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ORIGINAL ARTICLE

Pine and larch tracheids capture seasonal variations of climatic signal at moisture-limited sites

Liliana V. Belokopytova[1] · **Elena A. Babushkina**[1] · **Dina F. Zhirnova**[1] · **Irina P. Panyushkina**[2] · **Eugene A. Vaganov**[1,3,4]

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Abstract

Key message **Although the radial diameter and wall thickness of conifer tracheids from dry environments are climatic-sensitive across the full ring area, each cell parameter has a specific zone in a ring where its climatic response reaches the maximum.**

Abstract Seasonal dynamics of the timing and rate in cell production and differentiation imprint climate signals into intra-ring variations of anatomical wood structure (e.g. intra-annual density fluctuations). Despite recent methodological advances in quantitative wood anatomy, our understanding of xylem response to climate at the finest scale of intra-ring resolution is incomplete. The goal of this study is to investigate intra-ring changes of tracheid dimensions (cell radial diameter and wall thickness) controlled by moisture stress. Anatomical wood parameters of *Pinus sylvestris* and *Larix sibirica* from two drought-susceptible locations in Khakassia, South Siberia, were analysed. We found that inter-annual variation of tracheid parameters regularly exceeds the variation between radial tracheid files. This suggests that the climatic signal is recorded throughout the entire ring. However, each cell parameter has a specific zone in the ring where its climatic response reaches the maximum. The climatic response of the radial cell diameter has a temporal shift across the ring, which is particularly apparent in pine rings. The climatic response of cell wall thickness at the intra-ring scale has a more complex pattern. Our results facilitate investigation of the climate impact on tree rings at the finest intra-ring scale by quantifying the timing of climatic impact on ring structure and identifying specifically when climate impacts the formation of a particular cell.

Keywords Conifer trees · Xylem · Quantitative wood anatomy · Tree-ring structure · Climatic response · South Siberia

Introduction

Annual tree rings are affected by environmental factors including climate. On the level of cell production, tree rings record a climatic signal by means of changes in timing and rate of production (Prislan et al. 2013; Gričar et al. 2014; Swidrak et al. 2014; Balducci et al. 2016). Changes in cell differentiation further translate into variations of xylem anatomical structure (Yasue et al. 2000; Balducci et al. 2016; Ziaco and Biondi 2016). Quantitative wood anatomy can be used to address research questions related to how climate changes the ring's cell structure, and how xylem anatomical parameters could be utilised in climatic modelling (Panyushkina et al. 2003; Venegas-González et al. 2015; Singh et al. 2016; Castagneri et al. 2017; Wang et al. 2017). Recent advances in quantitative wood anatomy significantly improved the efficiency and accuracy of xylem anatomical measurements (von Arx and Carrer 2014; Gärtner et al. 2015; von Arx et al. 2016; Prendin et al. 2017;

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✉ Elena A. Babushkina
babushkina70@mail.ru

[1] Khakass Technical Institute, Siberian Federal University, 27 Shchetinkina St, 655017 Abakan, Russia

[2] Laboratory of Tree-Ring Research, University of Arizona, 1215 W. Lowell St, Tucson, AZ 85721, USA

[3] Siberian Federal University, 79 Svobodny Pr., 660041 Krasnoyarsk, Russia

[4] V. N. Sukachev Institute of Forest, SB RAS, 50/28 Akademgorodok, 660036 Krasnoyarsk, Russia

Peters et al. 2018). New methodological tools available for analysis of xylem anatomical data enable the employment of the wood structure parameters for climate reconstruction at very fine intra-seasonal scales well beyond the conventional use of ring widths with annual or seasonal time resolution (Wheeler and Baas 1993; Wimmer et al. 2000; Panyushkina et al. 2003; Eilmann et al. 2009; Fonti et al. 2010). For example, earlywood measurements of vascular parameters in ring-porous trees have been successfully used to evaluate the past moisture regime of the Mediterranean region and the past temperatures of the temperate climates in Europe (Pérez-de-Lis et al. 2016; Puchałka et al. 2016; García-González and Souto-Herrero 2017). It was also suggested that the intra-annual density fluctuations (IADFs) of tree rings from arid environments appear to be a good indicator for short-term droughts during the growing season (Battipaglia et al. 2010; Campelo et al. 2007; De Micco et al. 2012, 2016; Wilkinson et al. 2015; Zalloni et al. 2016). Analysis of the radial cell diameter and cell wall thickness of conifer tracheids from moisture-stressed environments has shown a high sensitivity of these parameters to moisture deficiency (Eilmann et al. 2009; Fonti and Babushkina 2016). Nevertheless, the temporal resolution of the xylem climatic signals is not well understood.

Another important approach of quantitative wood anatomy research is modelling kinetics of seasonal ring growth using estimates for the duration and rate of cell differentiation dynamics to theoretically validate parameters of tree-ring anatomical structure (Dodd and Fox 1990; Deslauriers and Morin 2005; Rossi et al. 2006; Rathgeber et al. 2016; Castagneri et al. 2017). The success of this approach results in the feedback scheme of climatic factors impacting wood anatomical structure through the control of key processes of morphogenesis (Seo et al. 2008; Cuny et al. 2013, 2014; Rathgeber et al. 2016). Some research claims that only latewood cells have "climatic potential" (Cuny and Rathgeber 2016), although this conclusion was drawn from small site studies. In contrast, other research indicates that climatic sensitivity of wood structure in the form of IADF is observed not only in latewood but throughout the entire tree ring (Campelo et al. 2006; Battipaglia et al. 2010, 2016, Babst et al. 2016). All these studies indicate that xylem anatomical parameters respond to climate variations at the time of their formation, and furthermore xylem formation may be responding to climatic stress with various strategies (Castagneri et al. 2017).

The main goal of this research was to evaluate the intra-ring dynamics of climatic signals in xylem anatomical parameters of conifer trees growing in a moisture-stressed environment in order to understand the climatic sensitivity of xylem at very fine intra-seasonal resolution. For this, we aim to (1) develop site chronologies of xylem anatomical parameters and evaluate their statistical characteristics; (2) determine the relationship between tree-ring width, cell number and mean cell size; (3) compare the intra-seasonal and inter-annual variability of xylem anatomical parameters, and (4) identify main climatic factors driving the anatomical ring structure. The study was conducted in the forest-steppe and steppe zones of South Siberia where conifer tree growth is limited by both temperature and precipitation, and summer droughts are often recorded. The forest stands comprise two dominant conifers, evergreen (Scots pine) and deciduous (Siberian larch), to facilitate a comparison of xylem anatomical traits between two different tree species.

Materials and methods

Site settings and climate

The study area is situated on the margins of the Sayan-Altai Mountains in South Siberia. The landscape comprises dry and cold depressions with steppes and forest-steppe ecotone, and mountain ranges covered predominantly with conifer forests. The samples were collected from two sites in the Minusinsk depression (Fig. 1a). The Minusinsk site (MIN, 53°45′N, 91°56′E, 300 m a.s.l.) is located 15 km east of the Minusinsk weather station (#29866, 53°41′N, 91°40′E, 250 m a.s.l.). The MIN site is covered with pine-birch forest on a chernozem soil layered with sand. The site is part of a large isolated tree stand surrounded by dry grasslands of the steppe zone called the Minusinsk forest. The forest vegetation in this dry environment is mainly sustained by extra moisture from numerous small lakes and rivers scattered throughout the area. The Bidja site (BID, 54°00′N, 91°01′E, 660 m a.s.l.) is located in the forest-steppe zone of the Batenevsky Range foothills, 60 km northeast of the Minusinsk weather station. The trees were sampled in the pine–larch open canopy forest on grey forest soils.

The climate of the study region is temperate extremely continental (Table S1; Alisov 1956). The annual average air temperature varies from year to year in range from − 1.5 to + 4.1 °C. Warmest temperatures occur from the end of June to the first half of July, when daily values sometimes exceed 30 °C. The annual sum of precipitation varies from 260 to 580 mm. About 90% of precipitation falls between April and October with a maximum in July. Vegetative season lasts approximately from the third decade of April to the beginning of October, when daily temperatures are higher than 5 °C. However, onset of cambial activity can be delayed by moisture deficit in May in extremely dry years (cf. delay observations in more arid conditions by Ren et al. 2015, 2018; Ziaco et al. 2018). Droughts may also occur later in the season.

The foothills generally receive more precipitation (ca. 140 mm per year) and less warmth (ca. 0.7 °C) than the

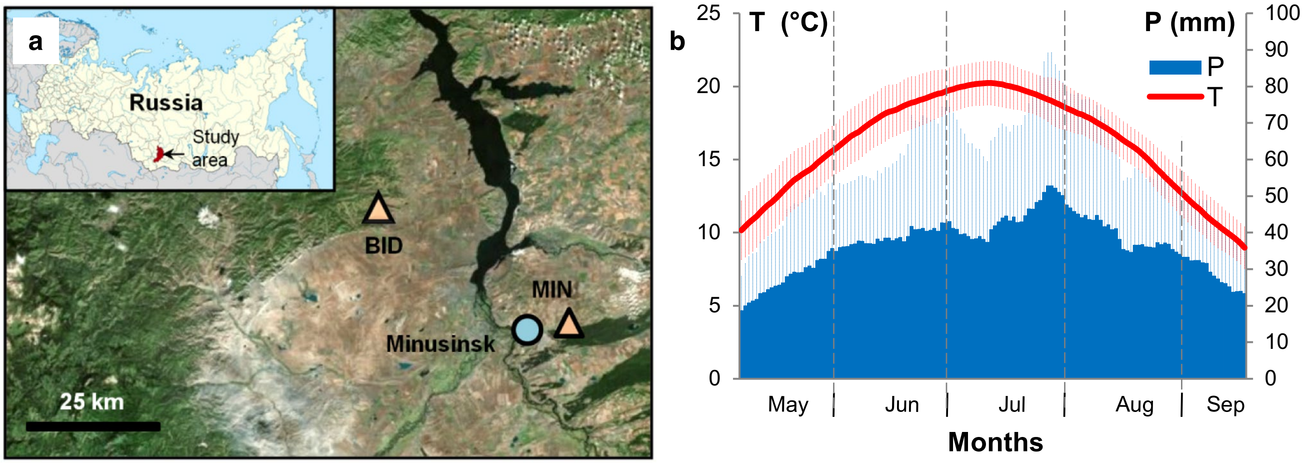

Fig. 1 Location and climate of study area. **a** Map of the central part of Minusinsk depression and position of the study area in Russia (upper-left corner insert). Triangles indicate location of tree-ring sampling sites. Circle is Minusinsk weather station. **b** Climograph of growing season May–September on the Minusinsk weather station for 1964–2011. Red is mean temperature (*T*) and blue is sum of precipitation (*P*) calculated from daily data with a 20-day moving window and 1-day step. Vertical red and blue lines are standard deviations of the inter-annual climatic series

Minusinsk forest, which is hotter and dryer due to the elevational and latitudinal differences (Table S1). However, the choice of sampling sites was aimed at reducing differences in soil moisture and microclimate conditions. We selected the BID site on dry slope of the south-aspect with high insolation and rapid runoff of precipitation. At the same time, the MIN site was selected on the flat landscape. Both sites have soils with below average humus content and water retention capacity (Kolyago 1971). The assumption of relative similarity in local conditions between sites was further supported by comparison of undercover vegetation (shrubs and herbs) at both sites, which comprised the same species and species with similar water supply requirements.

Tree-ring sampling and measurements

The increment cores from Scots pine (*Pinus sylvestris* L.) at the MIN site and Siberian larch (*Larix sibirica* L.) at the BID site were collected for this study. The wood surface preparation, tree-ring width (TRW) measurements and ring crossdating were carried out according to standard procedures of dendrochronology (Stokes and Smiley 1968). Two site TRW chronologies (indexed by detrending with negative exponential curves and then averaged; Cook and Kairiukstis 1990) were developed from 16 to 36 trees at the BID and MIN sites, respectively (Babushkina and Belokopytova 2014; Belokopytova et al. 2018). For the anatomical measurement, we selected five trees from each site that have high correlation with the site ring width chronology and were minimum 100 years old. Given the weak expression of the age trend in cell parameters, such a restriction reduces the age impact on the study results (Vysotskaya and Vaganov 1989; Lei et al. 1996; Eilmann et al. 2009).

After softening the cores by boiling in water, they were cut into thin sections (ca. 20 µm thick) with a sledge microtome (Microm HM 430; Thermo Fisher Scientific, USA) and then stained with an ethanol solution of 1% safranin. An image of each micro-section was captured with an image system built from a digital camera connected to a microscope (AXIOCam MRc5, Axio Imager D1; Zeiss, Germany, 400× magnification). Using captured images, we measured the following radial parameters of tracheids in each tree ring: cell number (*N*), radial lumen diameter (LD) and double cell wall thickness. For this study we replicated the tracheid measurements along five cell radial files per a ring. The optimum number of replications was determined by experimentation. Details are shown in the Electronic Supplementary Material (ESM). Accuracy of measurements is ca. 0.01 µm. The cell measurements were made for the interval 1965–2014 for MIN pine and the interval 1976–2011 for BID larch. Measurements of cell dimensions were processed with Lineyka software (Silkin 2010).

Cell chronologies

To distinguish cell dimensions developed during different phases of xylogenesis (Larson 1994), the measurements were transformed into radial cell diameter (CD = lumen diameter + double cell wall thickness) and cell wall thickness (CWT) using the ProcessorKR software (Silkin 2010). Because the radial number of cells varies between rings and within a ring, the cell diameter and wall thickness of each measured file were normalised to a constant number of cells per a ring (Vaganov et al. 1985), which allows inter-annual and intra-ring comparison, and correlations between studied anatomical parameters. In this case, we normalised the measurements to 15 cells (1...15). The ESM provides details on choice of this cell number and procedure of normalisation. The individual tree series of cell diameter and wall thickness for each of the 15 normalised cells were averaged from the five replicated file measurements and then for the five sampled trees. A total of 30 chronologies of tracheid anatomical parameters were developed for each site: 15 series for cell diameter and 15 series for wall thickness. Additionally, site cell number chronologies were built by averaging the number of cells per ring from the five replicated file measurements of the five sampled trees. TRW series were calculated as the CD sum for a radial cell file from a measured ring, and then used to crossdate cell chronologies. Crossdating was performed by comparison of TRW series calculated from cells and measured directly from the same core. Also, mean cell diameter CD_{mean} was calculated for each ring, and its time series for individual trees were investigated.

For inter-chronology comparison, the site cell chronologies were transformed into Z-scores (standardised to mean value of 0 and standard deviation of 1). Consequently, we analysed a dataset of 64 site chronologies: 15 CD, 15 CWT, TRW series, and N chronologies each for both pine and larch. The length of the cell chronologies is 50 years (1965–2014) for pine and 36 years (1976–2011) for larch parameters.

Statistical analysis

Key properties of variation in the cell parameters were described with arithmetic mean, standard deviation, and coefficient of variation, which is a ratio of standard deviation to arithmetic mean (Fritts 1976; Wigley et al. 1984). The variation of tracheid anatomical parameters was studied at various scales: inter-annual, intra-ring and inter-files, and visualised with time series (cell chronologies) and tracheidograms. A tracheidogram is a plot of intra-ring variation of an anatomical parameter in the radial direction according to the relative cell position within the ring as calculated for the 15 normalised cells per ring in this case (Panyushkina et al. 2003; Vaganov et al. 2006). The tracheidograms were also used to derive patterns of ring division in the earlywood, transition wood, and latewood. Latewood was defined on the basis of Mork's empirical criterion of $CWT > 0.25$ LD (Denne 1989). For the transition wood threshold was defined with $CWT > 0.10$ LD, which coincides with the onset of statistically significant increase of CWT.

Pearson correlation coefficients and simple linear regression models were calculated for evaluation of relationships between various cell parameters and their response to climate. In this study, daily observation data of mean temperature (T) and precipitation (P) for May–September season from the Minusinsk weather station for the interval 1964 to 2011 were used. In addition to the observations, we calculated two moisture regime monthly indices from T and P series of the Minusinsk station. Selyaninov hydrothermal coefficient (HTC) is calculated with the formula $\mathrm{HTC} = 10 \cdot \sum P / \sum T$ (Selyaninov 1937). The wetness index (WI) was adopted from Lei et al. (2014) and the equation was modified as $\mathrm{WI} = 10 \cdot \sum \log(P+1) / \sum T$ to take into account the possibility of zero P. To investigate climate–growth relationships, we used May–September daily temperature series averaged over a 20-day window with 1-day moving step, and precipitation series summed over the same window and step (Fig. 1b). This statistical approach has been recently used in analysis of ring cambial dynamics and cell parameters (e.g. Carrer et al. 2017; Castagneri et al. 2017). The climate correlation analysis was performed for chronologies of tree-ring width, cell number, and cell diameter and cell wall thickness for each normalised cell.

Additionally, pointer years were used to compare the wood anatomical structure formed under pluvial and drought conditions. This analysis was only performed for pine that has a longer interval of tracheid measurements than larch, and a sufficient number of pointer years. The pointer years were defined in the tree-ring width site chronology, where a TRW exceeding the mean plus 1σ indicates a positive pointer year and TRW less than the mean minus 1σ indicates a negative one.

Results

Mean of cell measurements and tree-ring width

Tree-ring width parameters strongly relate to the number of cells. Coefficients of determination for linear regressions between these two parameters are above 0.9 for individual trees of pine and larch, and ca. 0.89 for the averaged site series, with all relationships significant at $P \leq 0.0001$ (Fig. 2; Table 1). Since these two parameters are nearly proportional (intercept of the regression line is close to zero), the slope of linear regression can be considered to be an estimation of the mean radial cell diameter of individual trees CD_{mean}. Linear regression estimation of the mean cell diameter is ca. 3–4 μm higher than its directly calculated value (average value from all measured rings for individual tree). The individual tree series of mean cell diameters exhibit no statistically significant long-term age-related trends for either species ($P > 0.1$ for linear approximations of trends). The average number of cells per ring and the mean cell diameter are statistically independent regardless of the calculation method.

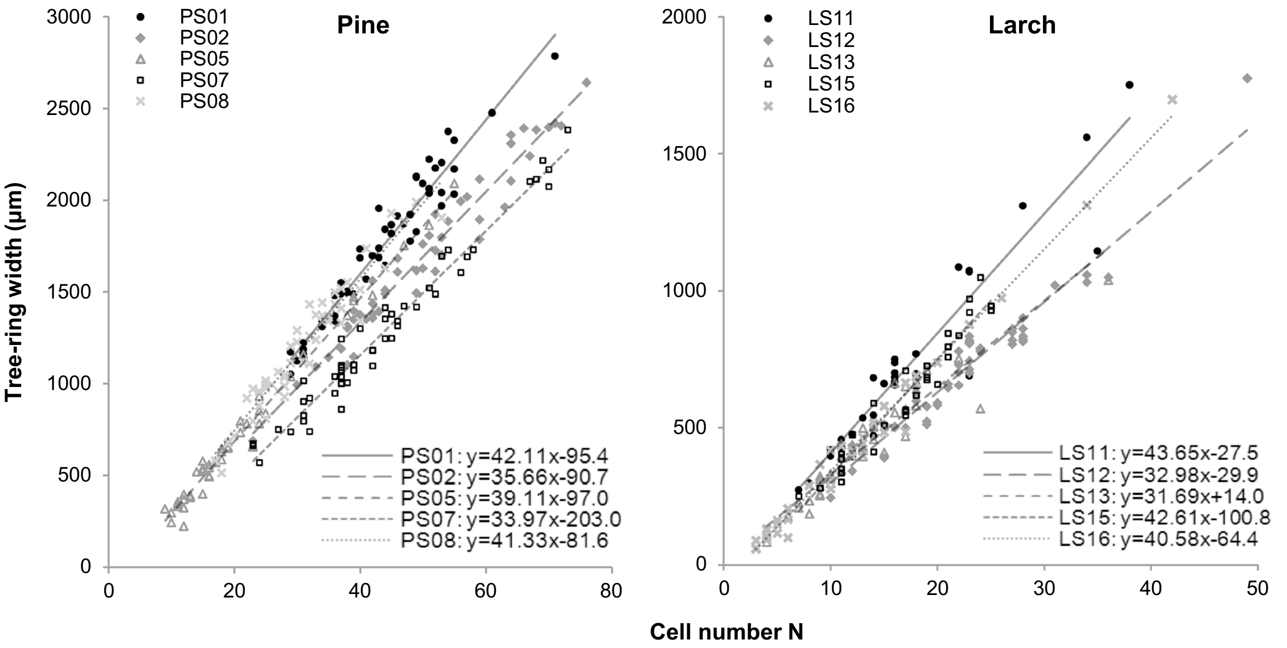

Fig. 2 Scatterplots of tree-ring width and cell number in the raw measurements of individual tree series. Lines show linear regression functions calculated for each tree

Table 1 Comparison of individual tree xylem anatomical parameters between pine and larch species

Individual tree characteristics	Pine trees					Larch trees				
	PS01	PS08	PS05	PS02	PS07	LS11	LS15	LS16	LS13	LS12
$CD_{mean}1$ (μm)	42.11	41.33	39.11	35.66	33.97	43.65	42.61	40.58	32.98	31.69
R^2	0.94	0.92	0.99	0.96	0.97	0.91	0.94	0.99	0.94	0.90
$CD_{mean}2$ (μm)	40.05	38.50	33.42	33.72	28.94	41.71	35.94	32.34	32.36	31.59
N_{mean}	44.0	31.5	20.8	50.0	43.4	17.6	16.5	11.8	13.7	22.3

$CD_{mean}1$ mean cell radial diameter, calculated as slope of linear regression TRW(N), R^2 determination coefficient of linear regression TRW(N), $CD_{mean}2$ arithmetic mean for individual tree series of mean cell radial diameter, N_{mean} arithmetic mean for individual tree series of cell number per ring

Variation of cell anatomical parameters

Analysis of replicated measurements indicates a small range of CD and CWT residual inter-file variations after averaging over five files. Coefficient of variation is on the average 4–5% and never exceeds 10%, without regularities within a ring (dotted line in Fig. 3). In contrast, the inter-annual variations of the cell anatomical parameters are much higher. In the earlywood zone defined by the first seven normalised cells for pine and first four normalised cells for larch, the CD and CWT size inter-annual variation is practically constant. In the transition zone (normalised cell positions 8…10 for pine and 5…8 for larch) it abruptly increases. In the latewood zone (normalised cell positions 11…15 for pine and 9…15 for larch) the inter-annual variation gradually declines (solid and dashed lines in Fig. 3). The inter-annual variation for CD changes throughout the ring with a smaller range than for CWT: maximum coefficients of variation for CD are 24% for pine and 43% for larch, and for CWT 33% and 54%, respectively. The main difference between species is relative width of different zones within the ring, with much wider latewood for larch. The CWT of earlywood is less variable in larch than in pine. This intra-ring pattern is consistent in our data. However, some fluctuations in the CD and CTW variations were observed between individual trees (Table S2). We noticed that trees with a larger mean cell diameter have a higher inter-annual variation of the earlywood CD. Trees with larger cell production (higher N) have a higher inter-annual variation of the latewood CD and CWT. Generally, the variation of site cell chronologies is considerably less than of their individual series. Additionally, the variation of site tree-ring width indexed chronologies is 20.6% for pine and 36.3% for larch, which is much higher than for cell parameters' site chronologies (Table S3).

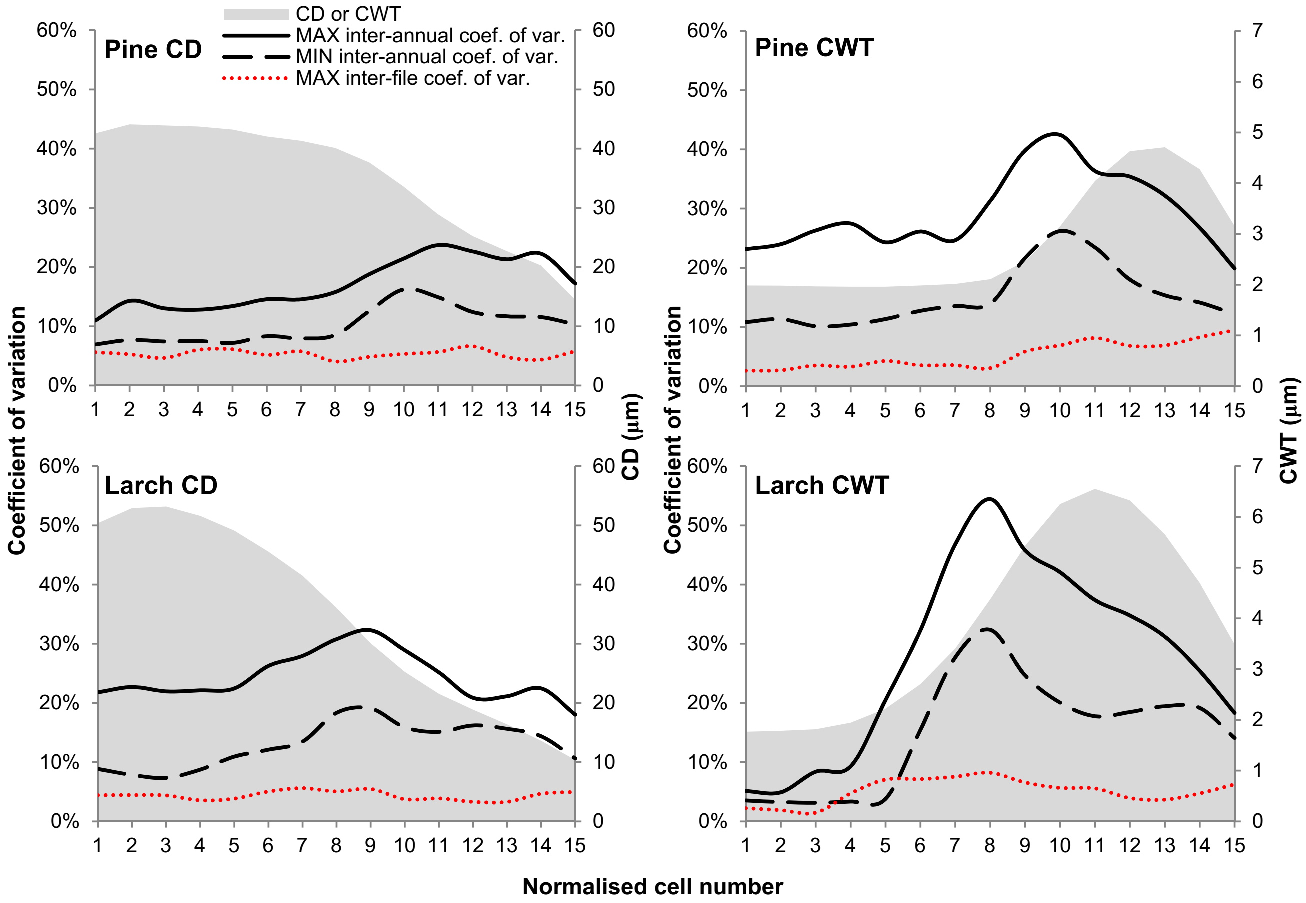

Fig. 3 Tracheidograms of pine and larch cell parameters normalised to 15 cells per ring and their variation. The pattern of inter-annual variation of cell parameters' series was calculated for each individual tree separately; its ranges (maximal and minimal values of the coefficient of variation among individual tree series for each normalised cell number) are delineated with solid and dashed lines (see legend on the top). Dotted red line is the maximum value of inter-file coefficient of variation calculated during diagnostic test for the number of replications (ESM). Left *Y*-axis is coefficient of variation (lines) and right *Y*-axis is value of the studied cell parameter (grey shade): *CD* cell radial diameter, *CWT* cell wall thickness

Common variance in cell chronologies

Figure 4 shows some of cell site chronologies and respective series of individual trees. The common component of variance in cell chronologies varies between cell parameters and ring zone. CD has the highest correlation between individual tree series in the transition wood (normalised cell positions 7…8 for pine and 4…5 for larch), whereas the lowest correlations are in the latewood (Table S4). The CWT correlation pattern is the opposite, with maximum in the middle of latewood (normalised cell number 13 for pine and 11–12 for larch), and the lowest correlations in the earlywood. Correlations of individual tree series and site chronologies are generally higher for the CD parameter.

Correlation between cell site chronologies of different normalised cell positions depends on the ring zone (Table S5, S6). The correlation coefficients between the cell chronologies have the maximum values between adjacent positions (reaching 0.94 for CD and 0.97 for CWT). Interestingly, most correlations between the cell parameters of earlywood and latewood are not significant. For both tree species, close correlations between the CWT chronologies extend to a greater distance within the boundaries of earlywood and latewood ring zones. CD, on the contrary, shows the highest correlations and greatest distances between significantly correlated cell chronologies in the transition zone. The inter-ring pattern matches for the studied tree species.

Correlation of chronologies with climatic factors

Tree-ring width (and cell number) has a complex response to climate, which is similar for both tree species: high temperature of the first half of growing season suppresses growth but amount of precipitation shows a positive effect (Fig. 5, Fig. S2). The negative impact of temperature reaches the maximum in late May and early July, then in mid-August.

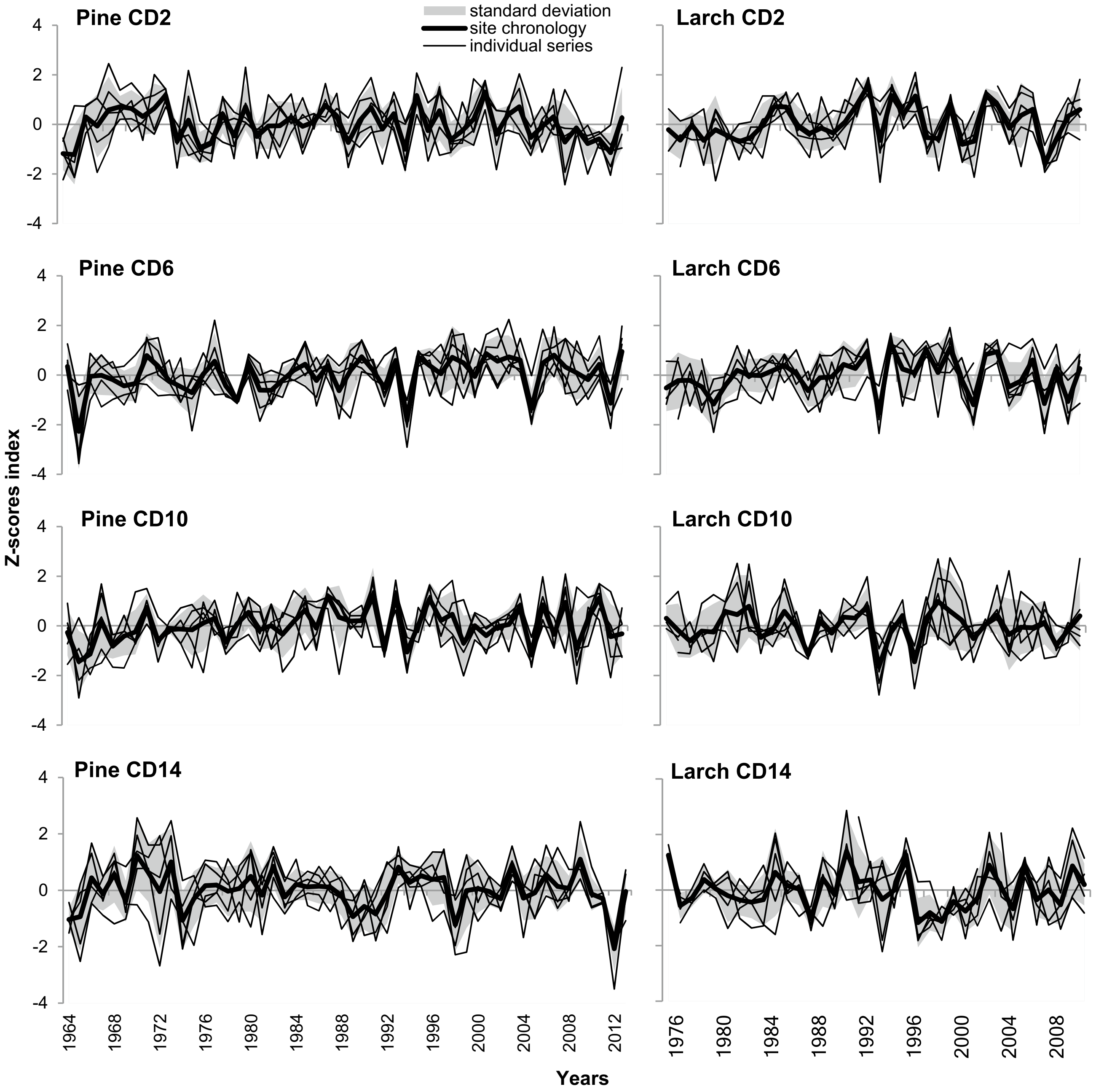

Fig. 4 Z-scores of individual series (thin lines) and site chronologies (thick line) of cell radial diameters (CD) for some of normalised cells: 2nd, 6th, 10th and 14th. Standard deviation (grey shade) was calculated for CD of five individual trees for each year separately

The periods of growth stimulated by moisture influx are almost the same: May to early June and first half of July. The response of tree-ring parameters to moisture indices HTC and WI differs very little from the precipitation response.

For pine, the CD response to climate shows a gradual change across the ring. Maximum correlations shift: they are observed from May to mid-June for first cells, in mid-July for the transition wood chronologies, and in the end of August for the latewood. The effect of precipitation on CD is more pronounced for the earlywood and transition wood. It should also be noted that the duration of the climatic response decreases in the last cells. CWT responds to the positive effect of precipitation between mid-July and mid-August. This relationship is significant only for the transition wood cells and the first few cells of latewood (cell positions 8…12). The negative effect of temperatures has a longer seasonal window ranging from July to August for the entire ring. We observed an inversion of the climate

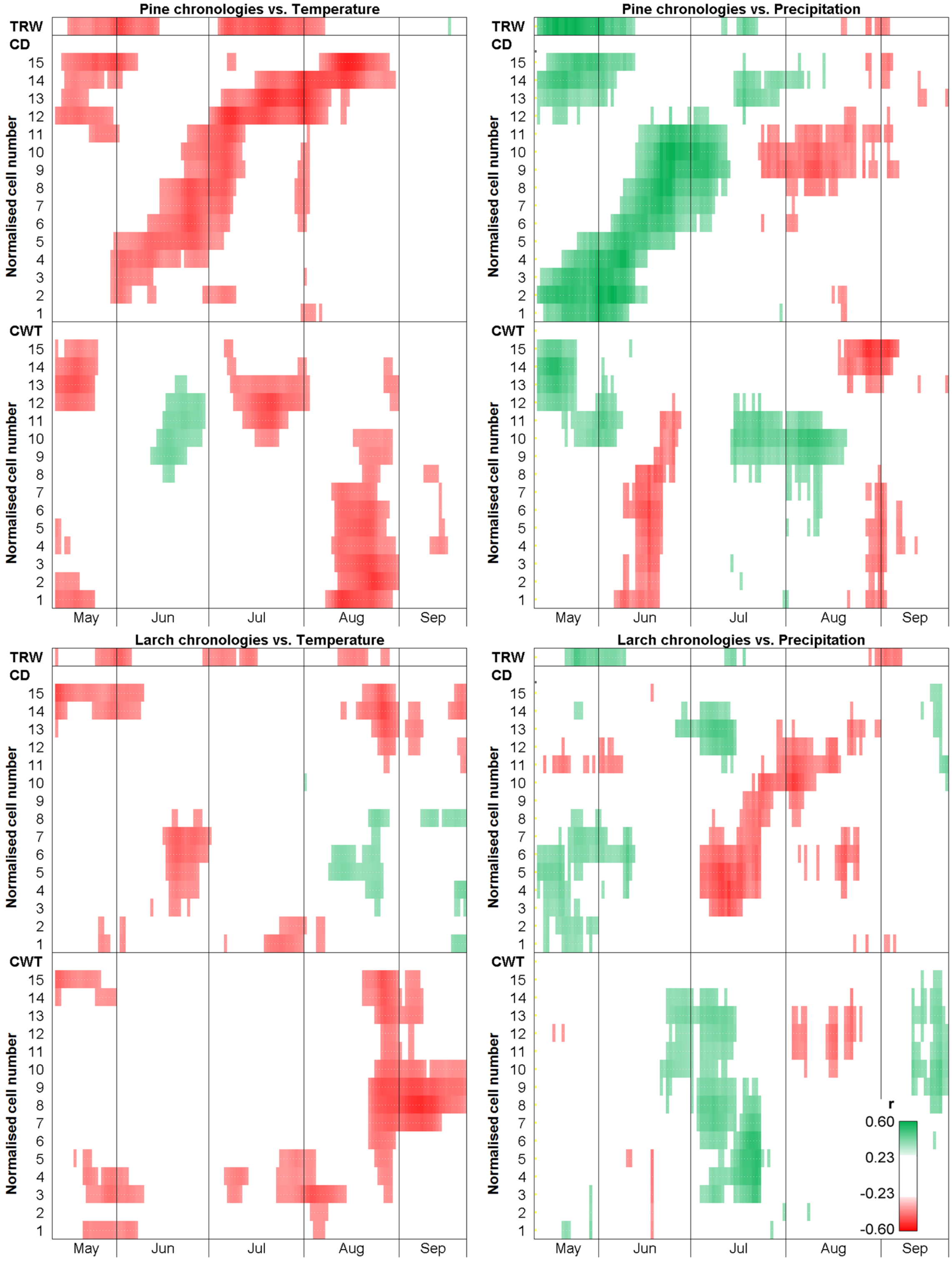

Fig. 5 Correlation coefficients between the site chronologies of tree-ring parameters and 20-day moving series of temperature and precipitation. TRW, ring width indexed chronology; *CD* cell radial diameter, *CWT* cell wall thickness. Correlation bar is shown at the low right corner of the last plot. Green is positive and red is negative correlation. Only significant correlations at $P \leq 0.05$ are shown

effect on CWT in June when dry and warm weather led to the formation of thicker cell walls throughout the ring. The maximum strength of this signal is recorded at cell positions 8…12. Furthermore, CWT is negatively correlated with both climatic parameters during the second half of August and the beginning of September.

For larch, CD and CWT responses are similar to the pine anatomical parameters, but the climatic signal is weaker. The positive impact of precipitation and negative impact of temperature on larch CD occur from May to early June in the beginning of earlywood and from late June to early July in the last cells of latewood. The climatic inversion can still be seen in the CWT series but with a much smaller magnitude. The precipitation impact is positive from mid-June to mid-July. The climatic signals of anatomical parameters for both studied tree species correspond to timing of corresponding phases of cell differentiation.

Pointer-year analysis for pine identified five negative (1964, 1965, 1974, 1998, 2012) and five positive (1970, 1971, 1982, 1995, 2007) pointer years. Figure 6 shows variations of climatic and anatomical parameters during these two sets of pointer years. Precipitation during the positive pointer years is up to 5 times more from May to the first half of June than in the negative pointer years, and up to 2.5 times more during the interval of July to first half of August. Temperatures, on the other hand, are significantly higher for the negative pointer years during the same periods (up to 3.7 °C and up to 2.6 °C, respectively). However, there is no significant difference between positive and negative pointer years at $P<0.05$ in the second half of June. Tracheidograms of the pointer years show that the tracheids are larger in the wet years than in the dry ones. The tracheids of the earlywood and latewood have significantly larger cell diameters: difference is 4–7 µm or 11–17% at cell positions 1…8, and 3–7 µm or 13–41% at positions 12…15, whereas

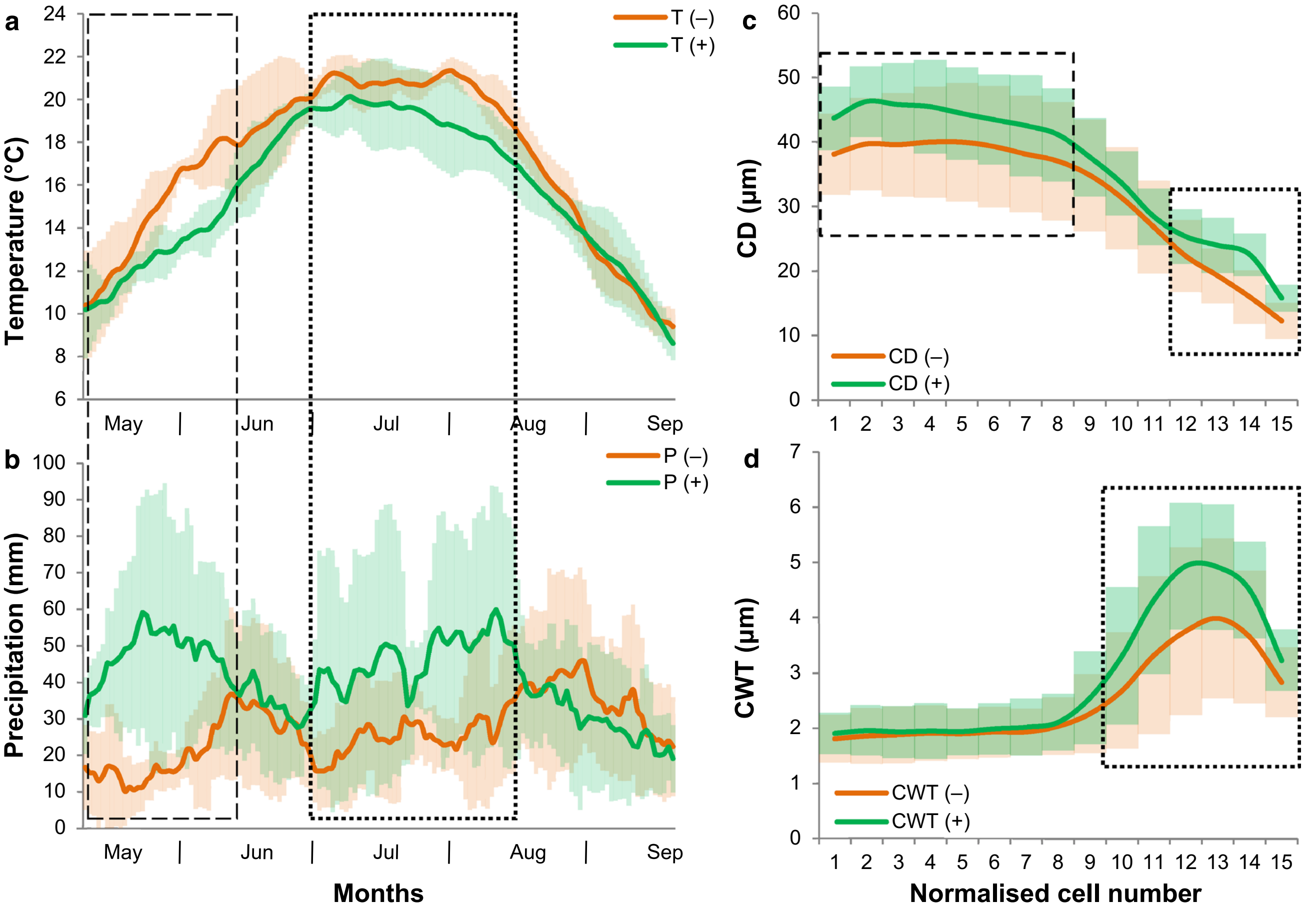

Fig. 6 Variations of **a** temperature and **b** precipitation, and **c** radial cell diameters (CD) and **d** cell wall thickness (CWT) of pine during negative (orange) and positive (green) pointer years. May to September climographs (**a, b**) are calculated from the Minusinsk daily data with a 20-day moving window. Tracheidograms (**c, d**) show fluctuations of cell parameters within 15-cell normalised ring. Lines mark the mean values and shades are ±1 σ range of studied parameters. Rectangles indicate the intervals with the significant at $P<0.05$ differences between positive and negative pointer years

the transition wood CD shows no significant difference between the positive and negative pointer years. The CWT is significantly larger (at $P < 0.05$) during positive years for cell positions 10…15 with maximum difference ca. 1.2 µm or 31% at positions 12.

Discussion

Relationships between cell parameters and cell production

Variance of wood anatomical parameters contains information independent of cell production and radial growth (Wimmer 2002; Rossi et al. 2012). Strong linear dependence of TRW on the cell number indicates that the average size of tracheids is stable during the observation period. The CD_{mean} does not have significant time dependency on age and size of individual trees or on climatic change. Age- and size-related decreasing rate and duration of cambial activity (leading to long-term trends in TRW and cell number) can last for centuries (Rossi et al. 2008; Li et al. 2013). However, for cell anatomical parameters and wood density as their derivative, there is evidence of such trends present predominantly during the first decades of tree lifespan (e.g. Pritzkow et al. 2014; Pacheco et al. 2016; see also theoretical reasoning by hydraulic requirements in; Carrer et al. 2015). This means that we can observe age trends in wood anatomy only when the pith wood is included in anatomical measurements (cf. Ziaco et al. 2016). Therefore in our study, absence of age trend in anatomical parameters is most certainly due to exclusion of the earliest 50 years (or more) of tree growth. The averaging of series between trees within one site slightly weakens the relationship between radial tree growth and cell production. Previous research found that the linear regression slope between TRW and N in larch trees in the study region varies depending on site habitat conditions (Babushkina 2011). Our results suggest the average size of tracheids depends on a combination of habitat (at site and individual tree scale) and tree genetics (Fonti et al. 2010).

A number of studies have shown that the relationship between tracheid size and cell production in all ring zones is described with an inverted negative exponential curve for narrow rings and horizontal straight line for wide rings (Vaganov et al. 1985; Babushkina 2011). The same relationship should be true for the mean cell diameter, but only a small share of rings are narrow enough to observe the dependence of cell size on the cell number (Fig. S3). It is possible that the lack of the relationship between the mean cell diameter and mean cell number is explained by relatively mild climatic conditions in the study area. CWT depends even less on cell production and shows a weak relationship with CN and TRW, since the wall maturation occurs later in the growing season.

Variation of anatomical parameters

Xylem anatomy records information about the climate impact on various scales: intra-ring and inter-annual. Intra-ring variations determine the ring structure, which includes earlywood (large-diameter thin-walled tracheids), transition wood, and latewood (small-diameter thick-walled tracheids). The procedure of normalising the measured radial cell files to a constant cell number divides a ring into narrow zones, and this ring partitioning isolates the variance pattern of anatomical parameters of each ring zone, and ascribes the climatic signal to these ring zones (Panyushkina et al. 2003; Deslauriers et al. 2003a; Vaganov et al. 2006; Olano et al. 2012). Another source of variance in the anatomical measurements arises from the position of tracheid across the circumference of the ring, i.e. tracheids from different radial files. Averaging xylem measurements over several cell files significantly reduces this type of variance (Seo et al. 2014).

Inter-annual variation of anatomical parameters is the main focus of dendroclimatic studies that use this fine temporal scale of year-to-year variance for modelling of retrospective variability of climate. Inter-annual variations of the average of five files of CD and CWT are higher than the inter-file variance. Our study suggests that the intra-annual variance is constrained by extrinsic factors (e.g. temperature and precipitation). The pattern of inter-annual variation changes across a ring, which makes it possible to track the inter-annual climatic signal between the ring zones. Cells of earlywood have a persistent intra-ring range in the CD and CWT within earlywood: CD has the maximum and CWT has the minimum for a given tree species at particular habitat. This specific property of earlywood cell variance also persists at the inter-annual time scale.

Additionally, the ratio between the earlywood and latewood also varies significantly from year-to-year, which leads to inter-annual offset in the position of the transition wood zone of the normalised tracheidogram. The switch of cells in the middle of tracheidogram between the earlywood and latewood introduces additional variance and results in an increased annual variability of cell parameters in transition zone. The seasonal processes involving nutrient accumulation are contingent on environmental settings, so they should also influence xylogenesis (Cuny et al. 2016). It is known that the formation of the secondary wall requires substantially more resources than the expansion of the primary wall (Hall et al. 2013; Overdieck 2016). This may explain the higher variation of CWT as compared to CD in the transition wood and especially latewood, and the stronger relationship of these cell series with climatic conditions. The duration of cell expansion decreases from the earlywood to latewood, whereas the duration of secondary wall deposition increases (Cuny et al. 2013, 2014; Rossi et al. 2006; Rathgeber 2017). This longer exposure of latewood cell wall deposition to climate influence induces a greater variation of the corresponding cell parameter. The variation of anatomical parameters of the last few cells decreases synchronously, since the secondary wall deposition is limited by the small size of the tracheids (CWT cannot exceed 0.5 of CD).

Inter-species differences

Our results suggest two studied conifer tree species have common patterns of variance of the anatomical parameters. The only visible difference between pine and larch xylem is seen in a greater proportion of latewood for larch. Similar ring structure is observed in oak, which is a well-studied ring-porous deciduous tree species (Büyüksarı et al. 2017). Large vessels developed at the very beginning of the growing season support the intensive emergence and growth of foliage. A wide zone of small vessels in the latewood determines the high density of oak wood. Something similar can be assumed for larch, which is also a deciduous species. We note that the radial diameter of cells (and consequently the lumen size) in larch earlywood is significantly larger than that of pine (Fig. 3). This phenomenon shifts the functional characteristics of larch ring structure closer to oak as well. The deployment of new needles for larch at the onset of the growing season is also coordinated with formation of large tracheids in the earlywood through the auxin synthesis in buds breaking en masse. Later, end of primary growth regulates a xylogenesis switch toward smaller tracheids with thicker walls. In turn, this switch requires a significant influx of nutrients into the xylem (Funada et al. 2001; Singh et al. 2012). On the other hand, climatic and soil-landscape conditions are not identical at both sites. This fact further reinforces differences in tree growth and its climatic response. For example, less significant climatic response of larch can be related to slightly cooler and wetter growth conditions. To distinguish functional species-specific differences and impact of local growth conditions with more certainty, further research is required.

Common variance of cell parameters

Our study showed distinctive partitioning of the common variance related to climate in the cell parameter chronologies. Firstly, the highest correlation between individual tree series occurs in the ring zone with the maximum size of anatomical parameters (Table S4). It suggests that the strength of cell parameter common variance including response to climate depends on the duration and rate (intensity) of the corresponding phase of tracheid differentiation, because these kinetic characteristics contribute to the final size of cell parameters (see Anfodillo et al. 2012; Cuny 2013; Cuny et al. 2013, 2014). Secondly, the shift of high correlations toward the transition wood is an indicator for synchronous fluctuation of the earlywood/latewood ratio at the site. It is driven by synchronised extrinsic factors (e.g. temperature, day length) that trigger the switch of cell formation from earlywood to latewood (Begum et al. 2015; Petterle et al. 2013), and climatically induced variance in cell production before and after this switch.

Intrinsic factors (genetics) impart stable wood structure and lessen common variance of the earlywood CWT series (Darikova et al. 2013). This assumption is also supported by other studies, e.g. low common variance in the mean CWT series observed in tree rings with predominant earlywood (Ziaco et al. 2016). This can explain the analogous dynamics of CWT in adjacent cell positions of the earlywood, which is especially evident for pine characterised by a relatively large proportion of earlywood in the ring (Table S6). The periods of tracheid differentiation partially overlap in close and especially adjacent tracheid positions; it means that common signals of CWT or CD chronologies overlap for close cell positions. This overlapping leads to the observed pattern of correlations between cell parameter series of different normalised cell positions (Table S5, S6, also see similar patterns in Panyushkina et al. 2003; Castagneri et al. 2017), i.e. as the distance between cell positions increases, the correlations decrease rapidly from very high values to insignificant ones.

Climate–growth relationships

Climatic impact on the radial growth of conifer trees is common in semi-arid regions. Moisture from precipitation stimulates tree growth, while high temperature promotes evapotranspiration and creates water stress. TRW integrates this impact mainly during cambial activity through the rate of cell production. We note that relatively high precipitation observed in late June and late July (Fig. 1b) significantly weakens the TRW climatic signal during this period (Fig. 5). This response is explained by the limiting role of both temperature and precipitation on the soil moisture and hydrological regime. This is also true for the response of chronologies to other climatic parameters related to humidity. Less pronounced climate response of larch TRW compared with pine TRW corresponds to the patterns of xylem climatic response. A short lag at the beginning of larch climate response observed in TRW and cell chronologies may be due to combination of later onset of growing season at the BID site and the necessity of development of assimilation apparatus (needles). Kraus et al. (2016) described a similar temporal pattern with the same time of bud burst and onset of cambial activity for evergreen spruce and a 3-week delay of secondary growth for deciduous beech.

The climate impact on CD shows a similar pattern, but the period of high impact shifts across the ring as new cells form (Fig. 5). Radial cell diameter is linked to weather conditions during the process of cell expansion (Deslauriers et al. 2003b; Vaganov et al. 2011). Additionally, the time interval with significant correlation of climate and CD can be partially amplified by the procedure of cell number normalisation, which bears more on the xylogenesis process then the calendar dates (Vaganov et al. 2006). Many previous studies noted that wood formation, including the cell division and differentiation, may start and end at different calendar dates in different years (Prislan et al. 2013; Gričar et al. 2014; Swidrak et al. 2014; Ziaco and Biondi 2016; Yang et al. 2017). In more arid areas, the timing of tree-ring development closely depends on both temperatures and precipitation, which was observed on the northeastern Tibetan Plateau and especially in the Mojave Desert mountains (Ren et al. 2015, 2018; Ziaco et al. 2018). A similar pattern can also be expected in the Minusinsk depression, as supported by simulation and seasonal observations of xylogenesis (Popkova et al. 2015, 2018). Therefore, we cannot exclude the influence of climate impact on the final radial diameters during the period when the cells are still situated within the cambial zone (Vaganov et al. 2006; Cuny et al. 2014).

Some anatomical parameters may have weak climatic response and low inter-annual variation in comparison to cell production and total ring growth. Cell number and TRW integrate the effect of climatic fluctuations over a much longer interval compared to anatomical parameters of individual cells, which results in higher values of annual variations. The effect of extrinsic factors on the process of cell division, duration and rate (the number of cells produced per time unit) changes in one direction (Rossi et al. 2014). This leads to nonlinear relationship of this effect with the cell production. As shown by Balducci et al. (2016), the kinetics of later cell differentiation processes has a built-in compensatory mechanism: suppression of the expansion rate of an individual cell or deposition of a secondary wall under the stressed conditions is partially compensated with increasing time for this cell residing in the corresponding zone of cell differentiation. Thus, the climate effect on the anatomical structure of the ring will be somewhat dampened. This phenomenon is possibly driven by the genetic mechanism of successive phases in tracheid differentiation that begins with division and ends with programmed cell death. This was confirmed by Darikova et al. (2013) for Scots pine and Siberian pine with genetically determined inter-species difference in cell growth that was monitored on a single plant (graft and rootstock), i.e. under uniform external conditions and hormone concentrations. Cuny et al. (2014) showed the intrinsic compensation mechanism with negative relationship between the rate and duration of cell differentiation processes.

The inversion of CWT climate response in June indicates that moisture deficit may prompt developing not only smaller but also thicker-walled cells. As a result, the cell's water-conducting capacity and subsequently transpiration decrease as a part of compensating mechanism for adapting trees to water stress (Nicholls and Waring 1977; Hacke and Sperry 2001; Sterck et al. 2008). CWT of the last tracheids in the latewood is limited by CD, which leads to their similar reaction to temperature.

The combination of climate responses for both anatomical parameters yields cumulative response of wood density to the moisture fluctuations. Unlike many other regions where maximum density is a proxy for temperatures, often having stronger climatic signal than TRW (Sun et al. 2016; Rathgeber 2017; Stine and Huybers 2017), in the studied region the ring wood density has a good potential for being a moisture proxy.

Our comparison of the ring xylem structure formed during the driest and wettest years (pointer years) suggests that even drastic differences in moisture availability are only moderately recorded in the studied anatomical parameters. This once again confirms the manifestation of a compensatory mechanism in the kinetics of cell differentiation. It is interesting that there is a zone of no significant differences between driest and wettest years in tracheidograms of both cell parameters, which for CWT occur in earlier cell positions than for CD. As for the seasonal climate, the second half of June appears to be the interval with minor differences in climate between pointer years. This points to the temporal shift in climatic effects on wood formation due to timing of cell differentiation at the intra-ring scale as discussed earlier.

Conclusion

The robust linear relationship between TRW and cell production contains no age-related changes, but varies between individual trees. The estimated variations in the cell parameters suggest the sensitivity of the wood structure to fluctuation of extrinsic conditions, albeit uneven, distributes throughout the entire ring. In contrast to the mean ring characteristics like TRW, the timing of environmental impacts is individual for each cell in accordance with the spatial–temporal organisation of the cell production and cell differentiation processes. In addition to the higher temporal resolution of the climate response, the cell parameters are less variable, which is associated with the genetically determined structure of tree rings and the compensatory mechanism in the kinetics of cell development.

The xylem anatomical parameters can provide valuable information on the retrospective variability of precipitation and temperature at very fine seasonal resolution. Although the radial diameter and wall thickness of conifer tracheids from dry environments are climatic-sensitive across the complete ring area, each cell parameter has a specific zone in a ring where its climatic response reaches the maximum or the minimum. This study indicates good potential for employing maximum wood density as a proxy of moisture regime in the semi-arid regions of South Siberia.

The results of this research open up new possibilities for studying the impact of climatic factors on the tree growth with very fine temporal resolution. Therefore, with respect to possible future research, it would be interesting to compare the seasonal kinetics of cell differentiation and the xylem anatomy–climate relationships to refine the theoretical algorithms of tree growth models.

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Author contributions EAV designed the study with input from EAB. DFZ supervised fieldwork and measurements. LVB performed statistical analysis and prepared figures. All authors contributed to discussion of results and writing the manuscript. LVB and IP wrote the English version of manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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