

# Moisture-driven shift in the climate sensitivity of white spruce xylem anatomical traits is coupled to large-scale oscillation patterns across northern treeline in northwest North America

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## Abstract

Tree growth at northern treelines is generally temperature-limited due to cold and short growing seasons. However, temperature-induced drought stress was repeatedly reported for certain regions of the boreal forest in northwestern North America, provoked by a significant increase in temperature and possibly reinforced by a regime shift of the Pacific decadal oscillation (PDO). The aim of this study is to better understand physiological growth reactions of white spruce, a dominant species of the North American boreal forest, to PDO regime shifts using quantitative wood anatomy and traditional tree-ring width (TRW) analysis. We investigated white spruce growth at latitudinal treeline across a >1,000 km gradient in northwestern North America. Functionally important xylem anatomical traits (lumen area, cell-wall thickness, cell number) and TRW were correlated with the drought-sensitive standardized precipitation–evapotranspiration index of the growing season. Correlations were computed separately for complete phases of the PDO in the 20th century, representing alternating warm/dry (1925–1946), cool/wet (1947–1976) and again warm/dry (1977–1998) climate regimes. Xylem anatomical traits revealed water-limiting conditions in both warm/dry PDO regimes, while no or spatially contrasting associations were found for the cool/wet regime, indicating a moisture-driven shift in growth-limiting factors between PDO periods. TRW reflected only the last shift of 1976/1977, suggesting different climate thresholds and a higher sensitivity to moisture availability of xylem anatomical traits compared to TRW. This high sensitivity of xylem anatomical traits permits to identify first signs of moisture-driven growth in treeline white spruce at an early stage, suggesting quantitative wood anatomy being a powerful tool to study climate change effects in the northwestern North American treeline ecotone. Projected temperature increase might challenge growth performance of white spruce as a key component of the North American boreal forest biome in the future, when drier conditions are likely to occur with higher frequency and intensity.

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## KEYWORDS

boreal forest, climate change, divergence, drought, pacific decadal oscillation, *Picea glauca*, plasticity, tree-ring width, wood anatomy

## 1 | INTRODUCTION

As the largest terrestrial biome, boreal forests play a key role in global carbon cycling and storage processes as well as the earth's energy budget (Bonan, 2008; Pan et al., 2011). Tree populations living at the latitudinal/cool margins of this biome are further considered important indicators of climate change impacts (Iverson, Schwartz, & Prasad, 2004; Travis & Dytham, 2004), as short growing seasons with low summer temperatures limit tree growth in these regions (Holtmeier, 2009; Körner, 1998, 2012).

Despite growing at cold margins, however, several studies have reported a decoupling, or even a negative reaction of radial tree growth to summer temperature, the so-called divergence effect, in numerous parts of the boreal forest biome since the second half of the 20th century (see D'Arrigo, Wilson, Liepert, & Cherubini, 2008 for a thorough review). This phenomenon was particularly observed in northwestern North America for white spruce (*Picea glauca* (Moench) Voss; e.g. D'Arrigo et al., 2008; Driscoll, Wiles, D'Arrigo, & Wilmking, 2005; Juday, Alix, & Grant, 2015; Lloyd & Bunn, 2007; Pisaric, Carey, Kokelj, & Youngblut, 2007; Porter & Pisaric, 2011; Wilmking, D'Arrigo, Jacoby, & Juday, 2005; Wilmking, Juday, Barber, & Zald, 2004). White spruce is the dominant tree species of the upland North American boreal forest (Scoggan, 1978) and constitutes one of the main treeline-forming species in Alaska and Canada (Lloyd, Wilson, Fastie, & Landis, 2005). One frequently reported explanation of the divergence effect in white spruce is temperature-induced drought stress (e.g. Barber, Juday, & Finney, 2000; D'Arrigo et al., 2008; Juday et al., 2015), as temperatures but not precipitation, have increased rapidly since the mid-1970s in Alaska (Stewart, Kunkel, Stevens, Sun, & Walsh, 2013). Furthermore, divergence was found to be more widespread in drier parts of northwest North America, mainly including continental inland sites (Griesbauer & Green, 2012; Juday et al., 2015), but also drier sites at northern treeline in Alaska and northwest Canada (Brownlee, Sullivan, Csank, Sveinbjörnsson, & Ellison, 2016; Porter & Pisaric, 2011; Porter, Pisaric, Kokelj, & deMontigny, 2013; Wilmking & Juday, 2005).

The 1970s temperature increase coincides with a regime shift of the Pacific decadal oscillation (PDO), a cyclic, (multi-) decadal variability in sea-surface temperatures, where negative phases lead to anomalously cool/wet, and positive phases to warm/dry climate regimes in NW North America (Mantua & Hare, 2002; Mantua, Hare, Zhang, Wallace, & Francis, 1997). The recent major 1976 PDO-shift from a negative, cool to a positive, warm phase is supposed to have reinforced ongoing temperature increase, possibly leading to drought stress-induced divergence in white spruce at latitudinal and elevational treelines in Alaska (Ohse, Jansen, & Wilmking, 2012) and Western Canada (Dearborn & Danby, 2018). However, the association between PDO regime shifts and the divergence effect in white

spruce is not well established and the exact underlying physiological processes of divergence are still poorly understood (e.g. Brownlee et al., 2016).

As is common with conifers, annual rings of white spruce are mainly formed by a single cell type, the tracheids, which are responsible for both the transport of water and nutrients (cell lumen) as well as mechanical support (cell wall; Brown, Panshin, & Forsaith, 1949). Besides the process of genetic adaptation through natural selection, which occurs rather slowly in long-living organisms such as trees (Chevin, Collins, & Lefèvre, 2013), cell formation can be a fast-reacting plastic process (e.g. Fonti et al., 2010; Rowe & Speck, 2005). Newly formed cells adapt to environmental conditions of the respective growing season in size, shape and number (e.g. Bryukhanova & Fonti, 2013; Gričar et al., 2014, 2015; Tremblay, Kašpar, Kuželová, & Gryc, 2015) in order to achieve best possible functionality regarding hydraulic efficiency (cell lumen and number) and safety (cell wall; Petit, Anfodillo, Carraro, Grani, & Carrer, 2011; Prendin, Mayr, Beikircher, von Arx, & Petit, 2018). In this way, cells can depict environmental conditions under which they were formed. More precisely, dimensions of cell lumen are restricted by temperature in cold environments (e.g. Petit et al., 2011) and by water availability under drought conditions (e.g. Bryukhanova & Fonti, 2013; Pellizzari, Camarero, Gazol, Sangüesa-Barreda, & Carrer, 2016), that is, cell lumen are smaller in cold or dry environments. Water sensitivity under drought was shown to be highest for cells formed in the early growing season (earlywood; Castagneri, Battipaglia, von Arx, Pacheco, & Carrer, 2018; Pacheco et al., 2017), as turgor pressure actively affects cell size during the cell enlargement process in the early growing season (Cosgrove, 2005). On the other hand, the carbon-demanding process of cell wall deposition mainly occurs at the end of the growing season and is typically correlated with late summer temperature in cold environments, especially in the latewood (Carrer, Unterholzner, & Castagneri, 2018; Castagneri, Fonti, Arx, & Carrer, 2017; Cuny & Rathgeber, 2016). The number of formed cells and their dimensions directly translate into the trees' radial and height growth and thus its hydrological functioning (Carrer, von Arx, Castagneri, & Petit, 2015), making wood anatomy a powerful tool to study tree vitality at high resolution (Pellizzari et al., 2016).

Thanks to recent methodological advances in quantitative wood anatomy (Prendin et al., 2017; von Arx & Carrer, 2014; von Arx, Crivellaro, Prendin, Čufar, & Carrer, 2016), time series of xylem anatomical traits (i.e. cell growth features) have been increasingly and successfully used to investigate physiological and functional responses to inter- and intra-annually changing climate conditions over long periods (e.g. Carrer, Brunetti, & Castagneri, 2016; Fonti et al., 2013; Pellizzari et al., 2016) and across climatic gradients (Borghetti, Gentilesca, Leonardi, van Noije, & Rita, 2017; Castagneri et al., 2017; Castagneri, Petit, & Carrer, 2015; Kulmala et al., 2017; Pacheco, Camarero, & Carrer, 2018). However, only few studies have

investigated long-term climate effects on wood anatomy of northern treeline conifers in general (e.g. Fonti et al., 2013; Pritzkow, Heinrich, Grudd, & Helle, 2014). Furthermore, anatomical studies on white spruce are limited to short periods in controlled experiments (Sebastian-Azcona, Hacke, & Hamann, 2018) or to technical applications (Gregory, 1971; Lenz, Cloutier, MacKay, & Beaulieu, 2010; Lenz, Deslauriers, Ung, MacKay, & Beaulieu, 2014; Marguerie, Bégin, & Cournoyer, 2000).

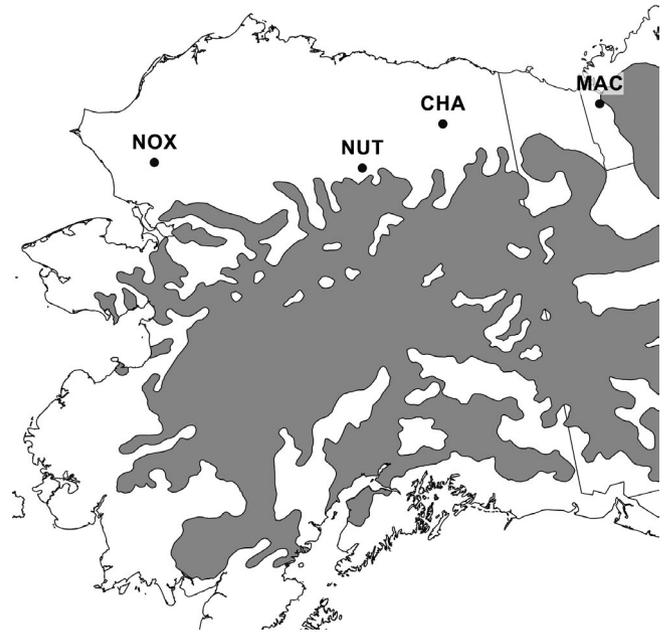
With this study, we made a first attempt to identify possible PDO-driven divergence in the climate–growth response of xylem anatomical traits in treeline white spruce using quantitative wood anatomy. We aimed at improving the mechanistic understanding of climate change effects on physiological processes and functioning of treeline conifers, which is essential for modelling spatio-temporal effects of future climate change on forest growth and distribution (Fonti et al., 2010). We analysed the functionally important xylem anatomical traits lumen area (LA), cell wall thickness (CWT) and cell number (CN), as well as the traditional tree-ring width (TRW) at four treeline sites along a >1,000 km west–east gradient of increasing continentality in northwestern North America and compared their sensitivity to climate across different PDO regimes. Assuming that conditions in positive PDO regimes were dry enough to provoke drought imprints in white spruce wood anatomical traits, we tested the following hypotheses:

1. Growth of xylem anatomical traits is more strongly water limited in positive (warm/dry) PDO regimes than in negative (cool/wet) regimes. This leads to reduced radial growth due to smaller LA and lower CN and consequently reduced hydraulic capacity under warm/dry conditions.
2. Sensitivity to water availability is highest in earlywood for LA and in latewood for CWT, leading to different consequences regarding the trees' functioning.
3. Signs of water-limited growth increase towards the eastern part of the gradient due to increasingly drier conditions.

## 2 | MATERIALS AND METHODS

### 2.1 | Study species and study area

White spruce, which is most widespread in Alaska and western Canada, grows best on well-drained, permafrost-free upland areas and south-facing treeline sites of the North American boreal forest, where it is the dominant species (Dyrness, 1980; Scoggan, 1978). It is commercially highly important (Burns & Honkala, 1990). Latitudinal treelines are quasinorthern elevational treelines in Alaska, as the Brooks Range stretches across the state from west to east, not permitting the boreal forest to expand beyond this topographic barrier (Rupp, Chapin, & Starfield, 2001). The NUT and CHA sites in the centre of the studied gradient (Figure 1) were established at such typical elevational south-facing treeline sites. The westernmost site (NOX) was a typical gallery forest growing on well-drained south-facing



**FIGURE 1** Distribution range of white spruce (*Picea glauca*) in northwestern North America (shaded area; Little, 1971) and study sites (black circles)

floodplains and high-terraces at the western foothills of the Brooks Range (Wilmking & Juday, 2005). The MAC site was located on a well-drained flat river alluvium underlain by permafrost (Nguyen, Burn, King, & Smith, 2009), where the active layer has increased in depth since the 1980s due to rising temperatures (Burn & Kokelj, 2009). All stands were typical for the respective areas, open canopy and nearly monospecific white spruce.

### 2.2 | Sample collection and processing

Mature white spruce trees were sampled at four latitudinal treeline sites in northwestern North America, following a gradient from Alaska's maritime Pacific northwest to the more continental Mackenzie River Delta in northwestern Canada (Figure 1; Table 1). One penetrating core (i.e. two radii) or two single cores were extracted per tree with an increment borer perpendicular to the slope in order to avoid reaction wood and to account for possible biases of uneven growth. Relevant tree measures (diameter at breast height, tree height) and site information (coordinates, elevation) were recorded (Table 1). TRW and genotype studies using data from NOX, NUT and MAC sites have been published before (for details see Eusemann et al., 2016; Ohse et al., 2012; Porter et al., 2013; Trouillier et al., 2018; Wilmking et al., 2017). For the present study, we focused on wood anatomical traits and selected eight trees per site (32 trees in total) from the existing and new datasets that (a) were similar in age and height as much as possible in order to reduce possible effects related to the trees' age (Carrer & Urbinati, 2004; Rossi, Deslauriers, Anfodillo, & Carrer, 2008) and ontogenetic differences that typically appear in trees of different age and size

**TABLE 1** Site metadata and mean values ( $\pm$  SD) of tree-ring width (TRW), cell wall thickness (CWT), lumen area (LA), CWT and LA: mean of all sectors) and cell number (CN) for the period 1925–1998. Mean dbh (diameter at breast height) for the MAC site was estimated from TRW. Coordinates and elevations represent mean site values as used to extract NRCAN climate data. Superscript capital letters indicate significant difference ( $p < .05$ ) between sites according to the pairwise Wilcoxon rank-sum test. The Holm correction for adjusted  $p$ -values was applied (Holm, 1979)

Site code (N)	Lat. (°N)/Long. (°W)	Elev. (m)	Mean age	Mean height (m)	Mean dbh (cm)	Mean TRW (mm)	Mean LA ( $\mu\text{m}^2$ )	Mean CWT ( $\mu\text{m}$ )	Mean CN
NOX <sup>A</sup> (8)	67.949/161.71	221	142 $\pm$ 44 <sup>D</sup>	12.1 $\pm$ 4.6 <sup>B</sup>	24.3 $\pm$ 8.4 <sup>BD</sup>	0.94 $\pm$ 0.29 <sup>D</sup>	644.5 $\pm$ 218.8 <sup>BCD</sup>	3.9 $\pm$ 0.7 <sup>CD</sup>	486 $\pm$ 150 <sup>BCD</sup>
NUT <sup>B</sup> (8)	67.946/149.74	855	142 $\pm$ 29 <sup>D</sup>	6.6 $\pm$ 1.6 <sup>AC</sup>	14.1 $\pm$ 5.9 <sup>A</sup>	0.51 $\pm$ 0.26 <sup>CD</sup>	455.8 $\pm$ 158.4 <sup>ACD</sup>	3.8 $\pm$ 0.4 <sup>CD</sup>	395 $\pm$ 115 <sup>ACD</sup>
CHA <sup>C</sup> (8)	68.730/144.81	803	117 $\pm$ 17 <sup>D</sup>	10.2 $\pm$ 2.5 <sup>B</sup>	17.9 $\pm$ 4.6 <sup>D</sup>	0.79 $\pm$ 0.22 <sup>BD</sup>	551.0 $\pm$ 184.5 <sup>ABD</sup>	3.5 $\pm$ 0.6 <sup>ABD</sup>	469 $\pm$ 205 <sup>ABD</sup>
MAC <sup>D</sup> (8)	68.45/135.52	9	242 $\pm$ 41 <sup>ABC</sup>	NA	13.4 $\pm$ 3.1 <sup>AC</sup>	0.25 $\pm$ 0.11 <sup>ABC</sup>	419.9 $\pm$ 162.6 <sup>ABC</sup>	4.0 $\pm$ 0.6 <sup>ABC</sup>	189 $\pm$ 72 <sup>ABC</sup>

(Carrer et al., 2015), (b) were mostly free from defects that are evidently not related to climate (e.g. compression wood, nodes, and rotten parts) and (c) were representative of the respective stands and therefore correlated well with the respective TRW site chronology. Even though we attempted to homogenize the dataset regarding tree age and height, trees at the MAC site were significantly older than trees from all other sites (Table 1). Due to different sampling efforts, data have different end years (NOX: 2009; NUT: 2012; CHA: 2015; MAC: 2006).

For measurement of annual ring width, cores were air-dried and mounted on wooden sample holders using water-soluble glue. Ring visibility was enhanced by either sanding the surface with progressively finer grit sandpaper or by smoothing it with a sledge microtome (Gärtner & Nievergelt, 2010). TRW was measured either using a LINTAB 5/TSAP-Win system (Rinn, 2003), a Velmex measuring system or the CooRecorder software up to version 7.7 (Cybis Elektronik & Data AB), which is based on visual scans of the core surface. Measurement precision was 0.01 mm (NOX, NUT) and 0.001 mm (CHA, MAC).

For measurement of xylem anatomical traits, cores of one radius per tree were unglued and cut into pieces of approximately 4 cm length. Transversal sections of 10–14  $\mu\text{m}$  thickness were cut from each piece using a rotary microtome (Leica RM 2245) following the standard protocol (von Arx et al., 2016). Thin sections were subsequently stained for at least 15 min in a 1:1 solution of safranin (1%) and astrablue (0.5%; both diluted in distilled water), cleaned and dehydrated with ethanol concentrated up to 95%, and permanently mounted on microscope slides using Eukitt (BiOptica) or Euparal. Digital images of the thin sections were acquired at 100 $\times$  magnification using a D-Sight 2.0 slide scanner (Menarini Diagnostics) or a Leica DFC450C digital camera attached to a Leica DM2500 microscope. While image sections acquired with the D-Sight slide scanner were automatically stitched within the same system, images acquired with the Leica DM2500 microscope were stitched afterwards using the ImageJ grid/collection stitching plugin that was developed for distortion-free stitching of microscope images (Preibisch, Saalfeld, & Tomancak, 2009). Dimensions of xylem anatomical traits were measured semiautomatically on generally 30–70 cell rows per ring with the ROXAS program (Prendin et al., 2017; von Arx & Carrer, 2014). Analysis was performed at least back to 1900 (except for a few younger trees), resulting in >6 millions of analysed cells.

Subsequent processing of xylem anatomical data was carried out using the R programming software v. 3.5.2 (R Development Core Team, 2018). In order to make use of the intra-annual resolution of xylem anatomical traits and to reflect different temporal stages of ring formation, each annual ring was divided into five sectors of equal width along the tangential direction from earlywood to latewood, that is, parallel with the rings (Pellizzari et al., 2016). In this way, we roughly obtained two sectors from the beginning of the growing season (earlywood), one sector of transition wood and two sectors from the end of the growing season (latewood). Compared to previous studies where rings had been divided into 10 sectors (e.g. Carrer et al., 2016, 2018)

we often encountered very narrow rings and therefore decided to use five sectors to keep the sample size of cells per sector reasonably high. For each sector, the 90th percentile of LA, the mean of radial and tangential CWT (Prendin et al., 2017) and potential hydraulic conductivity (KH) were computed based on the ROXAS output. KH was calculated in ROXAS as approximated by Poiseuille's law and adjusted to elliptical tubes (Nonweiler, 1975). Total CN was assessed per ring. Time series of individual trees were subsequently averaged into site chronologies per sector and trait. In this way, we obtained chronologies of 3 traits (LA, CWT, KH)  $\times$  5 sectors  $\times$  4 sites, plus one CN chronology per site, resulting in 64 xylem anatomical trait chronologies covering the 20th century.

Tree-ring width time series were averaged first per tree and then per site by applying the biweight robust mean in order to down-weight outliers. Crossdating of all TRW and anatomical series was verified using the software CDendro (Cybis Elektronik & Data AB). Since ring width, as well as xylem anatomical traits, contain trends related to ontogenesis (Carrer et al., 2015; Cook, Briffa, Shiyatov, Mazepa, & Jones, 1990) that are unrelated to climate, we standardized TRW and all trait chronologies by fitting a cubic smoothing spline of 30 years with 50% frequency cut-off, which removes the defined amount of the low-frequency variability (Cook et al., 1990). Averaging, validation of cross-dating, chronology building and standardization were carried out using the R-package dplR (Bunn, 2008) of the R programming software v. 3.5.2 (R Development Core Team, 2018).

## 2.3 | Climate data

Climate stations are scarce and records are fragmentary in north-western North America and particularly the Brooks Range due to its remoteness. Previous studies in this area often accessed stations from the lowlands, such as the long-lasting record of Fairbanks (e.g. Wilmking & Juday, 2005; Wilmking et al., 2004). The longest record in the Mackenzie Delta (Inuvik station, 68.30°N, 133.48°W) is located 85 km southeast of the MAC site and is restricted to the period 1957–2005. To explore possible regionally differing climatic effects across the entire gradient and to obtain a consistent dataset reaching back to the early 20th century, we decided to use site-specific modelled data provided by the Natural Resources Canada, Canadian Forest Service (hereafter NRCAN; <http://cfs.nrcan.gc.ca/projects/3/1>; McKenney et al., 2011). Monthly means of maximum and minimum temperature, as well as monthly precipitation sums, were obtained for each site based on its geographic location and spanning the period 1901–2013. Monthly mean temperature per site was calculated as the mean of the respective maximum and minimum temperatures. The NRCAN spatial climate models are based upon climate data from the respective nearest climate stations and modelled using the thin plate ANUSPLIN climate modelling approach, which accounts for topographic differences (McKenney et al., 2011). Data from this climate modelling project have been successfully applied in dendroclimatological

**TABLE 2** Relevant temperature ( $T$ ) and precipitation ( $P$ ) data per study site averaged across the 1901–2013 NRCAN data period

Site code	$T_{\text{mean}}$		Annual $T_{\text{mean}}$ (°C)	$P_{\text{sum}}$ July–August (mm)	Annual $P_{\text{sum}}$ (mm)
	January (°C)	July (°C)			
NOX	−21.8	12.1	−6.5	108	260
NUT	−23.8	11.1	−7.9	96	289
CHA	−25.3	8.5	−10.0	69	188
MAC	−27.9	12.7	−9.4	67	208

investigations of white spruce in NW Canada, including sites of different elevation (Dearborn & Danby, 2018), as well as for forest ecology assessments throughout Canada (e.g. Aubin et al., 2018; Hope, McKenney, Pedlar, Stocks, & Gauthier, 2016). Comparisons with station records from Fairbanks (all sites) and Inuvik (MAC site) reveal high correlations for mean temperatures of the growing season, but correlations of intermediate strength for precipitation (Table S1). While the modelled temperature data is probably very accurate regarding long-term trends and interannual variations, modelled precipitation data need to be interpreted with caution due to previously mentioned challenges (low station density, fragmentary records; McAfee, Guentchev, & Eischeid, 2014).

Averaged across the 1901–2013 NRCAN data period, January and July were the coldest and warmest months at all sites respectively. January mean temperatures decreased from west to east, while July temperatures were higher at low elevation (NOX, MAC) compared to high elevation sites (Table 2). Annual precipitation sums ranged between 188 and 289 mm, approaching reported minimum conditions for white spruce growth in northwestern North America (Juday et al., 2015; Thompson, Anderson, & Bartlein, 1999). Annual maximum precipitation is reached in July in NUT and in August at all other sites. Both annual precipitation sums and sums of July–August precipitation are distinctly higher at the two westernmost sites (Table 2).

## 2.4 | Statistical analysis

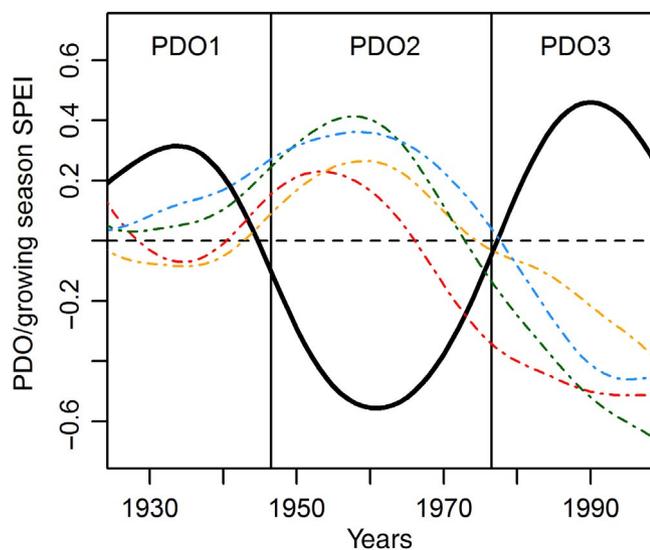
All statistical analyses were performed in the R software environment v. 3.5.2 (R Development Core Team, 2018).

In order to explore similarities and differences (a) among tree-ring traits and (b) between sites, we performed a principal component analysis (PCA; Jolliffe, 2002) using the standardized site chronologies of xylem anatomical traits as well as of TRW.

In order to investigate the effect of different climatic conditions prevailing in positive (warm/dry) and negative (cool/wet) PDO phases on wood formation, we selected the past three complete PDO phases of the 20th century based on Mantua and Hare (2002) for analysis (see also Ohse et al., 2012): 1925–1946 (positive, warm/dry; hereafter PDO1), 1947–1976 (negative, cool/wet; hereafter PDO2) and 1977–1998 (positive, warm/dry; hereafter PDO3).

As contrasting PDO regimes are mainly characterized by differing temperature and precipitation regimes, we tested and chose the standardized precipitation–evapotranspiration index (SPEI; Vicente-Serrano, Beguería, & López-Moreno, 2010), which contains site-specific information of temperature and evapotranspiration, as a suitable representative of climate forcing during different PDO regimes. Opposite to the PDO index, a positive SPEI generally indicates wet and cool conditions, while a negative SPEI is characterized by warm and dry conditions (Vicente-Serrano et al., 2010). In European and North American conifers of cold environments main tracheid production is assumed to occur between May and August (Deslauriers, Morin, & Begin, 2003; Mäkinen, Nöjd, & Saranpää, 2003; Schmitt, Jalkanen, & Eckstein, 2004; Seo, Eckstein, Jalkanen, & Schmitt, 2011; Seo, Salminen, Jalkanen, & Eckstein, 2010). Therefore, to unravel relationships between wood formation and the SPEI, the mean SPEI was calculated for the period of main cambial activity (May–August) using the Thornthwaite approach (Thornthwaite, 1948) in the R-package SPEI (Beguería & Vicente-Serrano, 2017). This growing season SPEI was negatively associated with the PDO index, supporting its suitability to represent the prevailing climate conditions of the respective PDO regime (Figure 2).

Finally, stationary bootstrapped (Politis & Romano, 1994) SPEI-growth Pearson correlation functions were computed for each standardized site chronology per trait and sector (where applicable) and for the three PDO phases using the R-package treeclim (Zang & Biondi, 2015). We further computed and plotted linear regressions of these same relationships to better represent correlation properties.



**FIGURE 2** Smoothed mean annual index of the Pacific decadal oscillation (PDO; Mantua et al., 1997) for the period 1925–1998 (black line) plotted against the smoothed standardized precipitation–evapotranspiration index (SPEI) of the main growing season (May–August; coloured dashed lines—red: NOX, yellow: NUT, green: CHA, blue: MAC), highlighting the similar pattern of the two indices. Both indices are dimensionless and their values were smoothed across their common data interval (1902–2013). Vertical lines mark shifts in the PDO regime (1946/1947 and 1976/1977) according to Mantua et al. (1997)

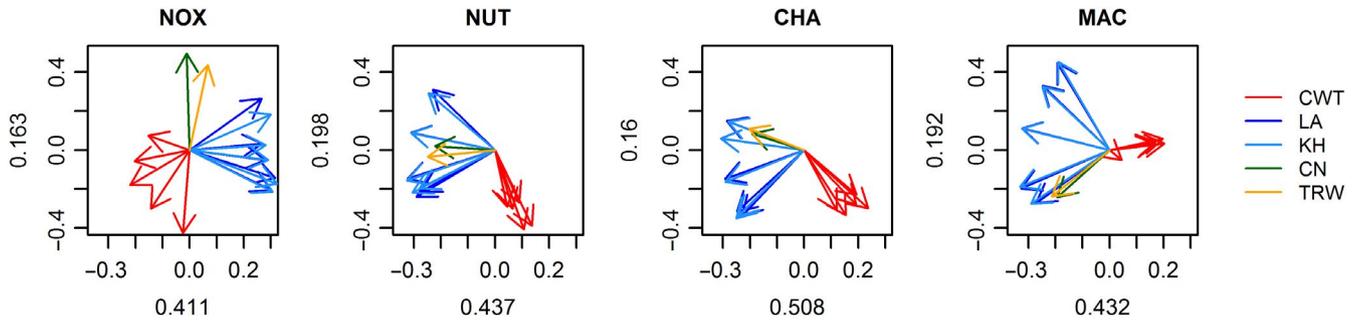
In order to enhance the reliability of our results, we repeated the climate–growth correlation analysis using the more traditional self-calibrating Palmer drought severity index (scPDSI; Palmer, 1965; Wells, Goddard, & Hayes, 2004). Above described precipitation and potential evapotranspiration data derived from the NRCAN climate model were used to compute the scPDSI in the R package scPDSI (Zhong, Chen, Wang, Lai, & Goddard, 2018). As the general correlation pattern was similar, but with overall lower and often nonsignificant correlation values (Figure S3), we based our further analyses and interpretation solely on SPEI-growth correlations. Additionally, in order to test the course of SPEI-growth relationships over the entire time period of data availability also including recent years, a moving window analysis was performed for all traits per site and the period 1925–2006/2013 (depending on the site) with a window size of 25 years and in steps of 1 year using the treeclim package (Zang & Biondi, 2015).

Since cells form annual rings, and in order to quantify relative importance, that is, the proportionate contribution (Johnson & Lebreton, 2004) of the different xylem anatomical traits to the formed tree ring (TRW), we built multiple linear regression models with LA, CWT and CN (mean of standardized values per ring) as regressors and the standardized TRW as the response variable. Given that observed explanatory variables can be interrelated, having both direct as well as combined effects on the response variable (Johnson & Lebreton, 2004), and as their position in the model can affect their contribution to the overall explained variance (Grömping, 2006), we assessed relative importance of the regressors using the metric 'lmg' incorporated in the R package relaimpo (Grömping, 2006). It considers the dependence of regressors by averaging over orderings, being one of the most suitable approaches to assess relative importance for observation data with causal relationships (Grömping, 2006). One model was built for each site and PDO period by adjusting the R code presented in Grömping (2006) to our data structure. In order to better compare contributions of the individual xylem anatomical traits, metrics were forced to sum to 100%.

### 3 | RESULTS

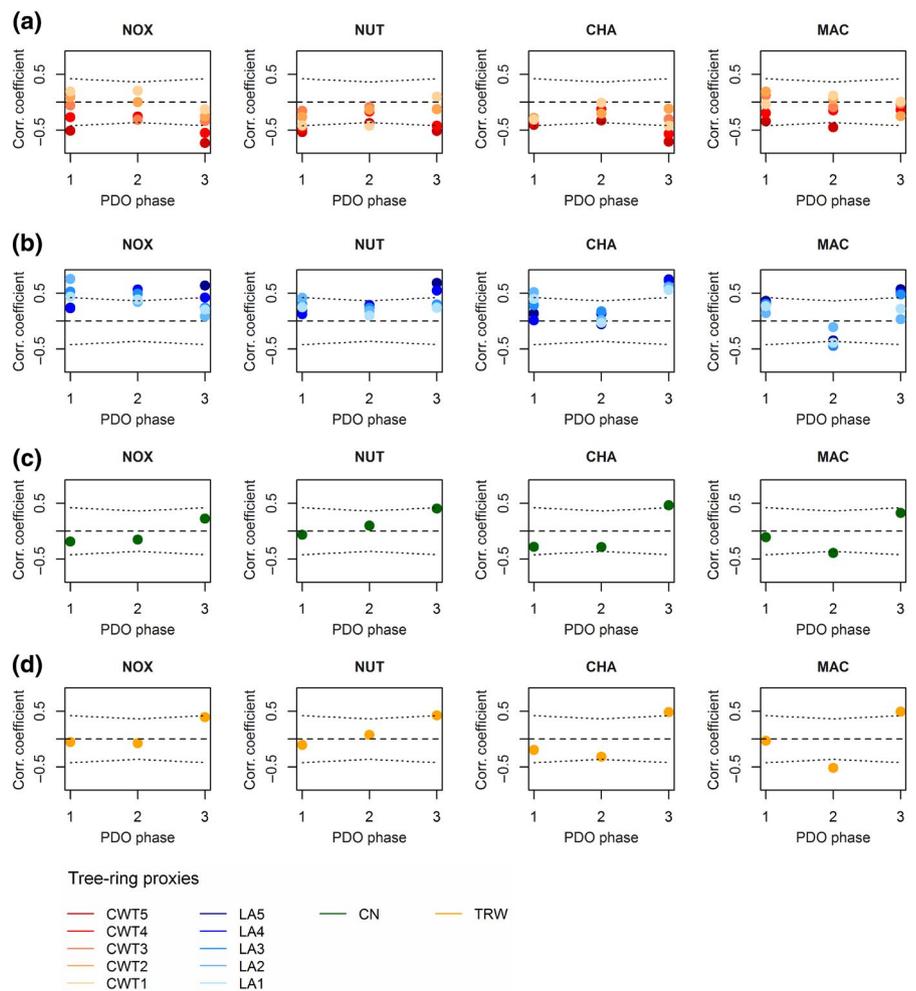
Principal component analysis of xylem anatomical traits and TRW chronologies revealed a clear pattern at each site, where the first two principal components explained 57.4%–66.8% of the total variance (Figure 3). LA and KH pointed into exactly the same direction; therefore we excluded KH as a synthetic measure from further analysis and exclusively used LA as the trait to represent hydraulic conductivity (e.g. Pellizzari et al., 2016). LA and CWT were generally clearly separated along the first axis. CN and TRW pointed into the same direction as LA in most cases.

Correlation signs of LA and CWT with SPEI were generally contrasting in all three PDO periods (Figure 4a,b), reflecting the pattern found by the PCA. CWT was generally negatively correlated with the growing season SPEI, while correlations of LA and SPEI were mostly positive. In other words, wetter conditions were associated



**FIGURE 3** Principal component analysis for the standardized trait chronologies reveals a positive association of LA and KH, a negative association of LA/KH and CWT, and a positive association of CN and TRW for the period 1925–1998 at all sites. Colours represent different traits: cell wall thickness (CWT, red), lumen area (LA, dark blue), hydraulic conductivity (KH, light blue; each for sectors 1–5), mean cell number (CN, green) and tree-ring width (TRW, yellow). Labelling values of the principal components (PC) refer to the amount of total variance explained by the respective PC

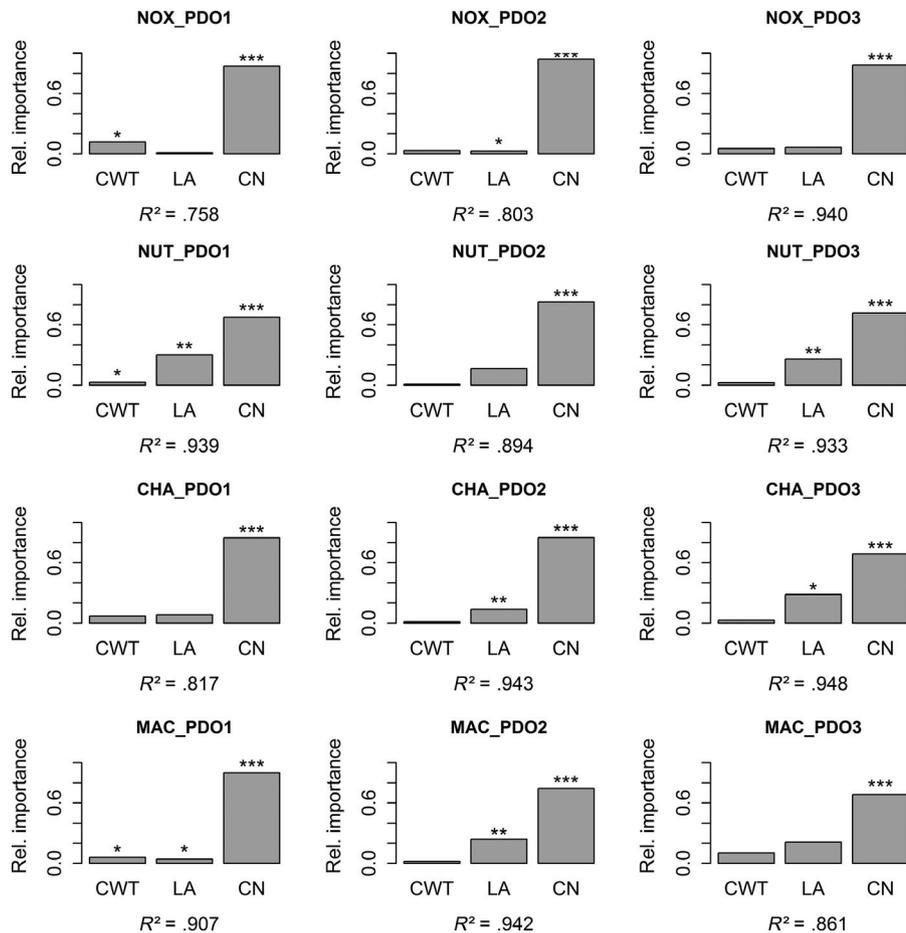
**FIGURE 4** Climate-growth Pearson correlations for the standardized trait chronologies per site with the growing season standardized precipitation–evapotranspiration index (SPEI; May–August) during the past three PDO (pacific decadal oscillation) regimes of the 20th century (numbers on the respective x-axis: 1 = 1925–1946; 2 = 1947–1976; 3 = 1977–1998). The four rows correspond to the four traits tested: (a) cell wall thickness (CWT; sectors 1–5), (b) lumen area (LA; sectors 1–5), (c) mean cell number (CN) and (d) tree-ring width (TRW). Sectors 1–5 for CWT and LA are counted from earlywood to latewood. Correlations beyond the dotted lines are significant ( $p < .05$ ). For colour coding of CWT and LA sectors please refer to the legend



with thinner cell walls and larger LA (Figure S4). For both traits, and across all sites, climate sensitivity was generally higher during positive PDO phases, particularly in PDO3 (mean of strongest absolute correlation values was  $0.46 \pm 0.07$  for CWT and  $0.46 \pm 0.23$  for LA in PDO1, and  $0.55 \pm 0.22$  for CWT and  $0.66 \pm 0.07$  for LA in PDO3) compared to the negative phase (mean of strongest absolute correlation values was  $0.38 \pm 0.07$  for CWT and  $0.36 \pm 0.17$  for LA in PDO2), during which correlations were mostly not significant. It

is notable that only at the MAC site, we found significant negative correlations between LA and the SPEI during PDO2, that is, LA were significantly smaller under wet conditions.

In most cases, and for both CWT and LA, climate sensitivity was strongest in the last ring sectors (mean of absolute correlation values of 4th and 5th sectors was  $0.37 \pm 0.18$  for CWT and  $0.35 \pm 0.22$  for LA) and weakest in the first ring sectors (mean of absolute correlation values of 1st and 2nd sectors was  $0.18 \pm 0.13$  for CWT and



**FIGURE 5** Relative importance of mean cell wall thickness (CWT), mean lumen area (LA) and mean cell number (CN) per ring contributing to annual tree-ring width per study site and per phase of the Pacific decadal oscillation (PDO1: 1925–1946; PDO2: 1947–1976; PDO3: 1977–1998), assessed based on multiple linear regression models. The overall explained variance ( $R^2$ ) for each model is reported underneath each subset. Significant contributions of the individual regressors to the respective model are marked with an asterisk:  $p < .001$  (\*\*\*),  $p < .01$  (\*\*),  $p < .05$  (\*). Metrics were forced to sum to 100%

$0.27 \pm 0.21$  for LA). Correlation patterns of CN and TRW were similar and differed from those of LA and CWT—CN and TRW were positively associated with water availability in PDO3 (except for NOX), but not in PDO1 and PDO2 (Figure 4c,d).

Moving window analyses revealed unstable SPEI-growth relationships across the whole study period, with correlations being strongest (and significant) around the time of PDO3 for all proxies, hereby confirming above described correlation patterns of the individual periods and for the different tree-ring traits (Figures S5 and S6). Positive correlations of LA, CN and TRW with the SPEI occurred earlier in time at the two westernmost sites NOX and NUT.

Assessment of relative importance revealed that CN contributed most to TRW formation (67%–94%), followed by LA (up to 30%). Contribution of CWT to the models was lowest, reaching max. 12% (Figure 5).

Trees differed in diameter at breast height, height, TRW, CWT, LA and CN (Table 1; Table S2) between sites, revealing the following general pattern (except for CWT; from largest to smallest, not all differences were significant): NOX, CHA, NUT, MAC.

## 4 | DISCUSSION

The aim of this study was to better understand the divergence effect and physiological growth reactions of treeline white spruce to climate regime shifts using quantitative wood anatomy. As hypothesized, we

found stronger signs of water-limited growth in warm/dry (positive) PDO phases, suggesting a shift in growth limiting factors between PDO periods and thus a high plasticity of xylem anatomical traits. Here we discuss signs and possible underlying processes of this shift including variations in time and space, as well as differences between traits.

### 4.1 | Changing drought sensitivity of LA and CWT points to a shift of growth-limiting factors

Under warm/dry PDO1 and PDO3 regimes, CWT was negatively correlated with water availability (SPEI), while LA showed a significant positive response at most sites, that is, cell lumen were smaller and cell walls thicker under drier conditions and the effect was inverted under increasingly wetter conditions. This opposing correlation pattern of LA versus CWT, which is supported by their opposite position in the PCA, was also found in previous studies (e.g. Carrer, Castagneri, Prendin, Petit, & von Arx, 2017; Castagneri et al., 2018). The positive association of cell size with water availability was previously interpreted as a typical sign of drought conditions for conifers in water-limited environments (Pellizzari et al., 2016) or subjected to irrigation experiments (Montwé, Spiecker, & Hamann, 2014). Under drought conditions, cell size is assumed to be smaller due to lower turgor pressure on the flexible cell walls (Cosgrove, 2005; Hölttä, Mäkinen, Nöjd, Mäkelä, & Nikinmaa, 2010; Hsiao, 1973), while cell

walls are thicker as the same amount of wall material is deposited in this smaller cell (Cuny, Rathgeber, Frank, Fonti, & Fournier, 2014). This growth reaction optimizes cell function under water-limited conditions by increasing the cell's stability and resistance to drought-induced cavitation (Hacke, Sperry, Pockman, Davis, & McCulloh, 2001). On the other hand, other cell growth reactions to drought have been reported as well (Eilmann, Zweifel, Buchmann, Fonti, & Rigling, 2009), but drought reactions can differ in conifers depending on species and age (Moran, Lauder, Musser, Stathos, & Shu, 2017), and positive correlations with SPEI indicate a clear association with moisture stress in our study. Our hypothesis that sensitivity of LA and CWT to water availability is highest in positive PDO regimes due to drier conditions is therefore supported.

Furthermore, it is obvious that drought sensitivity of LA and CWT was higher in PDO3 compared to PDO1, as PDO3 was warmer, and thus evaporative demand was higher compared to PDO1 (Figure 2; Figure S1). Based on the overall unstable relationship between LA/CWT and SPEI (present in PDO1, absent in PDO2 and again present in PDO3) we conclude that most likely a shift in growth limiting factors occurred between these PDO periods, where conditions in PDO2 were wet, drier in PDO1 and driest in PDO3. As no association with the SPEI was found in the wet PDO2 in most cases, anatomical traits were most likely temperature and not water-limited in PDO2, which would be the expected growth reaction in temperature-limited environments with sufficient water supply (e.g. Castagneri et al., 2015; Lenz, Hoch, & Körner, 2013; Petit et al., 2011).

This temporal pattern is partly in line with previous divergence studies on white spruce TRW in Alaska and Canada, which reported a positive association with water availability of the growing season in recent decades at northern treeline (Ohse et al., 2012), elevational treeline (Dearborn & Danby, 2018), or inland forest sites (Griesbauer & Green, 2012; Juday & Alix, 2012; Sullivan, Pattison, Brownlee, Cahoon, & Hollingsworth, 2016), also suggesting moisture stress as one possible explanation.

#### 4.2 | What drives CN and TRW?

Climate sensitivity of CN and TRW was similar in our study on white spruce, as has been shown for a variety of conifer species (Carrer et al., 2017, 2018; Castagneri et al., 2015; Gregory, 1971; Gričar et al., 2015; Little & Sundberg, 1991; Olano, Eugenio, García-Cervigón, Folch, & Rozas, 2012; Park & Spiecker, 2005). This is supported by our analysis of relative importance, showing that CN contributes a large amount to TRW's annual variation at our sites.

Similar to LA and CWT, the 1976/1977 shift towards drier conditions was indicated by positive correlations of TRW and CN with water availability at most sites in PDO3. This is striking, as CN is generally positively associated with temperature in cold environments (Carrer et al., 2017; Castagneri et al., 2015). But here, water availability really seems to limit radial tree growth in PDO3 by reducing the number of cells formed during a growing season.

However, no signs of water limitation were found in TRW and CN during PDO1 in contrast to LA and CWT. This reduced sensitivity might be (a) either related to the fact that PDO1 was slightly wetter and cooler than PDO3 (Figure 2) despite being defined as warm/dry phase (Mantua & Hare, 2002), or (b) to the trees being older and larger in PDO3 versus PDO1.

A slightly cooler and wetter PDO1 would suggest a different climatic threshold for CN compared to LA and CWT. Our findings are in line with the general divergence discussion, which mainly found positive precipitation signals after the 1970s as discussed before (D'Arrigo et al., 2008). Several authors found CN being positively associated with higher temperatures in spring and thus an earlier onset and a longer duration of cambial activity (Gričar et al., 2014; Lupi, Morin, Deslauriers, & Rossi, 2010). Indeed, temperatures were notably higher, but precipitation was also lower in PDO3 compared to the previous two regimes, possibly resulting in lower water availability in spring. As spring drought was previously reported to affect white spruce TRW (Dearborn & Danby, 2018; Ohse et al., 2012), we speculate that the positive effect of the early onset of growth might have been outweighed by the negative effect of lack of soil moisture in the slightly warmer and drier PDO3, leading to a reduced CN. Another explanation might be the presence of age or size effects in CN and TRW in PDO3, as our sampled trees were about 50 years older and potentially taller during PDO3. Size and age do influence drought susceptibility, with the TRW of older and larger white spruce trees showing generally more drought stress than younger and smaller trees even if data are standardized (Trouillier et al., 2019). The decreasing moisture sensitivity of CN and TRW in the early 2000s (Figure S6) might be due to a generally cooler and wetter regime prevailing after PDO3 (Newman et al., 2016), but also other effects (e.g. climate prior to the growing season) cannot be excluded. As the changeable sensitivity of CN to SPEI cannot be fully explained here, and as CN essentially affects radial growth as our analysis of relative importance has shown, and thus hydraulic conductivity by the formation of new cells (Petit et al., 2011), future studies should put more effort into understanding past performance of CN in order to assess future growth and survival of white spruce.

Finally, the higher climate sensitivity of LA and CWT presumably relates to the strength of the quantitative wood anatomy approach compared to traditional TRW analysis. In analysing xylem anatomical traits per sector, we were able to identify that part of the ring which was most sensitive to climate (in our study: latewood), while TRW contains information of the whole ring and therefore integrates environmental conditions of the complete growing season as well as the effect of reserves stored in the previous year.

#### 4.3 | Plastic latewood cells show highest sensitivity

As hypothesized, CWT was most sensitive to climate in the last ring sectors, which is in line with current research (Carrer et al., 2016, 2018; Cuny & Rathgeber, 2016). Cuny and Rathgeber (2016) showed that the impact of late summer climate conditions is entirely translated

into cell dimensions (particularly cell walls) of the last latewood cells, as no other compensation is possible at the end of the growing season when most cell formation processes are already completed for the respective season.

Unexpectedly, sensitivity was highest in the last sectors in most cases also for LA, which is in contrast to investigations on Mediterranean conifers where sensitivity of LA to water availability of the growing season was highest in the earlywood sectors (Castagneri et al., 2018; Pacheco et al., 2017). On the other hand, higher sensitivity to growing season climate of LA in latewood compared to earlywood was also frequently reported (Carrer et al., 2017; Castagneri et al., 2017; Gričar et al., 2015), which was ascribed to the fact that dimensions of earlywood cells were not controlled by climate conditions of the growing season in temperate and boreal regions (Castagneri et al., 2018; Cuny & Rathgeber, 2016; Park & Spiecker, 2005). Instead, it was suggested that cell enlargement is driven by the photoperiod and hormones (Castagneri et al., 2018; Cuny & Rathgeber, 2016; Cuny et al., 2014; Rossi et al., 2006), by ontogenetic adaptation to height growth (Anfodillo et al., 2012; Carrer et al., 2015), and climate conditions of the previous year (Björklund et al., 2017; Castagneri et al., 2015). The missing climate sensitivity in our earlywood cells might thus indicate that drought conditions at the beginning of the growing season were not as pronounced at our sites, potentially related to snow melt charging the soil water storage in spring (Dearborn & Danby, 2018).

Since correlations with the SPEI were of similar strength for LA and CWT, we cannot determine any of the traits as more reactive and conclude that both traits show similar levels of plasticity in the latewood at our sites. These findings of highly adaptive latewood cells are supported by a PCA performed per sector (Figure S2), showing that the differentiation of LA and CWT between sites increases towards latewood sectors. Our results are further consistent with findings from the field of dendroclimatology, which typically show higher climate sensitivity of latewood properties, especially maximum latewood density (Anchukaitis et al., 2013; Wilson et al., 2017). Moreover, moving window analyses revealed that correlation patterns over time were very similar between TRW, CN, and latewood LA, and inverted to those of latewood CWT, suggesting that latewood is not only the most sensitive part of a ring, but that it controls sensitivity of TRW to a certain extent. Overall, this highlights the link between TRW, latewood density and latewood cells (both lumen and wall) in general (Björklund et al., 2017) and suggests a general suitability of latewood cell features as a proxy to reconstruct summer climate. Since in contrast to earlywood, latewood cells have almost no effect on tree hydraulic performances (e.g. Pellizzari et al., 2016), we conclude that the identified high plasticity of latewood cells (for both LA and CWT) is likely not essential for the trees' survival.

#### 4.4 | Spatial patterns are potentially related to microsite and stand differences

In contrast to previous findings, which showed that drought stress increases towards the more continental east at northern treeline in

the Brooks Range (Wilmking & Juday, 2005), drought signals were present throughout all sites in our study.

This might have several reasons, possibly related to a combination of sample size, tree selection (tree age and height) and site selection (microsite conditions). In previous studies on divergence usually the majority of one site, but not all trees, responded to climate in the same way (e.g. Porter & Pisaric, 2011; Wilmking & Juday, 2005). The rather low sample size (eight trees per site) compared to previous TRW divergence studies did not permit to sort samples of one site according to their climate response, also we might have unknowingly chosen those trees in the west that are less drought tolerant. Even though a larger sample size would be desirable, 5–10 trees per site is a typical sample size for xylem anatomical studies due to labour-intensive sample preparation, especially when covering several decades and sites (e.g. Carrer et al., 2018; Pellizzari et al., 2016). Furthermore, trees in the west had a significantly larger LA and CN and were probably taller than trees at the MAC site (Table 1; Table S2), which would fit the allometric concept that taller trees build larger cells (Carrer et al., 2015). As tree height might affect climate sensitivity in white spruce more than age (Trouillier et al., 2019) and susceptibility to drought conditions increases with tree height (Prendin et al., 2018; Rowland et al., 2015), we speculate that the unexpectedly high drought sensitivity in the west might be partly due to taller trees in the west.

On the other hand, during the cold and wet PDO2 phase, LA, CN and TRW showed contrasting responses at both ends of this >1,000 km gradient. While for LA, the difference between PDO periods was most pronounced at the easternmost site (MAC), it was nearly absent at the westernmost site. Also, CN and TRW at the MAC site showed a clear negative climate–growth response during the negative PDO2 regime, indicating stressful conditions under wet climate regimes.

This extreme reaction of MAC site trees is potentially related to the underlying permafrost soils. As white spruce does not tolerate stagnant water (Burns & Honkala, 1990), wet, cool and anaerobic conditions of the poorly drained soils of the permafrost's active layer (Smith, Sheng, MacDonald, & Hinzman, 2005) might have reinforced the negative effect of the cool/wet PDO2 regime. These unfavourable soil conditions were potentially aggravated by the fact that all sites, but MAC, were located on south facing hillslopes with high solar radiation, and that conditions were among the wettest at MAC in PDO2 compared to other sites according to the SPEI (Figure 2), possibly leading to the most detrimental growing conditions (flat, cool and wet) at the MAC site during PDO2. At the westernmost site (NOX), in contrast, LA was equally sensitive to the SPEI during both cool/wet and warm/dry periods, that is, the positive effect of higher water availability existed in all PDO periods. Additionally to the previously discussed effect of tree height on drought sensitivity (Trouillier et al., 2019), NOX was among the sites with highest summer temperatures due to its low elevation (Table 2), and differences regarding moisture availability between PDO periods were smaller at NOX compared to other sites according to the SPEI, which altogether might have

contributed to higher moisture sensitivity of LA in NOX. Stand density or competition can also affect water demand of white spruce (Nicklen et al., 2019; Trouillier et al., 2018; Wilmking & Juday, 2005; Wright, Sherriff, Miller, & Wilson, 2018), but cannot be assessed here.

Overall, this flexible growth adaptation of xylem anatomical traits to different PDO regimes and site conditions is likely more a result of high phenotypic plasticity in response to environmental conditions (e.g. Byers, 2008) than of genetic adaptation, as the genetic component of wood anatomical and hydraulic-relevant adjustment to climate was found to be rather low in white spruce (Sebastian-Azcona et al., 2018) and other conifers (King, Gugerli, Fonti, & Frank, 2013; Ziaco, Truettner, Biondi, & Bullock, 2018). Plasticity is considered an essential ability for trees in order to survive when environmental conditions change (Chevin et al., 2013). However, a combined approach of different methods (e.g. common garden experiments, reciprocal transplants and experimental studies) is needed in order to quantify the relative importance of phenotypic plasticity and genetic adaptation (Merilä & Hendry, 2013), and its spatio-temporal variations in white spruce.

#### 4.5 | Summary and outlook

We found signs of higher sensitivity to drought in LA and CWT of treeline white spruce during positive warm/dry PDO regimes, indicating a plastic adaptation to shifts in growth-limiting conditions mainly in the stabilizing latewood cells. We showed that CN and TRW seem to be less sensitive to changes in the growing season water availability, as these traits only reflect the PDO shift of 1976/1977, but not that of 1946/1947. Overall, we showed that quantitative wood anatomy seems highly suitable for addressing short- and long-term reactions of white spruce growth to changing climate regimes. Future research should focus on unravelling underlying drivers of CN production and its climatic thresholds, as this is an essential component of radial growth and hydraulic conductivity, thus being highly relevant for future performance and survival of white spruce. The proportion of genetic versus plastic adaptation needs to be identified and microsite and stand effects on xylem anatomical traits need to be further explored in order to be able to extend inferences to a larger variety of white spruce habitats. A better knowledge of physiological growth reactions in white spruce will help to improve local and global vegetation and carbon cycle models (e.g. Hu, Moore, Burns, & Monson, 2010; Smith & Dukes, 2013) and to assess the (future) economic value of forests. Based on our study, all tested traits showed signs of water limitation in the warm/dry period of 1977–1998. As periods of drought might become more frequent and more severe under projected future warming (IPCC, 2014), the question remains whether white spruce at treeline will be able to cope with these conditions (genetically or phenotypically) or to expand its range northwards, which is certainly a challenge with the Brooks Range as a geographic barrier.

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#### CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

#### AUTHOR CONTRIBUTIONS

JL, MW and JWS conceived the study. JL, MP, TJP and MW collected samples and measured tree-ring width, JL measured xylem anatomical traits with the help of MC and MT. JL analysed the data with input from MC, MT, MW and TJP. JL wrote the manuscript with input from MW. All authors substantially contributed to the discussion of the manuscript and approved the submitted version.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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