= RESEARCH TECHNIQUES =

Transformation of Climatic Response in Radial Increment of Trees Depending on Topoecological Conditions of Their Occurrence

E. A. Babushkina^a, A. A. Knorre^b, E. A. Vaganov^a, and M. V. Bryukhanova^b

^a Siberian Federal University, Krasnoyarsk, Russia ^b Institute of Forest, Siberian Branch, Russian Academy of Sciences, Krasnoyarsk, Russia e-mail: aknorre@ksc.krasn.ru Received April 27, 2010

Abstract—We report the research results derived from identifying the regional climatic signal contained in the coniferous tree ring-width variability for different topoecological conditions in the forest-steppe of the Republic of Khakassia. It is found that under different growth conditions for trees of the same species the climatic signal undergoes a significant transformation. We demonstrate the possibility of using a combination of tree-ring chronologies of different tree species for an adequate dendroclimatic reconstruction of the leading climatic variables.

DOI: 10.1134/S1875372811010148

Keywords: radial increment, topoecological conditions, climate, species specificity, Khakassia.

INTRODUCTION

Substantial changes of the state of the environment as observed over the last several decades are reflected at different levels of ecosystem organization (organisms, species, populations, etc.). Identification of the species-indicators that signal such changes still remains the priority direction in research seeking to unravel the qualitative links between the species and the determining impact factor. Dendroindication is a key line of relevant investigations.

In areas dominated by one limiting factor, the influence of the topoecological conditions (relief, the thickness of the soil horizon, steepness and aspect of slopes, etc.) on variability in radial increment in woody plants does not reveal itself to a tangible extent. Therefore, the existing network of regional tree-ring chronologies identifies a significant climatic signal in the variability in increment in trees [1]. This is demonstrated emphatically for the Subarctic and mountainous regions where summer air temperatures (June-July) govern the time coincidence of radial increment across significant territories, while the generalized chronologies reasonably reliably represent regional temperature changes [2, 3]. Reconstructions for such regions serve to assess the natural climate variability in the preindustrial era, and the contribution of anthropogenic factors to current climatic fluctuations. As regards the steppe and semidesert territories, treering chronologies provide a reliable response of the increment in trees to humidification conditions thereby permitting reconstructions of the water levels in rivers and lakes, floods, and the fire regime [4–6].

Under optimal conditions, because of a less stringent limitation by the physical factors of the environment, there is an increase in species diversity in the composition of forest stands. In this case, the topoecological growth conditions start to play a significant role for the transformation of a common regional climatic signal in the variability of radial increment in trees [2, 7]. Moreover, the different species of woody plants growing under the same or similar ecological conditions transform the climatic signal in a species-specific manner as dictated by the characteristics of their seasonal growth and development [8, 9].

In the forest-steppe zone of Khakassia, at the forest-steppe interfaces, a single forest landscape may well include all woody species of this region, occupying different in the relief. This area provides a convenient research site for comparison of the climatic responses both from different timber species and from the same species occupying different topoecological niches. On this basis our intention here was to elucidate the following points:

- 1) What is the contribution of the climatic factors to the year-to-year variability in radial increment for different tree species depending on the topoecological conditions for their growth?
- 2) What are the climatic factors (temperature and humidity) that govern the dynamics of increment in woody plants under different topoecological conditions?
- 3) Is it possible to use the substantially differing tree-ring chronologies in higher quality reconstructions of the leading climatic factors?

MATERIAL AND INVESTIGATIVE METHODS

Material for our dendroecological investigation was collected in the forest-steppe zone of Shira district, Republic of Khakassia (54° 24'N, 89° 57'E). According to a climatic zoning, the territory of the district refers to the Altai-Sayan climatic zone of the temperate belt, with a moderately cold continental climate [10]. Data from the Shira meteostation indicate that the annual mean air temperature is 1.2 °C. The beginning of growing (the transition of diurnal temperatures across 5 °C) corresponds to the last ten-day period of April. The period with a temperature above 10 °C lasts 110– 120 days. The precipitation amount averaged 257 mm, with 72–90% of it corresponding to a warm season (April–October). Maxima and minima of atmospheric precipitation occur in July and February-March, respectively.

Material was collected in two areas extremely differing as regards the degree of soil humidification, namely the southern slope (SS), and the Tunguzhul' creek floodplain (CF). We investigated the variability in radial increment for four timber species: for the SS area – Siberian larch (*Larix sibirica* Ledeb.), common pine (*Pinus sylvestris* L.), and white birch (*Betula alba* L.), and for the CF area – Siberian larch and common spruce (*Picea obovata* Ledeb.). In the SS area, the upper and middle parts of the slope are dominated by larch and pine, respectively; birch trees occur only in the lower part of the slope.

Wood samples were collected in the form of cores using the Swedish increment borer at a height of 1.3 m for two radii of the tree stem. Collection, transportation and preprocessing of cores followed standard techniques adopted in dendrochronology [11], and the measurements were made with the semi-automatic LINTAB measuring system in conjunction with a specialized TSAP software package (as accurate as 0.01 mm) [12]. The dating of the samples (determination of the calendar year of each ring) was confirmed by correlation analysis using the COFECHA computer program forming part of the specialized DPL software package [13].

To extract the climatic signal influencing the tree-ring width, we undertook the procedure of standardization (indexation) in order to identify the climate-caused variability in radial increment [11, 14]. Standardization used a function of the prescribed form, namely the *spline function* (a picewise-conjugate function). The parameters of the increment curve with a specified spline window (67% of the length of the series) and with the prescribed variance suppression level (50%) were determined by fitting the values of the curve described by the piecewise-conjugate function, with the least standard deviation of approximation (the least square technique) [15].

The procedures of computations were performed in a specialized software package for dendrochronological investigations, namely DPL and STATISTICA'99 Edition [13, 16].

The individual indexed curves of increment as constructed for trees of the same species were then averaged to give a so-called *generalized* or local chronology for separate species and areas [14] with a dimensionless stationary series of increment indices where the mean is about 1.0, and the variance is temporally constant [17].

The standardization procedure was carried out using the ARSTAN computer program forming part of the DPL package. As part of its standardization, two data sets were obtained: standard generalizations of the chronology (std), and residual generalized chronologies (res) which eliminate to a significant extent the autocorrelation, i.e. a dependence of a current year's increment on a preceding year's increment [18].

Assessing the influence of climate on the dynamics of increment in trees was based on using monthly climatic data from the Shira meteostation for ground-level air temperatures (for the period 1966–2008), and for precipitation amounts (for the period 1937–2008). The correlation between radial increment in trees and temperature was examined for the period from September of a preceding year to September of a current year [2, 7].

Statistical analysis of the association of increment with climatic components was made from correlation coefficients between climatic factors and radial increment indices. The resulting histograms of correlation between temperature and atmospheric precipitation for separate months and increment indices were regarded as a proxy of the climatic response functions [7]. Reconstruction of the leading climatic factor from several tree-ring series used the technique of multiple linear regression [11].

RESULTS

Indices of Chronologies and Their Interrelations

For two selected areas (SS and CF) we constructed five tree-ring chronologies (for larch, pine and birch for the SS area, and larch and spruce for the CF area). For the SS area with deficient soil humidification conditions the three chronologies (Fig. 1, a-c) have a statistically reliably (90%) filled series as regards the number of samples and spans the period from 100 (for birch) to 200 years (for larch). The mean annual ring width indices are relatively high and vary from 0.76 mm (for larch) to 0.92-0.94 mm (for pine and birch). The standardized chronological series for larch and pine have similar indices of the values of variance, sensitivity and autocorrelation (Table 1). Furthermore, the extreme values of increments are virtually identical in these chronologies: maximum increment values correspond to 1808, 1819, 1859, 1870, 1915, 1926, 1986, and 1992, and the minimum values refer to 1838, 1845, 1849, 1862, 1875, 1900, 1908, 1944, 1964, 1998, and 2001. The chronology for birch also shows extrema in agreement with the chronologies for coniferous species, but it is characterized by slightly

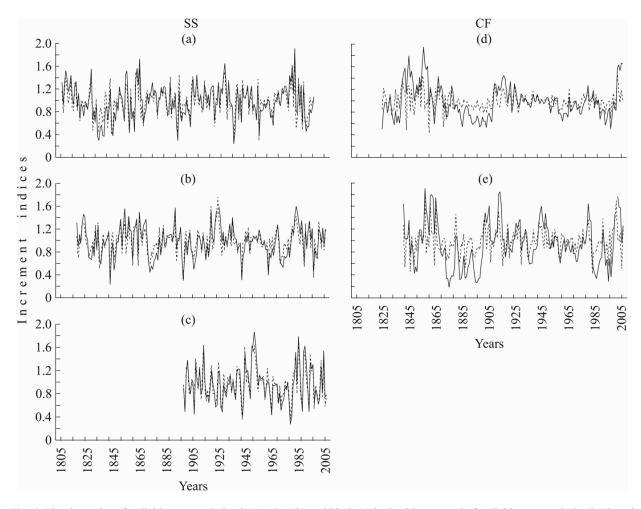


Fig. 1. The dynamics of radial increment in larch (a), pine (b) and birch (c) in the SS area, and of radial increment in larch (d) and spruce (e) in the CF area (indexed values, std – solid line, res – dashes).

Table 1. Statistical characteristics of tree-ring chronologies

		Number		std		res					
Chronologies	Period, years	of cores/ trees	Standard deviation (SD)	Sensitivity coef	Auto- correlation (AR)	Standard deviation (SD)	Sensitivity coef	Auto- correlation (AR)			
SS											
Larix sibirica (LS1)	1810–2008	14/2	0.31	0.29	0.35	0.28	0.32	0.01			
Pinus sylvestris (PS1)	1821–2008	15/2	0.29	0.26	0.46	0.24	0.28	0.01			
Betula alba (BA1)	1901–2008	11/2	0.35	0.30	0.47	0.30	0.34	0.01			
CF											
Larix sibirica (LS2)	1858–2008	12/2	0.42	0.22	0.82	0.23	0.25	0.04			
Picea obovata (PO2)	1886–2008	10/2	0.35	0.14	0.80	0.16	0.15	0.07			

higher values of SD and of the sensitivity coefficient. Visual comparison of the standard (std) and residual (res) chronologies for separate species growing on the southern slope shows their significant similarity. Nevertheless, correlation analysis of the chronologies reveals substantial differences (Table 2). While a

significant, rather high correlation exists between the chronologies for larch and pine (the middle and upper parts of the slope), the chronology for birch (in spite of the coincidence of separate extrema in increment) generally shows considerable differences from the chronologies for the conifers.

	std					res				
	LS1	PS1	BA1	LS2	PO2	LS1	PS1	BA1	LS2	PO2
LS1	1.00					1.00				
PS1	0.50	1.00				0.55	1.00			
BA1	0.21	0.19	1.00			0.15	0.17	1.00		
LS2	-0.08	0.14	-0.06	1.00		0.14	0.25	-0.09	1.00	
PO2	0.19	0.28	0.02	0.57	1.00	0.27	0.29	-0.03	0.38	1.00

Table 2. Relationship between standardized (standard (std) and residual (res)) tree-ring chronologies

Note. Significant (when p < 0.05) correlation coefficients appear in bold.

The chronologies for larch and spruce, obtained for the floodplain area (CF), do not exceed 180 years (see Fig. 1, d, e). The dynamics of radial increment in these species differs under identical growth conditions. Thus, beginning in 1945, the values of the tree-ring width (TRW) for spruce did not exceed 0.45 mm, whereas at the same period larch showed a significant increase in them, to 1.15 mm. Maximum increment indices were recorded in 1843, 1847, 1859, 1863, 1867, 1914, 1981, and 2003, and minimum indices were observed in 1851, 1875-1877, 1885-1887, 1897, 1900, 1960, 1996, and 1998. Standard and residual chronologies for separate time intervals differ substantially from one another. This points to the fact that at some periods nonclimatic factors of the environment have influence on increments in spruce and larch in the area of the creek floodplain. For instance, suppression of increment in larch and spruce was recorded from 1880 to 1910 and from 1875 to 1900, respectively (a marked difference between standard and residual chronologies).

Comparison of the standardized chronologies from different areas reveals that higher sensitivity is characteristic for the temporal series from the southern slope (0.26–0.30 for std), and lower sensitivity corresponds to the series from the creek floodplain (0.14–0.22 for std). These indices of the sensitivity coefficients testify that the climatic signal in the chronologies changes from significant to strong. The standard deviation characterizing the amplitude variability in increment varies for all series from 0.29 to 0.42 (for std). Upon removing from the std chronologies the first-order autocorrelation, the SD indices are somewhat decreased, whereas the sensitivity coefficient is increased (res chronologies).

Autocorrelation is due mainly to physiological factors and, to some extent, to the age trend of the chronology, but it can also be determined by a climatic cyclicity [14]. In the residual chronologies (res), unlike the standard chronologies (std), the autocorrelation is almost totally suppressed (the coefficients approach zero). The value of the variance, accounted for by a preceding year's increment (for standard chronologies) on the southern slope makes up 12 and 21% for larch and pine, respectively, and somewhat higher for birch (22%). In the floodplain area, this indicator constitutes 67% for larch and 64% for spruce.

Within each area the correlation between the changes in increment is much higher than that between the areas, which is also reflected in the higher values of the pair correlation coefficients (see Table 2). All the resulting chronologies are statistically significantly (p < 0.05) interrelated inside one area. The largest correlation coefficients between standard increment indices from chronologies of different kinds were recorded for pine and larch (R = 0.50) in the SS area, and for larch and spruce (R = 0.57) in the CF area. The smallest correlation coefficients are between chronologies for pine and birch (R = 0.19) in the SS area.

Response of Chronologies to Climatic Changes

The correlation coefficients between index values of radial increment in the tree species under investigation and the main climatic factors of the environment (temperature and humidity) are presented in Fig. 2. In general, the standard chronologies show a larger number of significant correlations (when p < 0.05) with the climatic factors for separate months when compared with the residual chronologies: 8 against 7 for the southern slope, and 5 against 2 for the creek floodplain. Nevertheless, the main factors that have a significant influence on increment in trees, are fully represented in both the standard and the residual chronologies.

Analysis of the climatic response showed that for the southern slope the influence of the same climatic factors on different species is different. Larch responds positively to an increase in the atmospheric precipitation amount in June and negatively to high temperatures at the onset of the growing period, namely May and June. The high June air temperatures have also a negative effect on radial increment in pine. In addition, increment in pine and larch correlates positively with October temperature (R = 0.35 for larch, and R = 0.34 for pine). For birch, a negative correlation of radial increment with April temperature (R = -0.33) and a positive correlation with September precipitation of a preceding year (R = 0.31) were revealed.

As regards the floodplain, temperature and precipitation influence differently the increment in larch and spruce. For instance, while the increment in spruce is to a larger extent dependent on the thermal regime of the onset of the growing period (the value

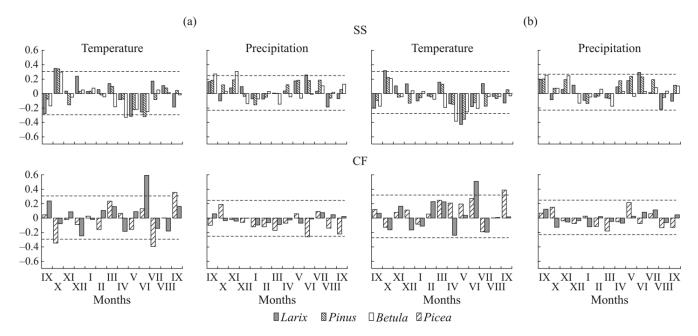


Fig. 2. The correlation coefficients of the indexed chronologies (a – std, b – res) with meteodata for the period 1936–2008 for atmospheric precipitation, and for the period 1966–2008 for temperatures (dashes correspond to the significant level).

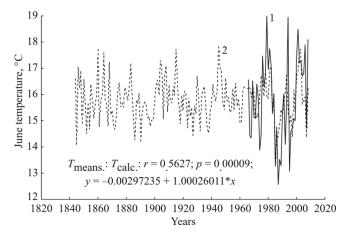


Fig. 3. The reconstructed June temperature series (dashes) and the series of observations (solid line) according to data from the Shira observatory.

of the correlation coefficient between TRW indices and June temperature is 0.59), the most significant factor influencing the increment in spruce is excessive humidification. The correlation between the spruce TRW and the precipitation amount in June has a negative character (R = -0.26). A rise in September temperature of a preceding year has a positive influence on the increment in spruce (R = 0.35).

Temperature of the active part of a season is the most significant factor in the increment variability for trees growing in the two habitats, but with the sign differing in the value and direction.

Reconstruction of Monthly Mean Air Temperature

Correlative analysis of the responses of radial increment in the conifers from two contrasting topoecological growth conditions shows that the chronologies for the trees from the southern slope and from the floodplain respond negatively and positively to the rise of June temperature, respectively. This permits us to use two chronologies in looking for the regression equation in which the climatic variable (June temperature) is a dependent variable, and the increment indices (IND) are independent variables. Finally, this searching led to a multiple linear regression model:

$$T_{June} = 14.09 - 1.489 \times IND_{pine} + 3.210 \times IND_{larch}$$

with the following statistical estimates: the multiple regression coefficient is 0.56; Fisher criterion F = 9.26, and p < 0.0005. A good agreement between actual (measured at the Shira meteostation) and calculated (from chronologies) values is evident in Fig. 3 where they are compared in their dynamics. Note that the slope of the regression, when the measured and calculated values are compared, does almost not differ from unity (thus emphasizing the quality and validity of the model). The mean values of the calculated and measured temperatures are in excellent agreement (15.79 and 15.81, respectively); however, the variances of the reduced series differ markedly (8.2 and 16.4), which corresponds to the variance level of the measured series. An independent verification involved comparing the reconstructed June temperature series from tree-ring chronologies with a longer (than that from the Shira meteostation) series of June temperature variation from the Minusinsk meteostation (about 120 km from the place of investigation). For a longer period of time the two series showed a highly significant correlation (R = 0.39; p < 0.001).

DISCUSSION

The goal of the research reported in this study was to study the formation characteristics of radial increment in coniferous wood under different topoecological conditions, and the transformation of the regional signal depending on the habitat conditions.

Undoubtedly the different species, even though they occur under almost identical habitat conditions, show differing responses to changes in the climatic conditions. Thus, birch on the southern slope responds more sensibly (than does pine or larch) to a rise in temperature at the very beginning of a season and shows a significant positive influence of atmospheric precipitation of the autumn and the onset of winter of a preceding year. This response of birch is due to the characteristic properties of the phenophases (the period of sap movement in trees and unfolding of leaves, and the seasonal dynamics of growth of leaves). In pine on the southern slope, the increment-suppressing temperature rise increases from May to June. Nevertheless, the climatic responses common to the habitat are present: a positive influence of the temperature rise in October (a potential lengthening of the growing period of the root system promoting an increase in radial increment during a next season through the use of additionally stored assimilates, namely nutrients and growth regulators [19]), and suppression of increment by high temperatures in April–June (indirect influence through an acceleration of soil drying).

The features of a different climatic response can be revealed by comparing the chronologies for larch and spruce in the creek floodplain area. Increment in pine sensibly responds to a rise of June temperature, which is accounted for mainly by adequate moving moisture under these conditions. On the other hand, the response of spruce to an increase in June temperature is not significant, whereas a rise of July temperature acts to suppress its increment markedly. Comparison of the structure of the root systems of these conifers under humidified habitat conditions suggests that it is the difference in the structure of the root systems which also explains the peculiarities of the climatic response. The root system in spruce that is nearer to the soil surface does not make it possible to take full advantage of the moisture in deeper horizons (available for larch), while at high July temperatures a drying of the subsurface horizons even in the creek floodplain leads to a deficit of moisture availability for the growing processes in spruce.

The tree-ring chronologies of the conifers on the southern slope exhibit higher sensitivity when compared with the floodplain area. Conceivably, on the southern

slope, the limitation (at certain periods of the season) by "temperature" is enhanced by one further factor of limitation by the "humidity deficit" which, at least at the initial period of the season, does not play any substantial role under the floodplain conditions. The higher values of the mean increment, the autocorrelation coefficient and of the percentage of the explained variance for woody plants growing in the creek floodplain area are indicative of the favorable conditions which level off the influence of a common limiting factor.

Dendroclimatic analysis is useful for identifying specific features of the response of trees to changes in weather conditions at different habitat locations. In spite of the fact that the selected areas are in immediate vicinity of each other, the different species of woody plants showed significant differences in the response of increment to climate, which characterizes their bioecological characteristics. The response of larch to the two entirely opposite growth conditions (a dry slope, and the humid conditions in the river floodplain) testifies its plasticity as a species.

Significant correlations were revealed between radial increment and temperature of the active part of the season: negative on the slope (May), and positive in the floodplain (July). Under the conditions of a moisture deficit (the slope), at the very beginning a the growing period whose onset for the given territory occurs in mid – end of May [20], a rise in air temperature promotes an increase in its evaporation. Meteorological measurements for the last 40 years indicate a considerable (by more than 1 °C) rise in May temperatures, which is responsible for the earlier beginning of growing [21]. Larch is characterized by an intense initiation of the growth processes just at the initial period of the growing season [22, 23]. Therefore, high air temperatures contribute to the drying-out of the soil thus causing a decrease in radial increment. Note that sensitivity to drying in larch is somewhat higher than in pine.

CONCLUSIONS

The results reported here testify that the growth topoecological conditions for growth of the same timber species transform substantially the regional climatic signal in the radial increment variability. At the same time, even under similar growth conditions (slope, floodplain) the coniferous and deciduous species show species-specific features in the climatic response. On the one hand, this enhances the possibilities of using tree-ring chronologies in analyzing the dependence of growth on climatic changes, and, on the other, opens up fresh opportunities for the more reliable dendroclimatic reconstruction of the leading climatic variables by using a combination of different tree-ring chronologies where these factors are significant. It was possible to exploit and illustrate such a possibility for reconstruction of the past variations in June temperature.

Of course, an approach of this kind also holds much

promise for other investigations where it is possible to use a set of long tree-ring chronologies for woody plants differing in topoecological growth conditions.

ACKNOWLEDGMENTS

This work was done with financial support from the Russian Foundation for Basic Research (09–04–01380, 09–05–00900, 09–04–92515), AVTs Program "Development of Scientific Potential in Higher School" (No. 2.1.1/6131), SFU Project (No. 1.7.09), and NSh–65610.2010.4.

REFERENCES

- 1. Briffa, K.R., Jones, P.D., Schweingruber, F.H., et al., Reduced Sensitivity of Recent Tree-Growth to Temperature at High Northern Latitudes, *Nature*, 1998, vol. 391, pp. 672-682.
- Schweingruber, F.H., Tree-Rings and Environment. Dendroecology, Bern; Stuttgart; Vienna: Haupt, 1996.
- 3. Briffa, K.R., Osborn, T.J., Schweingruber, F.H., et al., Low Frequency Temperature Variations From a Northern Tree-Ring Density Network, *J. Geophys. Res.*, 2001, vol. 106, pp. 2929–2941.
- 4. Andreev, S.G., Vaganov, E.A., Naurzbaev, M.M., and Tulokhonov, A.K., Using Annual Rings in Pine to Record Long-Term Fluctuations in Atmospheric Precipitation, the Runoff of the Selenga River and the Lake Baikal Level, *DAN*, 1999, vol. 368, no. 3, pp. 400–403 [in Russian].
- 5. Magda, V.N. and Zelenova, A.V., Radial Increment in Pine as the Indicator of Atmospheric Humidification in the Minusinskaya Depression, *Izv. RGO*, 2002, vol. 134, issue 1, pp. 73–79 [in Russian].
- 6. Meko, D.M., Cook, E.R., Stahle, D.W., et al., Spatial Patterns of Tree-Growth Anomalies in the United States and Southeastern Canada, *J. Clim.*, 1993, vol. 6, pp. 1773–1786.
- 7. Fritts, H.C., *Tree-Ring and Climate*, London; New-York; San Francisco: Acad. Press, 1976.
- 8. Vaganov, E.A. and Shashkin, A.V., *Growth and Structure of Annual Rings in Conifers*, Novosibirsk: Nauka, 2001 [in Russian].
- 9. Wilson, R. and Elling, W., Temporal Instabilities of Tree-Growth/Climate Response in the Lower Bavarian Forest Region: Implications for Dendroclimatic Reconstruction,

- Trees, 2003, vol. 18(1), pp. 19–28.
- 10. Alisov, B.P., *The Climate of the USSR*, Moscow: Izd-vo Mosk. un-ta, 1956.
- 11. Methods of Dendrochronology. Application in Environmental Sciences, Eds. Cook, E.R. et al., Dordrecht; Boston; London: Kluwer Acad. Publ., 1990.
- Rinn, F., TSAP V 3.6 Reference Manual: Computer Program for Tree-Ring Analysis and Presentation, Heidelberg, 1996.
- Holmes, R.L., Dendrochronology Program Library Users Manual, Tucson, Arizona. Updated September 1998 (Electronic Version), hhtp://www.ldeo.columbia. edu/trl.
- 14. Briffa, K.R., Wigley, T.M.L., and Jones, P.D. Towards an Objective Approach to Standardization, in *Methods* of *Dendrochronology*, Eds. K. Kairiukstis, Z. Bednarz and E. Feliksik, IIASA/Polish Academy of Sciences, Warsaw, 1987.
- Cook, E.R. and Krusic, P., Arstan, Version 2005. Tree-Ring Laboratory, Lamont-Doherty Earth Obs., http:// www.ldeo.columbia.edu/trl.
- 16. http://www.StatSoft.ru.
- 17. Matalas, N.C., Statistical Properties of Tree-Ring Data, *Bulletin of the International Association of Hydrology*, 1962, no. 7, pp. 39–47.
- Mazepa, V.S., Influence of Atmospheric Precipitation on the Dynamics of Radial Increment in Conifers in Subarctic Areas of Eurasia, *Lesovedenie*, 1999, no. 6, pp. 14–21 [in Russian].
- Sudachkova, N.E., Metabolism in Conifers and Formation of Wood, Novosibirsk: Nauka, 1977 [in Russian].
- 20. Butorina, T.N., *Bioclimatic Zoning of Krasnoyarsk Territory*, Novosibirsk: Nauka, 1979 [in Russian].
- 21. Knorre, A.A., Siegwolf, R., Saurer, M., et al., 20^{th} Century Trends in Tree-Ring Stable Isotopes (δ^{13} C and δ^{18} O) of *Larix sibirica* Under Dry Conditions in the Forest-Steppe in Siberia, *J. Geophys. Res.*, 2010, DOI: 10.1029/2009JG000930.
- Vaganov, E.A., Hughes, M.K., Kirdyanov, A.V., et al., Influence of Snowfall and Melt Timing on Tree Growth in Subarctic Eurasia, *Nature*, 1999, vol. 400, pp. 149–151.
- 23. Wang, L., Payette, S., and Begin, Y. Relationship Between Anatomical and Densitometric Characteristics of Black Spruce and Summer Temperature at Tree Line in Northern Quebec, *Canadian Journal of Forest Research*, 2002, vol.32, pp. 477–486.