



# Earlywood structure of evergreen conifers near forest line is habitat driven but latewood depends on species and seasons

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## Abstract

**Key message** Near upper forest line, values of conifer wood anatomical traits are species-specific, but relationships among traits are common. Growing season temperature significantly impacts wood anatomy only in its extremes.

**Abstract** Quantitative wood anatomy can provide detailed insight into adaptation of trees to changing environment, especially on the borders of species distribution ranges. This study investigated wood anatomy of *Pinus sylvestris* L., *Pinus sibirica* Du Tour, and *Picea obovata* Ledeb. near the forest line in the Western Sayan Mountains, where local climate changes rapidly. Anatomical traits reflecting three developmental stages of conifer tracheids (division = cell number, cell enlargement = radial diameter, and secondary wall deposition = cell wall thickness) were calculated for earlywood, latewood and total tree ring over 50 years. Similar earlywood anatomical structure and low between-trait correlations ( $r=0.21\dots.67$ ) were observed in all species, which supports prevalence of external impact on its formation, i.e. that shared habitat, climate, and similar habitus provide common trade-off between hydraulic efficiency and safety. Also, stronger nonlinearity of relationship between cell number and radial diameter in earlywood decreased correlations between them. In latewood, anatomical traits are strongly interconnected ( $r=0.63\dots.93$ ) for all species. However, Siberian pine has significantly less pronounced latewood; later switch from earlywood and different strategy of carbon allocation are proposed as possible reasons. Length of vegetative season and sum of temperatures above thresholds 5 °C and 8 °C have no significant correlations with anatomical traits, but extremes of these temperature variables led to forming more pronounced latewood (higher proportion of latewood cells with thicker walls) during warm/long vegetative seasons than during short/cool ones.

**Keywords** Quantitative wood anatomy · Earlywood · Latewood · Evergreen conifers · Cold environment

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## Introduction

Increasing temperature causes significant shifts in phenology and growth rate of the secondary growth of woody plants (Barber et al. 2000; Berner et al. 2013; Keenan et al. 2014; Cuny et al. 2015), leading to a consequent shift in the boundaries of plant communities (Grace and James 1993; Bocharov 2009; Kharuk et al. 2009) or even to massive forest decline due to increased droughts (Zamolodchikov 2012; Kharuk et al. 2013, 2017; Liu et al. 2013; Allen et al. 2015). Under predicted future temperature increase scenarios, the monitoring of the health state, growth and productivity of forest ecosystems, as one of the most important global carbon sinks, is of particular interest (Myneni et al. 2001; Pan et al. 2011; Pugh et al. 2019).

Tree rings are the most informative source of data on growth and carbon deposition in woody plants (Fritts 1976; Büntgen et al. 2019). Particularly, environmental factors impact the process of wood cells' formation and their anatomical traits during tree-ring development (Plomion et al. 2001; Hughes et al. 2010; Schweingruber 2012). The quantification of wood anatomical traits within tree rings does not only provide detailed insight into the earlywood and latewood width, density profiles, cell lumen size and cell walls thickness, but also on their variation over time when analyzed in long-term tree-ring series (Vaganov et al. 2006; von Arx et al. 2016; Arx et al. 2018; Bjørnklund et al. 2017; Rathgeber 2017; Ziaco and Liang 2019). Tree-ring based quantitative wood anatomy allows better understanding of physiological mechanisms in adaptation and acclimation of woody plants to changing environmental conditions (Chave et al. 2009; Fonti et al. 2010; Anderegg and Meinzer 2015), as well as revealing species-specific and regional patterns in phenology of cambial activity (Carrer et al. 2017; Castagneri et al. 2017). One of the significant questions in the study of the tree-ring structure being solved by quantitative wood anatomy is the fine balance between internal limitations and external factors as drivers of wood cells formation in the particular habitat conditions (climate, soil, landscape, etc.) and varying climatic characteristics of individual growth seasons (Fonti et al. 2010; Carrer et al. 2017; Castagneri et al. 2017; von Arx et al. 2018).

This study looks at selected wood anatomical traits of three species of conifers growing near the upper forest line in the Western Sayan Mountains (south of central Siberia). The harsh continental climate of this region is typified by high variation of temperature, thus location of the alpine treeline and tree growth at it can be controlled by temperatures and length of growing season as well as by severe winter frosts (Körner 1999; Körner and Paulsen 2004; Li et al. 2017). The evidences of reaction in growth and species distribution dynamics of various local trees to climate warming are

ambiguous (Kuznetsova 2007; Kharuk et al. 2009, 2013; Tchebakova 2011; Zamolodchikov 2012 and others) and need further investigating, especially at the boundaries of forested area. Selected sampling site in vicinity of the huge Sayano-Shushenskoe Reservoir can be considered as a unique polygon undergoing extremely fast climate warming (0.2–1 °C per decade depending on season; Babushkina et al. 2018a, 2020). All three evergreen conifers included in the study (*Pinus sylvestris* L., *Pinus sibirica* Du Tour, and *Picea obovata* Ledeb.) are of interest for forest management in Siberia, being widely spread in cold environments of alpine and boreal forests of the region. This study provides a conceptual framework to examine wood cells' traits reflecting three main developmental phases of any wood cell (division, enlargement, and the secondary wall deposition), namely cell number, radial diameter and cell wall thickness. We investigate the wood structure variability under rapidly changing climate over the last decades, and comparison of three species will allow us to infer balance between common environmental conditions and species-specific acclimation strategies in formation of aforementioned anatomical traits.

Common environment and similar height of investigated trees provide the same requirements to hydraulic and mechanical structure of their wood (Anfodillo et al. 2013; Piermattei et al. 2020). Thus, we expect comparable variability range for their anatomical traits, taking into account its natural dynamics within tree ring, i.e. distinction between earlywood and latewood. A second expectation is that pattern of relationships between anatomical traits should link them in tree-ring structure similarly for all three species, providing its functioning in cold conditions. For example, Piermattei et al. (2020) unraveled a complex interconnection between 65 wood anatomical traits of Norway spruce grouped according to their functions. However, unlike that study where only five outermost tree rings were considered, here we address a wider temporal range of climatic variability and its impact on the wood anatomical structure by investigating long-term tree-ring series. In connection with this, a third expectation is that the impact of temperature variation on wood anatomical structure during growing season should be similar for all three species and significant either in general or at least for years with extreme low or high temperatures (compare with Hantemirov et al. 2004; Neuwirth et al. 2007; Carrer et al. 2016). In summary, the tasks set out to achieve the aim of this study are the following: (1) to define the range of variability of tracheids' anatomical traits for each species; (2) to describe the relationships among these traits; and (3) to investigate how year-to-year temperature variations impact them.

## Materials and methods

### Study area

The research was performed on the Borus Ridge of the Western Sayan Mountains, most of which is covered by conifer forests (*Pinus sylvestris*, *Pinus sibirica*, *Larix sibirica*, *Picea obovata* and *Abies sibirica*). The soils are loamy, thin and stony, with numerous hard rock yields. The climate of the study area is sharply continental, with large daily and seasonal magnitudes of temperature fluctuations. Precipitation is unevenly distributed throughout the year, with a maximum observed in July and a minimum in February–March. As the elevation increases, temperatures decrease by an average of 0.65 °C per 100 m and annual precipitation increases approximately by 100–200 mm per 100 m (Polikarpov and Nazimova 1963; Maurer et al. 2002; Hamlet and Lettenmaier 2005; Babushkina et al. 2018a).

The climatic data needed for this study were collected at Cheryomushki weather station (Cher 1951–2014, 52.87° N 91.42° E, 330 m a.s.l.) located on the bank of the Yenisei River, 5 km north of the dam of the Sayano-Shushensky Reservoir. As shown in previous studies conducted in this area (Babushkina et al. 2018a, 2020), after the dam building, climate warming accelerated primarily in winter, the climatic dynamics of the warm season are still similar to the regional one. The interannual temperature dynamics is sufficiently synchronous within the region (as shown by comparison with data from other weather stations up to 100 km of distance) to use the daily temperature series of the Cheryomushki station, corrected for the difference in elevation between the station and the sampling site. To determine the dates of the temperature transition through certain threshold values  $T_{thr}$  in spring and autumn, temperature series were smoothed by 21-day moving average, and the first and last day of  $T > T_{thr}$  were found on the smoothed curve for each year (Online resource Fig. A1). Interval between these two dates was considered as estimation of vegetative period. In this study, threshold values of +5 °C and +8 °C were considered according to threshold temperature range approximately in the range of 5–8 °C for xylogenesis of conifers in boreal and mountain forests estimated in meta-analysis by Rossi et al. (2008). The sums of active temperatures above  $T_{thr}$  were calculated by summing up all positive values of  $(T - T_{thr})$  for the identified vegetative periods. The time series of the obtained variables are shown in Online resource Fig. A2.

### Sampling, processing, and measurements

The sampling site is located 9 km southeast of the weather station on the north-eastern mountain slope, 50–100 m under

forest line (52.81° N 91.51° E, 1300–1350 m a.s.l.). Forest stand here consists of *Pinus sylvestris*, *Pinus sibirica* and *Picea obovata* with mature trees of all three species forming its canopy. For the sampling of cores, living mature (cambial age > 80 years) dominant and subdominant trees without signs of mechanical damage were selected. The limitation of the minimum age allowed us to minimize age trends in the anatomical structure of tree rings for the period under consideration (cf. Vysotskaya and Vaganov 1989; Lei et al. 1996; Eilmann et al. 2009). The homogeneous height of the sampled trees also minimized the effect of the axial variation of anatomical traits (Anfodillo et al. 2013). Cores were taken with incremental borers at the chest height (~ 1.3 m). Thin (~ 15–20 µm) wood cross-sections were obtained from the cores on a sledge microtome and stained with safranin. Next, sections were dehydrated with alcohols of increasing concentration and fixed on permanent microscope slides with Canadian balsam. Anatomical measurements were carried out on microphotographs over a period of 50 years (1965–2014 for *Picea obovata*, 1968–2017 for the *Pinus* species); list of measured and calculated tree-ring traits is presented in Table 1. For each tree ring, we selected five radial files of cells (Seo et al. 2014; Belokopytova et al. 2019) and measured cell number ( $N$ ), lumen diameter ( $LD$ ) and double cell wall thickness ( $DWT$ ) with an accuracy of 0.01 µm (Vaganov et al. 1985; Larson 1994). Then, the corresponding series of radial diameter ( $D = LD + DWT$ ) and single cell wall thickness ( $CWT = DWT/2$ ) were calculated from the  $LD$  and  $DWT$  series.

### Separation of tree ring to zones and assessment of their traits

To separate earlywood and latewood, the Mork index (Mork 1928; Denne 1989) was adapted. The threshold value  $CWT/D = 0.125$  was empirically selected to be located in the area of the lowest density of cells' distribution between typical earlywood and latewood cells (Online resource Fig. A3). Note that the  $CWT/D$  values for typical earlywood cells are similar for all three species, which allowed the use of the common threshold value. Since drought-related intra-annual density fluctuations ( $IADF$ ) should not be observed in the cold and wet conditions of the study area, the almost complete absence (less than 1%) of rings where  $CWT/D$  after rising above the threshold returns to lower values testifies in favor of a correctly selected threshold value.

Then, for each ring as a whole and separately for earlywood and latewood, values of  $N$ , average  $D$  and average  $CWT$  were calculated. In addition, the maximum values of  $D$  and  $CWT$ , the position of the transition from earlywood to latewood  $PosLW$  (Online resource Fig. A4), and tree-ring width ( $TRW = \Sigma D$ ) were identified in each ring. To compare tracheidograms (series of intra-seasonal  $D$  and  $CWT$

**Table 1** Measured and calculated tree-ring traits

Description	Abbreviation	Unit of measurement
Cell number in tree ring (per radial file of cells)	$N$	–
Cell number in earlywood (per radial file of cells)	$N_{ew}$	–
Cell number in latewood (per radial file of cells)	$N_{lw}$	–
Lumen radial diameter	$LD$	$\mu\text{m}$
Double cell wall thickness	$DWT$	$\mu\text{m}$
Tree ring width	$TRW$	mm
Cell radial diameter	$D$	$\mu\text{m}$
Average cell radial diameter in earlywood	$D_{ew}$	$\mu\text{m}$
Average cell radial diameter in latewood	$D_{lw}$	$\mu\text{m}$
Average cell radial diameter in tree ring	$D_{mean}$	$\mu\text{m}$
Maximum cell radial diameter in tree ring	$D_{max}$	$\mu\text{m}$
Cell wall thickness	$CWT$	$\mu\text{m}$
Average cell wall thickness in earlywood	$CWT_{ew}$	$\mu\text{m}$
Average cell wall thickness in latewood	$CWT_{lw}$	$\mu\text{m}$
Average cell wall thickness in tree ring	$CWT_{mean}$	$\mu\text{m}$
Maximum cell wall thickness in tree ring	$CWT_{max}$	$\mu\text{m}$
Relative position of transition from earlywood to latewood cells in radial file	$PosLW$	%

variability) of the rings with different  $N$ , their normalization was used, i.e. compression or stretching of tracheidograms to a single value  $N = 15$  cells (Vaganov 1990; Belokopytova et al. 2019).

### Statistical analysis

To assess the relationships between anatomical traits, Pearson paired correlation coefficients and regression models were used; for each species, total set of 250 tree rings (5 trees  $\times$  50 years) was examined. In addition to linear regression models, we also used an exponential model with equation  $y = a_0 + a_1 \cdot \exp(a_2 \cdot x)$ , where the numerical coefficients are fitted with the least squares method. The determination coefficients for nonlinear models were calculated by the equation  $R^2 = 1 - \frac{\sum (y_{actual} - y_{model})^2}{\sum (y_{actual} - y_{mean})^2}$  (Kvålseth 1985).

## Results

### Variability of wood anatomy near forest line

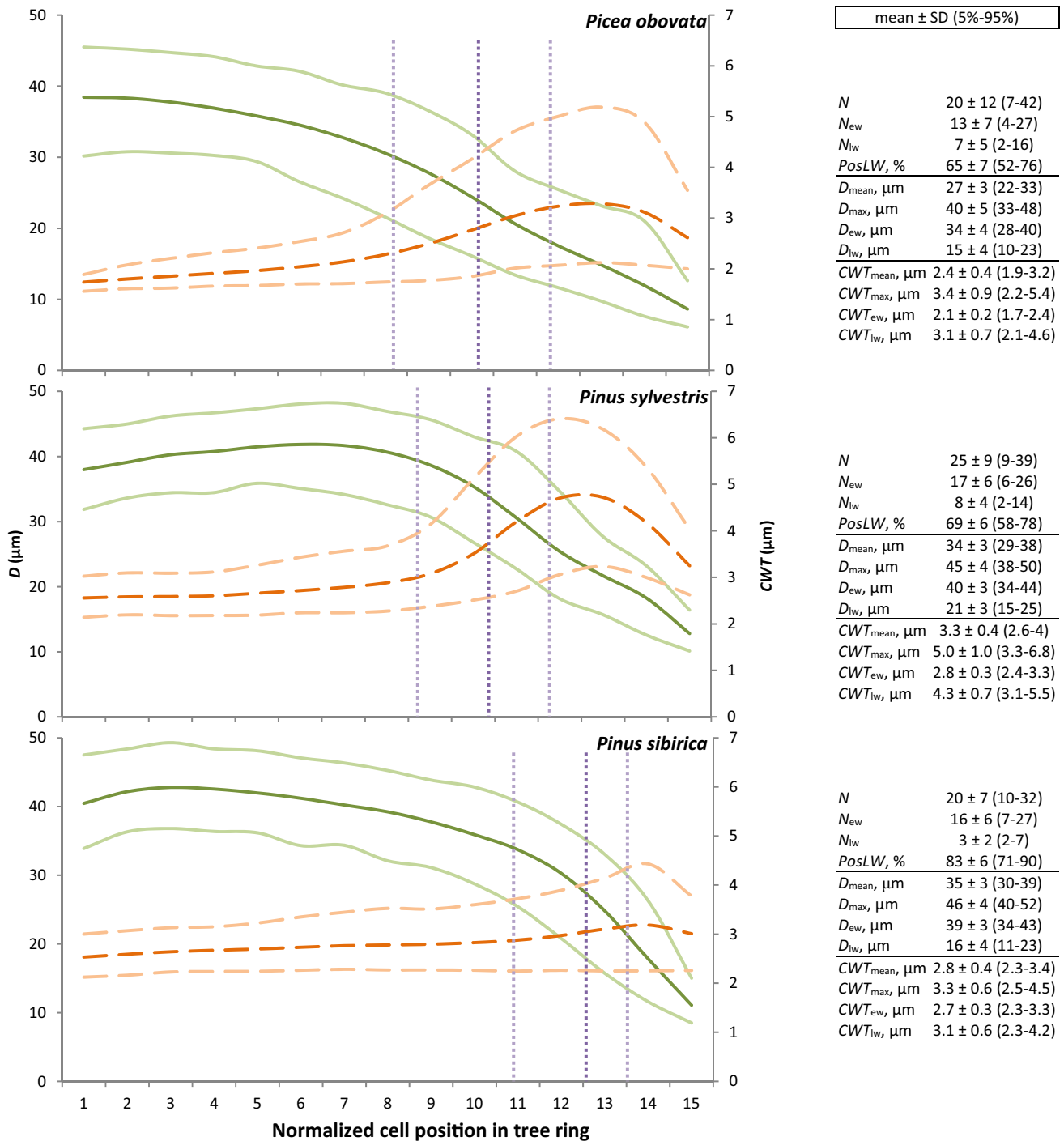
For each of the studied conifer species, average tracheidograms and range of variability for  $D$  and  $CWT$  for all measured rings show wood anatomical traits' dynamics within the tree rings (Fig. 1). The cell number  $N$  is comparable for all three species, while latewood occupies a much smaller fraction of the ring (17% on average) for Siberian pine than for Scots pine and spruce (31% and 35% on

average, respectively). The first tracheids in the earlywood have an average  $D$  over the 50 analyzed rings of 38–40  $\mu\text{m}$  in all species. In spruce, these cells are the largest, but in pine species,  $D$  increases slightly from the beginning of the ring, reaching a maximum of 45–46  $\mu\text{m}$  at 30–50% (*P. sylvestris*) or 10–20% (*P. sibirica*) of ring width. Then, in all species,  $D$  decreases to 9–12  $\mu\text{m}$  in the latewood; the most gradual decrease is observed in *Picea*.

Over the 50-year period, the  $CWT$  is stable in most part of the earlywood, i.e. it has similar average values (2.5–2.8  $\mu\text{m}$  for both *Pinus* species and 1.7–2.1  $\mu\text{m}$  for *Picea*) and low magnitude of inter-seasonal variability. Then, its values and the range of variability gradually increase to the middle of the latewood zone (average values: *P. sylvestris* —5  $\mu\text{m}$ , *P. sibirica* —3.3  $\mu\text{m}$ , *P. obovata*—3.4  $\mu\text{m}$ ), and toward the last cells decrease to 2.6–3.2  $\mu\text{m}$ . Cell wall thickness increase from earlywood to latewood is the least pronounced for *P. sibirica*, in the most extreme cases  $CWT$  remains stable ( $\sim 2.3 \mu\text{m}$ ) throughout the entire ring.

### Intrinsic patterns: relationships between anatomical traits

Pattern of strong and weak relationships is similar for all three species (Table 2). The production of tracheids in earlywood and latewood is significantly positively correlated with each other, which provides a strong positive relationship of  $N$  with both  $N_{ew}$  and  $N_{lw}$ . Wider earlywood ( $PosLW > 50\%$  in 98% of measured rings) leads to a stronger relationship between  $N$  and  $N_{ew}$  than between  $N$  and  $N_{lw}$ .



**Fig. 1** Tracheidograms of cell radial diameter  $D$  (solid lines), cell wall thickness  $CWT$  (dashed lines), and inter-annual range of transition to latewood  $PosLW$  (vertical dotted lines) for three species in the study area. Light lines represent 5% and 95% percentiles, dark lines

represent mean values over all 50-year period. On the table at the right from each plot, ranges of variation are presented: mean value, standard deviation, 5% and 95% percentiles for each investigated tree-ring trait

Note that  $PosLW$  correlates more strongly with  $N_{lw}$  than with  $N_{ew}$ , and does not have a significant correlation with  $N$ .

The dependences of the radial diameter traits on cell number are stronger after separation of ring into earlywood

and latewood: the positive correlation of  $D_{ew}$ ,  $D_{max}$ , and  $D_{mean}$  is maximum with  $N_{ew}$ ;  $D_{lw}$  is more strongly associated with  $N_{lw}$ . The increase in  $PosLW$  is associated with an

**Table 2** Correlations between anatomical traits

Traits	$N$	$N_{ew}$	$N_{lw}$	$PosLW$	$D_{mean}$	$D_{max}$	$D_{ew}$	$D_{lw}$	$CWT_{mean}$	$CWT_{max}$	$CWT_{ew}$
<i>Picea obovata</i>											
$N_{ew}$	<b>0.98</b>										
$N_{lw}$	<b>0.94</b>	<b>0.84</b>									
$PosLW$	-0.11	0.08	<b>-0.39</b>								
$D_{mean}$	<b>0.57</b>	<b>0.61</b>	<b>0.46</b>	<b>0.31</b>							
$D_{max}$	<b>0.44</b>	<b>0.45</b>	<b>0.39</b>	0.10	<b>0.85</b>						
$D_{ew}$	<b>0.44</b>	<b>0.43</b>	<b>0.41</b>	0.04	<b>0.92</b>	<b>0.89</b>					
$D_{lw}$	<b>0.83</b>	<b>0.76</b>	<b>0.87</b>	<b>-0.34</b>	<b>0.59</b>	<b>0.46</b>	<b>0.51</b>				
$CWT_{mean}$	<b>0.77</b>	<b>0.67</b>	<b>0.87</b>	<b>-0.48</b>	<b>0.50</b>	<b>0.43</b>	<b>0.51</b>	<b>0.90</b>			
$CWT_{max}$	<b>0.82</b>	<b>0.74</b>	<b>0.88</b>	<b>-0.36</b>	<b>0.57</b>	<b>0.45</b>	<b>0.52</b>	<b>0.93</b>	<b>0.95</b>		
$CWT_{ew}$	<b>0.64</b>	<b>0.60</b>	<b>0.64</b>	<b>-0.25</b>	<b>0.48</b>	<b>0.42</b>	<b>0.49</b>	<b>0.67</b>	<b>0.83</b>	<b>0.69</b>	
$CWT_{lw}$	<b>0.81</b>	<b>0.73</b>	<b>0.86</b>	<b>-0.35</b>	<b>0.57</b>	<b>0.44</b>	<b>0.52</b>	<b>0.93</b>	<b>0.96</b>	<b>0.99</b>	<b>0.70</b>
<i>Pinus sylvestris</i>											
$N_{ew}$	<b>0.96</b>										
$N_{lw}$	<b>0.87</b>	<b>0.71</b>									
$PosLW$	-0.09	<b>0.15</b>	<b>-0.52</b>								
$D_{mean}$	<b>0.66</b>	<b>0.75</b>	<b>0.38</b>	<b>0.33</b>							
$D_{max}$	<b>0.69</b>	<b>0.69</b>	<b>0.55</b>	-0.01	<b>0.85</b>						
$D_{ew}$	<b>0.66</b>	<b>0.67</b>	<b>0.52</b>	-0.01	<b>0.92</b>	<b>0.91</b>					
$D_{lw}$	<b>0.76</b>	<b>0.69</b>	<b>0.74</b>	<b>-0.26</b>	<b>0.69</b>	<b>0.67</b>	<b>0.71</b>				
$CWT_{mean}$	<b>0.42</b>	<b>0.25</b>	<b>0.63</b>	<b>-0.60</b>	<b>0.19</b>	<b>0.34</b>	<b>0.37</b>	<b>0.61</b>			
$CWT_{max}$	<b>0.57</b>	<b>0.44</b>	<b>0.68</b>	<b>-0.45</b>	<b>0.36</b>	<b>0.45</b>	<b>0.47</b>	<b>0.73</b>	<b>0.89</b>		
$CWT_{ew}$	<b>0.31</b>	<b>0.21</b>	<b>0.42</b>	<b>-0.34</b>	<b>0.22</b>	<b>0.30</b>	<b>0.34</b>	<b>0.41</b>	<b>0.87</b>	<b>0.64</b>	
$CWT_{lw}$	<b>0.50</b>	<b>0.37</b>	<b>0.63</b>	<b>-0.45</b>	<b>0.33</b>	<b>0.39</b>	<b>0.43</b>	<b>0.72</b>	<b>0.91</b>	<b>0.97</b>	<b>0.65</b>
<i>Pinus sibirica</i>											
$N_{ew}$	<b>0.98</b>										
$N_{lw}$	<b>0.74</b>	<b>0.59</b>									
$PosLW$	0.04	<b>0.22</b>	<b>-0.61</b>								
$D_{mean}$	<b>0.50</b>	<b>0.54</b>	<b>0.18</b>	<b>0.30</b>							
$D_{max}$	<b>0.43</b>	<b>0.44</b>	<b>0.25</b>	0.10	<b>0.82</b>						
$D_{ew}$	<b>0.40</b>	<b>0.38</b>	<b>0.32</b>	-0.03	<b>0.92</b>	<b>0.83</b>					
$D_{lw}$	<b>0.65</b>	<b>0.56</b>	<b>0.75</b>	<b>-0.38</b>	<b>0.41</b>	<b>0.33</b>	<b>0.42</b>				
$CWT_{mean}$	<b>0.61</b>	<b>0.53</b>	<b>0.70</b>	<b>-0.34</b>	<b>0.53</b>	<b>0.49</b>	<b>0.58</b>	<b>0.80</b>			
$CWT_{max}$	<b>0.70</b>	<b>0.62</b>	<b>0.74</b>	<b>-0.30</b>	<b>0.49</b>	<b>0.39</b>	<b>0.50</b>	<b>0.87</b>	<b>0.88</b>		
$CWT_{ew}$	<b>0.57</b>	<b>0.51</b>	<b>0.62</b>	<b>-0.26</b>	<b>0.54</b>	<b>0.52</b>	<b>0.58</b>	<b>0.70</b>	<b>0.97</b>	<b>0.78</b>	
$CWT_{lw}$	<b>0.63</b>	<b>0.56</b>	<b>0.66</b>	<b>-0.27</b>	<b>0.48</b>	<b>0.35</b>	<b>0.48</b>	<b>0.86</b>	<b>0.83</b>	<b>0.96</b>	<b>0.70</b>

increase in  $D_{mean}$ , does not correlate with  $D_{ew}$  and  $D_{max}$ , but has a negative correlation with  $D_{lw}$ . Cell radial diameter traits  $D_{ew}$ ,  $D_{max}$ , and  $D_{mean}$  have strong positive correlations between themselves but less pronounced correlations with  $D_{lw}$ . Among the interrelations of the cell wall thickness with other anatomical traits, the strongest positive correlations are with  $N_{lw}$  and  $D_{lw}$ , a negative relationship is observed with  $PosLW$ . At the same time, all  $CWT$  traits are closely correlated.

The relationships that were strongly significant for all species and not described directly with mathematical functions were considered in more details (Online resource Fig.

A5). The  $N_{lw}(N_{ew})$  dependence is close to linear, but the distribution of data points (tree rings) on the scatter plots has shape of a triangle rather than straight line. The  $D(N)$  dependences in both zones of the ring are nonlinear and are well described by a negative exponential functions with a horizontal asymptote in the area of wide rings ( $R^2$  of exponential models is stably higher than that of linear models, as well as their curves' visual fitness to actual data points). Application of exponential functions  $D(N)$  improves the quality of modeling the  $TRW(N)$  dependence in comparison with the simple linear model with constant average cell diameter (Table 3), allowing in one model to obtain the maximum

explained variation and plausible estimate of  $D_{\text{mean}}$  in wide rings. In other dependences, nonlinearity was not observed.

### Temperature variation and its impact on wood anatomical structure

Unlike winter climate of the study area, the temperature characteristics of the growing season did not undergo drastic changes after the construction of the reservoir and the launch of the hydroelectric station (Online resource Fig. A2). Nevertheless, long-term trends were observed: June to August temperatures increased on average by 0.12 °C per decade; the sum of active temperatures increased by 4–5 °C

per decade, depending on the choice of the threshold temperature value; every decade, the growing season began earlier by 0.8–1.0 days and ended later by 1.2–2.1 days (i.e. its duration increased by 2.1–3.0 days per decade). Note also that the most extreme years in terms of heat supply were unevenly distributed in the considered period (Table 4). The extremely cold and short vegetative seasons were more often observed before the reservoir was filled (the most extreme years were 1971, 1972, 1983, 1984, 1985) than after that (1995, 2014), and vice versa, the longest and warmest vegetative seasons were recorded after the filling of the reservoir: 1990, 1998, 1999, 2001, 2002, 2004, 2007.

**Table 3** Estimations of  $D_{\text{mean}}$  from various models  $TRW(N, D_{\text{mean}})$  and from actual time series

Tree species	$TRW = TRW_0 + D_{\text{mean}} \cdot N$			$TRW = D_{\text{mean}} \cdot N$		Nonlinear model <sup>a</sup>		Actual series		
	$TRW_0$	$D_{\text{mean}}$	$R^2$	$D_{\text{mean}}$	$R^2$	$D_{\text{mean}}^*$ <sup>b</sup>	$R^2$	$D_{\text{mean}}$	$D_{\text{mean}}^*$ <sup>b</sup>	$N_{\text{mean}}$
<i>Pinus sylvestris</i>	-0.0676	37.16	0.975	34.79	0.971	35.87	0.976	33.77	34.69 35.12 <sup>c</sup>	25.27
<i>Pinus sibirica</i>	-0.0711	38.90	0.965	35.66	0.958	36.65	0.965	34.81	35.91 36.19 <sup>c</sup>	19.76
<i>Picea obovata</i>	-0.0646	31.85	0.968	29.40	0.961	30.39	0.968	27.40	29.01 30.17 <sup>c</sup>	19.75

<sup>a</sup>Nonlinear model:  $TRW = N \cdot (D_{\text{mean}}^* - a_1 \cdot \exp(-a_2 \cdot N))$

<sup>b</sup> $D_{\text{mean}}^*$ —estimation of mean  $D$  in wide rings (asymptote in the exponential function  $D_{\text{mean}}(N)$  for each species, mean value for five widest rings for each tree in actual series)

<sup>c</sup>estimation of  $D_{\text{mean}}^*$  only for trees with  $N_{\text{mean}} > 20$

**Table 4** Years when the most extreme values of temperature variables were recorded (during 1968–2014, common period for anatomical measurements of the three species)

Values	Temperature variable	Low heat supply		High heat supply	
		Values	Years <sup>a</sup>	Values	Years <sup>a</sup>
June–August temperature	$T_{JJA}$ (°C)	9.2–9.8	<u>1985</u> , <u>1971</u> , 1988, 2010, <u>1984</u>	11.6–12.0	2005, 2008, <u>1998</u> , <u>2002</u> , 2012
Sum of active temperatures > 8 °C	$\Sigma T8$ (degree-days)	1040–1310	<u>1985</u> , <u>1971</u> , <u>1995</u> , 2006, 1970	1794–2036	<u>2004</u> , <u>2001</u> , <u>2002</u> , <u>1999</u> , <u>1998</u>
Sum of active temperatures > 5 °C	$\Sigma T5$ (degree-days)	1560–1690	<u>1985</u> , <u>1983</u> , <u>1972</u> , 2010, 1976	2040–2400	<u>2007</u> , <u>2002</u> , <u>2004</u> , <u>2000</u> , <u>2001</u>
Beginning of period with temperatures > 8 °C	$T8_{\text{beg}}$ (date)	12–21 Jun	<u>1995</u> , 1989, <u>1971</u> , <u>2014</u> , <u>1984</u>	14–19 May	<u>2004</u> , 1992, <u>2001</u> , <u>2002</u> , <u>1990</u>
Ending of period with temperatures > 8 °C	$T8_{\text{end}}$ (date)	14–21 Aug	1969, 2006, <u>1985</u> , <u>1972</u> , 1968	4–12 Sep	<u>2007</u> , <u>2004</u> , 1973, <u>1998</u> , 2010
Duration of period with temperatures > 8 °C	$T8_{\text{dur}}$ (days)	61–71	<u>1985</u> , <u>1995</u> , 1996, <u>1971</u> , 1969	104–122	<u>2004</u> , <u>2001</u> , <u>2002</u> , <u>1990</u> , <u>1999</u>
Beginning of period with temperatures > 5 °C	$T5_{\text{beg}}$ (date)	30 May–3 Jun	<u>2014</u> , <u>1984</u> , <u>1983</u> , 2010, 2013	25 Apr–9 May	<u>2007</u> , <u>1990</u> , <u>1999</u> , 1991, <u>2001</u>
Ending of period with temperatures > 5 °C	$T5_{\text{end}}$ (date)	28 Aug–2 Sep	<u>1972</u> , 1996, <u>1985</u> , 1968, 1974	19–23 Sep	1988, 2006, <u>2007</u> , 2012, <u>2002</u>
Duration of period with temperatures > 5 °C	$T5_{\text{dur}}$ (days)	99–103	<u>1972</u> , <u>1983</u> , <u>1985</u> , <u>2014</u> , 2013	130–149	<u>2007</u> , <u>2002</u> , <u>2004</u> , 1997, 2000

<sup>a</sup>For each temperature variable, 5 years are indicated in order from the most extreme to the less extreme value in each direction of the extreme. Underlined are years when extremes of the several variables, all in same direction, were registered

Typical for continental climate high magnitude of temperature fluctuations leads to an almost twofold difference in heat supply between the most extreme years; the vegetative season onset in spring has a fluctuation range of 38–39 days, its ending in autumn has range of 28–29 days, and duration varies by 50–61 days (according to estimates of temperature transition dates above and below considered threshold values).

No significant correlations were found between calculated temperature characteristics and the anatomical traits of earlywood, latewood, and total ring. However, in the most extreme years in terms of heat supply, similar deviations in the anatomical structure of tree rings were observed in all three species (Fig. 2). During extremely cold/short growing seasons, slightly larger but much thinner-walled cells were formed, and vice versa, during extremely warm/long seasons tracheids were slightly smaller but with much thicker walls. Significant differences ( $p < 0.05$ ) were observed in *CWT* at the border of earlywood and latewood (in 6–10th normalized cell positions for spruce, 7–14th positions for Scots pine, and 11–12th positions for Siberian pine), the difference in *D* is less stable (9–11th positions for spruce, 4th and 12th positions for Scots pine, 1st and 6th positions for Siberian pine).

## Discussion

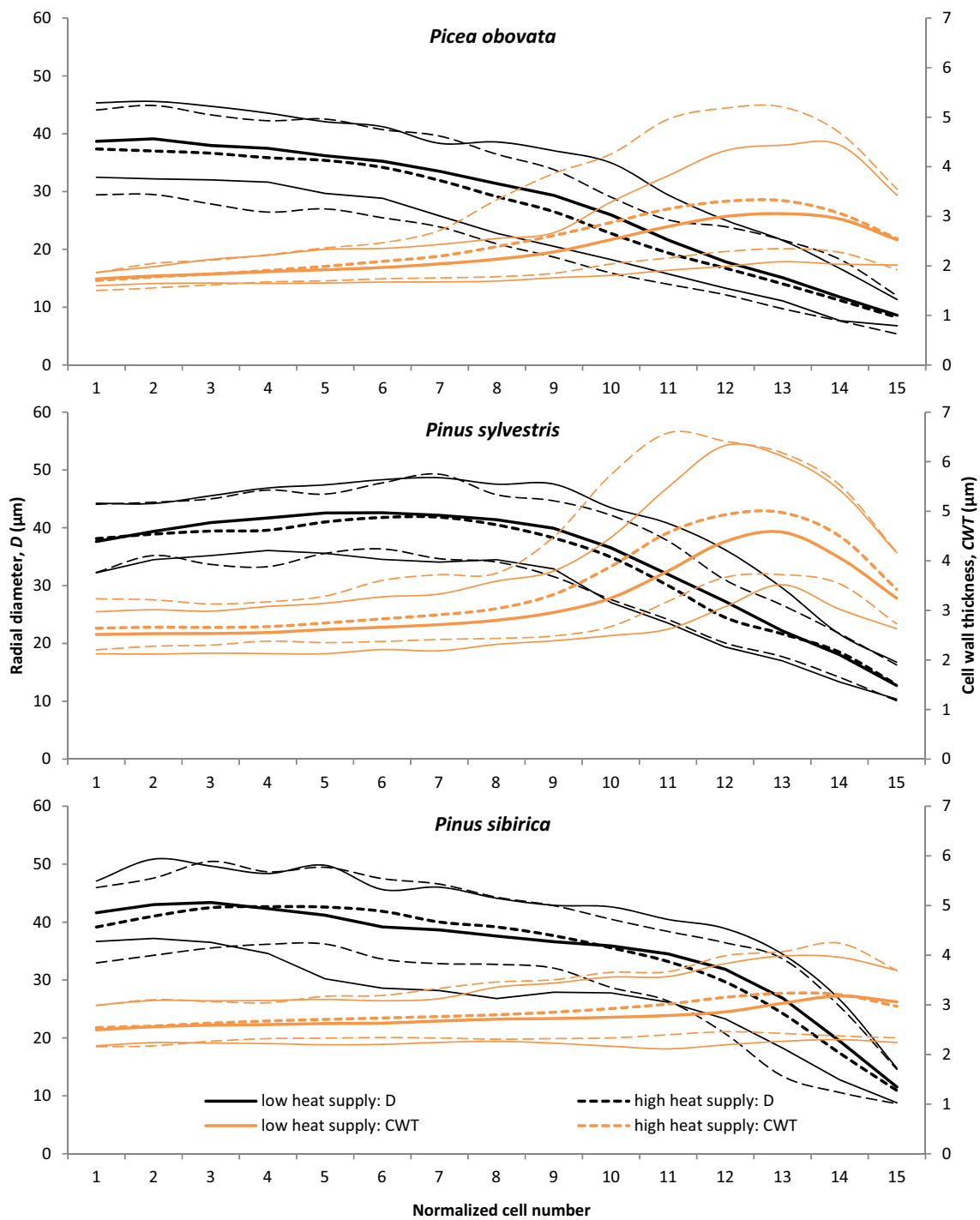
The study area is close to the upper boundary of the common species distribution range, i.e., at the left end of the bell-shaped curve of their temperature tolerance, according to Shelford's law (Shelford 1931), where low temperatures limit trees growth (Li et al. 2017). Taking into account the commonality of local conditions, like wind load or soil characteristics, we observe a plastic response of these conifers' morphology to environmental pressure of a similar direction and intensity. Common intra-seasonal timeframe of this pressure is provided by fairly minor differences (Babarykina and Grigoryev 2006; Ovchinnikova et al. 2011; Ovaskainen et al. 2020) and common patterns in primary and secondary growth phenology (e.g., cambial activity temperature threshold for conifers in Rossi et al. 2008; early beginning of photosynthesis in Suvorova et al. 2005, 2011; synchronous bud break and onset of cambial activity of evergreen conifers in Velisevich and Khutoroy 2009; Antonucci et al. 2015; etc.). This allows us to interpret any revealed differences in their wood anatomy primarily as the species specificity of growth processes' internal regulation and of the strategy of their adaptation to the cold and short vegetative season.

## General and species-specific patterns in the wood anatomical structure

The average cell number per radial file of tracheids in the tree ring has similar variation ranges for all three species. It seems that sharing habitat, habitus and phenological cycle as evergreen conifers provided common intra-seasonal patterns of the organic substances' synthesis and deposition in all three species. Furthermore, these common factors pressed the same requirements to the hydraulic architecture of xylem (Anfodillo et al. 2012, 2013; cf. Campelo et al. 2013), i.e. size and wall thickness of earlywood tracheids as main water conduits (Scweingruber 2012; Hacke et al. 2015). Small size of earlywood cells compared to warmer natural areas within the region (Babushkina et al. 2010, 2018b, 2020; Belokopytova et al. 2019) may be due linked to growth processes being limited by low temperature (Hoch and Körner 2003), slowing the production of new cells (Körner 1999; Körner and Paulsen 2004) and hindering deposition of macromolecules in the secondary cell walls (Crivellaro and Büntgen 2020). On the one hand, cold alpine forests are characterized by relatively low tree height, which is clearly linked to formation of smaller conduits at the stem base of mature trees (Anfodillo et al. 2013; Olson et al. 2014; Rungwattana and Hietz 2017). Moreover, combination of low temperatures and high relative air humidity during growth season in the study area reduces transpiration and cell turgor, leading to slower cell extension and eventually smaller tracheids (Lockhart 1965; Proseus and Boyer 2005). On the other hand, the limited size and relatively thick walls of the earlywood conduits, similar for all species, may have been selected for higher mechanical wood strength to resist high wind and snow loads, and also to minimize the risk of tracheids' damage by severe winter frosts (Davis et al. 1999; Mayr et al. 2002, 2006; Bigras and Colombo 2013; Hacke et al. 2015).

Differences in the latewood structure between the three species are more pronounced, namely its ratio in the ring and *CWT* values (see other observations comparing conifer species under similar conditions: Babushkina et al. 2010; Vaganov et al. 2010; Darikova et al. 2013; Carteni et al. 2018), with much lesser values of both traits for Siberian pine. Carteni et al. (2018) suggested that the transition to latewood is regulated by a sharp increase in the availability of carbohydrates in the lower part of the stem after cessation of the primary growth. Therefore, genetically predetermined (Kuznetsova 2007; Kuznetsova and Grek 2016) differences in the intensity and duration of the primary growth for Siberian pine, like longer needles, denser foliage, and especially additional development of the so-called summer shoots in mature trees during end of June—beginning of July (Goroshkevich 2006; Goroshkevich and Popov 2009; Velisevich et al. 2009), may lead to a retarded switch to latewood formation. The radial growth and anatomical structure also





**Fig. 2** Normalized tracheidograms of cell radial diameter  $D$  (dark) and cell wall thickness  $CWT$  (light) for years with extremely low (1971, 1972, 1983, 1984, 1985, 1995, 2014) and extremely high

(1990, 1998, 1999, 2001, 2002, 2004, 2007) heat supply. Thin lines represent 5% and 95% percentiles, thick lines represent mean values over 5 years

may be affected by competition for nutrients with reproductive processes (Innes 1994; Rovere et al. 2003; Olano et al. 2017), whose productivity is also typically higher for Siberian pine in comparison with other considered species and is shown to be strong competitor for resources in Siberian

pine provenances adapted to cold environments (Zhuk and Goroshkevich 2018). We suggest that a small ratio and low  $CWT$  of latewood for Siberian pine can be associated with a genetically fixed species strategy of diverting more resources to primary growth and reproduction, which is

realized through a low deposition rate of the tracheids' secondary wall compared to other species. However, this species is currently underappreciated as subject of research in the area of carbon assimilation and allocation. Therefore, to test this hypothesis, it would be interesting to conduct a meta-analysis of carbon deposition in various vegetative and reproduction organs on scale of comparison between different species and/or climatic zones of conifer distribution.

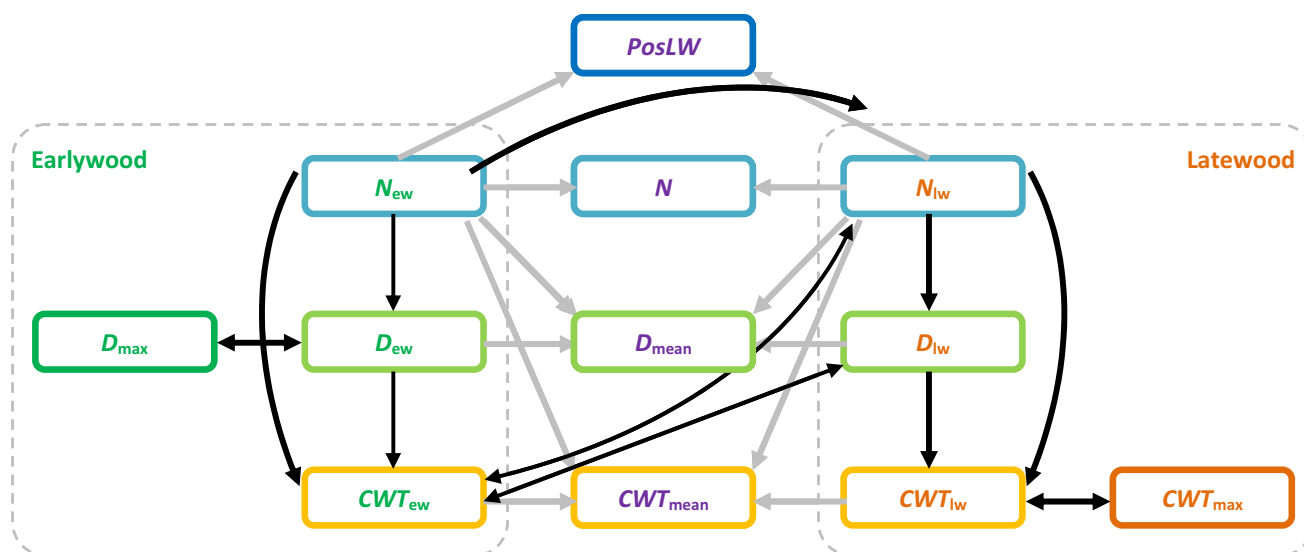
### Relationships between anatomical traits

Taking into account the functional dependences (Online resource Fig. A4) of the total ring traits on the traits of earlywood and latewood, the interconnections between anatomical traits common to all three coniferous species can be summarized schematically as presented on Fig. 3. The stability of the ratio of earlywood and latewood in the ring ( $PosLW$ ), regardless of radial growth rate, results from the tradeoff between water supply and carbon deposition/mechanical strength (Lachenbruch and McCulloh 2014). Since cambial activity during the season is regulated by the processes of primary growth through the synthesis of hormones and nutrients (Dodueva et al. 2014; Huang et al. 2014), it can be assumed that cell production in two zones of the ring is interconnected by feedback with the tree habitus and the characteristics of the photosynthetic apparatus both in process of its formation ( $N_{ew}$ ), and afterward ( $N_{lw}$ ).

A nonlinear dependence of the cell radial diameter on their number is found in both zones of the ring, but its non-linearity is more pronounced in earlywood. This may be due to the presence of two paths of regulation of cell expansion: (1) internal regulation of all secondary growth processes

by hormones and availability of nutrients (Vorobyova and Vorobyov 1999; Dünser and Kleine-Vehn 2015; Carteni et al. 2018); (2) external restriction of the growing cells' turgor and, accordingly, cell expansion by low temperature and high air humidity (Lockhart 1965; Proseus and Boyer 2005). As a result, in earlywood formed during relatively cool beginning of vegetative season, the second limitation blocks increase of cell size above certain threshold at  $N_{ew} > 10\text{--}15$  cells; latewood cells expand during the middle of the season at higher temperature and due to fast switch to cell wall deposition don't reach aforementioned size threshold, thus their expansion is mainly limited by decreasing concentration of growth hormones, and has more linear relationship with cell production.

In earlywood, the relationship between the results of successive stages of tracheid differentiation is relatively weak, which may be due to compensation mechanism in the kinetics of xylogenesis described by Balducci et al. (2016): an increase in the duration of a certain stage of tracheid maturation in the case of a decrease in its speed. Duration of the secondary cell wall deposition in latewood is limited by short duration of vegetative season, especially in cold alpine forests, which impedes the aforementioned compensatory mechanism (confer Cuny and Rathgeber 2016). Therefore, the rate of the corresponding process plays the prevailing role in the CWT values of this zone. In conditions of sufficient moisture, this rate is probably limited by the temperature dynamics and the efficiency of the photosynthetic apparatus, fully formed at this time of season. It should also be noted that, as seen in Online resource Fig. A3, the ratio of  $CWT/D$  in latewood has a definite maximum value of about 0.3–0.4, above which it practically does not rise. This is due



**Fig. 3** Intrinsic relationships between investigated tree-ring traits. Arrows indicate direction of statistical (black) and strictly functional (gray) relationships. Abbreviations of traits are presented according to Table 1

to the necessity to have enough inner space for organelles and cytoplasm until the very end of tracheid differentiation. Such an internal limitation leads to strengthening of the  $CWT(D)$  positive relationship in the last cells of the ring.

### The effect of heat supply and the duration of the vegetative season

At present, it is still not completely clear which of the two temperature-related factors limits the growth of trees in mountain ecosystems to a greater extent: the duration of the vegetative season (its onset and ending dates) or heat supply during xylogenesis (Bouriaud et al. 2005; King et al. 2013; Jochner et al. 2018). At the beginning of the season, an earlier onset of temperatures favorable for xylogenesis leads to an increase in the duration of the cambial activity (Gindl et al. 2001; Rossi et al. 2012, 2013). At the end of the vegetative season, a decrease in temperature primarily limits the process of organic substances' deposition in the structure of xylem (Hoch et al. 2002; Hoch and Körner 2003; Piper et al. 2006), leading to inhibition of cell wall thickening even before photosynthesis deactivation. On the other hand, the rate of growth processes (both the formation of new shoots and needles, and xylogenesis in the trunk) is regulated by heat supply during all the season, which can be expressed in terms of the sum of active temperatures. The difficulty in separation of the signal from duration and heat supply of the vegetative season is that these climatic variables are positively interrelated in the study area: most years with extremely high summer temperatures are characterized by an earlier beginning and/or late ending of the season, and vice versa (Table 4). Therefore, in this case, temperature extremes were considered in the complex. The absence of significant correlations between generalized anatomical traits and temperature variables may be due to the mismatch of the temporal scales. Even while generalized, cell numbers and measurements are regulated by climatic fluctuations over much shorter periods than full vegetative season ( $T > 8\text{ }^{\circ}\text{C}$  or  $T > 5\text{ }^{\circ}\text{C}$ ) or the most part of it (June–August).

At the same time, the analysis of tracheidograms of pointer (extreme) years showed more significant results. First of all, the extremes of heat supply and the duration of the vegetative season affect the deposition of the secondary cell wall. However, their influence is overridden by requirements for the hydraulic structure through internal regulation in typical earlywood cells, and by limitation of the minimum necessary lumen volume in the last cells of the ring. An unexpected reverse reaction of the radial cell diameter (the formation of larger cells during short/cold seasons) may be due to the fact that the result of cell expansion depends on its duration more than on rate (Denne 1972; Anfodillo et al. 2012; Cuny 2013), and increased by higher temperatures availability of nutrients stimulates a faster transition from

cell extension to wall thickening (Carteni et al. 2018). In addition, a decrease in the radial size and an increase in the cell wall thickness in the middle of the ring can be interpreted as shift to the higher proportion of latewood during warmer/longer growth season, which may be because of earlier beginning and later ending of latewood cells' production after completion of the primary growth. This hypothesis is supported by observations, for example, in the Natural Reserve “Stolby”, where regional warming trends led to not only earlier, but also faster development of foliage for all three studied conifer species (Ovchinnikova et al. 2011; Ovaskainen et al. 2020).

**Author contribution statement** EAV and EAB conceived the research idea and study design, planned the analyses. DFZ, EAB, LVB and collected the field data. LVB and AC performed the analyses and led writing the paper. All authors contributed critically to the drafts of this manuscript and gave final approval for publication.

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### Compliance with ethical standards

**Conflict of interest** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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