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Earlywood and Latewood Features of *Pinus sylvestris* in Semiarid Natural Zones of South Siberia[1]

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Abstract—Chronologies of the anatomical and integral parameters of the Scots pine (*Pinus sylvestris* L.) earlywood and latewood were investigated for two sites in the Minusinsk depression with different soil moisture conditions. Patterns of statistical characteristics and climatic responses of the chronologies were identified. Differences between sites were revealed in the cell diameter and wall thickness distributions. These differences are indicators of adapting pine wood structure to the moisture deficit.

Keywords: cell number, cell radial diameter, cell wall thickness, earlywood, latewood, semiarid conditions
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It is known that tree rings are a valuable natural archive for studying environmental conditions, including climate, and adaptation of ecosystems to their changes [1]. They can be used widely because of their annual temporal resolution with a possibility of precise dating, the longevity of trees life span, and the wide spread of forest vegetation around the globe [2, 3].

Tree ring width is the most frequently used parameter due to the simplicity of its measurement [4]. Considering the tree-ring formation, its width sums up the results of cell division and extension processes. At the same time, the structure and function of wood are also under influence of the result of the third cell differentiation stage: thickening of the cell wall [5, 6]. Therefore, given differences in the structure and functions of wood layers formed during the season, i.e. earlywood and latewood, the parameters of the wood cell structure can contain more detailed climatic information in comparison with the integral parameters of the tree ring [7, 8]. For conifers, the cellular structure is characterized by tracheids radial diameter and cell wall thickness. It should be taken into account that the combination of these parameters defines function of cells, including water transport and carbon deposition [6, 9], i.e. the developed ring structure subsequently has a long-term effect on the state of the tree as a whole and its further growth [10].

In connection with the foregoing, the anatomical characteristics of wood cells are an important source of data on the adaptation of trees to environmental changes, especially in conditions of insufficient moisture, where there is a high risk of hydraulic balance disruption in woody plants, leading not only to suppression of their growth, but also to an increase in mortality [11, 12]. Studies in this field are now particularly important due to the global increase of temperature and of the droughts frequency, especially in temperate latitudes [13, 14].

Research of the adaptation of trees to a lack of moisture is advisable on the lower and southern boundaries of the forest, where the tree growth is typically limited by the amount of precipitation. In temperate latitudes of the continental climate, including South Siberia, these conditions are represented by forest-steppes and isolated forest stands in the steppe zone. We set the following objectives: (1) to investigate the structure parameters of Scots pine earlywood and latewood in habitats with a deficit of precipitation; (2) to compare the climatic response in various tree ring parameters; (3) to identify the features of wood structure, characterizing the adaptation of pine to different growth conditions.

MATERIAL AND METHODS

Samples were collected from two sites in the Minusinsk depression (Fig. 1): Berenzhak (BER, 54°20′ N, 89°44′ E) is situated 32 km to the south-west from Shira village (weather station #29756 Shira, 54°30′ N, 89°56′ E); Minusinsk (MIN, 53°45′ N, 91°56′ E) is situated 15 km to the east from the Minusinsk town (weather station #29866 Minusinsk, 53°41′ N, 91°40′ E).

The climate of the study area is moderately cold continental [15] with the average annual air temperature 1–1.5°C. The transition of daily temperatures

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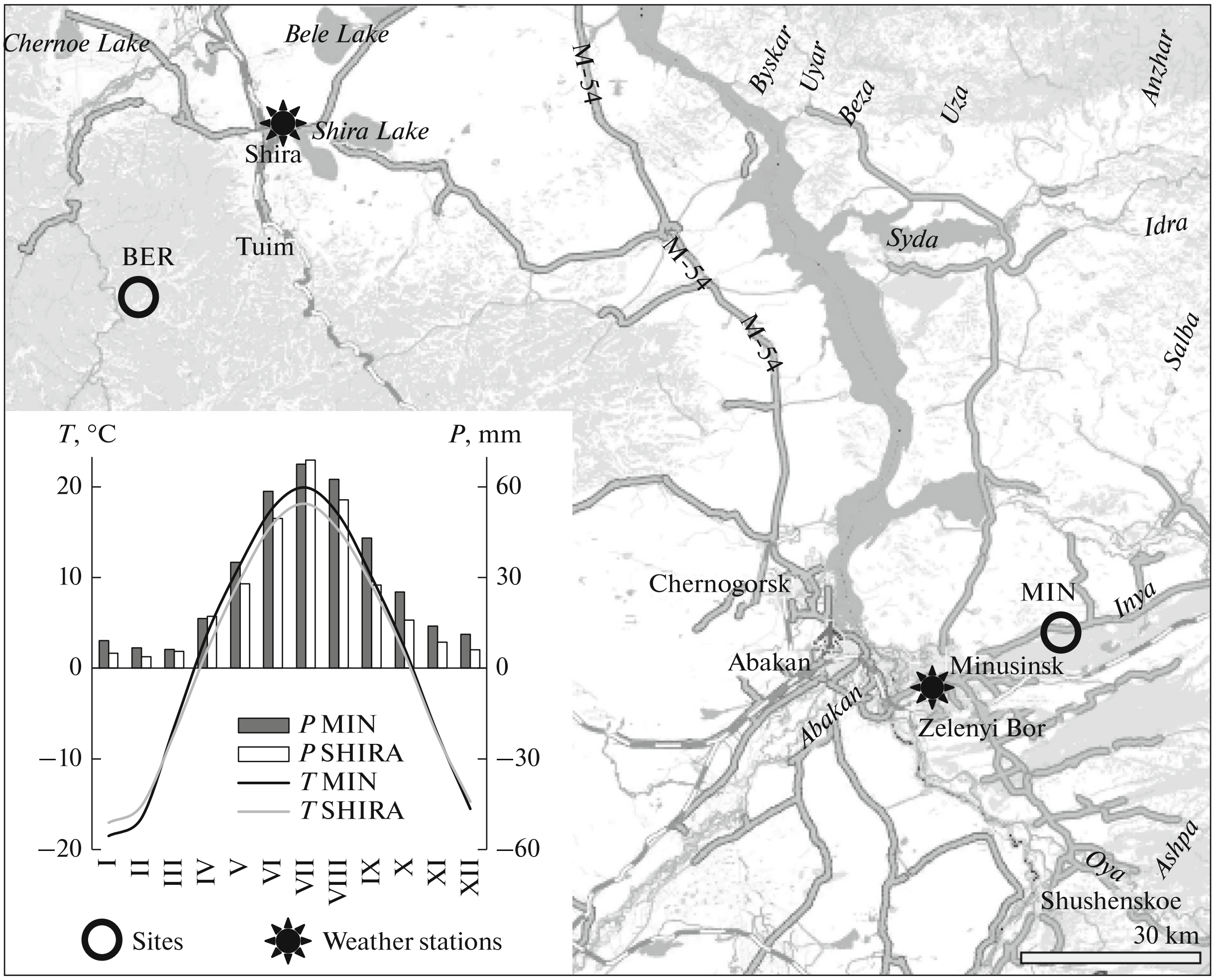

Fig. 1. Map of the study area (the Republic of Khakassia and South of the Krasnoyarsk Territory), and climatic diagrams of mean temperatures (lines) and the amount of precipitation (bars) based on data from the Minusinsk and Shira weather stations. Sites of the wood samples collecting and state weather stations are marked on the map.

through 5°C threshold occurs at the end of April. The average amount of precipitation per year is 300–350 mm. Its regime is characterized by a pronounced summer maximum: about 90% of precipitation falls during the period from April to October, the maximum is in July, the minimum is in February–March (Fig. 1). Differences between weather stations are insignificant. Monthly data on the mean temperature and the amount of precipitation for 1969–2008 were used in the work.

The BER site is located on the border of the forest-steppe zone and the southern taiga in the Kuznetsk Alatau foothills. It is represented by slope of the southern exposition (inclination 15°–20°) covered with pine-larch with birch motley-grass forest on mountain gray soil with rocks. The foothills are characterized by higher average amount of precipitation than it is recorded at the Shira weather station, located in flatlands. However, the combination of precipitation water flowing down and filtering to the slope base, and the increased influence of solar radiation leads to a pronounced deficiency of soil moisture on the site. The lack of moisture is also evidenced by prevailing such species of undergrowth as *Caragana arborescens*, *Spiraea chamaedryfolia*, *Spiraea trilobata* and the absence of moss cover.

The MIN site is located in the Minusinsk insulated forest. It is covered with birch-pine motley-grass forest on layered aeolian humus chernozems. The Minusinsk forest is situated in the steppe zone, where most of the summer precipitation is pulled to the Yenisei River. Therefore, the amount of precipitation is steadily lower in the investigated area than at the Minusinsk weather station. Nevertheless, the location of the site in a weakly expressed relief depression provides accumulation of precipitation and additional moistening from the nearest hydrological objects. As a result, the site has a pronounced moss cover (covering up to 50%), predominate species of undergrowth are *Rosa acicularis* and *Cotoneaster melanocarpus*. Thus, in spite

Table 1. Numerical parameters of cells normal distributions in the earlywood and latewood zones

Site	Earlywood (ew)							Latewood (lw)						
	percentage, %	CWT/D		D, μm		CWT, μm		percentage, %	CWT/D		D, μm		CWT, μm	
		μ	σ	μ	σ	μ	σ		μ	σ	μ	σ	μ	σ
MIN	65.6	0.046	0.014	41.4	8.2	1.88	0.34	34.4	0.203	0.049	23.6	5.6	4.46	1.32
BER	69.3	0.068	0.019	37.5	6.0	2.78	0.60	30.7	0.252	0.073	19.1	6.9	4.88	1.56

of the smaller amount of precipitation, moisture conditions at the MIN site are generally less extreme.

At each site, the cores of 5 living trees of Scots pine (*Pinus sylvestris* L.) with age of 80–120 years were selected for measurement. The age restriction, especially given the relatively weak expression of the age trend in the radial cell diameter and wall thickness, made it possible to exclude the possibility of a significant effect of the biological tree age on the study results [16–18]. Collection and transportation of cores were carried out according to standard techniques of dendrochronology [2]. To study the cell structure of tree rings, the cores were softened by boiling in water, and thin sections (20 μm) were obtained with a sledge microtome. On the microphotographs of these stained sections, the following anatomical parameters of the rings were measured: cell number (CN), radial diameter (D) and wall thickness (CWT) of each cell [19] for 5 radial files in each ring, followed by averaging between files. To make averaging over series with different CN possible, the initial measurements were normalized to the mean CN over all radial files [20]. The tree ring width (TRW) was calculated as a sum of D for all cells. The dating of the samples (determination of the calendar year of each ring) was carried out by comparing these TRW series with the chronologies available for the considered sites, which include cores of the same trees (see [21, 22]).

The Mork's empirical rule was used to separate zones of earlywood and latewood (Fig. 2a). This rule makes it possible to distinguish cells of early and late wood on the basis of a simple criterion: latewood includes cells for which the CWT is more than 0.25 of the lumen size [23]. Since the radial cell diameter is composed of a lumen and two walls, the $CWT/D > 1/6 \approx 0.17$ ratio should be fulfilled for latewood. However, taking into account later studies of the conifer wood anatomy and physiology [24, 25, etc.], it was decided to use a boundary criterion calculated from actual data. We plotted the density functions of cell distribution by the CWT/D ratio over all measured annual rings for each site, then modeled these distribution density functions in form of the sum of two normal distributions [26], representing the earlywood and latewood zones (Figs. 2a, 2b).

The values of the normal distribution numerical parameters (mean – μ, standard deviation – σ) were calculated by the least squares method (Table 1). As threshold values (k) of the CWT/D ratio we used the mean value between local minima on the empirical and modeled distribution density curves [27]. The k values were calculated separately for each site. To confirm the obtained threshold values, scatter plots of cell distribution in the CWT and D axes were developed (Figs. 2d, 2e). In these graphs, the k values of CWT/D are showed as straight lines with an angular coefficient k. Obviously, for both sites these straight lines are at an approximately equal distance between earlywood and latewood cell clusters.

After dividing rings into earlywood and latewood zones, for each year summing the radial cell diameters in each zone was performed to obtain the integral parameters values: earlywood width (EWW) and latewood width (LWW). Then the average D and CWT values in each zone were calculated. After averaging over all five trees within the site, local chronologies of the six anatomical and three integral parameters of tree rings were obtained. Significant long-term trends in the chronologies are not observed.

We used the following chronology statistical characteristics: arithmetic mean, standard deviation, variation coefficient (the ratio of standard deviation to arithmetic mean), sensitivity coefficient (the ratio of difference between two adjacent values of the variable to their arithmetic mean, averaged over the entire series) and first-order autocorrelation coefficient [4, 28]. In this case, the variation coefficient is a measure of the parameters variability in general, and the sensitivity coefficient is a measure of its part caused by rapidly changing external factors, primarily climatic ones. To analyze the climatic factors influence on the anatomical structure of wood, paired correlation coefficients of chronologies with temperatures and precipitation were calculated on base of monthly weather station data. The number of considered dendroclimatic relationships is comparable with the duration of the analysis period, so the significance level of the correlation coefficients was adjusted by the Benjamin-Hochberg procedure to account for the multiplicity of comparisons [29].

For analyzing pine tree rings structure under different local conditions of growth, the distribution density of cells by D and CWT were simulated in form of the sum of two normal distributions (earlywood and latewood), separately at each site.

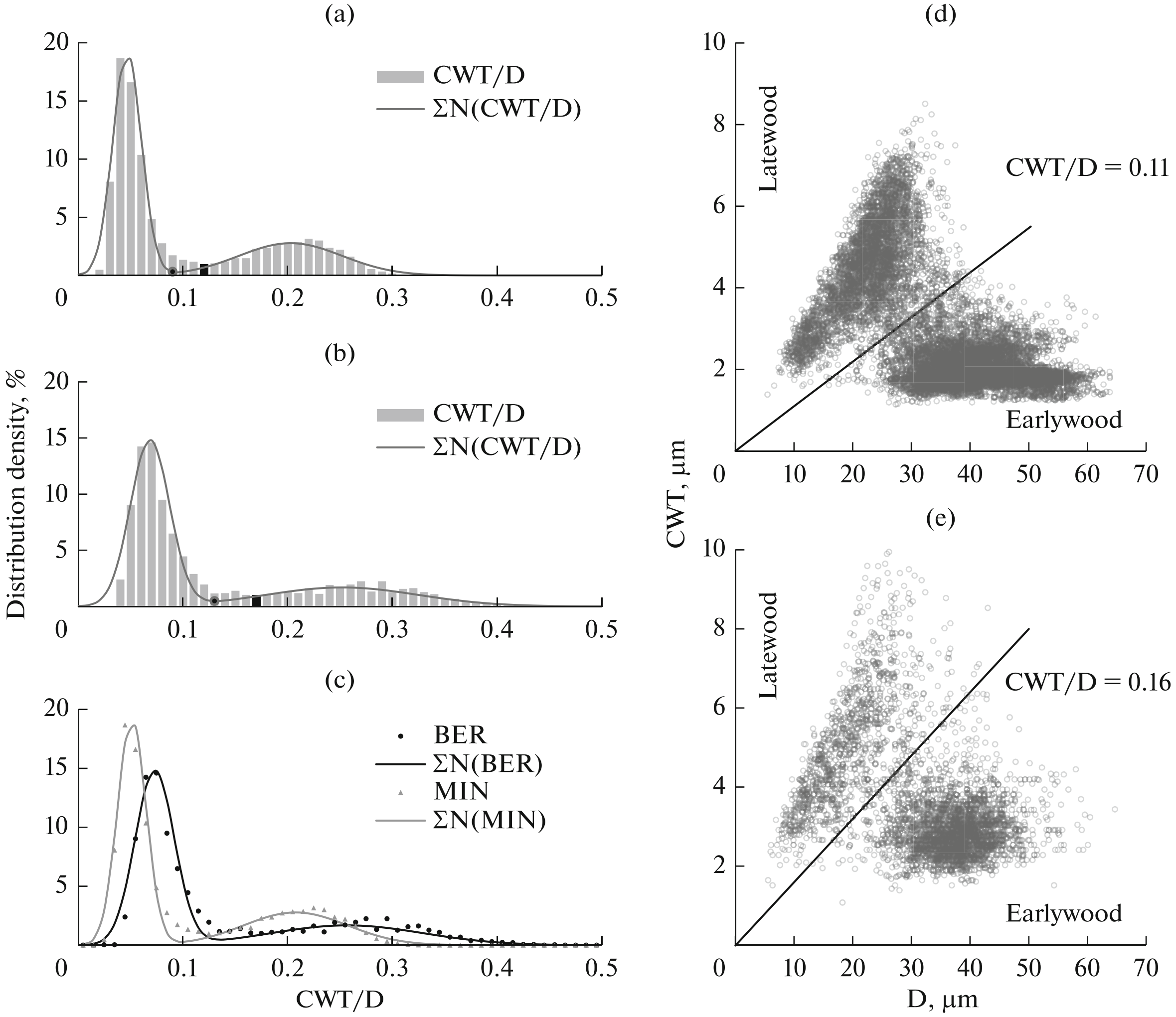

Fig. 2. Separation of tree rings into the earlywood and latewood zones. The empirical and calculated (the sum of two normal distributions) wood cell distribution density by the value of ratio CWT/D at the MIN (a) and BER (b) sites; threshold values CWT/D (local minima on the empirical and calculated curves) for the separation of zones are marked. Comparison of the cell distribution by CWT/D at two sites (c). The actual dependence of the cell wall thickness on the radial cell diameter and the threshold CWT/D value at the MIN (d) and BER (e) sites.

RESULTS AND DISCUSSION

During the process of dividing pine tree rings into earlywood and latewood zones, it was found that the ratio CWT/D is characterized by larger values and higher variability at the BER site than at the MIN site. Thus, at the BER site the threshold CWT/D value is higher by 45%, the calculated average CWT/D values are higher by 48 and 24% for earlywood and latewood respectively, and the calculated standard deviations are higher by 36 and 49% respectively (see Fig. 2c, Table 1).

The statistical characteristics of local chronologies at each site are given in Table 2. The growth of wood at the BER site is less intensive on average, which is reflected in production of a much lesser number of smaller cells in both zones and decrease in the integral parameters values. In contrast, the average CWT and variability of all parameters are lower at the MIN site. Among the anatomical parameters, the greatest differences between sites and variability within the site are observed for CN, especially in latewood. D and CWT are more stable, because their values are limited by functional requirements. Integral parameters accumulate these differences during the season, which leads to a higher variation compared to anatomical ones.

Differences in the statistical characteristics of all parameters are indicators of more extreme conditions at the first site due to an unfavorable landscape-soil combination. In the absence of additional sources of soil moisture, the relative moisture deficit leads to adaptation—the soil moisture saving by a more pronounced restriction of water transport and subsequent transpiration. It is manifested as a lumen size decrease due to the formation of smaller cells with thicker walls [30, 31]. In addition, the formation of a thicker wall

Table 2. Statistical characteristics of the wood parameters chronologies

Characteristic	CN ew	D ew	CWT ew	CN lw	D lw	CWT lw	EWW	LWW	TRW
MIN site (1964–2013)									
Arithmetic mean (mean)*	24.88	41.47	2.08	13.07	21.39	4.22	1.04	0.30	1.33
Standard deviation (stdev)*	4.36	2.17	0.13	3.54	2.08	0.45	0.20	0.10	0.27
Variation coefficient (var)	0.18	0.05	0.06	0.27	0.10	0.11	0.20	0.34	0.21
Sensitivity coefficient (sens)	0.17	0.06	0.05	0.27	0.10	0.10	0.21	0.33	0.19
First-order autocorrelation coefficient (ar-1)	0.28	–0.06	0.36	0.18	0.09	0.30	0.14	0.16	0.26
BER site (1969–2008)									
Arithmetic mean (mean)*	11.96	36.68	2.86	5.30	17.99	4.52	0.39	0.09	0.48
Standard deviation (stdev)*	2.85	3.47	0.24	1.79	2.00	0.55	0.19	0.05	0.23
Variation coefficient (var)	0.24	0.09	0.08	0.34	0.11	0.12	0.49	0.57	0.49
Sensitivity coefficient (sens)	0.26	0.11	0.07	0.31	0.11	0.13	0.36	0.40	0.32
First-order autocorrelation coefficient (ar-1)	0.19	–0.01	0.37	0.33	0.19	0.20	0.56	0.60	0.63

* Mean and stdev values are in [μm] units for D and CWT, in [mm] units for EWW, LWW and TRW, and dimensionless for CN parameters.

Table 3. Correlation coefficients between the wood parameters chronologies

Parameter	Dew	CWTew	CNlw	Dlw	CWTlw	EWW	LWW	TRW
MIN site								
CNew	**0.57**	0.25	**0.61**	**0.61**	**0.54**	**0.98**	**0.61**	**0.95**
Dew		0.01	0.26	**0.49**	**0.47**	**0.55**	**0.99**	**0.78**
CWTew			**0.35**	**0.33**	**0.47**	**0.72**	**0.29**	**0.64**
CNlw				**0.76**	**0.64**	0.17	**0.32**	0.25
Dlw					**0.80**	**0.63**	**0.82**	**0.77**
CWTlw						**0.54**	**0.67**	**0.65**
EWW							**0.57**	**0.95**
LWW								**0.79**
BER site								
CNew	**0.57**	**0.42**	**0.56**	**0.42**	**0.51**	**0.97**	**0.61**	**0.95**
Dew		**0.54**	0.23	**0.57**	**0.50**	**0.54**	**0.97**	**0.69**
CWTew			**0.58**	**0.64**	**0.70**	**0.67**	0.26	**0.62**
CNlw				**0.34**	**0.64**	**0.47**	**0.59**	**0.53**
Dlw					**0.82**	**0.48**	**0.46**	**0.51**
CWTlw						**0.54**	**0.69**	**0.62**
EWW							**0.78**	**0.99**
LWW								**0.86**

Significant at $p < 0.05$ coefficients are bold.

reduces the vulnerability of earlywood tracheids to cavitation by increasing their strength, which is important in dry conditions [32]. In latewood, the increase in CWT is an indicator of a higher intensity of nutrient storage in a plant at the end of the growing season, because it is caused by the same physiological processes. Since the stored nutrients are used by the plant at the beginning of the next growth season, including the processes of wood formation, this is reflected in the presence of autocorrelational dependence in the chronologies at both sites.

Most of the chronologies have significant positive correlations between each other (Table 3). In earlywood, the correlation between CN and D is expressed,

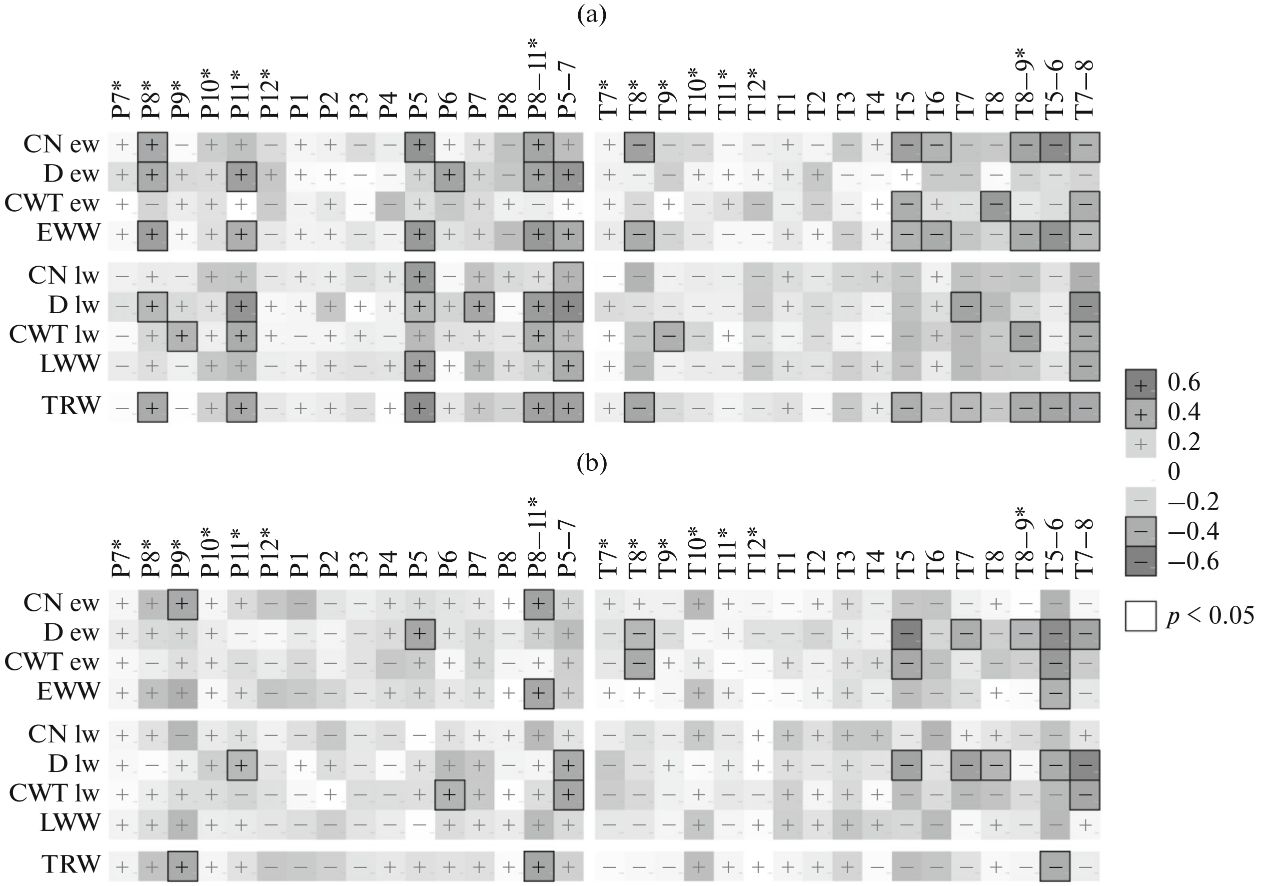

Fig. 3. Paired correlation coefficients of the wood parameters chronologies with temperatures (T) and precipitation (P) of the individual months and longer periods (1969–2008) at the BER (a) and MIN (b) sites. Asterisks (*) mark months of the year preceding the development of a tree ring. The coefficients significant at $p < 0.05$ with the correction for multiple comparisons are marked.

CWT for this zone is relatively constant (see the lower cluster of cells on Figs. 2d, 2e). In latewood, all three anatomical parameters are closely interrelated, which is explained by the tendency to form cells with a minimum lumen, i.e. relatively constant ratio CWT/D (see the upper cluster of cells on Figs. 2d, 2e), and by the dependence of all three cell differentiation stages intensity on external conditions [33]. Given the partial overlap in the time of earlywood and latewood development, the presence of positive correlations between the parameters of different zones is also evident. The close relationship between TRW, EWW and CN of earlywood has been repeatedly noted for Scotch pine and other conifer species, for example in [34] and the sources mentioned in it, while the parameters of latewood are weaker associated with TRW, since they contribute less to it.

Correlation dendroclimatic analysis (Fig. 3) showed that the climatic response of the wood anatomical parameters in the study area has the same basic patterns as ones of the TRW due to moisture limitation [33]. Precipitation as a source of moisture affects the tree rings development positively in the second half of the previous growing season and in the first half of the current one. The temperature of these periods is an indirect negative factor, because its growth leads to evapotranspiration increase too and subsequent soil draining. The influence of the temperature and precipitation of the previous year can be explained, on the one hand, by the accumulation of reserve nutrients at the end of the growing season, and on the other hand by the general effect of favorable or unfavorable conditions on the tree vital state and its growth, leading to the appearance of first-order autocorrelation in all parameters. Since the soil moisture conditions are more favorable at the MIN site, there the climatic response is also significantly weakened during the warm period in comparison with the BER site. Comparison of the climatic response of different parameters shows the presence of certain time shift in the transition from CN to D and then to CWT and from earlywood to latewood according to the timing of the end of the corresponding cell differentiation stages in each zone. The climatic response of EWW and LWW is similar to the response of CN of the same zones, but in most cases it is less pronounced due to the contribu-

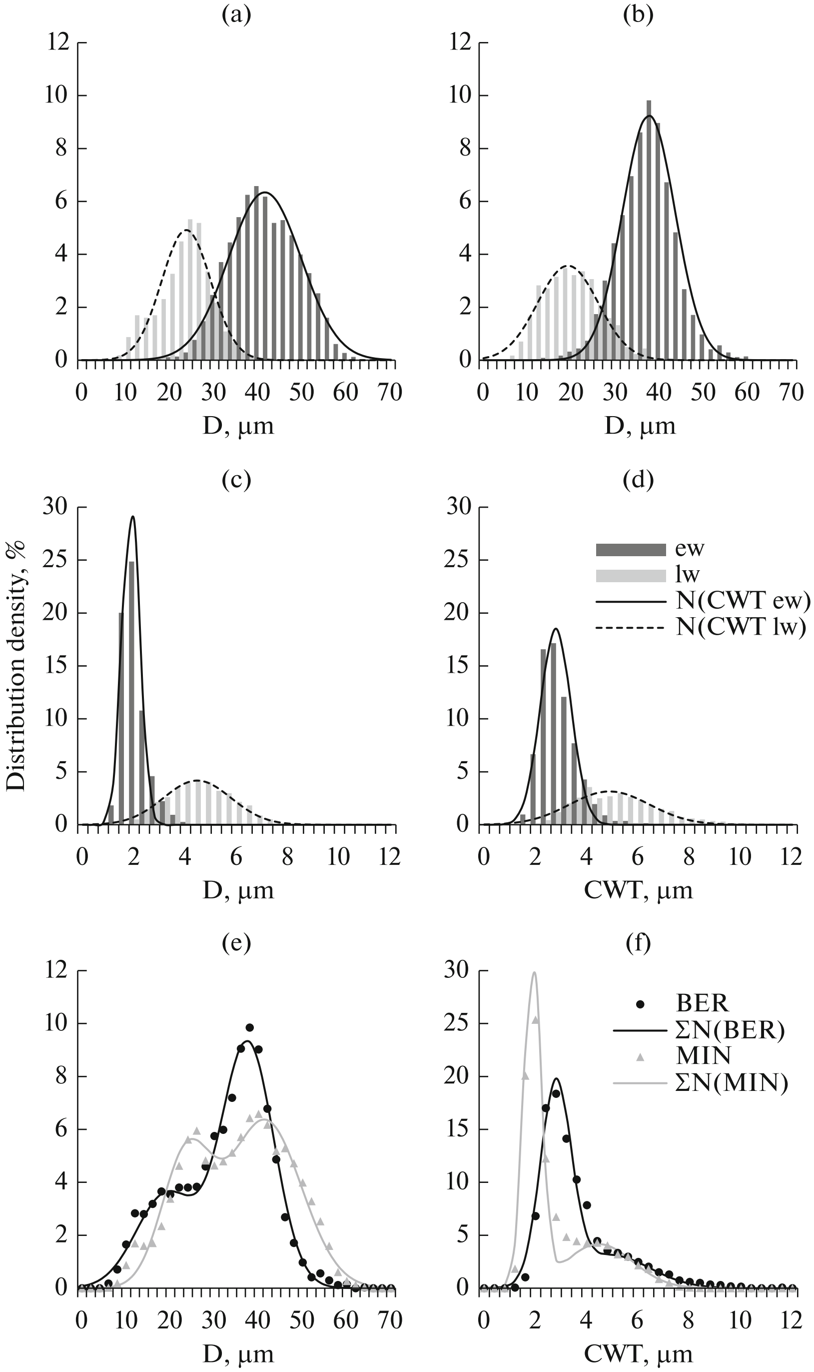

Fig. 4. Empirical and calculated (normal distribution) density of earlywood and latewood cells distributions by D and CWT: distributions of cells by D at the MIN (a) and BER (b) sites; distributions of cells by CWT at the MIN (c) and BER (d) sites; comparison of the summary distributions of cells by D (e) and CWT (f) between two sites.

tion of D oscillations to these integral parameters. The climatic response of the TRW chronologies is more similar to EWW, but LWW contribution to the total ring width is also evident.

The distribution density functions of cells by D and CWT calculated for all measured tree rings at each site are close to the sum of two normal distributions for the earlywood and latewood zones, despite typical for pine wood smooth transition between zones, i.e. the so-called transition zone [20] (Fig. 4, Table 1). Parameters of the transition zone cells are determined by the overlap of these two distributions. Despite the differences in growing conditions, the unity of the regional climate causes a similar earlywood to latewood cell number ratio at both sites. Differences between the sites in the distribution shape show that more pronounced moisture limitation leads to the adaptation of wood structure, which occurs in the following directions: (1) cells become smaller throughout the entire ring, while in earlywood the dispersion of D also decreases; (2) CWT increases in both zones, which significantly increases the wall strength, while reducing the lumen.

Thus, the wood anatomical structure reflects the restriction of water transport and the increase in the cell wall strength in more extreme moisture conditions.

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