

Article

Contribution of Xylem Anatomy to Tree-Ring Width of Two Larch Species in Permafrost and Non-Permafrost Zones of Siberia

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Abstract: Plants exhibit morphological and anatomical adaptations to cope the environmental constraints of their habitat. How can mechanisms for adapting to contrasting environmental conditions change the patterns of tree rings formation? In this study, we explored differences in climatic conditions of permafrost and non-permafrost zones and assessed their influence on radial growth and wood traits of *Larix gmelinii* Rupr (Rupr) and *Larix sibirica* L., respectively. We quantified the contribution of xylem cell anatomy to the tree-ring width variability. Comparison of the anatomical tree-ring parameters over the period 1963–2011 was tested based on non-parametric Mann-Whitney U test. The generalized linear modeling shows the common dependence between TRW and the cell structure characteristics in contrasting environments, which can be defined as non-specific to external conditions. Thus, the relationship between the tree-ring width and the cell production in early- and latewood are assessed as linear, whereas the dependence between the radial cell size in early- and latewood and the tree-ring width becomes significantly non-linear for both habitats. Moreover, contribution of earlywood (EW) and latewood (LW) cells to the variation of TRW (in average 56.8% and 24.4% respectively) was significantly higher than the effect of cell diameters (3.3% (EW) and 17.4% (LW)) for the environments. The results show that different larch species from sites with diverging climatic conditions converge towards similar xylem cell structures and relationships between xylem production and cell traits. The work makes a link between climate and tree-ring structure, and promotes a better understanding the anatomical adaptation of larch species to local environment conditions.

Keywords: tree-ring structure; latewood; earlywood; number of cells; cell diameter; cell-wall thickness; climate factors; cryolithozone; forest steppe

1. Introduction

Tree growth depends on a number of internal and external factors and their effect on tree radial growth are reflected in the structure of the xylem [1–4]. For different forest ecosystems, climate can explain up to 40%–60% of the variance in the seasonal variability in tree-ring anatomy [2,5,6]. Due to a wide plasticity, coniferous trees are able to adapt an anatomical structure under the influence of external factors, and *Larix* spp. being the main tree species in the Siberian permafrost is well adapted to extreme climatic and soil conditions [7–9]. The variability of tree-ring width and its anatomical characteristics, e.g., number of cells, radial lumen size and cell-walls thickness, are closely related to the dynamics of tree-ring formation, especially to the kinetics of cell production [2,10]. Previous studies reveal an impact of the processes of cell differentiation on anatomical structure of tree rings [2,11–14]. Therefore, the endogenous factors of cell growth and maturation, combined with external conditions result in the final tree-ring structure of conifers [2,15–17].

A variety of aspects of tree-ring formation at different locations with different climate conditions show, that at high latitudes temperature is the main factor determining radial growth irrespective of the species [12,18–21]. Quantitative wood anatomy intensively developing in last decades [22–24] can be used to address research questions related to how climate affects the ring's cell structure, and how xylem anatomical parameters could be used in eco-physiological modelling [25,26].

It is still an open question how the contrasting external conditions influence the rate of tree radial growth (tree-ring width) and tree-ring structure of conifers [2,25,27,28]. In this study, the impact of climatic conditions on radial growth was compared between larch species growing in permafrost and non-permafrost zones in Central Siberia. The continuous permafrost zone is dominated by Gmelin larch (*Larix gmelinii* Rupr (Rupr)). The forest-steppe zone is dominated by Siberian larch (*Larix sibirica* L.), a species growing on non-permafrost soils (Figure 1). Because of the contrasting growth conditions, the two environments host different species, which prevents to disentangle the species from its environment. The positive temperature trends observed at high latitudes and the existing global warming scenarios (IPCC, 2008; 2014) are stimulating potential changes in the distribution of species, namely Siberian Larch could replace Gmelin larch due to the predicted shift in permafrost further north.

We hypothesized that larch species have similar contributions of earlywood and latewood cell production and cell sizes to tree-ring width variability, but the absolute values of cell parameters (tracheid diameter and cell-wall thickness) are different due to xylem adjustment to local climate.

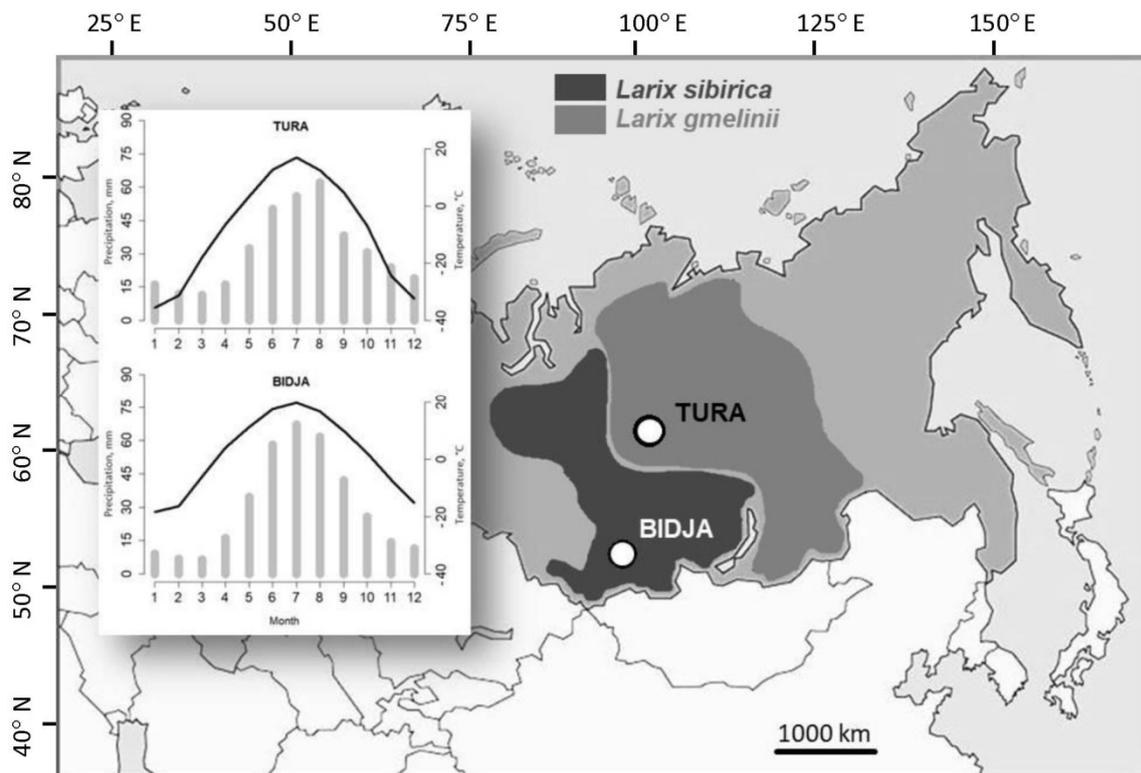


Figure 1. Map of the study area. Left panels show the climatic diagrams of the study sites with mean monthly temperature (black lines) and monthly sum of precipitation (grey bars). The meteorological data covers the common period 1963–2011. Colored zones on the map indicate areas where studied larch species (*Larix sibirica* L.—dark grey area; *Larix gmelinii* Rupr (Rupr)—light gray area) are distributed. The studied sites with tree-ring width and anatomical parameters are marked with circles.

2. Materials and Methods

2.1. Study Areas and Tree Selection

The study took place in two sites in Siberia, Russia (Figure 1). The first one (TURA; 64°18′ N, 100°11′ E, 150 m a.s.l.) is located in continuous the permafrost zone in the northern taiga with stands mainly dominated by Gmelin larch. The climate is continental, the annual air temperature is $-9\text{ }^{\circ}\text{C}$ and the annual precipitation is 370 mm according to data from the meteorological station located in the region (TURA, 64°16′ N, 100°13′ E, 205 m a.s.l.). The growing season usually starts at the end of May and ends in late August [9,29]. The southern site (BIDJA, 54°00′ N, 91°01′ E, 660 m a.s.l.) is located close to the Sayan-Altai Mountains and the Batenevsky Range in the forest-steppe zone. The meteorological station in Minusinsk (53°41′ N, 91°40′ E, 254 m a.s.l.) is located 60 km from the study site, with mean annual temperature of $1.0\text{ }^{\circ}\text{C}$ and annual precipitation of 330 mm. BIDJA experiences a longer growing season compared to TURA, ranging between late April and early October [30]. The trees were sampled in the pine-larch open canopy forest on grey forest soils. The site is represented by Siberian larch forest mostly with 110-year old trees.

2.2. Wood Sampling and Preparation

Wood cores from *Larix sibirica* L. and *Larix gmelinii* Rupr (Rupr) were collected in 2012 from 16 and 18 trees in BIDJA and TURA, respectively. Annual tree-ring width (TRW) was measured with 0.01 mm precision using a LINTAB measuring system and program TSAP (Rinntech, Heidelberg, Germany). To control a quality of cross-dating, we used the COFECHA program [31]. TRW chronologies were detrended with negative exponential curves. An auto-regressive modeling was applied to remove

the auto-correlations from the detrended time-series, which were averaged using a biweight robust estimate of the mean [32]. Five 100-year old trees per site characterized by the highest correlation coefficients with the site chronology (0.6–0.8) were selected for anatomical measurements. Wood cores were taken at 1.3 m stem height with the 5 mm increment borer (Haglof, Sweden) perpendicular to slope direction to avoid reaction wood.

Each core was softened by boiling in water, and thin cross sections (20 μm) were cut by using a sledge microtome (Reichert, Germany) and stained with a water solution of safranin (1%). All anatomical characteristics were measured at magnification of 400 \times under a microscope equipped by a digital camera (AXIOCam MRc5, Axio Imager D1; Carl Zeiss, Germany,). Five cell rows were selected in each ring to measure the number of cells (N), cell diameter (D), cell-wall thickness (CWT). Measurements were obtained with Lineyka software [33]. According to the Mork index [34], the ratio of double cell-wall thickness (2CWT) to radial size of the lumen (D) in each the ring was used to provide the sizes of zones of earlywood (EW, $2\text{CWT} < \text{LD}$) and latewood (LW, $2\text{CWT} \geq \text{LD}$), for each of which the average values of linear and area tracheid parameters were calculated. Measurements covered the time window 1963–2011 for TURA and for one tree in BIDJA trees. The other trees in BIDJA were measured from 1976. The measurements were performed for trees >100 years old, when the age/tree geometry effect on tree-ring width and structure at both sites as well as the impact of post-wildfire active layer thickness changes on tree growth rate at TURA [35,36] could be considered marginal.

2.3. Dendroclimatic and Statistical Analyses

The stability of climate-growth relations was analyzed by using a bootstrapped response function analysis [37]. The climatic signal was estimated by the Pearson correlation (r) between the tree-ring indexes and monthly values of mean temperature and precipitation (from previous June to current September) from the nearest climate station by the “treeclim” package in R [38], which applies a bootstrap procedure to estimate the error using random data sets. It uses 1000 bootstrapped samples to compute response and correlation coefficients, and to test their significance at 0.05.

Using the Mann-Whitney-Wilcoxon U Test [39], we considered whether there is a difference for two independent groups of tree-ring anatomical characteristics without assuming them to follow the normal distribution.

The effect of anatomical characteristics (number of cells and cell diameter) and site on tree ring width (TRW) was evaluated using generalized linear models (GLMs) [40]. The cell diameter, number of cells and the indicator of site were included as independent variables to quantify their effect on tree ring width. The distributions of raw data and residuals were estimated, and the relationships between cell size and TRW were linearized for the analyzed impacts. Multiple regressions were performed to assess the effects of the independent variables on TRW. The r -squared (coefficient of determination) interpreted as a statistical measure of how well the regression predictions approximate the real data points assume that the coefficient should be at least 50%. Results with determinacy coefficient higher than 80% can be considered good enough. A sensitivity analysis was used to determine the specific contribution of each independent variable [41]. Bootstrapped t-tests were applied to evaluate the impact of the relative variations on the results of the model. T-statistics were repetitively calculated by randomly resampling the original data set and estimating the 95% confidence intervals of the distribution [42]. Bootstrapping was performed 10,000 times to improve the robustness of results [12]. Differences were considered significant when both confidence intervals were either higher or lower than zero. All transformations were performed taking into account the assumption of normality. The normality of distributions was checked based on Shapiro-Wilk’s tests. All statistical analyses were performed using R [43].

3. Results

3.1. Climate Sensitivity of TRW

Bootstrapped response function analysis was performed relating tree-ring growth to monthly mean temperature and seasonal sums of precipitation from June of the previous year to September of current year for the period 1963–2011 (Figure 2).

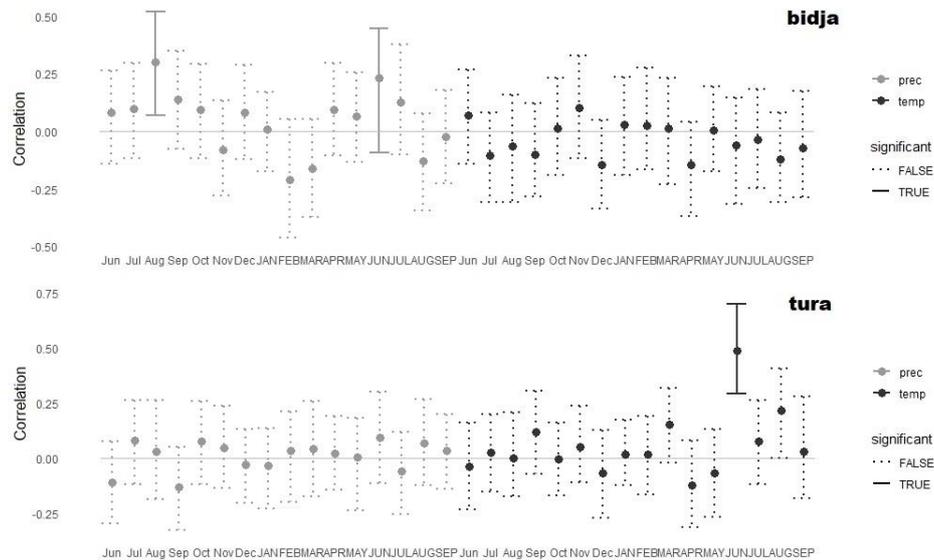


Figure 2. Bootstrapped Pearson correlations between tree-ring indices and monthly climate variables (mean temperature and precipitation) for the period 1963–2011. Monthly correlation coefficients were calculated for previous to (abbreviated by lower-case letters) and the current year of tree-ring formation (abbreviated by upper-case letters). Bold bars show significant correlations at $p < 0.05$.

Results of dendroclimatic analysis of BIDJA indicate that summer precipitation in previous year August and in current year June influenced positively and significantly TRW ($r = 0.31$ and 0.25 , $p < 0.05$, respectively). At TURA, current year June temperature positively influences tree-ring growth ($r = 0.57$, $p < 0.05$).

3.2. Xylem Cell Features

An analysis of the radial increment variability for the studied period showed different year-to-year dynamics (Figure 3). Annual rings in the southern site BIDJA were wider on 51% than in the northern site TURA. In terms of number of cells, the annual increment for TURA trees varied from a minimum of 3 to a maximum of 37 with the average of 12 tracheids (± 2.04 SD) per ring. In BIDJA the number of cells ranges from six to 73, on average of 18 tracheids (± 6.68 SD) per ring. Therefore an average cell production is a 33% lower in TURA (Figure 3). The average cell-lumen diameters were $33.7 \mu\text{m}$ and $30.1 \mu\text{m}$, for BIDJA and TURA, respectively, which means a 10% difference between the sites. Cell-wall thickness in EW was 50% thinner in BIDJA compared with TURA (Figure 3).

A difference between the two chronologies of tree-ring anatomical characteristics estimated by Mann-Whitney U test detected the significant differences between the two sites in all lines except the cell-wall thickness in latewood (Table 1).

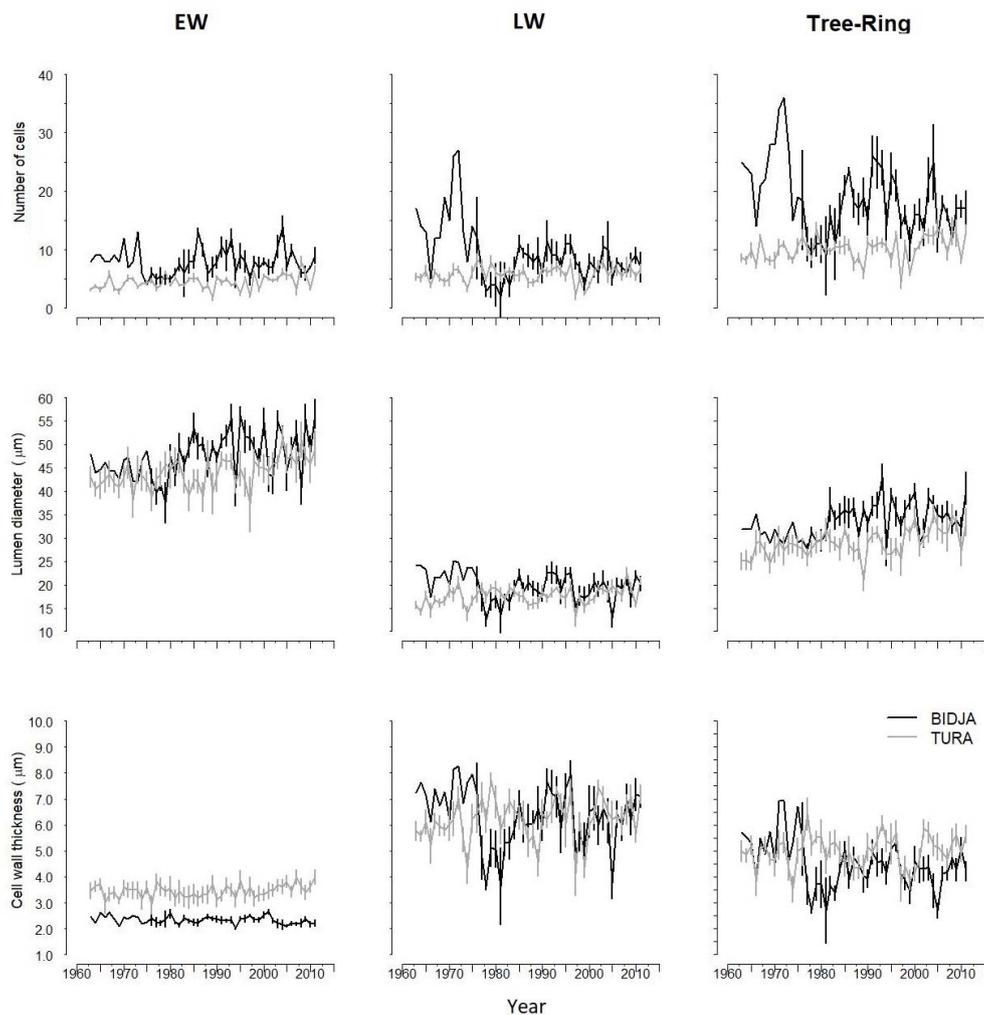


Figure 3. Mean anatomical characteristics (mean \pm standard deviation (vertical bars)) obtained for the five monitored trees from the two studied sites illustrated by number of cells, lumen diameter, cell-wall thickness in earlywood (EW) (left panel), in latewood (LW) central panel), and in total ring (Tree-Ring) (right panel).

Table 1. Estimated parameters of the Mann-Whitney U-test for anatomical characteristics of the study sites.

		U-Value	p-Value
Number of cells	EW	2230	$2.28 \times 10^{-13} *$
	LW	1866	$2.53 \times 10^{-6} *$
	Ring	2236	$2.25 \times 10^{-13} *$
Lumen diameter	EW	1716	$1.90 \times 10^{-4} *$
	LW	1761	$4.79 \times 10^{-5} *$
	Ring	2025	$5.21 \times 10^{-10} *$
Cell-wall thickness	EW	0	$2.20 \times 10^{-16} *$
	LW	1353	$2.82 \times 10^{-1} *$
	Ring	749	$1.18 \times 10^{-3} *$

* The sign indicates the significance; EW—earlywood; LW—latewood; Ring—total ring.

3.3. Relations between Main Anatomical Characteristics of Tree Rings

The relationship between tree-ring width (TRW) and the number of cells (N) for both sites and types of wood (earlywood and latewood, EW and LW) can be considered as linear (Figure 4a,b). Pearson correlation between TRW and N in EW was 0.89 and 0.88 ($p < 0.001$) for TURA and BIDJA, respectively, well matching with the similar linear relationships between TRW and LW (0.91 and 0.92 ($p < 0.001$) for TURA and BIDJA, respectively). Non-linear relationship between tree-ring width (TRW) and cell diameter (D) was observed for earlywood and latewood cells at TURA and BIDJA sites (Figure 4c,d).

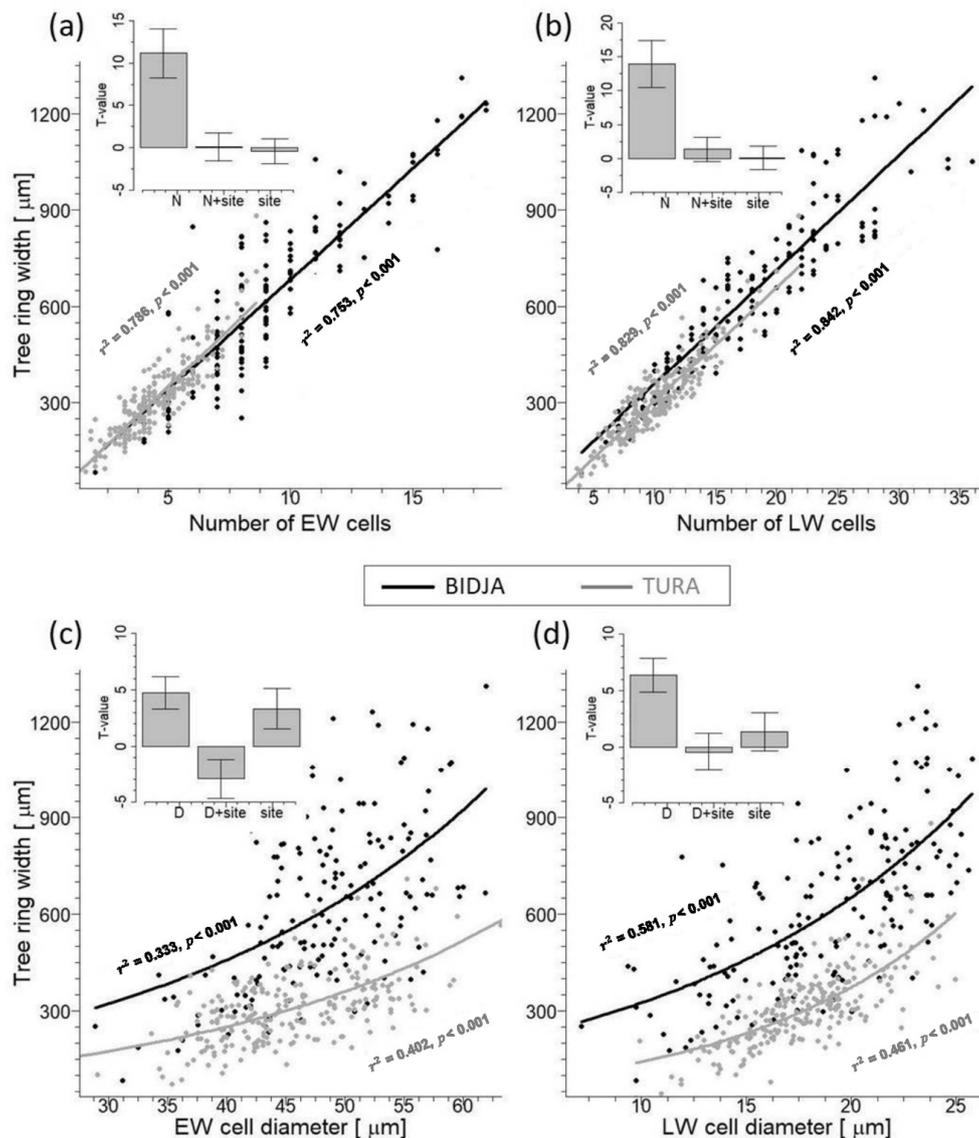


Figure 4. Linear relationships between tree-ring width (TRW) and number of cells in earlywood (EW) (a) and latewood (LW) (b). Nonlinear relationships between TRW and cell diameter in earlywood (EW) (c) and latewood (LW) (d) smoothed by an exponential function. The results are in black for TURA studied site and in grey for BIDJA studied site with corresponding r^2 and levels of significance. The enclosed vertical bars represent mean and 5% and 95% confidence intervals of the bootstrapped T-statistic based on 10,000 replications. A T-test is considered significant when both confidence intervals are either higher or lower than zero.

The r^2 between TRW and D for TURA was weaker in EW (0.33, $p < 0.001$) in comparison with LW (0.58, $p < 0.001$) (Figure 4c,d). For BIDJA the r^2 in EW and LW was nearly equal (0.41 vs. 0.46, $p < 0.001$). The resulting boxplots in Figure 4a–d show the distribution of all variables (N, cell diameter in EW (LW) and site locations) that measure their significance in TRW formation. In most cases, the indicators of site were insignificant except boxplot in Figure 4c, where both confidence intervals are visibly lower than zero. If the limits at boxplots in Figure 4 were equal to zero or extremely narrow and close to zero, it was determined as statistically non-significant results.

Contribution of each anatomical parameter to the TRW variability was showed in Figure 5 resulting from the analyses performed on the two studied sites. By the results of sensitivity analysis, the effect of number of EW and LW cells on the variation of TRW was on average 56.8% and 24.4% respectively (Figure 5). Cell diameter effect was expectedly weaker representing on average, 3.3% (EW) and 17.4% (LW). Should also be noted the intensified influence of LW cell diameter in BIDJA, which was about a quarter (23%) of the total variance in TRW (Figure 5).

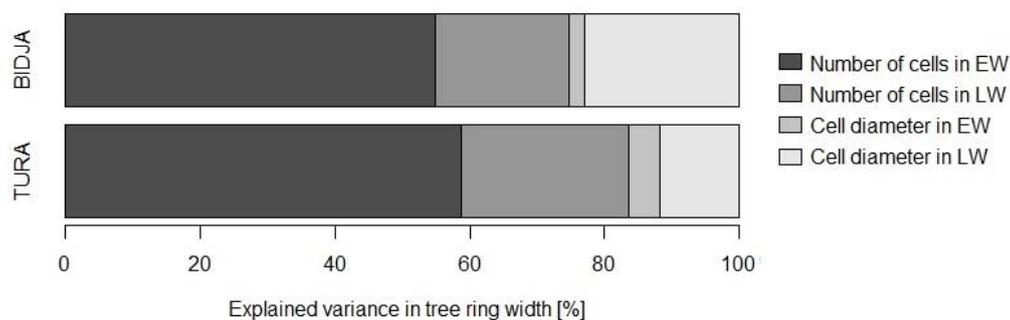


Figure 5. Contribution of number of cells and radial cell diameter in EW and LW to the total variability of tree ring width for both sites.

4. Discussion

This study investigated the differences in tree-ring climatic response and anatomical characteristics of xylem between two larch species growing in permafrost and non-permafrost sites. The results have showed how external factors change the tree-ring cell structure and affect the radial growth in Siberia. The monitoring involved two species because Gmelin and Siberian larch grow under different conditions and have non-overlapping distributions. Investigations of intra- and interspecific differentiation demonstrated a low genetic diversity within the larch genus, and in particular between the two study species [8,44–46]. This low genetic difference also results in similar wood anatomical traits. Particularly, it was shown that interpopulation genetic variability is significantly higher (85%) within one species than interspecies differences between *Larix gmelinii* and *Larix sibirica* (15%) [46].

The traditional dendroclimatology approach was applied to estimate the impact of climate variables on the tree-ring growth of Siberian larch and Gmelin larch. It is worth noting that significant influence of different climate factors (June temperature in permafrost site and June precipitation in southern non-permafrost site) on TRW was found. Climate-growth analysis for TURA had showed that the June temperatures had the most significant positive effect on the tree growth which confirmed by the previous results obtained for permafrost-growth larch [47,48]. The results obtained for BIDJA indicated the significantly positive influence of summer precipitation on tree growth. As it was noted earlier, high precipitation in late June and late July increased tree ring width of conifers in Southern Siberia [49,50].

A comparison of tree-ring anatomical parameters over the period 1963–2011 showed differences of tree rings formed under contrasting (permafrost-non-permafrost) conditions (Figure 3). Due to high correlation between tree-ring width and number of cells, wider rings of larch in BIDJA have more cells in comparison with narrower rings with less cells in TURA. Further, parameters of earlywood and latewood were analyzed separately due to their adaptive response to environmental changes

to achieve an optimal balance between competing needs for transport and mechanical functions. For studied boreal ecotones, as well as for the areas where seasonality is well pronounced, cells with large lumen and thin cell wall are considered as earlywood, while latewood cells are characterized by small lumen and wider cell wall [51,52]. One should note here that this tree-ring formation mechanism in extratropical conditions is described by some process-based models [14]. In our study it was shown that cell production of earlywood was lower under permafrost conditions in comparison to non-permafrost. The same pattern was observed for the lumen diameter of earlywood cells, namely, the EW lumens in the northern site were significantly smaller than the lumens in the southern site. It can be considered as an adjustment of the transport system to the dry conditions of Southern Siberia, as was mentioned earlier for pine at the same environment [53]. This might be also confirmed by studies that hydraulic conductivity of conifers is maximized by increasing tracheid diameters in locations where freezing is rare [54,55]. The narrow tracheid diameters protect against freezing-induced embolism in cold climates [56].

An opposite pattern was observed in the cell-wall thickness variability of the earlywood tracheids: The cell wall in the north (TURA) was thicker than in the south (BIDJA). However, no differences of CWT was found for latewood zone or whole ring between the sites. The thicker cell walls in latewood of trees from permafrost might be explained by the need to achieve a high mechanical strength against of harsh environmental conditions, which correspond well with other studies at North [18]. The optimization of the xylem structure to required mechanical support occurs by increasing the cell-wall area and the changing ratio of early- to latewood. A possible explanation for the phenomenon of thinner call-wall of tracheids in the southern site is relatively drier conditions, when trees faced the insufficient amount of available soil moisture due to high air temperatures and increased transpiration under limited amount of precipitation, while for trees growing in the cryolithozone it is possible to use additional sources of water from the seasonal soil thawing. In the studied conditions of Southern Siberia an increase of summer temperature with the minimum amount of precipitation or even their absence in the middle of the growing season causes a water deficit and might suppresses the processes of photosynthesis and the assimilates formation [57], which can subsequently be used to build tracheid cell walls. In this regard, the amount of precipitation in the second half of summer allows continued tree growth [58] and increases the area of the cell wall in latewood.

Obtained results confirmed our hypothesis, that absolute values of cell parameters (tracheid diameter and cell-wall thickness) are different due to xylem adjustment to local climate at permafrost and non-permafrost environment. Despite the obvious differences in the growing conditions and related tree-ring formation, relationships between TRW and the number of cells and cell diameter in EW and LW have been proven as non-specific to environmental conditions. It was shown how number of cells, cell diameter and climate specifics affect tree-ring formation in contrasting environments. Our second hypothesis that the earlywood and latewood cell production and cell sizes have a similar contribution to tree-ring width was accepted. Cell production in early- and latewood explain 56.8% and 24.4%, respectively, of the tree-ring width variability, which is fully consistent with the hypothesis of a linear relationship between total cell production, rate of cell production, and tree-ring width [2]. This relationship between TRW and the number of cells is typical to conifers from various ecological conditions. The dependence between the radial cell size in early- and latewood and the tree-ring width becomes exponential for both northern and southern sites. Only in case of dependence between the EW cell size and the tree-ring width was the site effect was significant, which requires additional analysis.

5. Conclusions

Climatic conditions and anatomical characteristics of *L. sibirica* and *L. gmelinii* were compared in contrasting conditions to assess their impact on radial growth. Results of bootstrapped response function analysis for southern site BIDJA indicated that summer precipitation in August of the previous year and in June of current year influenced positively tree radial growth. The same analysis for TURA revealed a significant positive correlation with the temperature of June of the current year. Tracheids

with smaller lumen and wider cell wall were observed under permafrost conditions. The relationship between the tree-ring width and the cell production in early- and latewood are assessed as linear, whereas the dependence between the radial cell size in early- and latewood and the tree-ring width becomes significantly non-linear for TURA and BIDJA. The results show that different larch species from sites with diverging climatic conditions converge towards similar xylem cell structures and relationships between xylem production and cell traits. The relations obtained for tree-ring anatomical features of larch species in different climatic zones answer to the question on the consequences of the current warming and the associated changes in the hydrothermal regime of soils on wood growth and xylem anatomy. Our results help to clarify the link between climate and xylem functioning, and can be a tool to improve the developing models of tree growth [58,59]. This approach promotes a better understanding the anatomical adaptation of larch species to local environment conditions.

Author Contributions: M.I.P., V.V.S. and S.R. conceived and designed the study; M.V.F. and E.A.V. provided the anatomical data; A.V.K., E.A.V. and J.-G.H. provided the valuable discussion and ideas; M.I.P., V.V.S., E.A.V., M.V.F., A.V.K., E.A.B., J.-G.H. and S.R. wrote the paper. All authors have read and agreed to the published version of the manuscript.

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