition of Bliss, 1997). Four sites were sampled along a climatic gradient, ranging from oceanic climate in the western coastal area (site 1) to the more continental conditions further inland (site 4) (Fig. 1). The mean seasonal temperatures at the four climate stations in the study area (Table 1) reflect the temperature gradient between the oceanic and continental climates in the Nuuk Fjord (Taurisano et al., 2004). Total precipitation throughout the growing season (June–August 2010) is 234 mm in Nuuk, 137 mm in Qussuk, and 81 mm in Kapisillit, which is the typical precipitation gradient recorded along the transition from oceanic to continental conditions in the Nuuk Fjord (Taurisano et al., 2004). During the past decades there has been a significant increase in temperature in the study area (Hanna et al., 2012), whereas no significant precipitation change has been observed (Mernild et al., 2014), thus leading to potential water limitation for vegetation growth.

A total of 21 plants sampled in July–August 2013 were used for quantification of wood anatomical traits: two plants from site 1, five plants from site 2, four plants from site 3, and ten plants from site 4. The investigated plants were sampled along oceanic–continental and elevational gradients and provided a representative sample across the two main climatic factors describing these gradients (Fig. 2). At each site, circular plots with a diameter of 10 m (~79 m^2) were distributed along an elevational gradient, and plots were separated by 50 vertical meters. The first plot was established at 10 m a.s.l., and the last one at a maximum elevation of 850 m a.s.l., which caused the uneven sampling among sites as the elevational gradient limited

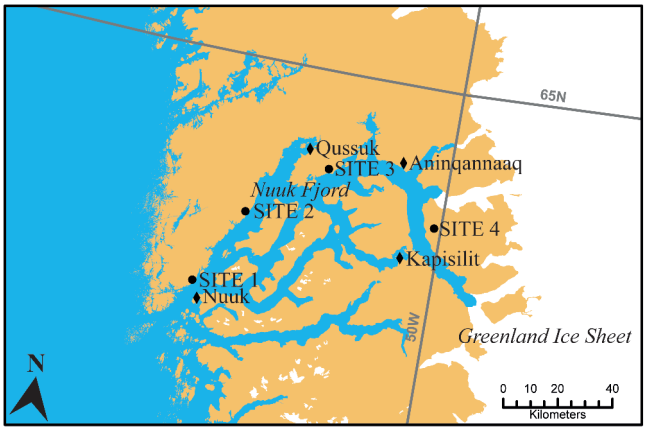


FIGURE 1. Location of the four sampling sites of *B. nana* located along the Nuuk Fjord in western Greenland (64.18°N, 51.72°W) as well as the location of the four climate stations that were used to assess the correlation between monthly variation in climatic conditions at Nuuk and other sites in the Nuuk Fjord.

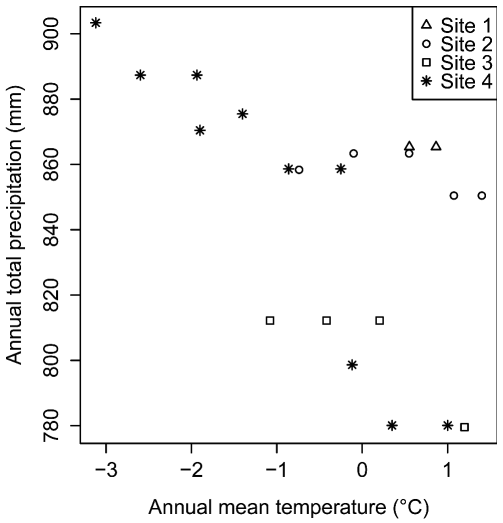


FIGURE 2. The distribution of samples along the two main climatic factors (annual mean temperature and total annual precipitation) describing the oceanic-continental and elevational gradients in the study area. Note that the samples are relatively evenly distributed in climatic space although they are unevenly distributed geographically as indicated by the different symbols for the different sites.

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TABLE 1

Seasonal mean, minimum, and maximum temperatures (°C) at the four climate stations in the Nuuk Fjord illustrating the oceanic-continental gradient in the study area.

	Seasonal mean, minimum, and maximum temperatures, 2008–2009 (°C)			
Climate station	Summer (June–Aug.)	Fall (Sept.–Oct.)	Winter (Nov.–Mar.)	Spring (Apr.–May)
Nuuk	7.1, 1.5, 21.0	1.6, –9.0, 8.6	–7.0, –24.7, 6.3	–0.2, –8.4, 10.6
Qussuk	8.7, 0.6, 21.5	0.4, –15.1, 13.3	–10.4, –34.4, 9.0	–1.9, –14.6, 14.0
Aningannaaq	8.4, 0.1, 19.4	0.1, –15.3, 14.3	–8.2, –25.3, 11.3	–1.5, –15.0, 14.6
Kapisillit	9.2, 1.7, 21.7	1.2, –12.8, 16.4	–8.8, –31.4, 13.2	0.6, –14.5, 13.4

the sampling. An additional plot with a diameter of 2 m (~3 m^2) was established nested within each of these plots. The largest individual in terms of volume occurring in each 79 m^2 plot was collected. In each 3 m^2 circular plot information about elevation, slope inclination, and slope aspect was recorded. The terrain within the larger plots was generally homogeneous. Therefore, the measured plot properties, such as slope inclination and aspect, were assumed to represent the conditions experienced by the collected shrub. Slope inclination and slope aspect were combined to a solar radiation index (SRI), a measure of the insolation received by each plot at summer solstice at solar noon (Keating et al., 2007).

Climatic Variables

Climatological data on average monthly temperature and average monthly precipitation were obtained from WorldClim (2016) (version 1.4) for the period 1960–1990 at a 30 arc-second resolution (Hijmans et al., 2005). To account for within-grid-cell topographic variation in temperature, we adjusted the extracted temperature for each plot by using a standard lapse rate (6.49 °C/1000 m) and the known elevation of the plot in relation to the elevation extracted from WorldClim (2016) (Hijmans et al., 2005) of the grid cell in which the plot is situated. For some plots located near the sea no climatic information was available in WorldClim (2016). For these plots, we used the value of the nearest terrestrial cell.

The fluctuations in monthly mean temperature within each year were calculated based on climate station data from Nuuk (64.18°N, 51.72°W; Danish Meteorological Institute [2016]). This is the only climate station in the Nuuk Fjord for which continuous monthly data is available during the investigated time span (2001–2011). However, temperature data from Nuuk and the other climate stations in the Nuuk Fjord were highly correlated ($r > 0.9$) during the overlapping, but shorter (4–9 years) time spans. Therefore, annual variation in monthly mean temperatures for each plot was estimated by adding the difference between the monthly mean WorldClim temperature (1960–1990) at Nuuk and the monthly mean WorldClim temperature at each plot to the yearly resolved monthly mean temperature DMI data from Nuuk. Similarly, annual variation in total precipitation during the growing season (June–August) was calculated based on WorldClim differences in total precipitation between Nuuk and each plot and monthly DMI data from Nuuk.

The mean monthly data for temperature and precipitation were combined in five climate variables: mean summer temperature (Summer.temp, June–August), mean fall temperature (Fall.temp, September–October), mean winter temperature (Winter.temp, November–March), mean spring temperature (Spring.temp, April–May), and total summer precipitation (Summer.pre, June–August). None of the mutual correlations among variables exceeded ±0.7 when tested for multicollinearity.

Xylem Anatomical Traits

Samples were cut at approximately 1/3 of the height from the base of the plant to ensure that only stem tissue was collected. Thin sections (~20 μm) of entire stem cross sections were produced using a WSL-Lab-microtome (Gärtner et al., 2015). Sections were stained with safranin and astrablue to differentiate between lignified (safranin) and non-lignified (astrablue) parts of the secondary tissues. The microtome sections were then dehydrated by rinsing with alcohol and xylol. Finally, sections were embedded in Canada balsam and oven-dried at 60 °C for about 24 h (Gärtner and Schweingruber, 2013). Digital overlapping micrographs of selected sections were acquired at 40× magnification corresponding to 0.945 pixels·μm^{-1}. The resulting images were stitched together using the software PTGui (PTGui v. 10 ®2000–2015 New House Internet Services B.V., Rotterdam, Netherlands).

Visual cross dating within each stem sample was performed using line measurements of growth ring

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width performed along 2–4 radii in the software ImageJ (Abràmoff et al., 2004). Wedging of the rings was revealed by carefully observing the growth ring boundaries throughout their entire circumference. Cross dating between stem samples was performed by visually matching the growth patterns and by verification of problematic or missing rings in the cross sections. Indications of a few missing rings (2) were found, a feature typically observed in arctic shrubs because of the harsh growing conditions (Buchwal et al., 2013). This gave us the stem age of the sample, hereafter referred to as age. Growth ring widths possibly decrease with age (Bär et al., 2005), vessel size increases with plant height/age (Carrer et al., 2015; Lehejcek et al., 2016), and vessel grouping increases with age (Zhao, 2015). To account for these effects, we (1) measured growth as basal area increment (Bär et al., 2005; Buras and Wilmking, 2014) based on the determination of growth ring boundaries with the image analysis tool ROXAS v1.6 (von Arx and Dietz, 2005; von Arx et al., 2013; developed for Image Pro Plus v6.1, Media Cybernetics, Inc., Silver Spring, Maryland, U.S.A.), (2) removed at least the five innermost growth rings before analyzing the xylem anatomy, as the age trend is most evident there (Fonti et al., 2010), and (3) included age as a variable in the analysis. The oldest sample contained 86 growth rings, while the youngest had 16 growth rings. Sampling was performed in July–August 2013, and the innermost (see above) and outermost growth rings were removed. The latter was done as overlaying bark hindered the analysis of the outermost rings in some samples. This resulted in the study period 2001–2011 covered by all samples.

Based on the analysis of digital images of stem cross sections, two anatomical features were derived for individual growth rings: vessel size and vessel grouping. The ROXAS software automatically determined vessel position, vessel lumen area, and vessel grouping patterns. The lower limit for vessel size recognition was set to 500 μm^2 to ensure all bigger vessels were recognized while avoiding difficulties in distinguishing the smallest vessels from similar-sized fiber cells. Automatic vessel recognition was manually improved before measurement to remove problems with unrecognized vessels and separate merged neighboring vessels because of low contrast in some sections. Growth ring boundaries were manually drawn. For each growth ring the following variables were calculated by ROXAS: (1) Basal Area Increment (BAI, mm^2), henceforth referred to as growth/BAI; (2) Maximum Vessel lumen Area (MVA, μm^2), henceforth referred to as maximum vessel size/MVA; and (3) Vessel Grouping index calculated as mean number of vessels per group (VG; von Arx et al., 2013), henceforth referred to as vessel grouping/VG (Fig. 3). Because of a few missing rings, the 21 shrubs and the study period of 11 years resulted in 229 measurements of each variable.

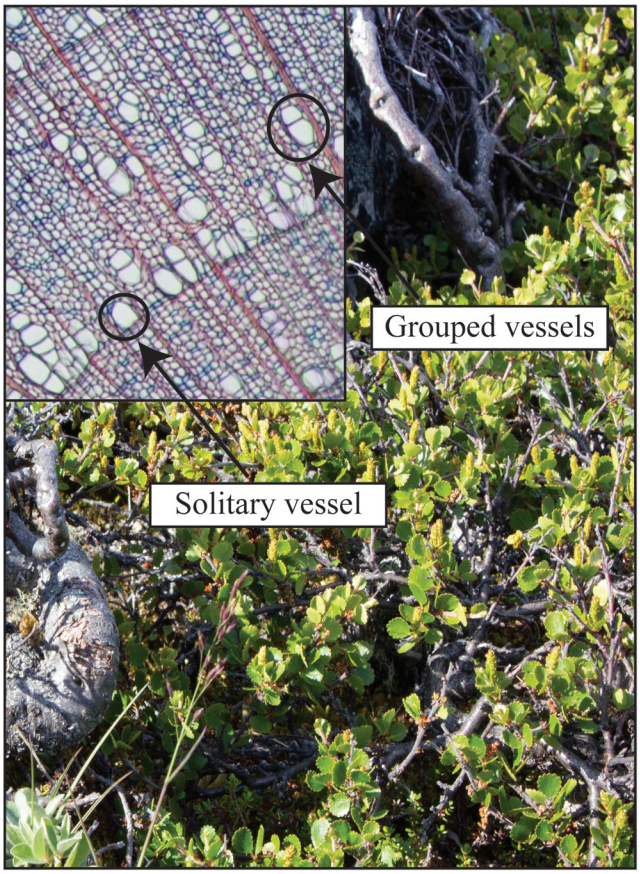


FIGURE 3. ***B. nana*** **growing in the Nuuk area. Inset showing a cross section with grouped and solitary vessels marked.**

Statistical Analysis

Structural equation modeling (SEM) was used to investigate the causal and temporal interactions between MVA, VG, and BAI and how these are affected by climatic conditions and age for the period 2001–2011. In SEM a hypothesis of the causal relationships between the measured variables in a system is fitted to observed data. The main use of SEM is to quantify the possible direct and indirect causal pathways that are most influential on a variable, and whether the influences of different factors on a variable are positive or negative (Grace et al., 2010). The main advantage of using SEM in this study is that it allows multiple variables to interact simultaneously. This makes it possible to test at once for hypothesized interrelationships between climate, xylem anatomical traits, and growth (Alivifar et al., 2012).

We hypothesized that BAI was affected by a number of variables: (1) Summer.temp, (2) Winter.temp, (3) Fall.

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temp, (4) Spring.temp, (5) Summer.pre, (6) Age, (7) MVA, and (8) VG. We hypothesized MVA and VG to be affected by the six first-mentioned variables above. To account for the differences among individual plants caused by local conditions, we included the plant-specific averages of each xylem anatomical trait and growth in the analysis (BAI.mean, MVA.mean, VG.mean); this ensures that the analysis is not driven by the differences between shrubs but by the annual variation. BAI, MVA, and VG were tested for normality. The validity of the model was tested by the comparative fitness index (CFI) and standardized root mean square residual (SRMR). CFI is relatively independent of sample size and ranges between 0 and 1; a CFI value close to 0.95 indicates a good fit (Hu and Bentler, 1999). SRMR evaluates standardized differences between observed and predicted covariance matrices; SRMR below 0.08 indicates a good fit (Hu and Bentler, 1999).

Multiple linear regression (MLR) analysis was used to investigate drivers behind spatial variation in the means of the plant-specific variables estimated across the entire time period from 2001 to 2011 (BAI.mean, MVA.mean, VG.mean). Mean growth (BAI.mean) was regressed against mean maximum vessel size (MVA.mean), mean vessel grouping (VG.mean), solar radiation index (SRI), slope, mean winter temperature (Win.t.mean), and mean total summer precipitation (Sum.p.mean). Mean maximum vessel size (MVA.mean) was regressed against mean summer temperature (Sum.t.mean), mean spring temperature (Spr.t.mean), solar radiation index (SRI), and slope, whereas mean vessel grouping (VG.mean) was regressed against mean winter temperature (Win.t.mean), solar radiation index (SRI), and slope. Due to the low sample size (21 samples) we would risk over-fitting the model if all climatic parameters were included, so we based our selection of climatic parameters in the spatial models on our findings in the temporal model.

All statistical analyses were performed in R (R Core Team, 2015). The package "lavaan" (Rosseel, 2012) was used for SEM with maximum likelihood as an estimator. The package "dplR" was used to investigate the time series of growth and xylem anatomical variables (Bunn, 2008, 2010; Bunn et al., 2017).

Results

Across all growth rings the mean annual growth was 3.2 mm^2 (SD 2.5), the mean maximum vessel size in each growth ring was 1593 μm^2 (SD 1315), the mean vessel grouping in each growth ring 1.4 (SD 0.2), and the mean age 32.2 years (SD 17.1). Visual inspection of the annual variation in the time series for growth, maximum vessel size, and vessel grouping (Fig. 4) revealed a higher similarity within sites than among sites.

The SEM showed a significant positive effect of annual maximum vessel size (p-value < 0.01) and vessel grouping (p-value < 0.01) on annual growth with bigger and more grouped vessels leading to increased growth (Fig. 5). The annual variation of maximum vessel size, vessel grouping, and growth were significantly and positively correlated with the plant specific averages of these variables (p-values < 0.01) (Fig. 5). The SEM showed a positive effect of winter temperature (p-value < 0.05) and summer precipitation (p-value < 0.05) and a negative effect of age (p-value < 0.1) on annual growth. There were positive effects of summer temperature (p-value < 0.01) and fall temperature (p-value < 0.1) and negative effects of spring temperature (p-value < 0.01) and summer precipitation (p-value < 0.1) on maximum vessel size. Finally, there was a positive effect of winter temperature (p-value < 0.1) on vessel grouping. In total, 50.0% of the total variation in BAI, 71.0% of the total variation in MVA, and 66.0% of the total variation in VG were explained. The SEM evaluation gave a SRMR of 0.027 (recommended < 0.08) and a CFI of 0.88 (recommended > 0.95). As a result, we consider the SEM robust (Hu and Bentler, 1999; Ullman, 2006).

The multiple regression models revealed that solar radiation (SRI) had a positive effect (p-value < 0.05) on the overall spatial variation in growth (BAI.mean) ($R^2 = 0.1$) (Table 2), but did not provide an explanation for the spatial variation in maximum vessel size (MVA.mean) or vessel grouping (VG.mean).

Discussion

In this study we explored the links among climate, xylem anatomical features, and spatio-temporal patterns in growth variation in the arctic shrub species *B. nana*. Structural equation modeling revealed how variation in maximum vessel size and vessel grouping possibly positively impacts growth annually and that the variation of xylem anatomical traits is driven by climatic conditions (Fig. 5). Our results suggest that *B. nana* is able to adjust key xylem anatomical traits in response to environmental conditions, which will eventually influence the growth rate.

We found growth to be positively affected by winter temperature and summer precipitation. A similar relationship with summer precipitation has been found for *B. nana* during warm years in Siberia where drought stress occurs (Li et al., 2016). In our study, *B. nana* most likely experiences drought stress in the innermost part of the Nuuk Fjord with the most continental climate, and the positive effect of summer precipitation is there-

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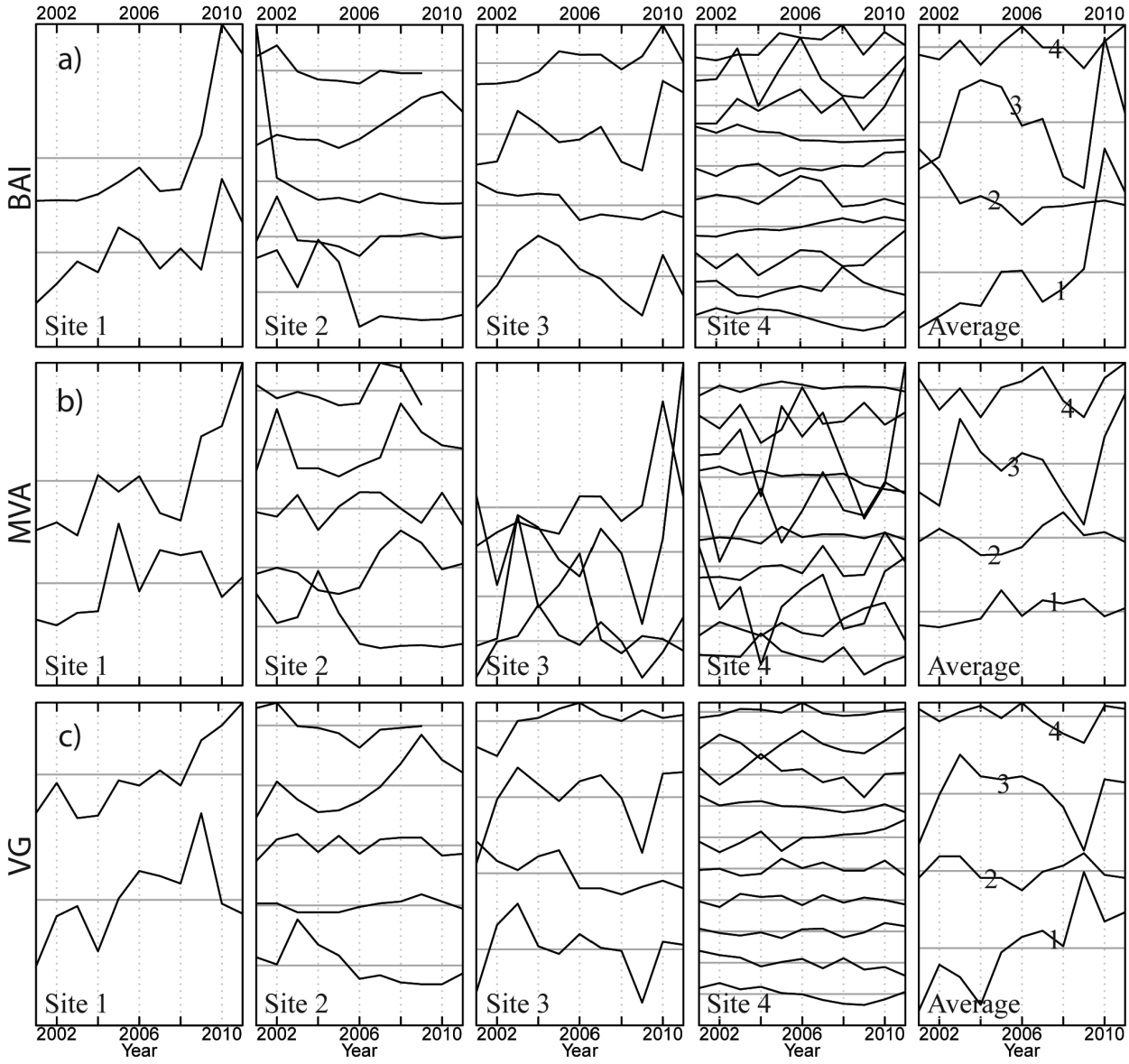


FIGURE 4. The inter-annual variation in (a) growth (basal area increment, BAI), (b) maximum vessel size (MVA), and (c) vessel grouping (VG) in the study period (2001–2011) for each *B. nana* sample within the four sites and the averages for the four sites. No values are shown at the *y*-axes because the aim of this figure is to illustrate patterns, not absolute values.

fore not surprising. Hollesen et al. (2015) likewise documented that growth of *B. nana* is positively influenced by winter temperature in western Greenland. The positive effect of winter temperature may be caused by a possible earlier onset of the growing season or by an increase in the availability of nutrients because of warmer soil temperatures and thereby higher microbial activity (Hollesen et al., 2015). In some arctic areas summer temperature has also been found to have a positive effect on radial growth, while in other areas, for example, western Greenland, no effect or a negative effect has been identified (Myers-Smith et al., 2015). The missing direct effect of summer temperature in our study might be related to either very little increase in summer temperature during the study period or summer temperature in some areas acting indirectly by changing the local moisture regime. Radial growth expressed as basal area increment (BAI) did not show a consistent age trend.

As expected, maximum vessel size was positively related to growth. This is most likely an effect of increased efficiency of the water transport leading to increased growth as pointed out by Olano et al. (2013). We found maximum vessel size to be positively affected by summer temperature in agreement with Lehejcek et al. (2016). A

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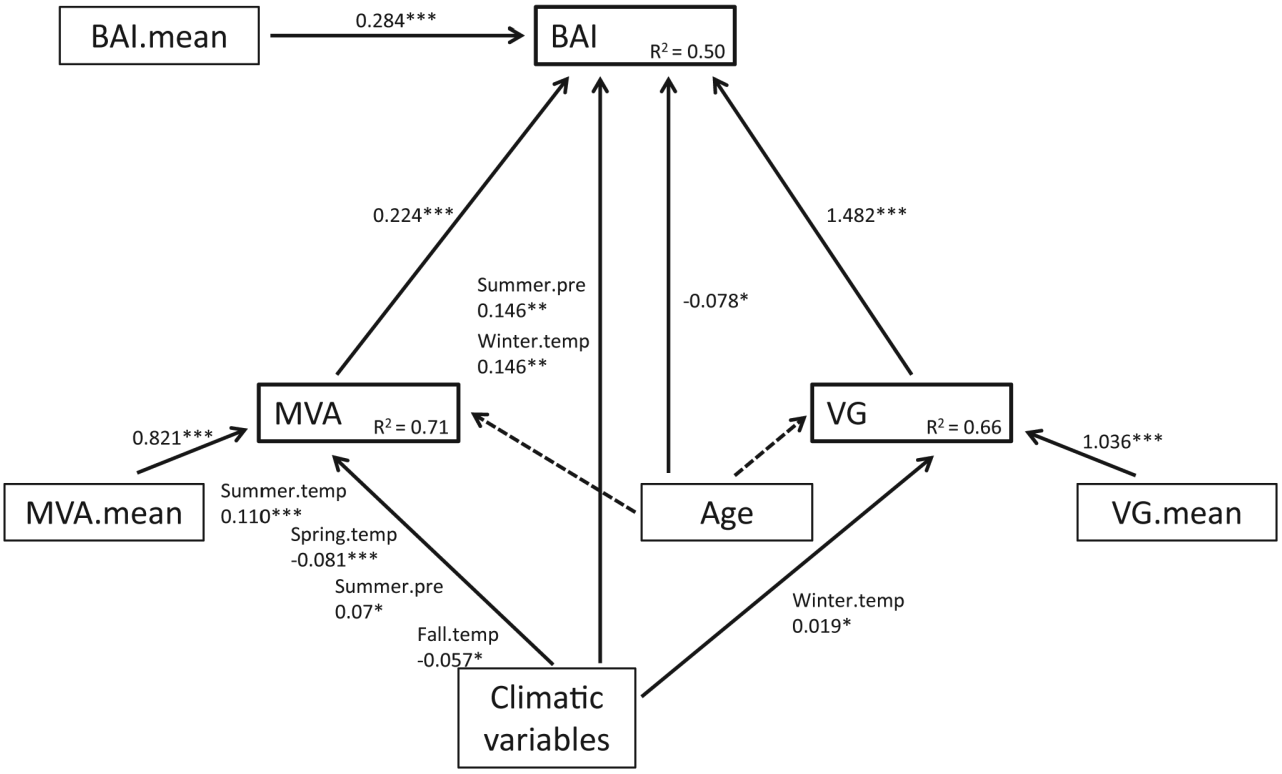


FIGURE 5. Structural equation model describing the interactions between the shrub variables: basal area increment (BAI), maximum vessel size (MVA), vessel grouping (VG), mean values of basal area increment (BAI.mean), maximum vessel size (MVA.mean), vessel grouping (VG.mean), and age of growth ring (Age) and the environmental variables: mean temperature in the four seasons Spring (April–May, Spring.temp), Summer (June–August, Summer.temp), Fall (September–October, Fall.temp), Winter (November–March, Winter.temp), and total summer precipitation (Summer.pre) for the study period 2001–2011. For a better overview only climatic variables with a significant effect in the model are included in the illustration. Model statistics: CFI = 0.88 and SRMR = 0.027. The numbers next to the arrows show standardized regression weights. R^2 is the explained variance for each parameter. *: $p < 0.1$, **: $p < 0.05$, ***: $p < 0.01$.

TABLE 2

Standardized parameter estimates for the linear model for the period 2001–2011 explaining the variation in mean growth (BAI.mean), mean maximum vessel size (MVA.mean), and mean vessel grouping (VG.mean) for each *B. nana* shrub by the explanatory variables mean maximum vessel size (MVA.mean), mean vessel grouping (VG.mean), Age, mean summer temperature (Sum.t.mean), mean spring temperature (Spr.t.mean), mean winter temperature (Win.t.mean), mean total summer precipitation (sum.p.mean), SRI (Solar Radiation Index, a measure of the insolation received by each plot at summer solstice at solar noon), and slope.

	Explanatory variables									
Response	MVA. mean	VG.mean	Age	Sum.t.mean	Win.t.mean	Spr.t.mean	Sum.p.mean	SRI	Slope	Adj. R^2
BAI.mean	–0.01	0.32	–0.01	—	0.24	—	0.11	0.5*	–0.01	0.10
MVA.mean	—	—	0.43	0.80	—	–1.07	—	0.16	–0.06	0
VG.mean	—	—	–0.18	—	–0.01	—	—	0.11	–0.26	0

* = $p < 0.05$.

putative eco-physiological explanation for this could be a decreased risk of freezing when temperatures increase causing a shift of the trade-off between efficiency and safety toward efficiency (Tyree et al., 1994; Gorsuch et al., 2001; von Arx et al., 2012). We hereby also show that summer temperature has an indirect positive effect

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on growth suggesting a mechanism behind the positive relationship between summer temperature and growth found in other studies (Myers-Smith et al., 2015). The causal relationship behind the observed negative effect of spring temperature on maximum vessel size is less obvious, however. It could be because warmer temperatures lead to earlier snow melt and earlier growth in *B. nana* (Borner et al., 2008). This increases the risk of late frost events that can be hazardous to the plant, especially if the vessels are wide (Fonti et al., 2007, 2010). It could also be explained by a shortening of the growing season caused by cold spring temperatures and increased selection for rapid growth performed by wider vessels when the temperatures are finally suitable. The effects of summer precipitation and fall temperature on maximum vessel size are less obvious in our study. The positive effect of summer precipitation could be attributed to the fact that bigger vessels are more prone to air seeding caused by drought due to their bigger inter-vessel pits, which will be selected against under dry conditions (Loepfe et al., 2007). The negative effect of fall temperature on the maximum vessel size could indicate a critical role of temperature for the formation of the resting cambium from where the vessels are formed the following spring. Age had no effect on maximum vessel size, which is most likely because the increasing trend in vessel size during ontogeny usually can be ignored when short time periods are studied, or when plants have reached their maximum height (Carrer et al., 2015).

Vessel grouping also affected annual growth positively as hypothesized because of the increase in conductivity (Loepfe et al., 2007). The variation in vessel grouping could be explained either by more grouped vessels at sites prone to cavitation events as suggested by Carlquist (1984, 2009) or by less grouped vessels in dry years as suggested by Loepfe et al. (2007). The latter could explain the positive effect of summer precipitation on growth in warm years found by Li et al. (2016), which we have also documented. However, we did not find a direct effect of precipitation on vessel grouping. Instead, we found a weak positive effect of winter temperature on vessel grouping, which could be explained in three different ways: (1) warmer winter temperatures may cause reduced snow cover and increase the risk of frost damage, which means that vessel grouping may be an advantage as the water can bypass cavitated vessels and thereby enhance the fitness of the plant (cf. Carlquist, 1984, 2009); (2) warmer winter temperatures lead to increased snowmelt and higher water availability; grouped vessels may be selected for because they are more efficient when the risk of drought-induced embolism is low (cf. Loepfe et al., 2007); or (3) reduced snow cover caused by warmer winter temperatures may lead to drier soils in spring and grouped vessels may be selected for to counteract the negative effects of cavitated vessels (cf. Robert et al., 2009). At the specific scale of this study it should be pointed out that spatial variation in water retention capacity is typically high and therefore caution should be exercised when concluding on causal relationships. Future studies should monitor water availability and other key environmental parameters as experienced by the individual plants.

The SEM also showed significant relationships among the mean values of growth, maximum vessel size, and vessel grouping (BAI.mean, MVA.mean, VG.mean) and their respective annual variables (BAI, MVA, VG). These significant effects reveal that plant-specific differences of growth, maximum vessel size, and vessel grouping are present as expected because the mean values explain some of the annual variation within plants, indicating a difference between plants. To study this variation in space we made linear models of these plant-specific mean values of growth, maximum vessel size, and vessel grouping. Linear models of the spatial variation in mean growth revealed a positive relationship with solar radiation index (SRI), while no patterns in the spatial variation of xylem anatomical traits were found. The lack of relationship among climatic parameters, xylem anatomical characters, and growth in space may be a consequence of the insufficient detail of the climate data. In this study, we combined monthly data from a single climate station with monthly regional means. This does not capture the full monthly, topographic, and oceanic-continental variation throughout the area, nor the microscale variation in temperature caused by, for example, snow cover and shielding. Furthermore, the difference in average, minimum, and maximum temperature during the four seasons between Nuuk and Kapisillit is around 2 °C, suggesting that microscale temperature variation might have greater amplitude than macroscale temperature gradients. Microscale environmental variation can be critical for biomass production (Bär et al., 2008) and survival (Graae et al., 2011) in arctic tundra. We investigated the importance of microclimatic conditions by including proxies for local environmental conditions, for example, solar radiation, and found as earlier mentioned a positive effect of solar radiation on mean growth. Hence, our results show the importance of local conditions for spatial variation in shrub growth. Quite contrary, Meinardus et al. (2011) found that *B. nana* individuals in Norway responded in a similar way to selected macroclimatic variables even though they were growing under different local conditions. In our study the time series of growth measurements showed local synchrony in some years and local asynchrony in

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others (Fig. 4). Studies of *B. glandulosa* also reveal local variation in plant response to macroclimatic conditions. Dumais et al. (2014) recently demonstrated how radial growth of this species depends on elevation, as the complexity of the climate-growth relationships increases with elevation in a study from Canada. Another study from Canada showed that the growth of *B. glandulosa* is driven by different climatic factors that are sensitive to topographic heterogeneity (Ropars et al., 2015). Warmer summer temperatures thus promote growth on terraces and hilltops, whereas winter precipitation promotes growth in snowbeds. Finally, the most recent study of *B. glandulosa* from Canada has revealed that radial growth of roots shows higher sensitivity to macroclimate than stems and consequently that it may be more difficult to find a shared macroclimatic signal when investigating growth based on stems only (Ropars et al, 2017). Similarly, Meinardus et al. (2011) found a shared climatic growth signal in their study of root collars. Because we studied only cross sections from stems, this could thus explain the missing macroclimatic signal in our data.

Conclusion

We have shown that maximum vessel size and vessel grouping are affecting radial growth positively, that they provide a mechanistic explanation for the annual variation in growth, and that the variation in xylem anatomical traits is driven by climatic parameters. This plasticity of the hydraulic system could be a key factor in understanding *B. nana's* response to climate change. More specifically, a plant's capacity for xylem anatomical adjustments may enhance its ability to compete with other species (Meinardus et al., 2011). The main climatic drivers behind temporal variation in growth were winter temperature and summer precipitation, whereas the main drivers behind maximum vessel size were summer temperature and spring temperature. Finally, the main driver behind vessel grouping was winter temperature. This strongly suggests a system of explanatory variables that interact in complex ways. Despite a relatively small sample size and low spatial resolution of the climate data, we found that a surrogate variable for local variation in growing conditions such as solar radiation was better at explaining spatial variation in growth than climate variables measured at the regional level. More studies based on denser sampling and addressing multiple spatial scales will undoubtedly improve our understanding of the causal relationship between climate, anatomical traits, and shrub growth. This is particularly pertinent for our ability to forecast vegetation changes in the vulnerable arctic ecosystem.

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