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No effect of snow on shrub xylem traits: Insights from a snow-manipulation experiment on Disko Island, Greenland

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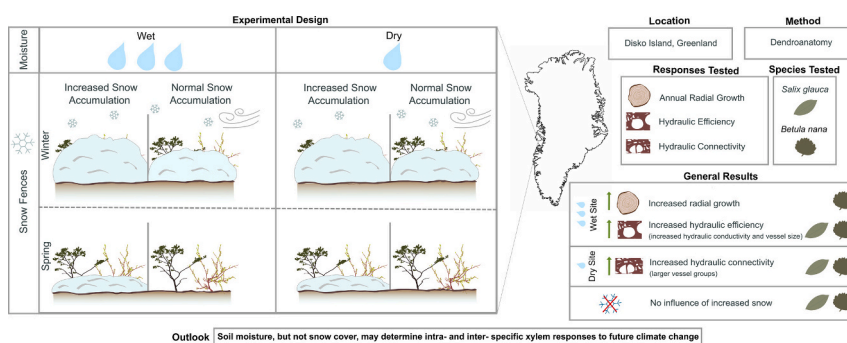
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HIGHLIGHTS

- Using dendroanatomy we assessed how shrub xylem is influenced by snow and moisture.
- No differences were observed in growth or anatomy with small increases in snow.
- Hydraulic efficiency and vessel grouping differed between moisture regimes.
- Radial growth of *Betula nana*, but not *Salix glauca*, was higher at the wet site.
- Soil moisture may drive heterogenous xylem responses to future climate change.

GRAPHICAL ABSTRACT



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ABSTRACT

Widespread shrubification across the Arctic has been generally attributed to increasing air temperatures, but responses vary across species and sites. Wood structures related to the plant hydraulic architecture may respond to local environmental conditions and potentially impact shrub growth, but these relationships remain understudied. Using methods of dendroanatomy, we analysed shrub ring width (RW) and xylem anatomical traits of 80 individuals of *Salix glauca* L. and *Betula nana* L. at a snow manipulation experiment in Western Greenland. We assessed how their responses differed between treatments (increased versus ambient snow depth) and soil moisture regimes (wet and dry). Despite an increase in snow depth due to snow fences (28–39%), neither RW nor anatomical traits in either species showed significant responses to this increase. In contrast, irrespective of the snow treatment, the xylem specific hydraulic conductivity (Ks) and earlywood vessel size (LA95) for the study period were larger in *S. glauca* ($p < 0.1$, $p < 0.01$) and *B. nana* ($p < 0.01$, $p < 0.001$) at the wet than the dry

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site, while both species had larger vessel groups at the dry than the wet site ($p < 0.01$). RW of *B. nana* was higher at the wet site ($p < 0.01$), but no differences were observed for *S. glauca*. Additionally, *B. nana* Ks and LA95 showed different trends over the study period, with decreases observed at the dry site ($p < 0.001$), while for other responses no difference was observed. Our results indicate that, taking into account ontogenetic and allometric trends, hydraulic related xylem traits of both species, along with *B. nana* growth, were influenced by soil moisture. These findings suggest that soil moisture regime, but not snow cover, may determine xylem responses to future climate change and thus add to the heterogeneity of Arctic shrub dynamics, though more long-term species- and site- specific studies are needed.

1. Introduction

Arctic regions at the northernmost limits of woody plants have experienced warming four times that of the global average (AMAP, 2021; Rantanen et al., 2022), leading to widespread increased woody plant productivity including changes in shrub abundance and growth (Büntgen et al., 2015; García Criado et al., 2020; Myers-Smith et al., 2011; Tape et al., 2006). However, responses vary among individuals, species, and sites (Young et al., 2016), with some areas seeing decreases in productivity (Ackerman et al., 2017; Myers-Smith et al., 2015), making it challenging to predict future vegetation patterns, and thus overall Arctic ecosystem functioning. While there has been a general increase of productivity with temperature, recent studies have found a decoupling between growth and temperature; this “divergence problem” has been found in trees (Babst et al., 2019; D’Arrigo et al., 2008) as well as in low-statured Arctic and Alpine shrubs (Francon et al., 2021; Gamm et al., 2018). This suggests a potential shift toward vegetation being limited by other climatic variables (Carrer et al., 2019) or complex micro-site near-surface conditions and dynamics (Dobbert et al., 2021a, 2022; Francon et al., 2020) in a warmer world. Thus, although rising growing season temperatures typically benefit Arctic shrubs (e.g., Boyle et al., 2022; Buchwal et al., 2022), reduced water availability and increased transpiration rates might counteract these advantages (Buchwal et al., 2020; von Arx et al., 2012).

Arctic deciduous shrubs have been found to store insufficient water in their stems than is necessary for potential transpiration, suggesting a reliance on soil moisture, rather than stem storage, to meet transpiration requirements (Clark et al., 2022). Indeed, soil moisture has been identified as a driver of plant productivity (Berner et al., 2020) and shrub growth (Ackerman et al., 2017; Gamm et al., 2018) in the warming Arctic, with water availability potentially determining plant distribution and growth rates at some sites (Ackerman et al., 2017; Buchwal et al., 2020; Davis et al., 2021; Gamm et al., 2018). Plant available water in the Arctic often comes from permafrost, runoff, and snow melt, rather than precipitation, making it localised and challenging to quantify (Westergaard-Nielsen et al., 2017, 2020). Snow-melt water, an important part of the hydrological cycle (Liu et al., 2021), has been found to be used by plants, particularly early in the growing season (Hu et al., 2013; Zhang et al., 2021) and during dry periods (Zhu et al., 2022).

Thus, snow, a prominent feature of the Arctic, may mediate or amplify climate impacts on vegetation (Callaghan et al., 2011; Sturm et al., 2001; Wipf et al., 2009), but the net effect can be difficult to predict. For example, increased snow may positively influence shrubs either directly (e.g., providing protection from frost (Larcher and Siegwolf, 1985; Slatyer et al., 2022)) or indirectly by altering local growing conditions (e.g., increasing soil temperatures (Pattison and Welker, 2014; Sanmiguel-Vallelado et al., 2021), nutrients (Brooks et al., 2011), and water availability (Jespersen et al., 2018)). On the contrary, as snow-melt date may dictate the timing of the growing season for low-lying shrubs (e.g., by influencing access to direct sunlight and near-surface temperatures), increased snow may also shorten the length of the growing season (Assmann et al., 2019; Kelsey et al., 2021; Pedersen et al., 2018; Rixen et al., 2022), and potentially counteract any of the positive influences (Fig. 1). Understanding the effects of snow on shrubs is important as changes in shrubs can further influence the Arctic

ecosystem, for example with larger shrubs increasing snow depth and potentially promoting increased shrubification (e.g., the shrub-snow hypothesis (Sturm et al., 2005, 2001)).

Snow manipulation experiments, such as passive snow fences, can be used to study these potential impacts of snow on vegetation by altering snow-depth and melt timing (Rixen et al., 2022; Wipf and Rixen, 2010). Such experiments provide valuable insights into shrub responses to changes in local growing conditions (Wipf and Rixen, 2010), despite uncertainties related to predicting Arctic precipitation patterns and landscape-scale snow cover (Bintanja et al., 2020; McCrystall et al., 2021; Rixen et al., 2022). However, shrub responses to snow vary, with both negative (e.g., lower live cover (Cooper et al., 2019)) and positive (e.g., increased stem length (Blok et al., 2015)) influences observed on Arctic shrubs across different species, studies, and habitat types (Mörsdorf and Cooper, 2021). Our understanding of the overall effect of changing snow-cover on Arctic shrub dynamics remains limited due to these varying responses, exacerbated by a lack of studies focused on the influence of snow cover on radial growth and the underlying cellular mechanisms (Power et al., 2022).

Quantifying xylem cell traits can establish mechanistic links between radial growth and climatic or environmental factors, as these traits have been demonstrated to adjust to growing conditions and concurrently influence plant growth and survival. The plant water-transport system, in particular, can be influenced by internal (e.g., ontogeny and allometry (Anfodillo et al., 2013; Olson et al., 2020; Zhao, 2015)) as well as external factors (e.g., climate and herbivory (Nielsen et al., 2017; Prendin et al., 2020)). Larger vessels, according to Hagen-Poisuille’s law (Baas and Schweingruber, 1987; Hacke and Sperry, 2001), contribute to greater hydraulic efficiency (Fonti et al., 2010), and thus may potentially lead to increased growth rates (Nielsen et al., 2017). Additionally, the spatial arrangement of these vessels can influence xylem functioning (Martínez-Vilalta et al., 2012); vessels can be grouped together, allowing for transport among conduits (Carquist, 2009; Loepfe et al., 2007). Larger vessels and vessel-groups, while increasing conductance, also pose a higher risk of embolism occurrence and spreading (Loepfe et al., 2007; Tyree et al., 1994), impacting survival during extreme conditions such as drought and freeze-thaw events (Brodribb et al., 2020; Feild and Brodribb, 2001; Gorsuch and Oberbauer, 2002; Mayr et al., 2007; Tyree and Sperry, 1989). Hence, the two critical properties of the overall transport system, conductance and resistance to embolism, tend to favour contrasting traits (Loepfe et al., 2007). Understanding the factors influencing phenotypic plasticity and genetic variability of the hydraulic architecture can offer insights into the mechanisms underlying responses at individual, species, and site-specific levels, especially as temperatures, and the frequency of extreme events, increase across Arctic ecosystems (Gorsuch et al., 2001; Nielsen et al., 2017; Pedersen et al., 2015; Wang and Callaway, 2021).

Here, using methods of dendroanatomy, we analyse responses of two widespread deciduous Arctic shrub species *Salix glauca* L. and *Betula nana* L., in a snow manipulation experiment in Western Greenland. We examine the impact of snow accumulation and soil moisture on radial growth and xylem anatomical traits, focusing on annual ring width and traits related to water transport and hydraulic efficiency (Table 1). Specifically, taking into account allometric and ontogenetic variability, we 1) test the species-specific effects of the snow accumulation

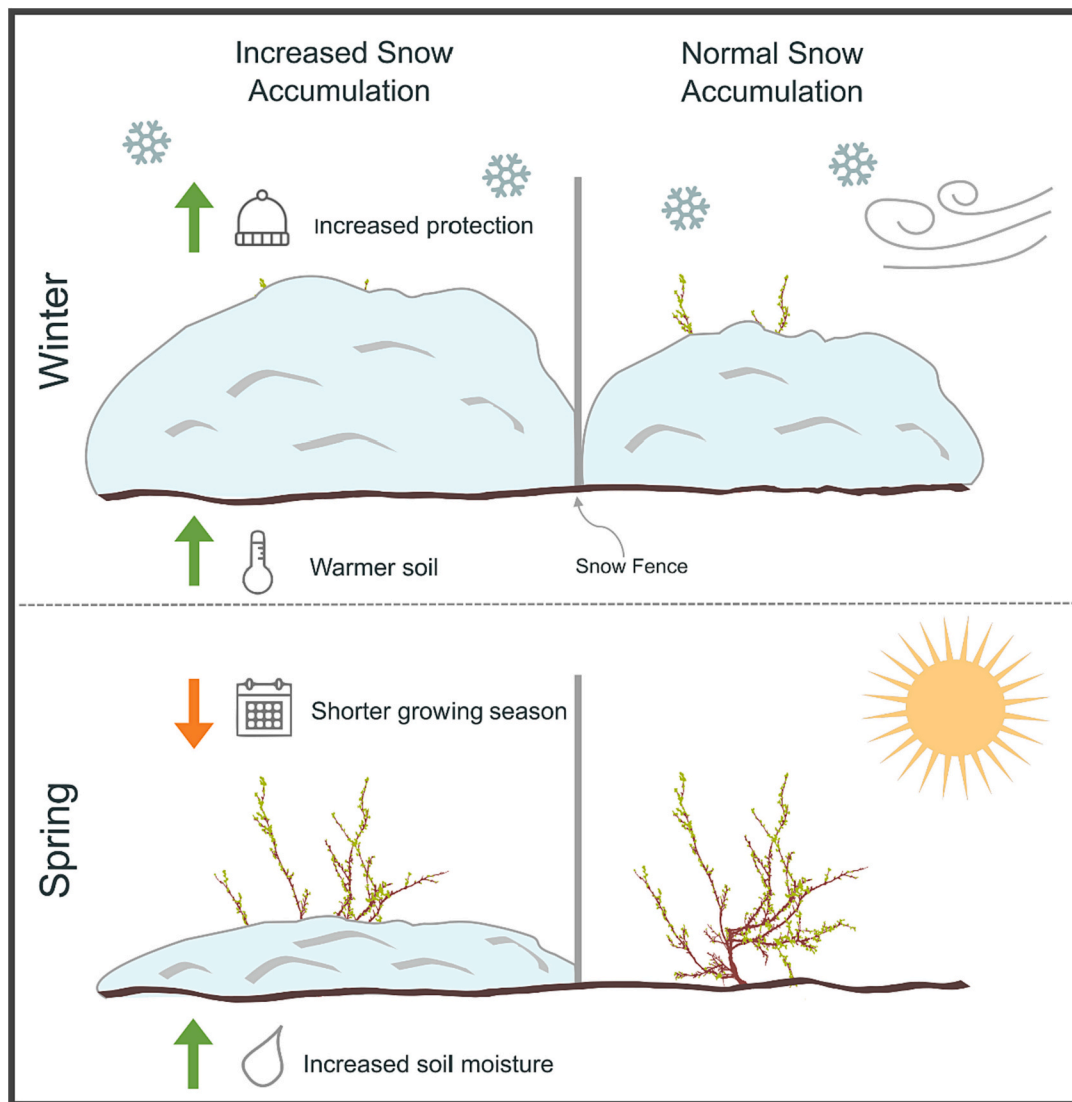


Fig. 1. Schematic of a snow fence in both winter and spring, showing the potential influences of the snow treatment on the growing conditions. Arrows indicate our hypotheses of how each effect may influence shrub growth and anatomy. Green arrows indicate a positive influence (i.e., increased growth and increased hydraulic efficiency) while orange arrow indicates a negative influence (i.e., decreased growth and decreased hydraulic efficiency).

treatment, and 2) test the differences in the shrub responses between the wet and dry site.

We hypothesise, due to increased water availability in the beginning of the growing season and more protection in the winter, annual radial growth and hydraulic efficiency (i.e., hydraulic conductivity and vessel size) and connectivity (i.e., vessel group size) will be greater in the individuals under increased snow accumulation (H1). In addition, we hypothesise, due to the increased water availability and less threat of drought during the growing season, radial growth and hydraulic efficiency and connectivity will be higher in the individuals growing at the wet site compared to the dry site, irrespective of snow treatment (H2).

2. Methods

2.1. Site and experimental design

The study area is located in the transition zone between continuous and discontinuous permafrost in the Blæsedalen valley on Disko Island (Qeqertarsuaq) (69°16'N, 53°27'W), in Greenland (Kalaallit Nunaat). The samples were collected from areas adjacent to snow fences within a snow manipulation experiment established by the Center for Permafrost

(CENPERM) and the Arctic Station, both University of Copenhagen. The experimental setup has 12 fences, each 14.7 m in length and 1.5 m in height, in two distinct vegetation types, approximately 200 m apart: six fences in a well-drained tundra heath (the “dry” site) and six fences in a wetland characterised by grasses (the “wet” site) (Voříšková et al., 2019) (Fig. S1). The vegetation is taller at the wet site (Christiansen et al., 2017), dominated by *Carex* ssp., *Eriophorum angustifolium*, *Paludella squarrosa*, *Tomentypnum nitens*, *Salix arctophila* and *Dryas octopetala* (Voříšková et al., 2019). While the dry site is dominated by a mix of shrubs including *Vaccinium uliginosum* L., *B. nana*, *S. glauca*, *Empetrum nigrum* L., and *Cassiope tetragona* (Lindwall et al., 2016). The soil consists of basaltic rock fragments, with the dry site having a thin (~5–10 cm) organic horizon and the wet site having a thick (~20 cm) peat layer (Voříšková et al., 2019). The permafrost table is lower in the dry site (>3 m below the ground) than at the wet site (~0.5 m below the ground) (Christiansen et al., 2017).

The fences were installed in July 2012 (dry site) and July 2013 (wet site) to allow for accumulation of wind-drifted snow on the lee (“snow”) side of the fence (South) and ambient levels of snow on the windward (“control”) side (Fig. S2).

Table 1

Descriptions of anatomical variables quantified in this study (Anadon-Rosell et al., 2018). Based on high correlations between the quantified variables, we selected the variables in bold for analyses and discussion.

Function	Parameter	Acronym	Units	Reference
Growth	Annual ring width	RW	μm	–
Hydraulic Efficiency	Theoretical xylem-specific hydraulic conductivity	Ks	$\text{m}^2 \text{MPa}^{-1} \text{s}^{-1}$	(Tyree and Ewers, 1991)
	Theoretical hydraulic conductivity	Kh	$\text{m}^3 \text{MPa}^{-1} \text{s}^{-1}$	(Tyree and Ewers, 1991)
	Mean hydraulic diameter	Dh	μm	(Kolb and Sperry, 1999)
	95% percentile of vessel lumen area	LA95	μm^2	(Anadon-Rosell et al., 2018)
Spatial Vessel Distribution	Mean group size of non-solitary vessels	V_M	–	(von Arx et al., 2013)
	Vessel density	CD	no./ mm^2	–
	Vessel grouping index: Mean number of cells per group (including solitary cells)	V _G	–	(Carlquist, 2001)

2.2. Environmental data

2.2.1. Snow

To further assess how the snow fence treatment impacted the growing conditions in general and to characterise the wet and dry site, we utilized the following variables in relation to snow: snow melt date (2013–2020) and spring snow depth (2014–2020). These variables were measured at four fences: three in the dry site and one in the wet site.

Snow depths were estimated from approximately 18,000 photos taken from 2012 to 2020 with Cannon 1000D cameras fixed on tripods. Each of the four fences was photographed three times daily from April to September (Fig. S2). Snow surveyor poles (approximately 160 cm tall with 20 cm increments marked) were installed at the snow and control sides of each fence. Snow depths were then manually estimated from the photos based on the distance between the snow surface and the top of the pole, with a resolution of 0.8 cm of snow depth per pixel (Liu et al., 2023).

For spring snow depth, we defined spring onset day each year as the day following April 1st when daily mean air temperature exceeded 0 °C, recorded at a climate station located within 200 m of the dry site.

2.2.2. Soil temperature and soil moisture

To characterise our study sites and assess the impact of the fences on the local growing conditions, we used daily soil temperature and moisture (measured at the same four fences as the snow data, see above). Soil temperature was measured hourly at a 5 cm depth using TinyTag PB-5001 loggers (Gemini Data Loggers, UK). Soil moisture was measured every 10 min as volumetric water content using Decagon EC-5 sensors (Decagon Devices, USA), giving integrated measurements of the 0–5 cm topsoil. Monthly mean values of soil temperature and moisture from 2013 to 2020 were used for the analyses.

Due to data availability, the time frames of the environmental data differ from those of the shrub responses. However, we used the entire time-series available to provide insight on how the fences influence the growing conditions in general.

2.3. Shrub sampling

The shrubs were sampled in August 2018 (dry site) and August 2020 (wet site). We aimed to collect five individuals of each species on each side of each fence; if fewer than five individuals were present, samples were taken from available individuals. To account for any microsite variation within the sampling plots, we sampled *S. glauca* and *B. nana* individuals growing relatively close to each other, when possible. Collected shrubs of the same species were approximately 2 m apart, where possible, to avoid sampling clonal individuals (Fig. S1 B). To ensure control individuals were not impacted by the fence, we selected those growing at least 2–4 m from the control (North) side of the fence, while snow side individuals were within ~1–2 m from the fence, i.e., within a distance that experienced increased localised snow accumulation.

Using gardening shears, a section of the main stem (at least 25 cm from the tip) of each individual was collected in the field (root collars could not be sampled due to ongoing experiments). The distance from the cut to the tip of the stem, as well as the distance to the fence, the vegetative height, and the stem diameter were measured and recorded for each individual.

In total, 210 shrubs were sampled (60 *S. glauca* at the wet site, 60 *S. glauca* at the dry site, 30 *B. nana* at the wet site, and 60 *B. nana* at the dry site).

2.4. Dendroanatomical analyses

Samples were cut into 12–15 μm thick micro-sections with a rotary microtome (RM2245, Leica, Heidelberg, Germany). Sections were stained with 1 % safranin and 0.5 % astrablue and permanently fixed with Eukitt (BioOptica, Milan), following standard protocols (Gärtner and Schweingruber, 2013; von Arx et al., 2016). Digital images of each section were captured at 100 \times magnification (D-sight, Menarini Diagnostic, Florence, Italy (1.99 pixel/ μm) and Axio Scan Z1, Zeiss, Germany (2.26 pixel/ μm)). From the 210 individuals sampled, we selected a subset of 80 (ten samples per treatment, per moisture regime, per species) to be analysed in this study, based on sample age (minimum age of ten years) and being of high enough quality for conducting the anatomical analyses. This number of replicates is in line with recent shrub dendroanatomical studies (eg., Anadon-Rosell et al., 2018; Ganthaler and Mayr, 2021; Piccinelli et al., 2023).

Growth rings were first measured using Coorecorder (Larsson, 2014), with at least two radii measured for each cross-section, taking care to include wedging rings. Visual crossdating was performed within and between individuals, and the output was statistically checked using COFECHA (Holmes, 1983).

Within each cross-section, we defined a wedge, centered at the pith and with a consistent angle ($\alpha = 60^\circ$), to be analysed using ROXAS v.3.0.548 (von Arx et al., 2013; von Arx and Dietz, 2005). We selected the wedge based on its quality (i.e., avoiding imperfections such as cracks and broken cell walls) and inclusion of as many rings as possible that were present in the sample. Annual rings were manually traced in ROXAS, with reference to the measurements in Coorecorder to ensure inclusion of wedging or missing rings. In total we analysed 1167 radial rings (634 in *S. glauca* and 533 in *B. nana*).

For each growth ring, we quantified the following hydraulic related variables: a) vessel density (CD), b) vessel lumen area at 95 % percentile (LA95), c) vessel grouping (mean group size of grouped vessels per annual ring (V_M), and the mean number of vessels per group, including solitary vessels (V_G)), e) mean hydraulic diameter (Dh), and f) hydraulic conductivity (theoretical hydraulic conductivity (Kh) and theoretical

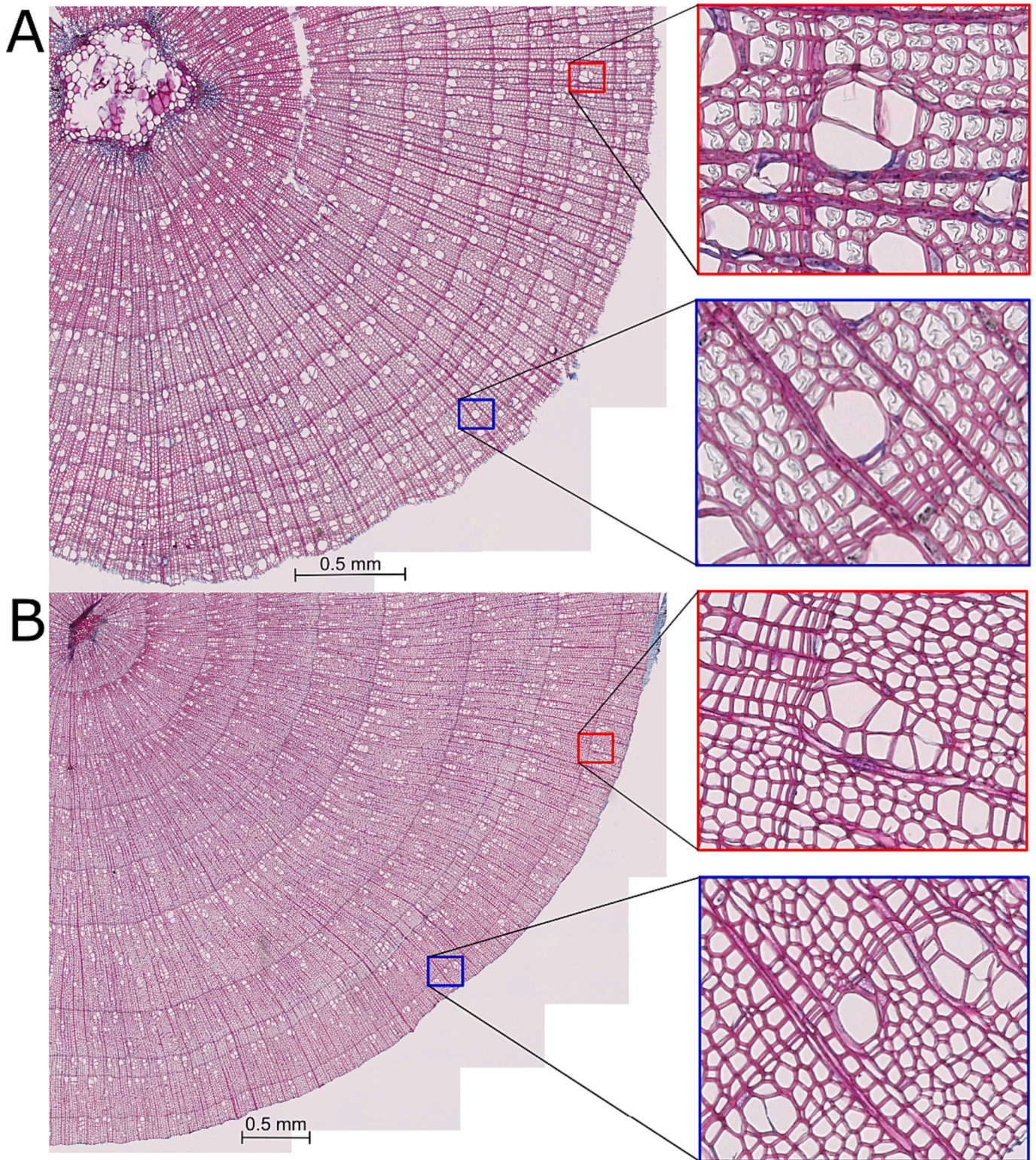


Fig. 2. Cross-sections of A) *Salix glauca* and B) *Betula nana*, both from the wet site. Insets highlight an example of a solitary vessel (in the centre of the blue box) and a vessel group (in the centre of the red box) from each sample.

xylem specific conductivity (K_s) (Table 1). As the variables within each group (grouped by general function) were highly correlated with each other, as well as with RW, we selected a subset of anatomical variables to present: theoretical xylem-specific hydraulic conductivity (K_s) to represent hydraulic conductivity, the largest vessels (LA95) to represent earlywood vessel size, and the mean group size of grouped vessels per

annual ring (V_M) to represent spatial vessel distribution (Anadon-Rosell et al., 2018) (Fig. 2). Correlations between RW and the quantified hydraulic related variables are shown in Fig. S3. In total we analysed 49,866 vessels (28,823 in *S. glauca* and 21,043 in *B. nana*). The entire quantified ring width and anatomical time-series covered the period 1991–2019 for *S. glauca* (wet site: 1991–2019, dry site: 1991–2017) and

1998–2019 for *B. nana* (wet site: 1998–2019, dry site: 2003–2017) (Fig. S4).

2.5. Statistical analyses

To assess the differences in growing conditions (soil moisture, soil temperature, snow depth, and snow melt date) between the treatments within each site and between the sites, we performed paired wilcox tests using the “compare_means” function in the ggpubr package (Kassambara, 2023).

To investigate the effects of treatment and site on radial growth and anatomical traits, we first accounted for ontogenetic trends (Carrer et al., 2015) by calculating the residuals of each response variable in relation to cambial age. The residuals were calculated using the tune package (Kuhn, 2023) within the tidymodels meta-package (Kuhn and Wickham, 2020), fitted with a natural cubic spline using the “ns” function in the splines package (R Core Team, 2022). To determine the most reasonable number of degrees of freedom to use in the spline, we divided the dataset into a training set (75 % of the dataset) and a test set (25 % of the dataset). A hyperparameter grid ranging from 2 to 18 degrees of freedom, in intervals of 2, was used to evaluate nine alternatives. We then used a random tenfold cross validation within the training set to select the best model based on the root mean square error (Kuhn and Johnson, 2018). Once the best hyperparameter of the degrees of freedom was selected, we trained the model with this number of degrees of freedom. This process was followed for each response variable and species separately for years with a minimum of five individuals per species (across all sites and treatments). Although age-related trends were not prominent for all variables, for consistency we used the residuals as the response variables for all models (Fig. S5).

To examine the effect of the snow treatment and moisture (site), we employed linear mixed effects models. All models were fit using the “lme” function from the nlme package (Pinheiro et al., 2022; Pinheiro and Bates, 2000). In each model, individual ID was used as a random effect to account for individual differences and dependencies within measurements. Using the measured distance of the wood cut to the tip of the stem, we reconstructed the retrospective distance to the stem apex for each year, assuming constant rate of primary growth per year. This reconstructed distance was included in all models as a fixed effect to account for allometric trends. We included a residual auto-correlation structure (corAR1) (Pinheiro et al., 2022) to account for temporal dependence of response variables within individuals. Assumptions of normality and homoscedasticity of residuals were visually assessed and accepted for each model (Zuur et al., 2010). We tested each model for collinearity by using Generalized Variance-Inflation Factors (GVIF) in “vif” function in the Car package (Fox and Weisberg, 2019). Marginal and conditional pseudo R^2 for each model was calculated with the function “r.squaredGLMM” in the MuMIn package (Barton, 2023).

See sub-sections below for the fixed effects included in the different models based on our hypotheses (“full_{hyp}”) for the treatment and site analyses, respectively. To test if any observed differences were due to the treatment/site and not due to temporal trends, individual variability, or allometric trends, we performed an ANOVA on each of the full_{hyp} models and two alternative models: 1) the null model, including just the autocorrelation term and the random effect of ID, 2) the null_{dist} model, the same as the null model, but with distance to apex as a fixed effect. We accepted the full_{hyp} model if the ANOVA showed it was significantly ($p < 0.05$) different from each of the alternative models.

Due to differences in shrub ages, sampling year, and fence installation years, the response variables for each species/site combination had varying timeframes: the treatment period (i.e., years after fence installation) was 2013–2017 for the dry site and 2014–2019 for the wet site. To test for treatment effects, we analysed an equal number of years before and after the fence installation (i.e., five and four years before and after the fence installation for the wet and dry sites, respectively). For the site analyses (i.e., examining the influence of moisture regime), only

the common time period between the sites and species (2004–2017) was included.

2.5.1. Treatment models (H1)

To investigate differences in growth and anatomical traits of *B. nana* and *S. glauca* before and after the installation of the snow fences (H1), we fit separate linear mixed effect models for each combination of species, site, and response variable (RW, Ks, LA95, V_M). We created two factor variables: period (years before the fence installation as “pre” and years after as “post”) and treatment (“snow” and “control”). In all full_{hyp} models, the distance to apex and an interaction between treatment and period were included as fixed effects.

2.5.2. Site models (H2)

To investigate the effect of site (wet versus dry) on radial growth and xylem traits (H2), we fit linear mixed effect models for each species and each of the four response variables. In all full_{hyp} models we included the distance to apex and an interaction between site and year. A random effect of treatment, along with ID, was first included to account for variation among individuals growing on the different sides of the fence, whether this variation was due to the treatment or due to unexplained variation between the plots. However, as the inclusion of this factor did not change the results, and the models with and without treatment as a random effect were not significantly different ($p > 0.05$), we present the models with ID as the only random effect.

2.5.3. Post-hoc comparisons

We performed post-hoc tests on the estimates from the full_{hyp} models to determine significant differences between factors (treatments and sites) using the “emmeans” and “pairs” functions from the emmeans package (Lenth, 2023). For the treatment models (H1), we compared the mean of each of the responses before and after the fence establishment at the control and treatment plots, respectively. Contrasting significance between treatment and control sides (i.e., a significant difference on one side of the fence, but not on the other) would suggest an effect of the treatment. For the site models (H2), we compared both the mean response and the change in response (i.e., slope), between the sites. While differences in means would indicate an overall difference between the sites, a difference in slopes suggests a difference in the trend over our study period.

All the analyses were performed in R version 4.2.1 (R Core Team, 2022).

3. Results

3.1. Snow depth effect (H1)

As expected, the fences increased snow accumulation and delayed snow melt at the snow plots (Table 2). Snow plots had on average an

Table 2

Average monthly values (± 1 S.E.) of the environmental variables quantified from 2013 to 2020 for each treatment (control = ambient and snow = increased snow) and site. Units: soil moisture – decimal volume %, soil temperature – temperature degree days over 0 °C, snow depth – cm, snowmelt date – day of year.

	Wet ($n = 1$ fence)		Dry ($n = 3$ fences)	
	Control	Snow	Control	Snow
Avg. Soil Temp	57.9 (± 14.4)	67.0 (± 12.8)	66.9 (± 6.7)	64.9 (± 6.5)
Avg. Soil Moisture	0.272 (± 0.026)	0.273 (± 0.021)	0.091 (± 0.0039)	0.098 (± 0.0051)
Avg. Snow Depth	67.1 (± 1.13)	85.9 (± 0.95)	54.2 (± 1.04)	72.3 (± 0.85)
Avg. Snow Melt Date	156.2 (± 1.69)	160.3 (± 1.42)	153.8 (± 0.92)	158.4 (± 0.85)

increase in snow depth of 21.1 cm (39 %) (3.1–44.4 cm) at the dry site and 18.8 cm (28 %) (-2.8 [i.e., the control had 2.8 cm more snow than the treatment] – 31.1 cm) at the wet site (Figs. S6, S7). Snowmelt was delayed by an average of 5 days per year (2–9 days) at the dry site and 4.6 days per year (1–9 days) at the wet site. Despite this, we did not find a significant effect of the snow fences on the average monthly soil moisture or temperature (Figs. S6, S7).

Contrary to our hypotheses, we did not detect any significant ($p < 0.05$) influence of the snow treatment on RW, Ks, LA95, or V_M for either species (Figs. 3, 4, Table 3). The full_{hyp} model did not significantly differ from the null model for eight of the 16 models, and did not differ from the null_{dist} model for 12 of the 16 models, indicating minimal evidence of any effect of the snow treatment, once taking into account temporal, ontogenetic, allometric, and individual related variation. Detailed outputs can be found in Tables S1, S2, and S3.

Furthermore, post-hoc comparisons confirm this lack of significant difference in xylem traits before and after the fence installation (Fig. 4, Table S3). While Ks and LA95 for *S. glauca* at the wet site and RW and LA95 for *B. nana* at the dry site showed differences before and after the fences were installed, these differences were observed on both the control and snow sides, indicating they were not due to the snow treatment. In addition, the RW of *S. glauca* and V_M of *B. nana*, both at the dry site, showed significant differences at the control and snow sides of the fences, respectively. However, neither of these models are significantly different from their respective null models ($p > 0.1$), suggesting this difference is not due to the treatment.

3.2. Site effect (H2)

As expected, average monthly soil moisture was higher at the wet site

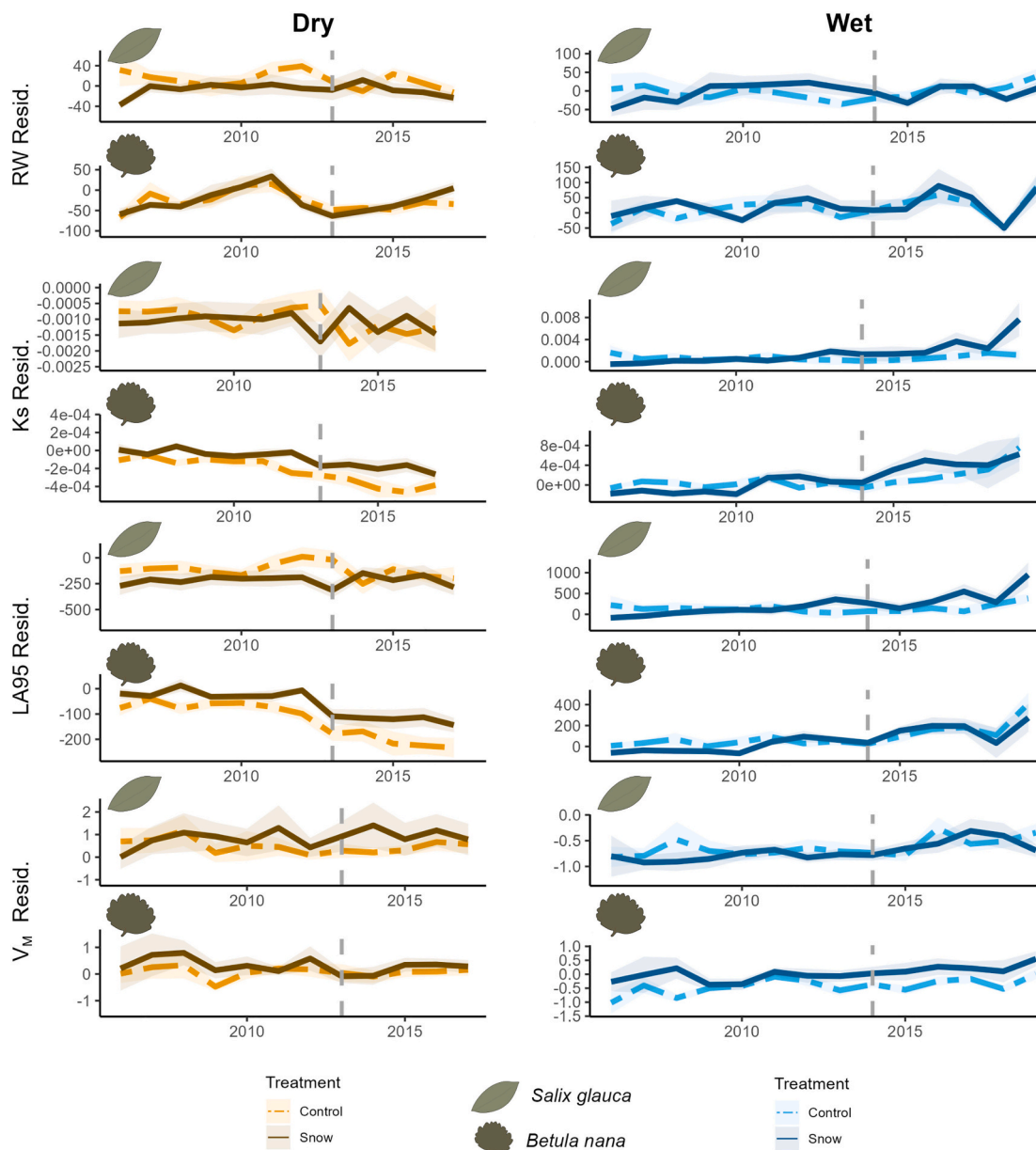


Fig. 3. Time-series of mean response variables (as residuals based on cambial age), separated by species and site. The vertical gray dashed lines represent the installation of the snowfences. The darker, solid lines represent responses of shrubs growing on the lee side of the fence that experienced increased snow accumulation after the installation of the snow fence (“snow”). The lighter, dashed lines represent responses of shrubs growing on the control side of the fence that experienced ambient snow depths both before and after the installation of the fence (“control”). Coloured ribbons show the standard error. Note the differences in the y-axis scales.

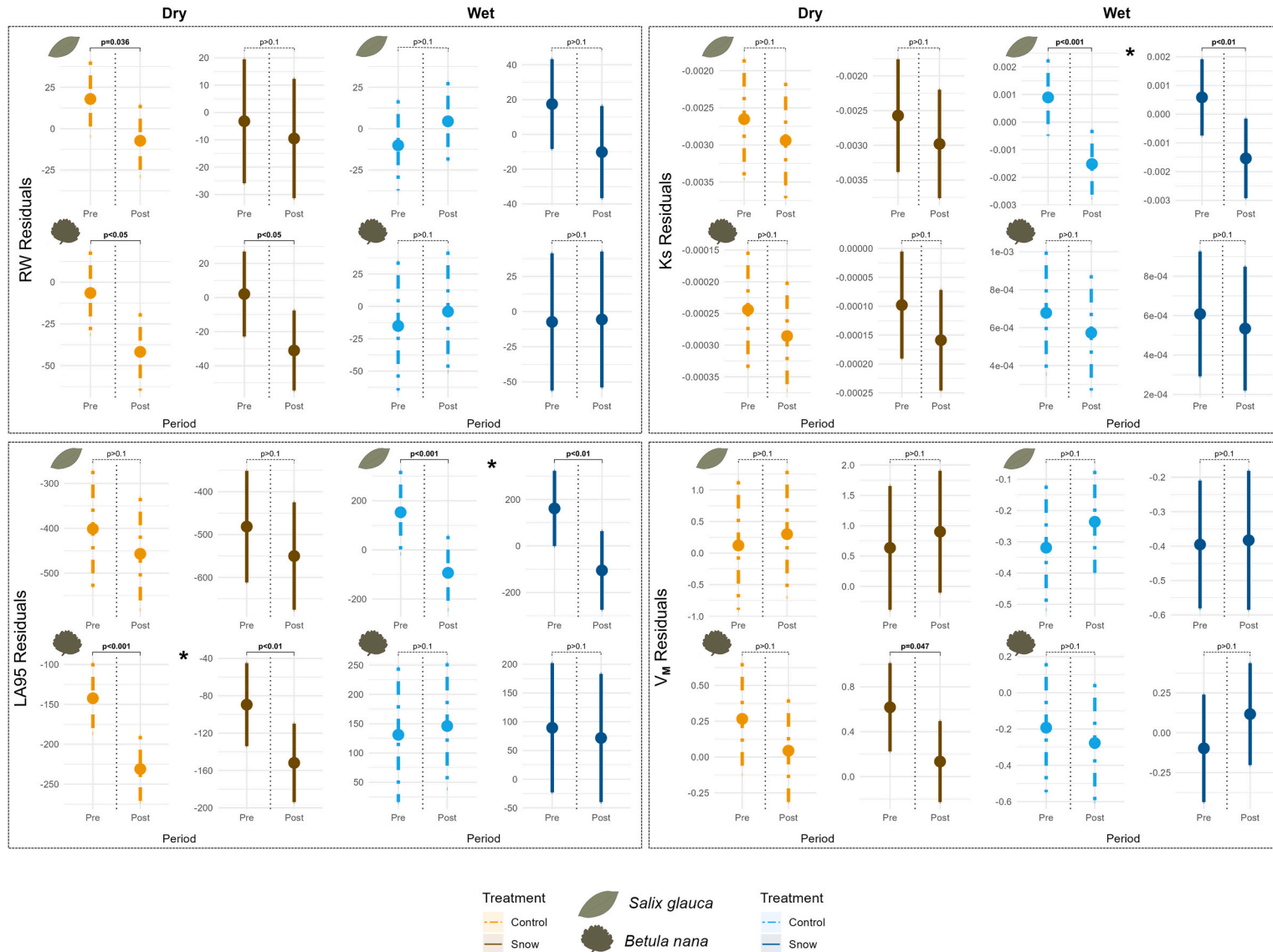


Fig. 4. Estimated responses for each species (*Salix glauca* and *Betula nana*) and site (wet and dry) combination before and after the installation of the snow fence (dotted gray vertical line). Dashed lines represent shrubs with ambient snow levels in the “post”-snow fence period (“control”), while solid lines represent shrubs with increased snow accumulation in the “post”-snow fence period (“snow”). Both “control” and “snow” shrubs experienced ambient snow levels during the “pre”-snow fence period. Values represent estimated means and standard errors based on lme models, accounting for ontogenetic and allometric trends, autocorrelation, and individual differences. P-values are from post-hoc comparisons, with $p > 0.05$ indicating no significant difference in response variables before and after fence installation. Significant models are denoted with “*”, while the rest of the models do not significantly differ from the null models.

compared to the dry site ($p < 0.001$), while soil temperature did not significantly differ ($p = 0.28$) (Fig. S8). Spring snow depth was also greater at the wet site ($p < 0.05$), while spring snow melt date did not significantly differ ($p = 0.82$).

As we did not find evidence of an effect of the snow treatment, we performed the site analyses with both treatments combined. Overall, we found greater influence of site than treatment; seven of the eight models significantly differed from both the null and null_{dist} models. Detailed outputs can be found in Tables S4, S5, and S6.

3.2.1. Mean hydraulic efficiency higher at wet site for both species, while RW only greater for *B. nana*

Ks was significantly higher at the wet site for *B. nana* ($p < 0.01$) and marginally higher for *S. glauca* ($p = 0.094$) for the study period overall (Fig. 5, Table S6). LA95 was higher at the wet site for both species ($p < 0.01$), and mean V_M was significantly higher at the dry site for both species ($p < 0.01$). Mean RW for *B. nana* was greater at the wet site than at the dry site ($p < 0.01$), while no difference was observed in *S. glauca* RW between the sites ($p > 0.1$) (Table S6).

3.2.2. No difference in growth trends observed between sites, but negative trends in hydraulic efficiency in *B. nana* at the dry site

In addition to mean differences, post-hoc analyses revealed differing site-specific trends (i.e., slopes) over the common 13-year period (2004–2017) (Figs. 6, S9). Trends in RW of *B. nana* and *S. glauca* did not significantly differ between the sites ($p > 0.1$). However, the trends in Ks and LA95 of *B. nana* differed, with the dry site exhibiting a negative trend compared to the wet site ($p < 0.001$). Meanwhile, no significant differences in trends of Ks or LA95 were found for *S. glauca* or for V_M for either species.

4. Discussion

Contrary to hypothesis one, we did not observe a significant effect of the snow treatment on any response variables for either species at either site. In support of hypothesis two, we found significantly different responses between the wet and dry sites. However, these responses varied among the traits and species analysed. Notably, both species exhibited higher LA95 and Ks at the wet site, while V_M was higher at the dry site. Only Ks and LA95 in *B. nana* showed differences in adjustments over time, with positive trends observed at the wet site and negative at the dry site. Additionally, RW was greater at the wet site for *B. nana*, but *S. glauca* RW showed no differences between the sites. Our results, therefore, indicate an influence of soil moisture – rather than snow – on xylem anatomy. Anatomical traits showed increased hydraulic efficiency at the wet site, corresponding with increased RW in *B. nana* but not *S. glauca*.

4.1. No observed influence of snow fence treatment on either shrub species

Although our study had comparable delays in snowmelt (wet: 5 days, dry: 4.6 days) to other snow fence studies, the increase in snow depth (wet: 17 cm, dry: 21 cm) was lower than the average reported in Arctic and alpine snow fence studies (80 cm) (Rixen et al., 2022). Given the natural variability in snow depths and melt dates for Arctic shrubs, this small increase may not have been sufficient to induce significant changes in above ground shrub xylem responses (Mallik et al., 2011; Rixen et al., 2022). Our results, then, suggest that *S. glauca* and *B. nana* growing at our study site are currently exposed to wide variations in snow-cover, potentially indicating a level of resistance to changes in snow patterns due to continued climate change (Gehrmann et al., 2020; Rixen et al., 2022).

Further explanation for this apparent resistance to the snow treatment may be attributed to the complex and multi-faceted effects of increased snow cover, which may affect plants in various and potentially opposing ways (Fig. 1). Thus, the overall impact relies on the balance

Table 3 Summary of sample size, ages, growth (RW) and anatomical traits (Ks, LA95, V_M , Vessel Lumen Diameter (VL)) of analysed shrubs for each species (BN – *Betula nana*, SG – *Salix glauca*), treatment, and site (Table 1) for the entire available timeframes. VL was derived from LA95. Note these ages reflect that of the organ sampled, not the actual age of the shrub, since the main stem, not the root collar, was collected. Values represent mean (± 1 S.E.). Units are as follows: Age – years, RW – μm , Ks – $\text{m}^2 \text{MPa}^{-1} \text{s}^{-1}$, LA95 – μm^2 , V_M – number of cells, VL – μm .

Species	Wet						Dry					
	Control			Snow			Control			Snow		
	BN	SG	n	BN	SG	n	BN	SG	n	BN	SG	n
# of Samples	10	10	10	10	10	10	10	10	10	10	10	10
Avg. Age	13.6 \pm 0.2	15.7 \pm 0.5	13.8 \pm 0.4	12.6 \pm 0.2	11.7 \pm 0.2	11.1 \pm 0.1	17.0 \pm 0.4	11.1 \pm 0.1	11.1 \pm 0.1	11.1 \pm 0.1	16.1 \pm 0.3	21
Max. Age	17	29	22	16	15	13	27	27	13	13	21	21
Avg. RW	142.2 \pm 7.0	92.1 \pm 6.3	151.3 \pm 10.0	94.6 \pm 6.3	99.3 \pm 6.1	103.8 \pm 5.6	91.6 \pm 4.6	91.6 \pm 4.6	103.8 \pm 5.6	103.8 \pm 5.6	81.8 \pm 4.5	81.8 \pm 4.5
Avg. Ks	6.6 $\times 10^{-4}$ \pm 5.5 $\times 10^{-5}$	4.3 $\times 10^{-3}$ \pm 2.7 $\times 10^{-4}$	6.5 $\times 10^{-4}$ \pm 6.5 $\times 10^{-5}$	4.8 $\times 10^{-3}$ \pm 4.2 $\times 10^{-4}$	2.6 $\times 10^{-4}$ \pm 1.7 $\times 10^{-5}$	2.7 $\times 10^{-3}$ \pm 1.3 $\times 10^{-4}$	2.6 $\times 10^{-4}$ \pm 1.7 $\times 10^{-5}$	2.7 $\times 10^{-3}$ \pm 1.3 $\times 10^{-4}$	3.6 $\times 10^{-4}$ \pm 2.1 $\times 10^{-5}$	3.6 $\times 10^{-4}$ \pm 2.1 $\times 10^{-5}$	2.6 $\times 10^{-3}$ \pm 1.3 $\times 10^{-4}$	2.6 $\times 10^{-3}$ \pm 1.3 $\times 10^{-4}$
Avg. LA95	456.4 \pm 23.8	877.7 \pm 42.3	450.4 \pm 24.8	934.3 \pm 49.9	206.0 \pm 7.7	605.0 \pm 22.5	254.6 \pm 10.1	605.0 \pm 22.5	254.6 \pm 10.1	254.6 \pm 10.1	521.5 \pm 19.5	521.5 \pm 19.5
Avg. V_M (± 1 S.E.)	2.7 \pm 0.0	2.5 \pm 0.0	3.1 \pm 0.1	2.5 \pm 0.0	3.1 \pm 0.1	3.5 \pm 0.1	3.5 \pm 0.1	3.1 \pm 0.1	3.4 \pm 0.1	3.4 \pm 0.1	3.8 \pm 0.2	3.8 \pm 0.2
Avg. VL	24.1 \pm 0.6	33.4 \pm 0.9	23.9 \pm 0.6	34.5 \pm 0.9	16.2 \pm 0.3	27.8 \pm 0.6	16.2 \pm 0.3	27.8 \pm 0.6	18.0 \pm 0.4	18.0 \pm 0.4	25.8 \pm 0.5	25.8 \pm 0.5

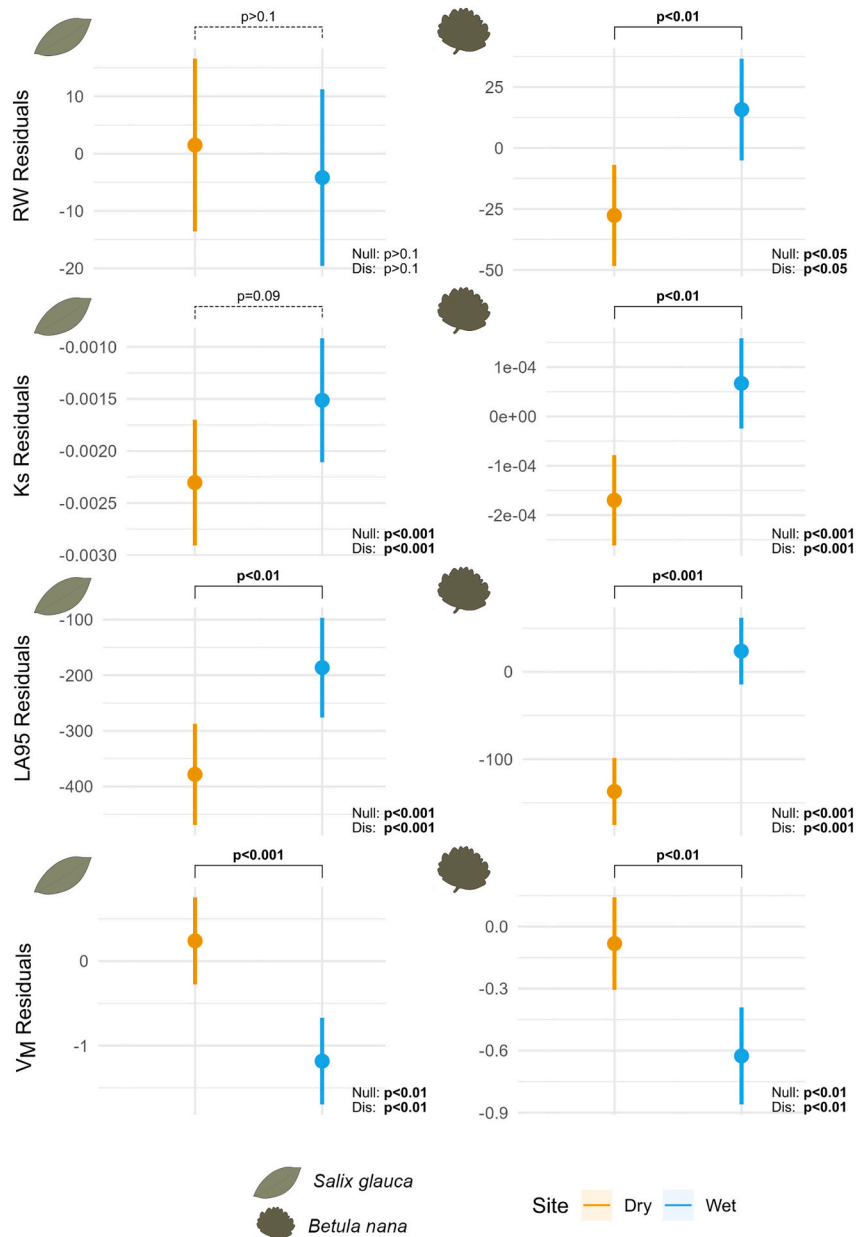


Fig. 5. Differences in estimated responses between study sites for each species. Values represent estimated means and standard errors based on lme models, accounting for ontogenetic trends, autocorrelation, and individual differences. P-values are from post-hoc comparisons, with $p > 0.05$ indicating no significant difference in mean response variables between the sites. Other variable outputs, including site-year interactions, are not displayed here and can be found in Table S4. Note the varying y-axis scales. P-values in the bottom right corner of each panel represent if the model is significantly different from the Null (only including the random structure) and Null_{dist} (same as Null but with distance to apex as a fixed effect). Note the varying y-axis scales.

between the positive and negative effects of this increased snow (Cooper et al., 2019); for example, any potential benefits of warmer soil may be negated by a shortened growing season, as delayed snow melt may also delay onset of xylogenesis (Vaganov et al., 2005). Moreover, unaccounted site-specific characteristics may have counteracted any effect of the increased snow, possibly explaining the lack of differences in the measured soil characteristics. For instance, the melt water from increased snow may not have been retained in the soil due to the slope, or, any impact may have been offset by a naturally occurring nearby snow drift supplying meltwater to both the snow and control sides of the fences.

Lastly, while our analyses focused on four xylem responses, other aspects of shrub growth and development - such as phenology, primary growth, leaf and root traits, and other anatomical characteristics - may

exhibit responses not captured in our study (e.g., Assmann et al., 2019; Blok et al., 2015; Christiansen et al., 2018; von Arx et al., 2012). Additionally, the hydraulic architecture may vary within individuals across different parts of the shrub; thus, the analysed section may not necessarily represent the plant's overall hydraulic architecture (Meinzer et al., 2010).

In our analyses, the random effect of individual shrub explained much of the variation, compared to the treatment or site effects (Table S1, S4). This highlights the wide range of variability between individuals perhaps related to intrinsic intra-specific differences (e.g., genetic (Pfenninger et al., 2021)) or individual adjustments to micro-site conditions not accounted for within each site (Dobbert et al., 2021a). This high amount of inter-individual variation is not atypical for dendrochronological-based studies, as wood formation in each

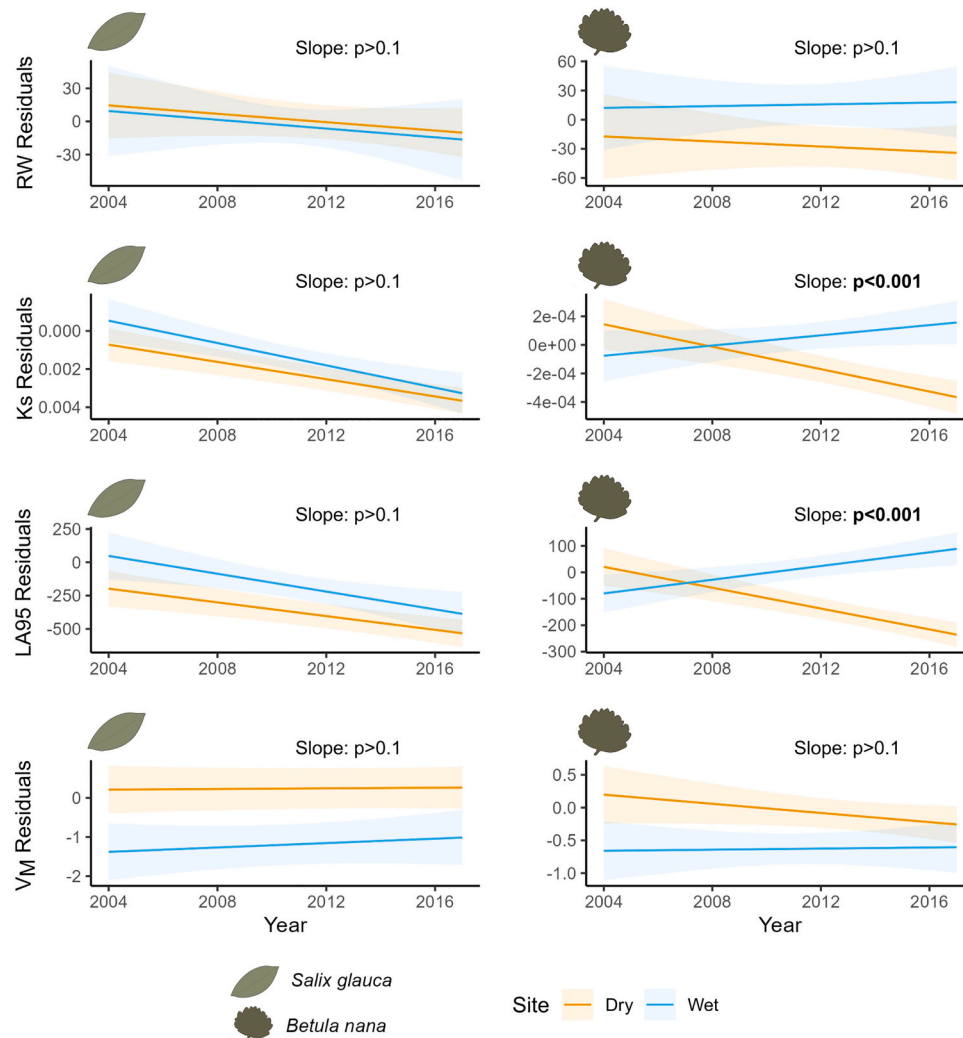


Fig. 6. Differences in trends, represented as linear relationships, of estimated responses between study sites for each species from 2004 to 2017. Plots are based on models for each response variable and species combination. P-values represent significance of differences in slope between the sites, based on post-hoc comparisons. Significance of explanatory variables, including interaction between site and year, are not shown, and can be found in Table S4. Note the varying y-axis scales.

individual is based on a multitude of unique intrinsic and extrinsic variables (Trouillier et al., 2018). However, this high level of variation may have obscured some patterns related to the treatment in our data.

While our study has not found a response to the increases of snow in our experiment, other studies have found snow to be an important driver of shrub growth, for example being identified as the key driver of radial growth of *Juniperus communis* L. in the Alps (Carrer et al., 2019) and that of *Salix alaxensis* in Western Canadian Arctic (Zalatan and Gajewski, 2006). However, the influence of snow on shrubs is complex, as it involves many co-varying factors and potential feedback mechanisms. For example, radial growth of *Vaccinium myrtillus* L., also in the Alps, was greater at sites with late snowmelt, but only in years with cold summers (Rixen et al., 2010). Therefore, future studies incorporating different snow treatments (e.g., manual snow addition and removal) and assessing a broader range of environmental conditions and shrub traits over an extended period could provide further insights into the effects of changing snow depths. This would help clarify if the observed lack of shrub responses in our study was due to the specific conditions at our study site or due to xylem in our study species being resilient against relatively small changes in snow cover.

4.2. Drought-related stress and freeze-thaw cycles may play a role in vessel size and grouping

As there may be a trade-off between efficiency (i.e., water and nutrient transport) and safety in the xylem hydraulic architecture (Prendin et al., 2018; Tyree et al., 1994), phenotypic plasticity may enable shrubs to adjust their anatomical features to better cope with changing growing conditions (Anderegg, 2015). At the wet site, where drought-related stress is less likely, the larger vessels promote enhanced water and nutrient transport, while conversely, the smaller vessels at the dry site enhance resistance to cavitation during dry periods (Jacobsen et al., 2005; Liu et al., 2019). Thus, the smaller vessels in each species at the dry site may be interpreted as a response to cope with extreme conditions (Gorsuch et al., 2001). Additionally, the larger V_M at the dry site may provide alternative pathways in times of drought, so nutrient and water transport may continue even if some vessels experience embolisms (Carlquist, 1984, 2009). As we observed greater vessel groups overall at the dry site (i.e., static for the study period), but no difference in slope (i.e., plastic over the study period), this difference may be a result of either phenotypic or genotypic variations between the sites (Anderegg, 2015; Callaway et al., 2003; Chevin et al., 2010; Matesanz et al., 2010).

While our study focused on moisture, and thus drought-induced

stress, shrubs may also respond to frost-related stress by favouring safety over efficiency. As both arid areas and regions prone to freeze-thaw events are expected to trigger similar shrub xylem responses – i.e., increased protection against cavitation (Ewers et al., 2007; Maherali et al., 2004) – it is difficult to distinguish between these potential drivers in our study. However, if freeze-thaw stress was the predominant driving factor at our study site, we would expect a significant influence of the increased snow, as it would likely provide protection against such events. Additionally, we would expect substantial evidence of frost damages (i.e., frost rings) in the xylem. However, we observed minimal evidence of such damages in our samples, and a similar lack of frost damage has been previously noted in *B. nana* and *S. glauca* also growing in Western Greenland (Young et al., 2016). Lastly, it is feasible that shrubs growing in this environment have adapted to cope with repeated freeze-thaw cycles (e.g., Dobbert et al., 2021a, 2021b), while the water-limitation due to increased temperatures would be a relatively novel challenge.

4.3. Radial growth of *B. nana*, but not *S. glauca*, responsive to soil moisture

The assessed responses provide insight on the ability of shrubs to adapt to their growing conditions by adjusting the xylem structure. Although differences were observed in hydraulic efficiency and vessel spatial distribution in both species, they coincided with differences in radial growth only in *B. nana*. This moisture limitation to *B. nana* growth is in line with recent findings also in Western Greenland (Gamm et al., 2018), and may suggest potential declines in *B. nana* growth rates at dry Arctic areas with increasing temperatures. In contrast, *S. glauca* did not show sensitivity to soil moisture, suggesting growth in this species may be more limited by other factors such as air temperature (e.g., Ackerman et al., 2018). However, it is also possible that the lack of response in RW is due to *S. glauca* having a more lagged response; being more influenced by allometric or ontogenetic trends; or, as growth responses vary within individuals (Ropars et al., 2017), it is also possible that growth rings at different parts of the shrub, i.e., at the root collar or roots, may be more influenced by soil moisture than at the stem.

The greater RW for *B. nana* at the wet site, likely due to the increased efficiency of water transport, is similar to findings from Nielsen et al. (2017), where increased ring widths were also found in relation to increased hydraulic conductivity in *B. nana* growing in Western Greenland. However, the relationship between growth and hydraulic traits can be complex, with results varying between species, studies, and sites. This is evidenced, for example, by greater LA95 in *S. glauca* at the wet site not coinciding with increased growth in our study, and Anadon-Rosell et al. (2018) observing increases in growth in *Vaccinium myrtillus* related to rising temperatures without an increase in vessel size. Our results suggest that hydraulic efficiency is limiting for *B. nana* growth, but not *S. glauca* at our study site, and indicate that metrics related to hydraulic properties may provide more insight into functional responses in *S. glauca* than ring width (von Arx et al., 2012).

4.4. Implications and outlook

Shrubs possessing larger vessels and higher xylem conductivity tend to have a competitive advantage due to the increased uptake of water and nutrients, potentially resulting in increased photosynthesis and growth rates (Nielsen et al., 2017). However, they are also more vulnerable to cavitation that could lead to decreased productivity or even death of individuals. Moreover, it has been previously estimated that plants having conduit diameters of 30 μm and greater are particularly vulnerable to freezing induced cavitation (Davis et al., 1999; Gorsuch and Oberbauer, 2002). We found that *S. glauca* at the wet site, having larger vessels overall, reaches this threshold (34.0 μm at the wet site, 26.8 μm at the dry site), while *B. nana* is well below this threshold at both sites (24.0 μm at the wet site and 17.1 μm at the dry site) (Table 3).

While larger vessels may promote *S. glauca* growth and competitive ability, potentially allowing it to outcompete smaller statured plants, including *B. nana*, loss in conductivity due to damages during extreme events may lead to decreased growth and long-term survival rates (Gorsuch and Oberbauer, 2002; Hacke and Sperry, 2001). This may thus give more of an advantage to *B. nana* and other species with safer hydraulic architectures in a more uncertain future.

Our study species, being dominant shrubs with circumpolar distributions, are among the drivers of Arctic greening trends (e.g., Bonta et al., 2023; Forbes et al., 2010). As vessel size is expected to increase with rising temperatures (e.g., in *S. pulchra* (Gorsuch and Oberbauer, 2002) and in *B. nana* (Nielsen et al., 2017)), these increases may drive further Arctic shrubification. Larger deciduous shrubs, such as *S. glauca* and *B. nana*, could continue to impact species diversity by outcompeting smaller species, including lichens, bryophytes, herbaceous plants, and evergreen shrubs (e.g., Fraser et al., 2014; Gorsuch et al., 2001). However, as previously discussed, this advantage may be counteracted if extreme events also increase. A deeper understanding of how growing conditions influence the plant water transport system may help explain the heterogeneity of shrub responses across, and even within, sites. As shrubification can have far-reaching ecological impacts, such as those related to nutrient and carbon cycles (Mekonnen et al., 2021; Schore et al., 2023; Vowles and Björk, 2019), understanding shrub anatomical plasticity can lead to a better understanding of Arctic ecosystem processes in a changing climate.

5. Conclusion

Based on our analysis of 80 *S. glauca* and *B. nana* shrubs in a snow manipulation experiment, we found the xylem hydraulic architecture, along with growth in *B. nana*, was dependent on soil moisture but not the snow treatment. Understanding the physiological plasticity of these species is important for predicting future shrub expansion, as changes in these traits can be directly linked to a species' ability to cope with changing growing conditions (Dobbert et al., 2022). Our findings provide a mechanistic perspective for differential success of two dominant shrub species growing in different moisture regimes. Here we provided insights from one site in Western Greenland, though more long-term and site-specific studies employing multi-proxy and integrative approaches are needed to enhance our understanding of how snow and moisture will influence shrub heterogeneity across the Arctic. Increasing our understanding of Arctic vegetation at the cellular level can ultimately improve our insights into the underlying mechanisms driving shrub responses and inform projections of ecological change in the region.

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CRediT authorship contribution statement

Candice C. Power: Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Signe Normand:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing. **Georg von Arx:** Project administration, Resources, Supervision, Writing – review & editing. **Bo Elberling:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing. **Derek Corcoran:** Methodology, Writing – review & editing. **Amanda B.**

Krog: Investigation, Writing – review & editing. **Nana Knakkergaard Bouvin:** Investigation, Writing – review & editing. **Urs Albert Treier:** Conceptualization, Project administration, Resources, Writing – review & editing. **Andreas Westergaard-Nielsen:** Investigation, Writing – review & editing. **Yijing Liu:** Investigation, Writing – review & editing. **Angela L. Prendin:** Investigation, Methodology, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on reasonable request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.169896>.

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