ISSN 1062-3590, Biology Bulletin, 2017, Vol. 44, No. 6, pp. 634–642. © Pleiades Publishing, Inc., 2017.
Original Russian Text © V.V. Fakhrutdinova, V.E. Benkova, A.V. Shashkin, 2017, published in Izvestiya Akademii Nauk, Seriya Biologicheskaya, 2017, No. 6, pp. 665–674.

ECOLOGY

Climatic Signals in Tree Ring Anatomical Structure of *Larix gmelinii* Growing under Contrasting Hydrothermal Conditions within the Forest-Tundra Ecotone

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Received April 20, 2016

Abstract—The results of comparative analysis of tree-ring anatomical structure in the trunk of *Larix gmelinii* (Rupr.) Rupr. growing in the forest-tundra ecotone in the north of Middle Siberia in contrasting hydrothermal conditions of permafrost soils are discussed. It is found that the best soil hydrothermal conditions affected the formation of relatively large tracheids in earlywood and latewood during the whole period investigated. Current climate warming has caused a positive trend in annual changes in the cellular characteristics in trees growing in relatively favorable soil conditions and has not caused observable changes in trees growing in adverse conditions. The wood anatomy structure of the water–conducting (earlywood) zone in the tree ring in favorable conditions is determined by the weather of late May and June, and in adverse conditions it is determined by the weather in late April and May.

DOI: 10.1134/S1062359017050089

The width of the tree rings is a sensitive character of the wood structure, "reacting to any change in the growth conditions" (Yatsenko-Khmelevskii, 1954; Chavchavadze, 1979). Numerous dendrochronological studies have revealed that changes in the width of tree rings depends significantly on climatic conditions of the region and the geographic location of growth (Shiyatov, 1973; Fritts, 1976; Schweingruber, 1996; etc.). It was found that at high latitudes the width of tree rings statistically is closely related to summer air temperature mainly in June and July, which allows us to monitor its current and past changes (Vaganov et al., 1996; Khantemirov, 1999; Esper and Schweingruber, 2004; Vaganov and Shiyatov, 2005; etc.). In recent decades, the correlation between these indicators has somewhat weakened (Briffa et al., 1998; etc.). Researchers attribute this to the current climate warming in the zone of continuous distribution of permafrost accompanied by weakening of the limiting role of air temperature and the increasing direct effect of other external factors on tree growth, such as precipitation (Mazepa, 1999), the depth of snow cover and date of snow disappearance from the soil surface, and the hydrothermal properties of the seasonally thawing layer (Vaganov et al., 1999; Kidryanov et al., 2003; Tabakova et al., 2011; Ben'kova et al., 2012, 2014; etc.).

If the width of a tree ring and the number of tracheids in conifers determine radial growth overall for the season, the feature of the anatomical structure of tree rings reflects the intraseasonal dynamics of radial growth (Lobzhanidze, 1961; Larson, 1994; Vaganov and Shashkin, 2000). Mature tracheids formed in different periods of the growth season are noticeably different in their wall size and thickness. Analysis of changes in these indicators provides the opportunity to discover intraseasonal changes in the tree growth rate and to identify the causes of the formation of the particular tree ring structure (Denne and Dodd, 1981; Larson, 1994; Vaganov and Shashkin, 2000; Schweingruber et al., 2006; Fonti et al., 2013; Bryukhanova et al., 2014). At high latitudes specific features of the environment exist. They are associated mainly with the presence of permafrost and low air temperatures, which cause a short growing season. Woody plants there are peculiar in having a high sensitivity to changes in environmental conditions and climate (IPCC..., 2001 etc.). False, frost- and light rings of different types of structure often occur in the trunks of trees (Schweingruber, 1996; Gurskaya and Benkova, 2013; etc.).

Table 1. Parameters of larch stands at sample sites

Parameter	SP1	SP3
Crown coverage	0.2	0.4
Mean diameter of trees, cm	7.95	6.08
Mean tree height, m	4.72	3.21
Mean crown length, m	1.23	0.94
Mean crown diameter, m	2.07	1.14
Mean growth rate for last 44 years, mm/year	0.86 ± 0.07	0.11 ± 0.04

Earlier studies within the ecotone of the Polar timberline on Taymyr Peninsula (Benkova et al., 2012) showed that *Larix gmelinii* (Rupr.) Rupr., growing directly on the border with the tundra, differs from the trees growing at a certain distance from the boundary in its higher intensity of radial growth and better biometric parameters. It was suggested that the observed differences are conditioned by various hydrothermal conditions of the soil. Evidently, the growth of trees in different hydrothermal conditions of the soil depends on the xylem transport function depending on the structure of the water-conducting system. Elements of the latter in conifers are conducting earlywood tracheids, by which upward flow of water and dissolved nutrients occurs from the roots to the crown. Earlywood tracheids are formed in physiologically active tree rings adjacent to the cambium. These rings form the water-conducting area of the trunk, named "sapwood" (Esau, 1965).

This work aims at study of the influence of the same climatic factors on the tree ring anatomical structure characteristics modified by local micro-ecological conditions of growth, mainly hydrothermal features of the soil.

MATERIALS AND METHODS

This study was conducted on Kotuiskaya Upland (Taimyrskii Dolgano–Nenetskii region of Krasnoyarskiy krai), in the middle current of the Kotuy River (70°52′53″ N, 102°58′26″ E). The general climatic characterization of the area is as follows: subarctic thermal regime, continuous distribution of permafrost, mean temperatures of January and July of −29.6°C and +12.5°C, respectively, a mean annual temperature of −13°C, and annual precipitation of 247 mm. Tree stands to 100% consist of *Larix gmelinii* (Noreen, 1978; Abaimov et al., 1997).

Xylotomic material were collected in two sampling plots (SPs) established in 2008 on the north–northeastern slope (4°–7°) of Odikhincha Mountain. SPs varied in the hydrothermal regime of soil, tree stand biometric characteristics, as well as by the degree of living moss cover development. SP1 was established in a sparse larch dwarf–shrub shrub–moss area in the upper part of the slope (303 m a.s.l) directly at the border with the tundra. The thickness of the moss cover was 2–4 cm. At the time of observation on July 20, 2009, the depth of the seasonally thawing layer reached 90 cm. The temperature on the surface under moss was 10.5°C, and the volumetric moisture content was 34%. SP3 was situated in the lower part of the slope (71 m a.s.l.), 300 m from the river and 40 m above the water surface, at a distance of 1700 m from SP1, in sparse sedge–horsetail–moss larch forest. For SP3 high humidity and low soil temperature throughout the vegetation period is typical. The relatively small depth of seasonal thawing, 68 cm, due to presence of thicker moss (7 cm) and peaty organic layers (thickness 15 cm, five times more than on SP1), prevents heating of the soil. At the time of observation on July 20, 2009, the temperature on the surface under the moss cover was 5.5°C, while the volumetric humidity was 50%. The temperature of the soil was measured with a soil thermometer, and the volumetric moisture content was measured by the equipment Sense^{TM} Hydro (Campbell Scientific Australia Pty. Ltd., Australia).

It was found earlier that the larch on SP3 has the worst biometric characteristics (Table 1) and its radial growth has higher sensitivity to changes in the climatic factors (Benkova et al., 2012).

On each SP five larch trees were chosen. The average diameter of a tree at the height of 1.3 m from the soil surface in SP1 and SP3 was 9.8 and 7.8 cm and the respective height was 6.98 and 6.64 m. The trees were more than 80 years old, so the age factor affected slightly the size of the last tree rings and its cellular structure. The disk was taken from the stem of each tree at 1/4 of the stem height above the soil surface. The sampled disks at a width of 5–8 mm were taken from two chosen radii. Air-dry samples of the larch were softened by boiling in water for 1–2 h. Then, using a sliding microtome, we prepared transverse sections with a thickness of 15–17 μm. The sections were stained with a solution of methylene blue for 2–3 min when the details of the structure became more visible. For producing temporary preparations, the best sections were chosen, including the last 45 outermost rings of sapwood, which were formed in 1964–2008. Then the sections were washed with water, placed on a glass slide in a drop of a glycerin–water mixture (1 : 2), and covered with a cover glass (Chavchavadze et al., 1992). Temporary preparations were examined on the device of computer image analysis (Image Analysis System, Carl Zeiss, Germany). In the tree rings from the inner boundary to the outer one, the radial dimension of tracheids formed five rows (D) and the double tracheid wall thickness (2CWT) were measured with a precision of 0.2 μm. To obtain the mean cell characteristics of the ring, the data obtained for five rows were averaged. The significance of differences of the obtained mean values was assessed using t-test.

Table 2. Mean anatomical characteristics of tree rings formed in the period 1964–2008 in the larch trees

SP	Early wood				Late wood			
	De, μm	CWTe, μm	Ne	EWe, μm	Dl, μm	CWTl, μm	Nl	LWl, μm
SP1	36.2 ± 1.2	3.1 ± 0.2	22 ± 2.9	775.3 ± 80.8	5.6 ± 0.4	4.7 ± 0.4	8 ± 1.0	133.6 ± 20.9
SP3	32.4 ± 1.0	3.1 ± 0.2	3 ± 0.2	86.5 ± 6.8	3.4 ± 0.1	3.6 ± 0.2	2 ± 0.2	22.9 ± 2.7

SP, sampling plot; De, Dl, mean radial sizes of tracheid in earlywood and latewood; CWTe and CWTl, mean cell wall thickness; Ne and Nl, mean (by tree rings) number of tracheids in the radial row in the earlywood and latewood; EWe and LWl, mean (by tree rings) width of the earlywood and latewood in the ring.

To perform comparative analysis of tree rings by tracheid anatomical characteristics, normalization was carried out. For this task tracheidograms (the graphs of the change in radial size and wall thickness of tracheids in a radial row from the inner boundary of the ring to the outer one) were built.. The number of cells in the row from the inner tree ring boundary to the outer one was normalized to a single standard number of cells (N). Normalization "shrinks" or "stretches" the original tracheidogram on the x-axis, adjusting the number of cells in the ring to the number N, and leaves the values on the y-axis unchanged. In this case details of the ring structure do not undergo deformation. The operation of normalization and the method of tracheidogram construction was described in detail earlier (Vaganov et al., 1985). In our case, normalization to the mean number of cells in the tree ring ($n = 20$) for 1964–2008 was carried out.

In the tree rings of larch, the boundary between water conducting earlywood and latewood, as a rule, was visually expressed clearly but not in all cases. For clear attribution of tracheids to earlywood or latewood, numerical criteria were developed. We used the Mork criterion (Denne, 1988): tracheids having a double cell wall thickness greater than or equal to the size of the lumen were considered as latewood tracheids.

For determination of the time periods within the growing season with a significant influence of climatic factors on cellular characteristics of the tree rings, moving correlation analysis of climate response function was used. We calculated the correlation of the radial dimensions of earlywood and latewood tracheids (De and Dl) and their cell wall thickness (CWTe and CWTl) with series of the mean daily temperatures and daily precipitation, averaged in a "window" of 20 days, moving by the time axis with an increment of five days. Earlier these values were shown to be a "20-day window" and "5-day step" optimal for places characterized by short growth season (Simanko et al., 2013).

Daily climatic data for the Khatanga meteorological station were taken from the National Weather Service, Internet Weather Source ftp:/ftp.ncdc.noaa.gov/pub/data/ghcn/daily/.

RESULTS

The low rate of the larch radial growth on SP1, as compared with the trees on SP3, affected excessive content of cold soil water. The trees on SP1 and SP3 also have significant differences in the average wood anatomical characteristics of the trunk (in 1/4 height from the soil surface). All indicators (Table 2) in SP1, except for the cell wall thickness of the earlywood tracheid (CWTe), were significantly larger than in SP3. The characteristics of earlywood zone of tree rings on SP1 and SP3 differ greatly, especially in the number of tracheids in the radial row (seven times) and in the earlywood zone width (nine times), while the characteristics of latewood zone differ by only the number of tracheids (1.5 times). Thus, according to anatomical characteristics, we can conclude that the water transportation system in the stem of the trees from SP1 is more developed: the water-conducting (earlywood) zone occupies a larger area in the tree rings: the width of the earlywood is about 90% of the ring width on SP1 and 78% on SP3. Relatively large tracheids capable of transporting a greater volume of water per unit time.

The distribution of tracheids by the radial dimensions is an integral feature of wood anatomy structure of woody sample (Vaganov and Shashkin, 2000) which contains information on the quality and physicomechanical properties of xylem. By the number and size of large (earlywood) and small (latewood) tracheids, we can estimate the efficiency of xylem transport and its mechanical properties. For each SP we estimated the distributions of cells by the radial dimensions in the tree ring series formed in 1964–2008, averaged for the trees investigated. The distributions have a bimodal character (Fig. 1) and consist of two overlapping maxima.

In the trees growing on SP1 in relatively favorable hydrothermal conditions on the boundary of the tundra, the first maximum is composed of cells 20–25 μm in size (14.5%) and the second (blurred) maximum of cells 35–45 μm in size (31.8%). The size of 12.4% of the cells corresponds to the mean value for all rings (30.6 ± 0.9 μm) , and the proportion of very small cells (up to 10 μm in size) is only 4.2%. In the trees growing in SP3, the maxima on the graph of distributions are expressed more clearly. The first maximum (21.4%) consists of small cells (up to 10 μm), the second maximum (18.3%) is of cells 35–40 μm in size, and 7% are

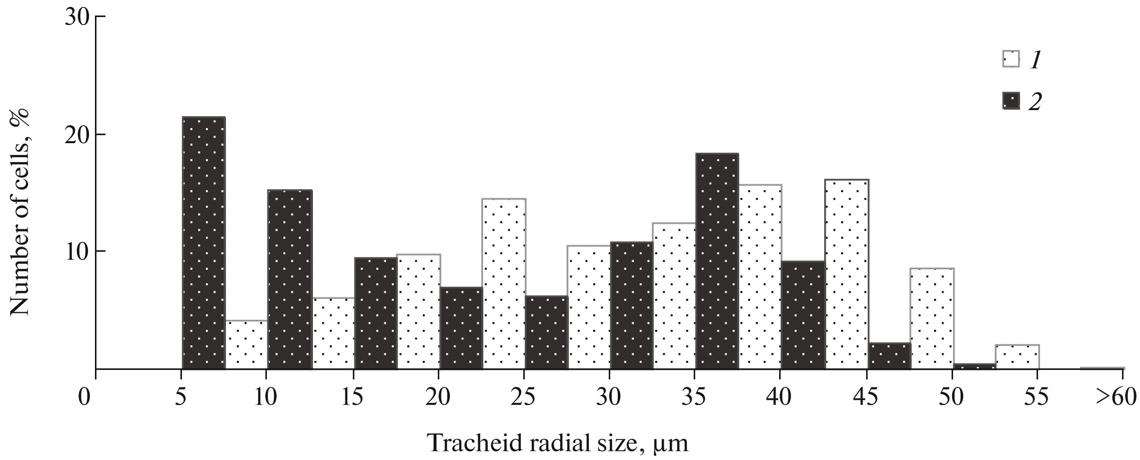

Fig. 1. Distribution of tracheids by radial sizes in tree rings (1964–2008) in *Larix gmelinii* on sampling plots SP1 (*1*) and SP3 (*2*).

cells the sizes of which correspond to the value mean for all rings (24.7 ± 0.8 μm). Thus, the main difference between the distributions of tracheids by the radial dimensions building for SP1 and SP3 is that in the trees grown on SP3 the cells are more definitely separated by size into small and large, with small tracheids the radial size of which is <10 μm being approximately 3.5 times more numerous than in the trees growing on SP1. We can conclude from the analysis of distributions that such a cellular character of the xylem as "the mean tracheid size" is less informative, because tree rings contain very few cells of these sizes : in our case, 7 and 13%.

Detailed information on the major patterns of intraseasonal changes in growth dynamics is contained in tracheidograms of the tree rings. Tracheidograms (Fig. 2) showed following:

(1) In the "normalized" tree ring, all cells in the trees on SP1 are notably larger than on SP3, except for marginal cells which have same sizes.

(2) In the trees on SP3, the maximum cell wall thickness is held by the cells forming the third quarter of the ring, and on SP1, by the cells located closer to the outer boundary of the ring. The maximum cell wall thickness in the trees on SP1 is 1.34 times more than that on SP3. In general, all cells in the trees on SP1, which form the second half of the tree rings, have significantly thicker walls. At the same time, the mean values of this parameter by the tree rings in the trees from SP1 and SP3 for period 1964—2008 were not significantly different: 3.8 ± 0.2 and 3.6 ± 0.1 μm, t-test <2.01, $p < 0.05$. Therefore, this parameter, as well as the mean radial size of tracheids, is of little informative value for comparative anatomical analysis.

(3) Rather high annual variability in the radial size of the cells that compose the first half of the tree rings (which includes the earlywood) was found in the trees on both SPs. At the same time, the variability of wall thickness of the tracheids that compose the second half of the tree rings, which includes the latewood, is substantially higher in the trees on SP1. Variability of the anatomical characteristics is caused, apparently, by the variability in the annual and seasonal changes in the weather conditions during the formation of tree rings. Analysis of tracheids revealed that the sensitivity of xylem to changes in weather factors is different in the trees growing on SP1 and SP3 in different hydrothermal conditions.

Analysis of the influence of climatic factors on anatomical characteristics of tree rings was carried out by cell chronologies and by "moving correlation climate response functions" separately for the earlywood and latewood. The latter were selected using the Mork criterion.

On the cell chronologies (Fig. 3), an increasing trend of radial sizes and wall thickness of tracheids on SP1 is clear. Annual variability in climatic conditions (Fig. 3) influences the size of earlywood tracheids on SP3 more clearly as compared to SP1. At the same time, the trees on SP1 have higher variability in the size of latewood tracheids and their walls.

Despite the differences in cell chronologies, conditioned by differences in growing conditions, the variability of the cell parameters obtained in SP1 and SP3 (Fig. 3) is characterized by a high synchronism: correlation coefficients $R = 0.60–0.94$ at a significance level of $R = \pm 0.30$, $p < 0.05$. Therefore, the tracheid chronologies obtained on both SPs have a common climate signal.

The moving correlation response functions for 1964–2008 (Fig. 4) revealed time periods within the growth season, when climatic factors (air temperature and precipitation) significantly affect the cell characteristics of tree rings. In the trees growing on SP1, a positive correlation between the radial size and the wall thickness of latewood tracheids with an air temperature from the third ten-day period of May to the end of June was determined (Figs. 4a, 4c, curves *2*).

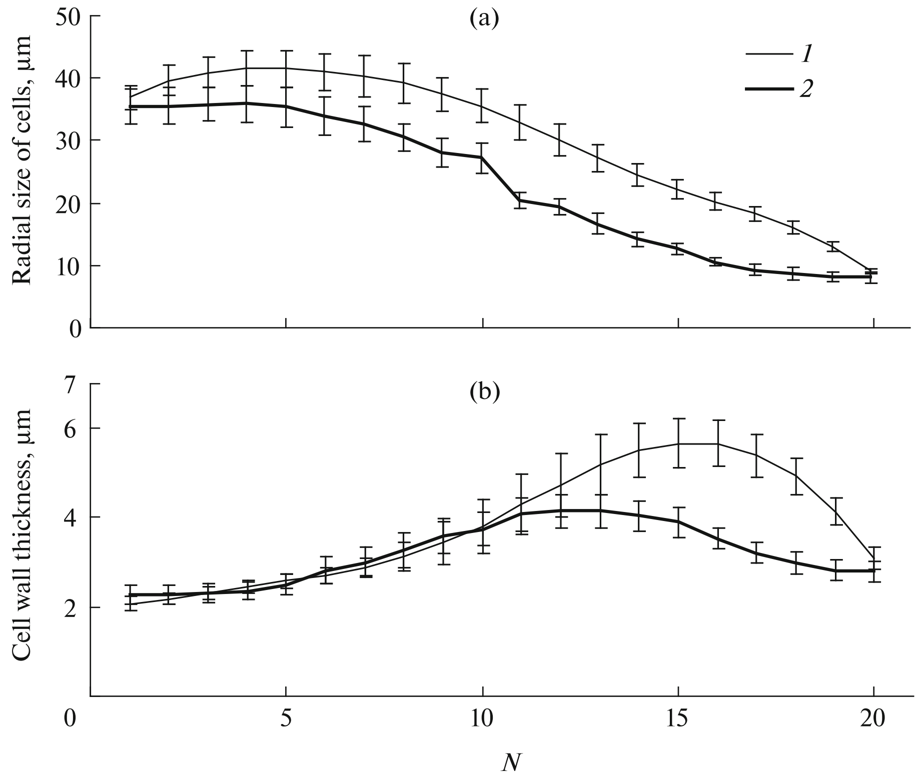

Fig. 2. Tracheidograms of tree rings (1964–2008) by radial size (a) and cell wall thickness (b) of tracheids in *Larix gmelinii* on SP1 (*1*) and SP3 (*2*). *N*, number of a tracheid in the radial row of tree ring cells normalized to 20.

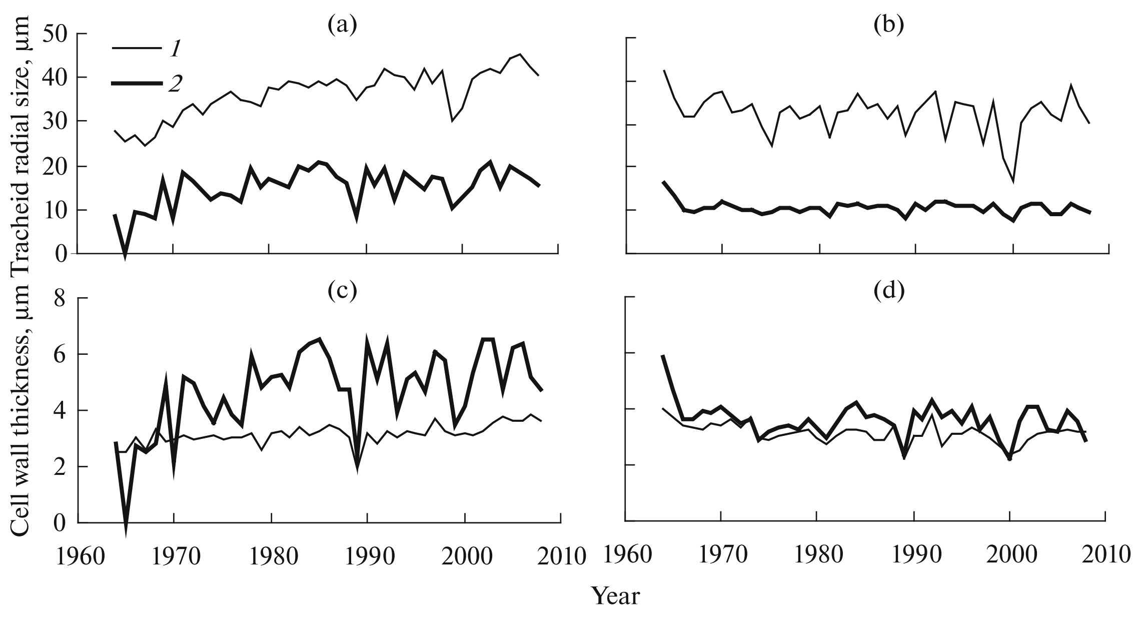

Fig. 3. Time series of tracheid radial size (a and b) and cell wall thickness (c and d) in earlywood (*1*) and latewood (*2*) of tree rings (1964–2008) in *Larix gmelinii* on SP1 (a and c) and SP3 (b and d).

On similar characteristics of earlywood tracheids (cell wall thickness and radial sizes), the temperature factor, judging by the values of *R*, has no visible effect (Figs. 4a, 4c, curves *1*). A negative correlation between the radial size of earlywood tracheids (Fig. 4b, curve *1*), radial size and wall thickness of latewood tracheids (Figs. 4b, 4d, curves *2*) with the amount of precipitation was detected in the same period as that of temperature. The thickness of the walls in earlywood tracheids was not significantly connected to precipitation (Fig. 4b, curve *1*).

Thus, in the trees on SP1, the weather conditions from May 20 until the end of June influence significantly in the wood anatomy characteristics of tree rings. The latewood are more sensitive to the effects of both climatic factors, while the earlywood (conductive) only to precipitation: the more rain that falls in the indicated period of the season, the smaller the earlywood tracheids formed.

In the trees grown on SP3, a negative correlation between the radial size and cell wall thickness in earlywood and the cell wall thickness in latewood with air temperature was detected from middle April until the third ten-day period of May (Figs. 4e, 4g, curves *1, 2*). The temperature does not influence significantly the radial size of traceids in latewood (Fig. 4e, curve *2*). The correlation of all parameters studied with precipitation was insignificant or at the limit of significance (Figs. 4f, 4h, curves *1, 2*).

DISCUSSION

The results represent an example of how in the xylem under relatively rapidly changing external conditions (climate warming, high annual variability in summer temperature and/or decrease of the available soil water in the seasonally thawed layer) signs appear that indicate its "local adaptation" directed to maintenance or restoration of the transport function in the tree (Gamalei, 2011). It was found that on SP1, located in the upper part of the slope directly on the border with the tundra, healthy trees are grown with a well-developed crown and tree rings that are more than two times wider than those of trees of the same age grown on SP3 on the lower part of the slope. According to the daily values of air temperature obtained at the weather station Khatanga from 1964 to 2008, the mean monthly temperatures of May and June display a pronounced positive trend (the first increased by 3.2°C and the second at 2.6°C). At the same time, the mean monthly temperatures of July and August have not changed. The increase in the mean air temperature of May and June over the past decades has improved growing conditions on SP1. This is manifested in the dynamics of radial growth (Benkova et al., 2012) and in cell chronologies of *Larix gmelinii* (Fig. 3).

V. Benkova et al. (2012) provided arguments allowing the conclusion that favorable conditions for growth are provided by the hydrothermal properties of soil which were considerably better than on SP3. Evidently, the temperature on the soil surface beneath poorly developed moss cover on SP1 has also increased over recent decades. Together with the increase in activity of the root system, the intensity of growth processes (photosynthesis, transpiration, etc.) increased, which was accompanied by an increase in the water-conducting efficiency. Larger tracheids were formed in the tree rings capable of transporting larger volume of water per unit time, it is evidenced by the positive trend of mean sizes of the tracheids in earlywood tracheids in annual rings in (Fig. 3). Adverse soil conditions on SP3 have not improved, and have possibly deteriorated due to the increase in time of the moss–lichen layer thickness. Due to the increased intensity of water runoff along the slope, the amount of excess soil moisture seems to have increased on SP3; the temperature of water in the soil level of high larch root concentration has not increased according to measuring data in 2008 (Benkova et al., 2012) and has remained fairly low (close to 0°C) due to the thermally isolating thick lichen–moss cover. Thus, even in recent May–June warming, soil water remains "inaccessible" to the roots, while potential transpiration in connection with the increase in air temperature increases. In connection with the disturbance of the water balance, the risk of embolism in the water-conducting system in xylem appears. To reduce this risk, the smaller tracheids in earlywood are form but the size of those is not influenced by climate warming (Fig. 3).

We emphasize that the formation of distinctive features in the cell structure of tree rings in larch trees under contrasting soil hydrothermal conditions occurs under the influence of various factors identified by the moving correlation climate response function (Fig. 4). In the larch on SP3, a significant influence of weather conditions on the wood anatomy characteristics appears earlier and takes less time than on SP1. Phenological observations (Karbainova, 2006) revealed that the appearance of needle shoots in *Larix gmelinii* in the area of our research is closely linked with June temperatures and is highly variable from year to year in connection with their high annual variation: over 14 years of observations, the actual amplitude of variation in the dates of this phenophase was 34 days, from June 10 to July 14. Evidently, the date of start of the radial growth is closely connected with the beginning of needle shoot growth and it should be associated also with June temperatures. The May period preceding the beginning of radial growth corresponds to preseason reactivation of the cambium, which can last quite long, up to two months. (Prislan et al., 2011). Thus, the results obtained by the moving climate response function confirm the hypothesis proposed earlier based on the analysis of the influence of climatic factors on radial growth (Benkova et al., 2012): the season of radial growth on SP3 starts earlier than on SP1.

The explanation of the obtained correlations (Fig. 4) is as follows: on SP1 the increase in the soil moisture in relation to heavy precipitation in late May and June negatively affects the efficiency of water conduction. The increase in precipitation is usually accompanied by decrease in temperature and, hence, decrease in transpiration. Abundance of soil water and low tran-

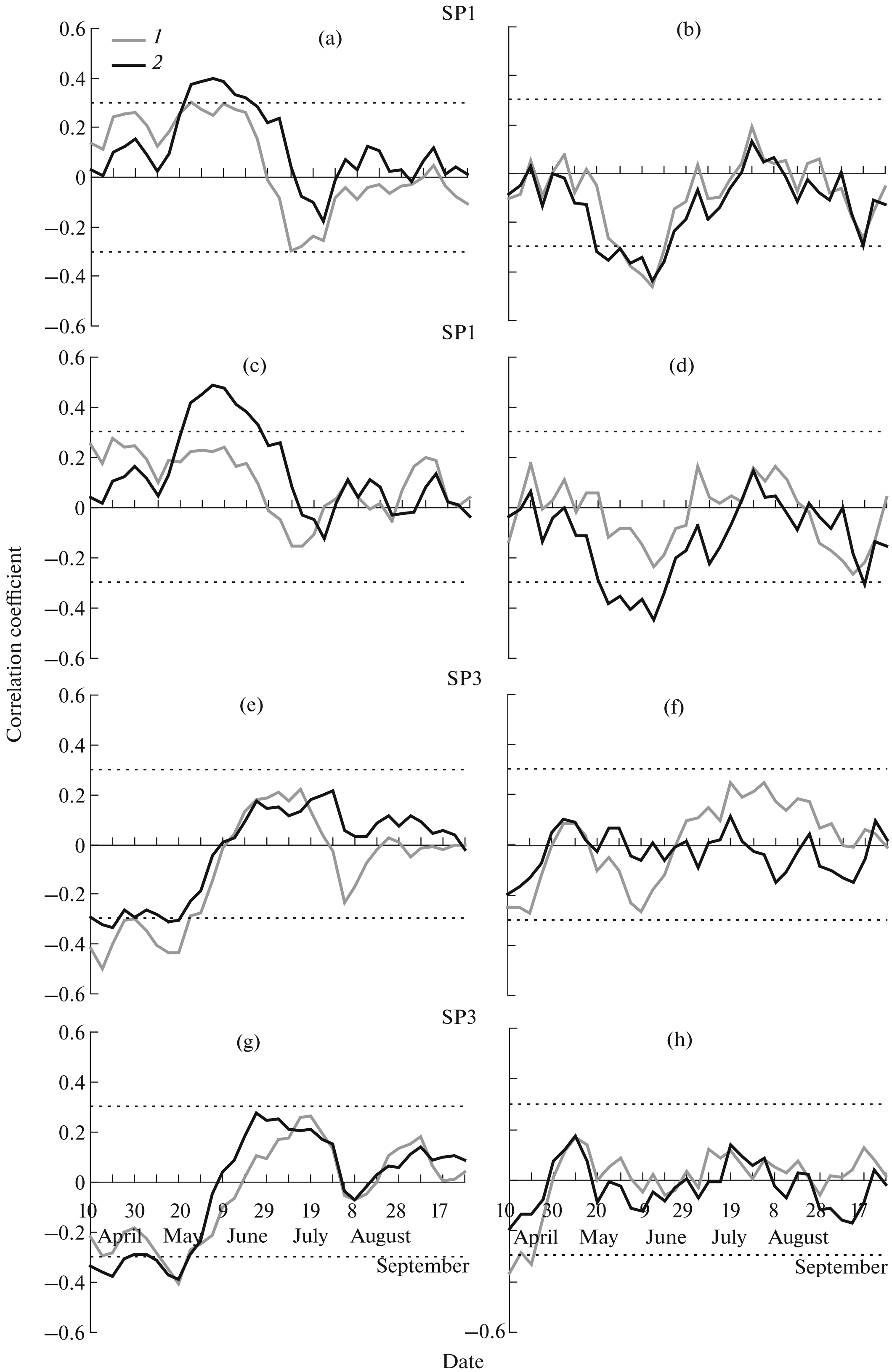

Fig. 4. Moving correlation 20-day response functions of the tracheid radial size (a, b, e, and f) and cell wall thickness (c, d, g, and h) of the earlywood (*1*) and latewood (*2*) to air temperature (a, c, e, and g) and precipitation (b, d, f, and h) in *Larix gmelinii* on SP1 and SP3 (1964–2008).

spiration create the conditions for low efficiency of water transport from roots to crown.

We consider the latewood in the tree ring as a "buffer" zone between this and the next tree ring; the thick latewood cell walls as a "sponge," in which micro- and submicrocapillary water (it is there in the bound state) and dissolved nutrients are reserved. The tree can use these reserves in the next year if there are unfavorable weather conditions at the beginning of the growth season. The increase of air temperatures in late May and June of the current season is accompanied by an increase in intensity of photosynthesis and an larger amount of metabolic products that are used to formation of the relatively thick cell walls in latewood, capable of reserving a greater amount of water.

The preseason period, from April 20th to the end of May, which is earlier than that on SP1, has great importance in the formation of the tree ring anatomical structure on SP3. Relatively high air temperatures at this period provoke early preseason reactivation of the cambium. Water and nutrients stored in the previous season are spent on this activity. Meanwhile, frozen soils covered with a thick thermo insolating moss cover do not allow their completion through the root system over a long time, and the tree at the beginning of radial growth season can experience soil water deficit. In connection with poor turgor, the cells formed have a relatively small final size. Small tracheids in earlywood are poorly efficient for water conduction but protect against embolism.

CONCLUSIONS

The trees of *Larix gmelinii*, which grow within the forest-tundra ecotone on SPs located at a relatively short distance from each other, in contrasting hydrothermal soil conditions differ in the cell characteristics of annual increment and by the duration and degree of influence of climatic factors on them.

Better soil hydrothermal conditions have conditioned the formation of relatively large tracheids in earlywood and latewood for the whole period investigated (1964–2008).

Current climate warming affects tree ring anatomical structure in the trees growing in different soil hydrothermal conditions differently: this has led to a positive trend in the annual changes in the xylem characteristics of the larch growing in favorable soil conditions aimed at preserving the xylem transport function and has not caused significant changes in the trees growing in unfavorable conditions.

The structure of water-conducting zones of tree rings in the trees growing in different soil hydrothermal conditions determine different times of the growth season: in relatively favorable conditions, this is the end of May–June, corresponding to the entire period of seasonal activity of the cambium, and in unfavorable conditions, it is the end of April–May, i.e., the preseason reactivation of the cambium, on which start of the seasonal growth depends.

ACKNOWLEDGMENTS

This work was supported by the Russian Foundation for Basic Research, project no. 14-04-00443.

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Translated by S. Kuzmin