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The Relationship Between Variability of Cell Wall Mass of Earlywood and Latewood Tracheids in Larch Tree-Rings, the Rate of Tree-Ring Growth and Climatic Changes

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Keywords

Larch
Earlywood
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Tracheid
Cell wall mass
Mass deviation index
Potential of cell development
Critical threshold of tree-ring width

Summary

Mass accumulation dynamics in earlywood and latewood cell walls of larch from northern regions of Central Siberia are investigated and correlations among cell mass of different tree-ring zones, radial tracheid sizes and tree-ring width are found. A linear relationship exists between cell wall mass and radial cell size. The deviation of cell mass from the regression line (index of mass deviation) and the mean density of the respective tree-ring zone are similarly functionally dependent on the radial cell size and reflect the realization of the potential determined during the period of cell formation. There is a critical value of larch tree-ring width in relation to cell mass. For the tree-rings with width less than this critical value the difference in the mass of earlywood and latewood cells increases with decreasing tree-ring width. The cell wall mass correlates with the monthly temperatures of June and July. Under favorable growing conditions tracheids with similar mass of cell walls are formed in earlywood and latewood, while under unfavorable conditions cell wall mass accumulation in latewood is severely limited. A comparative analysis of the cell wall mass in earlywood and latewood indicates that mass accumulation is independent of the switching processes from earlywood production to the production of latewood.

Introduction

Mass of tracheid walls is a direct indicator of stem mass accumulation and depends on the photosynthesis rate during the period of tracheid formation and development (Richardson 1964; Schweingruber 1996). Data on the relationship between the mass of early- and latewood tracheid walls cannot be considered comprehensive, as they were obtained, as a rule, for only small quantities of material. Some data have shown the mass of tracheid walls in earlywood and latewood to be equal (Skene 1969; Sastry and Wellwood 1971). Others have shown that the mass of earlywood and latewood tracheid walls can be both equal and different (Antonova *et al.* 1995; Vaganov *et al.* 1985). So, we can assume that both situations are possible, depending on the ontogenesis period of a tree and its environmental conditions.

The goal of our work is to investigate the dynamics of the mass of earlywood and latewood tracheid walls and to correlate cell wall masses with other parameters of tree-ring structure and climate, using a large number of data on cell sizes and wood density obtained from tree-rings of larch in the north of Central Siberia.

Materials and Methods

Wood samples (cores) were collected from *Larix sibirica* Ledeb and *L. gmelinii* (Rupr.) Rupr. in 3 sites in the north of Central Siberia (Russia) (Fig. 1). Here up to 70% of the tree-ring width variability is explained by summer temperature (Vaganov *et al.* 1996a). Tree-ring width changes due to tree age are practically impossible since cell size measurements were carried out for the last 100 tree-rings of 250-year-old larch trees, *i.e.* for the period when tree growth is stable.

The sites GA (71°17'N, 93°53'E) and IK (70°30'N, 89°25'E) are very open larch stands (canopy closure is less than 0.1) typical for the forest tundra. The site KURL, situated 250 km south from the northern timberline (68°03'N, 89°10'E), is a mixture of larch, spruce and birch. All study stands grow under wet conditions.

The tracheid mass can be measured by means of maceration and weighing (Sastry and Wellwood 1971). However, indirect measurements based on the geometrical size of tracheids (Skene 1969) or on a combination of different techniques, for example densitometry, are much more productive. The latter method was used in our investigation to evaluate the mass of cell wall (calculated per unit of tracheid length). Tree-rings, cell sizes and density data for the present study were obtained by Kirdyanov and Zarharjewski (1996) and Vaganov *et al.* (1996b). Then

$$M = P_Z D T \qquad (1)$$

where M is the specific mass of the tracheid wall, P_Z is the density of the tree-ring zone (earlywood or latewood), D, T are the radial and tangential size of tracheids in this zone.

The error in the calculation of M can be estimated by the general equation for the estimation of indirect measurement errors ($f(x)$), where n is the number of independent variables (Goldin *et al.* 1983):

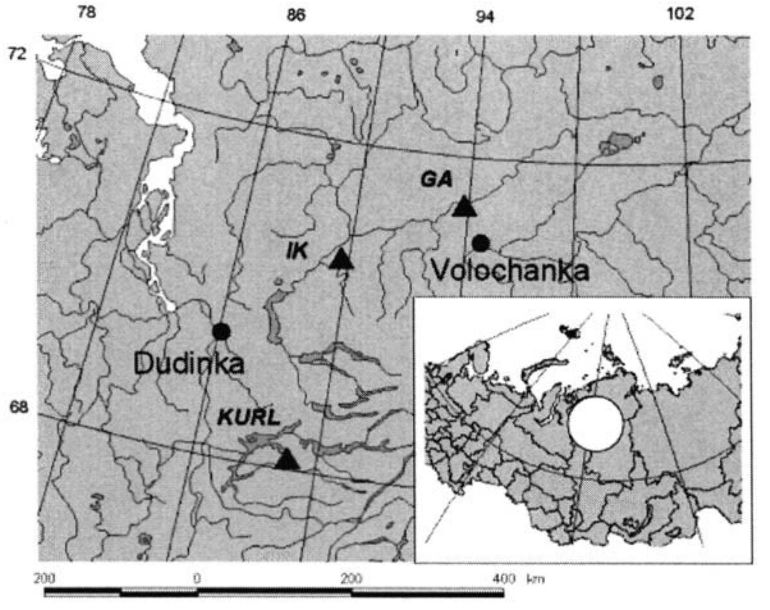

Fig. 1. Location of tree-ring sites (▲) and meteorological stations (●).

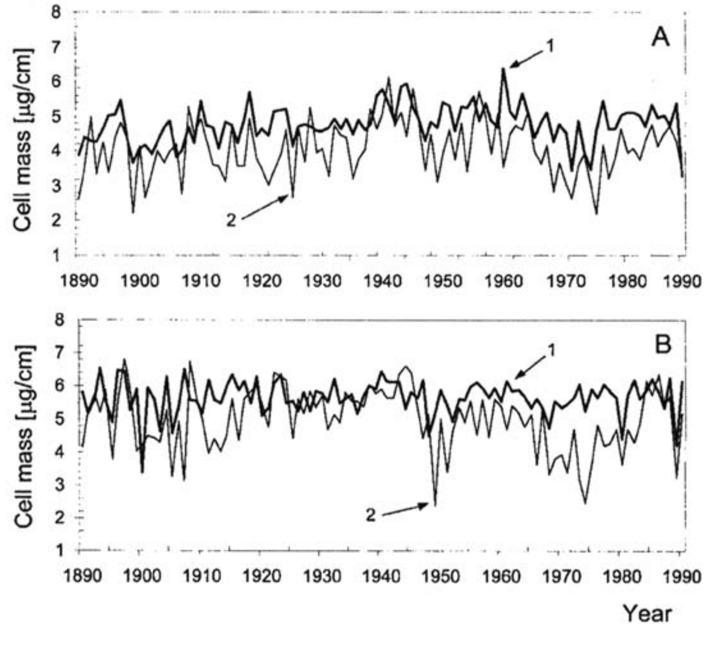

Fig. 2. Year-to-year cell wall mass changes in: 1 - earlywood, 2 - latewood; A,B - sites IK and KURL, respectively.

$$\sigma f(x) = \sqrt{\sum_{i=1}^{n}\left[\frac{\partial f(x_i)}{\partial x_i}\Delta x_i\right]^2} \qquad (2)$$

In the present study it is 0.4×10^{-6} g (0.4 µg), *i.e.*, 10%.

The measurements of tree-ring density profiles were carried out according to the standard technique with the densitometer DENDRO-2003 (Schweingruber 1996) for, at least, 10 trees per site and 2 radii per tree. All individual density curves obtained were averaged for each site. Radial tracheid sizes in 5 radial files randomly chosen in each tree-ring were measured using a semi-automatic device (Vaganov *et al.* 1985). To compare tree-rings with different cell numbers, the standardization of individual cell files to the standard cell number (15 cells) was done according to the technique described in Vaganov *et al.* (1985). Tangential tracheid dimension measurements showed that the value is close to 35 µm.

The mean density of earlywood and latewood tracheids measured by densitometry was taken as P_Z. If the length of earlywood and latewood tracheids does not significantly differ (Larson 1994), *M* can be considered as the mass of cell wall in earlywood and latewood.

To estimate the influence of climatic changes on cell wall formation, dendroclimatic analysis was done. Monthly temperature and precipitation records from two nearby meteorologi-

Table 1. Correlation between the mass of earlywood and latewood cells, their difference (ΔM) and tree-ring width (TRW) for the sites investigated

Site	Correlation between:			
	cell wall mass of			
	earlywood vs. latewood tracheids	earlywood tracheids vs. TRW	latewood tracheids vs. TRW	ΔM vs. TRW
GA	0.64	0.51	0.84	-0.72
IK	0.54	0.50	0.76	-0.48
KURL	0.34	0.25	0.84	-0.73

All coefficients are significant at $p<0.05$.

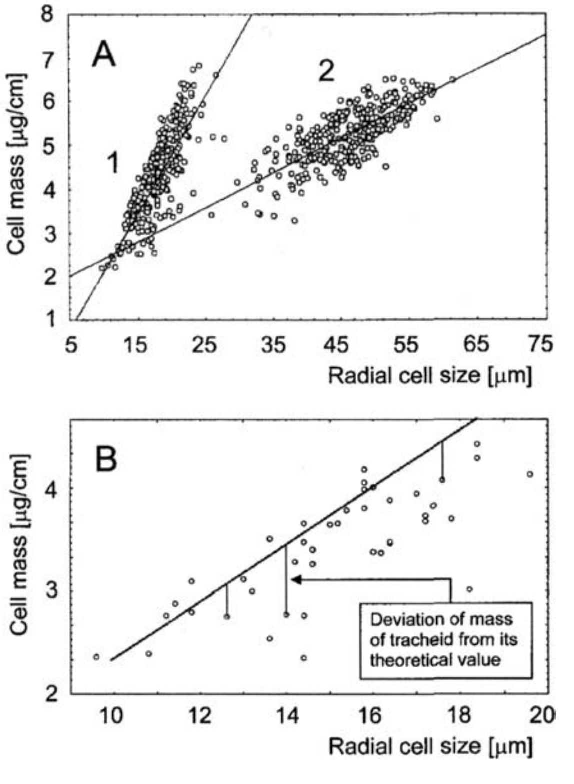

Fig. 3. Relationship between cell wall mass and radial cell size: 1 - latewood, 2 - earlywood; A - sites GA, IK and KURL, B - example of cell wall mass deviation.

cal stations were availabale. Data from the station Volochanka were used for the site GA and from Dudinka for IK and KURL (Fig. 1).

Results

A comparison of earlywood and latewood cell masses shows that they can be either equal or different, depending on the year when the tree-ring was formed (Fig. 2). The dynamics of early- and latewood cell mass is synchronous. Significant positive correlation was found between the mass of earlywood and latewood tracheids and tree-ring width for all sites investigated (Table 1). Consequently, environmental conditions favourable for cell production are also favourable for mass accumulation in the cells of earlywood and latewood.

There is a linear relationship between the mass of cells and their radial size (Fig. 3a), but the respective linear equations are different for earlywood and latewood tracheids. Similar results were obtained by Sviderskaya (2000) for basal cell wall area of pine tracheids. Quantitatively these relations can be approximated by the regression equation $Y = kX + b$. Coefficients of the equation are shown in Table 2. The slope of the plane curve calculated for latewood cells is 3-4 times larger than for earlywood cells. In other words, latewood cells accumulate 3-4 times more cell wall mass per unit of radial dimension than earlywood cells.

It is also seen from the data in Figure 2 that the ranges of cell wall mass changes for earlywood and latewood are very similar, but the range of radial cell size changes is 2-2.5 times wider for the earlywood cells than for the latewood ones. The average values of cell mass in different tree-ring zones do not differ significantly: 5.2 ± 1.0 µg for earlywood and 4.4 ± 1.4 µg for latewood. These differences do not significantly exceed the absolute error of measurements (0.4 µg). Nevertheless the mass stored in earlywood cells is larger than that in latewood of the same tree-ring. The X-coordinate of regression line intersection point (Fig. 3a) is close to the radial dimension of the cells in the cambial zone (7-8 µm).

Let us define the index of mass deviation I as the deviation of cell mass, obtained for a certain radial tracheid dimension, from the regression line:

$$I = \frac{M}{M_t} = \frac{M}{k\,D + b} \tag{3}$$

where M is the cell mass for defined cell size, M_t the theoretical cell mass for the same radial cell size, D the radial cell size and k and b represent parameters of the regression line. Between the index of mass deviation and the mean density of the same tree-ring zone there is a high correlation. For all sites it is close to 1.

The difference between earlywood and latewood cell wall mass is characterized by:

Table 2. Parameters of the regression equations $Y = k X + b$ for the relationship between cell wall mass and radial cell size

Site	Tree-ring zone	k, $\mu g \times cm^{-1} \times \mu m^{-1}$	b, $\mu g \times cm^{-1}$	R^2
GA	Earlywood	0.099	1.03	0.68
	Latewood	0.28	-0.8	0.68
IK	Earlywood	0.093	0.6	0.75
	Latewood	0.22	0.13	0.59
KURL	Earlywood	0.067	2.2	0.56
	Latewood	0.26	-0.03	0.74
Data summarized for GA, IK, KURL	Earlywood	0.077	1.67	0.56
	Latewood	0.27	-0.6	0.68

R^2 is coefficient of determination, significance level p<0.00001.

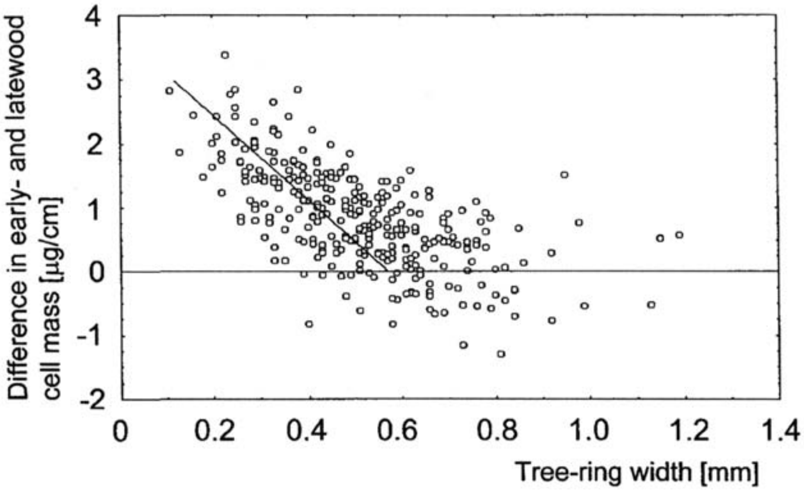

Fig. 4. Relationship between difference in cell wall mass in early- and latewood and tree-ring width.

$$\Delta M = M_{ew} - M_{lw} \tag{4}$$

where M_{ew}, M_{lw} are masses of early- and latewood cells of the same tree-ring. Figure 4 represents the relationship between ΔM and tree-ring width, the main indicator of seasonal productivity. The correlation coefficient between these two variables is negative and significant for all sites studied (Table 1). It indicates that the worse the environmental conditions for tree-ring growth, the greater the difference between the masses accumulated in early- and latewood cell walls. The relationship of ΔM with TRW shows that up to some critical threshold (TRW_c), ΔM decreases gradually, but for $TRW > TRW_c$ the difference between cell mass of early- and latewood is not larger than the error of indirect measurements of ΔM (0.6 µg). This can be explained by the assumption that during seasons unfavorable for tree-ring growth (when $TRW < TRW_c$) the quantity of "building material" is not enough to form a wide tree-ring with thick cell walls. The suppression of the biosynthetic processes of secondary cell wall formation in larch tree-rings at the northern timberline is more obvious for latewood cells because $\Delta M > 0$ (*i.e.*, $M_{ew} > M_{lw}$).

To estimate the effect of environmental changes on cell wall formation and development, coefficients of sensitivity (Shiyatov 1986) were analyzed (Table 3). The influence of environmental factors on cell wall mass accumulation is 1.6-2.5 times higher in latewood than in earlywood. For all sites investigated, the coefficient of sensitivity calculated for mass of latewood tracheids is higher than for maximum latewood density and less than for tree-ring width.

A dendroclimatic analysis was made using monthly temperature and precipitation records from October of the previous year to September of the current year. Correlation coefficients between cell wall mass and monthly temperature are shown in Figure 5. The summer temperature regime is the only parameter that significantly correlates with this tree-ring characteristic.

Correlation coefficients between cell mass and monthly temperature for the period from June to August are presented in Table 4. Correlation coefficients of

Table 3. Coefficients of sensitivity calculated for wall mass of tracheids *M*, maximum latewood density P_{max} and tree-ring width TRW

Site		Coefficients of sensitivity		
		M	P_{max}	TRW
GA	Earlywood	0.08	0.14	0.31
	Latewood	0.20		
IK	Earlywood	0.12	0.12	0.29
	Latewood	0.20		
KURL	Earlywood	0.09	0.10	0.26
	Latewood	0.18		

Table 4. Correlation coefficients between monthly temperature and cell wall mass *M*, radial cell size *D*, mean density of tree-ring zone P_m, maximum latewood density P_{max} and tree-ring width TRW

Site		Tree-ring parameter							
		Earlywood			Latewood				
		D	*M*	P_m	*D*	*M*	P_m	P_{max}	TRW
GA	June	0.18	0.30*	0.17	0.08	0.36*	0.46*	0.46*	0.33*
	July	0.17	0.12	-0.13	0.17	0.42*	0.55*	0.55*	0.46*
	August	-0.18	-0.14	0.06	-0.11	0.10	0.27	0.26	-0.08
IK	June	0.24	0.45*	0.43*	-0.02	0.41*	0.68*	0.69*	0.41*
	July	0.26	0.21	-0.06	0.09	0.34*	0.48*	0.48*	0.42*
	August	-0.27*	0.08	0.34*	-0.26	0.14	0.52*	0.52*	0.18
KURL	June	0.50*	0.56*	-0.07	0.23	0.55*	0.70*	0.71*	0.41*
	July	0.14	0.11	-0.07	0.13	0.26	0.33*	0.33*	0.39*
	August	0.11	0.28*	0.14	-0.14	0.06	0.36*	0.34*	0.04

* coefficient significant at $p < 0.05$.

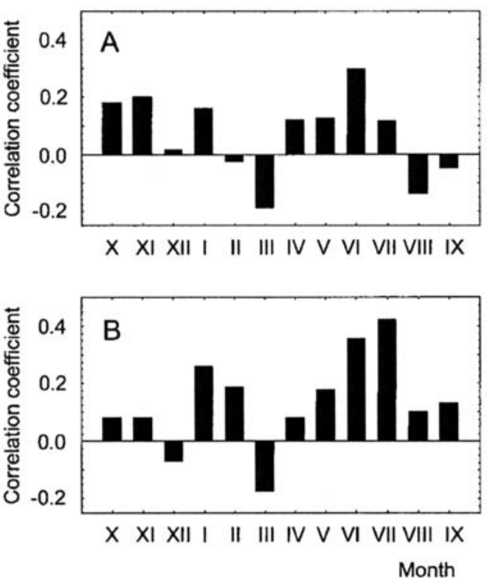

Fig. 5. Correlation of cell wall mass obtained for GA and monthly temperature: A - earlywood tracheids, B - latewood tracheids.

other tree-ring structure parameters (radial cell size, mean earlywood density, tree-ring width and maximum latewood density) with the same climatic variables are also shown.

The dendroclimatic analysis shows that the mass of earlywood tracheids correlates positively with temperature of June and latewood cell mass with June and July temperatures. The results are in agreement with observations on the seasonal formation of cells in different tree-ring zones of larch growing at the northern timberline (Vaganov *et al.* 1999). The mass of cell walls is in direct proportion to radial cell size and mean density of the same tree-ring zone. Nevertheless, the mass of cell wall of earlywood has a higher correlation coefficient with temperature than earlywood cell size and mean density.

ΔM correlates negatively with monthly temperature of individual summer months, and for the southernmost site KURL the correlation coefficient of this parameter is higher with June temperature than with July temperature.

The xylem of conifers consists mostly of tracheids. It can be assumed that the mean density of any part of a tree-ring can be considered as density calculated for the "mean" tracheid from the same zone. The density of a cell (Fig. 6) can be calculated as cell mass divided by its volume:

$$P_c = \frac{M}{V} = \frac{M}{D\,T\,L} \qquad (5)$$

where P_C is mean cell density, *V* is cell volume, *T* is tangential size of tracheid and *L* represents length of tracheid.

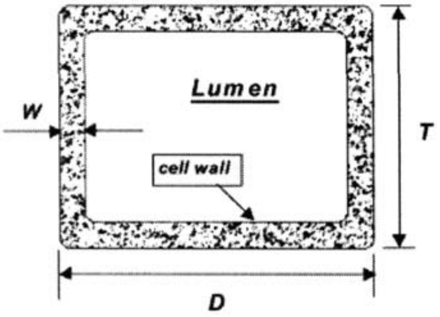

Fig. 6. Scheme of the cross-section of a tracheid. *D, T* - radial and tangential sizes of cell. *W* - cell wall thickness.

The mass of cells can be found as the product of cell wall density P_w and volume of cell wall V_w:

$$M = P_w V_w \quad (6)$$

$$V_w = (S - S_l)L = (2W(D + T) - 4W^2)L \quad (7)$$

where S is the area of cross-section of tracheid, S_l the area of cross-section of lumen and W the cell wall thickness. From equation (6) and (7):

$$M = 2WP_wL(D + (T - 2W)) \quad (8)$$

Consequently, mean cell density can be calculated from (8) and (5):

$$P_c = \frac{2\,W\,P_w}{T}\left(1 + \frac{T - 2\,W}{D}\right) \quad (9)$$

On the other side, index of mass I can be found from (8) and (3), where L is taken as 1:

$$I = 2\,W\,P_w\left(\frac{D}{k\,D + b} + \frac{T - 2\,W}{k\,D + b}\right) \quad (10)$$

If one compares equations (9) and (10) and takes into consideration the amplitude of variation of the coefficients k and b (Table 2), it is seen that M and I are inversely related to radial cell size D. This relationship can explain a high correlation between the density of tree-ring zone and amplitude of cell mass deviation from its theoretical value.

Discussion

Let us consider the regression line calculated using the highest values of cell mass obtained for each radial cell size, but not for all the tracheid mass values (Fig. 3b). This line is expected to show the highest cell mass possible for each radial cell size. Then the deviation of mass from its potentially maximum value predetermined during the beginning period of cell formation (in cambial zone) and, consequently, density of this part of the tree-ring are the index of realization of cell development potential and, therefore, index of environment suitability during the period of cell wall mass accumulation. It supports the concept by Vaganov (1996) that the tracheid sizes in trees along the polar tree line are defined to a great extent in the beginning of the growing season, *i.e.*, this period is the key one for further cell development. During this interval the potential for cell development is predetermined and this potential can be realized or not, depending on weather conditions. The importance of early summer conditions has been pointed out in a number of papers.

The number of cases where the deviation of cell mass from the regression line calculated for all the data obtained for each site is not higher than the error of its measurements is, on average, 83.2 ± 1 % and 61 ± 4 % for earlywood and latewood cells, respectively. It indicates that earlywood cells realize the potential of growth better than latewood cells. Little data on the seasonal dynamics of tree-ring growth at the northern timberline show that formation and development of secondary cell wall in earlywood tracheids take place during the interval of vegetation period with more favorable conditions than in latewood cells. Worse environmental conditions in the second part of the growing season can lead sometimes to the termination of cell wall development.

Consequently, early- and latewood tracheid mass changes (Fig. 2) show that the potential of growth of all cells is determined by the conditions in the first part of the growing season. The level of photosynthesis apparatus development, *i.e.*, needles development, seems to play the leading role in this process. This is a reason why year-to-year variability of tracheid mass in different zones of a tree-ring are quite synchronous. Similarity of values of early- and latewood cell mass indicate that environmental conditions during the vegetation period were quite favorable to realize the potential of cell development predetermined in the beginning of the growing season but differences in mass reveal that conditions were much worse at the end of the vegetation period.

During favorable years, when differences in mass of cells in different tree-ring zones is are small, latewood cells realize their potential of growth. It indirectly indicates that accumulation of cell wall mass is independent from the processes of cell differentiation.

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