INFLUENCE OF CLIMATE CHANGES ON TREE-RING CHARACTERISTICS OF SCOTS PINE PROVENANCES IN SOUTHERN SIBERIA (FOREST-STEPPE)

by

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SUMMARY

Scots pine provenances from all over Russia planted in 1964 at the forest-steppe zone were analyzed. Eight tree-ring characteristics from 12 different provenances were measured densitometrically. The time span of tree-ring observation covers the period from 1969 to 1997. The sensitivity coefficient of latewood width, latewood and maximum densities and latewood percentage decreases in relation to the increasing latitude of the provenances. The growth of all studied provenances is dictated by the local weather and climate. The correlation coefficients of indices between the local provenance and the other provenances are not lower than 0.46-0.97, and the synchronicity coefficients are minimally 0.84. The Euclidean distances vary from 0.11 to 0.13 between the local provenance and the other provenances. All statistical parameters show that the interannual variability reflects the prevailing influence of the local weather conditions. Variability of weather conditions determines up to 87% of the growth variability in the forest-steppe of southern Siberia.

Key words: Tree-ring width, tree-ring density, plantation, provenance, dendroecology.

INTRODUCTION

A provenance trial of Scots pine was established from 1964 to 1967 in the Krasnoyarsk forest-steppe zone, southern Siberia by the Institute of Forest SB RAS, Krasnoyarsk (Iroshnikov 1977), in order to study height growth and survival characteristics.

Tree rings are controlled by genetic predisposition and environmental factors (Barnett 1981; Larson 1994; Savidge 1996). The analysis of tree-ring characteristics in different provenances can be a tool for evaluation of the genetic control of xylem differentiation. In Siberia only two extensive dendrochronological studies on different provenances have been made. Isaeva and Cherepnin (1988) studied tree-ring parameters such as tracheid wall thickness and latewood percentage of 5 Scots pine provenances planted in the Krasnoyarsk forest-steppe plantation. They concluded that all provenances are very well adapted to new environments. Another study was conducted by Savva et al.

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(2002a) on 16 Scots pine provenances planted in the southern taiga (Boguchany). They found that most of the interannual variability for all the provenances reflected the local weather variations.

Very rapid warming due to an increase in atmospheric concentrations of CO_2 and other greenhouse gases is predicted by Briffa et al. (1998) and Flanagan and Ehleringer (1998). Therefore it is of great interest to study the behaviour of different provenances under identical ecological conditions. Here we study the adaptation of tree-ring formation.

The genetic influences on wood formation are not well known and the results are contradicting (Zobel & Van Buijtenen 1989). For instance, McKimmy and Nicholas (1971) have shown that genetic and environmental components significantly affect the wood density of 50-year-old *Pseudotsuga menziesii* (Douglas fir) while Ericson (1960) found that different *Pinus sylvestris* (Scots pine) genotypes are only weakly influenced by environmental conditions. Conversely, Rink and Thor (1973) found that the influence of environmental factors on wood density in *Pinus virginiana* exceeds the genetic influence.

Densitometrical analysis has several advantages. In a way it integrates several tree-ring characteristics. Moreover, the densitometrical characteristics summarize the influences of climatic conditions and genetic reaction of a tree over long periods of time (whole life span).

In this paper we studied the genetic potential of Scots pine by using the densitometric measurements of tree-ring width, earlywood and latewood widths, earlywood and latewood densities, minimum and maximum densities and latewood percentage. Scots pine is unique because it has a very wide ecological range, it grows on extremely dry sites in semi-arid climates and also on wet sites in bogs (Ellenberg 1974). The geographical range is very large. The western border lies at the Sierra Nevada of Spain and extends as far east as Yakutiya in Russia. We had the opportunity to compare the reaction of Scots pine provenances from all over Russia, from about 50-64° N and 56-127° E, grown at the same site near Krasnoyarsk.

The objective of the study is to evaluate the response of Scots pine *(Pinus sylvestris* L.) to annual weather conditions through testing twelve provenances in the forest-steppe, southern Siberia, using densitometric measurements of tree rings.

MATERIALS

The Laboratory of Forest Genetics and Breeding of the Institute of Forest (A.I. Iroshnikov) raised seedlings in 1964. A field trial of 3-year-old plants was established in three plots in 1967. The plantation is on formerly ploughed and entirely tilled sod-podzol soil. The seedlings were planted in rows 1.5* 0.75 m apart. We selected the biggest trees in the plot, based on dbh to avoid the influences due to competition.

We collected 292 increment cores from 12 pine provenances. The location of provenance origins and their forest type are given in Table 1. For each provenance, 15-25 trees were sampled. For each tree, one core was taken, which included tree rings of two radii. Cores were taken at approximately 50 cm above ground. This height above

Table 1. Data on the 1964 Scots pine provenance trial. Provenances are listed in order of decreasing latitude of origin.

No.	Provenance	Latitude [°N]	Longitude [°E]	Number of trees analysed	Forest type
10	Sangarsk	63° 58'	127° 28'	15	Northern taiga
9	Lensk	60° 43'	114° 53'	17	Middle taiga
11	Olekma	60° 22'	120° 24'	21	Middle taiga
6	Boguchany	58° 23'	97° 26'	24	Southern taiga
1	Perm	58°	56° 20'	22	Southern taiga
5	Kazachinsk	57° 43'	93° 17'	25	Forest-steppe
2	Sverdlovsk	56° 50'	60° 50'	18	Southern taiga
3	Miass	55°	60°	21	Forest-steppe
12	Tygda	53° 06'	126° 21'	19	Southern taiga
8	Ulan-Ude	51° 49'	107° 35'	18	Forest-steppe
7	Dzhida	50° 40'	106° 10'	23	Forest-steppe
4	Leninogorsk	50° 20'	85° 33'	20	Mountain taiga

the base represents a loss of about 4 years of growth in relation to the total tree age. Analysis was carried out on tree rings formed in the age period from 4 to 33 years.

The climate of the Krasnoyarsk forest-steppe territory is continental (Zyubina 1974), with the coldest month being January (average temperature is -18-21°), and the warmest month in July with an average temperature of 18-19°. The duration of the vegetation period is on average 140-150 days. A year-by-year variability of the humidity regime is characteristic for the forest-steppe zones of Siberia. The average annual precipitation varies from 394 mm to 494 mm (Zyubina 1974). The average annual temperature varies between 0.2° to -1.7°. Approximately 50% of the precipitation falls in June-August.

METHODS

Cores were analyzed with a DENDRO-2003 densitometer. Detailed descriptions of the technique have been given by Schweingruber (1988) and Eschbach et al. (1995). Tree-ring width, early wood width, latewood width, percentage latewood (radial growth chronologies), minimum and maximum densities, earlywood and latewood densities (density chronologies) were measured and cross-dated. We delimited earlywood and latewood on the 50% density level between the maximum and minimum densities. Measurements were taken for eight tree-ring characteristics from each tree (individual series) in each provenance (provenance chronology).

To exclude age trends in the radial growth, and minimum and earlywood density chronologies we used a negative exponential function. The latewood and maximum density chronologies were standardized by the second degree polynomial function and the latewood percentage chronologies by a linear function. Then indices were calculated by dividing the values from measured characteristics by the values obtained from the fitting curve (Cook et al. 1990). The age trend is similar for each provenance (Fig. 1); therefore the indexed chronologies of different provenances are comparable.
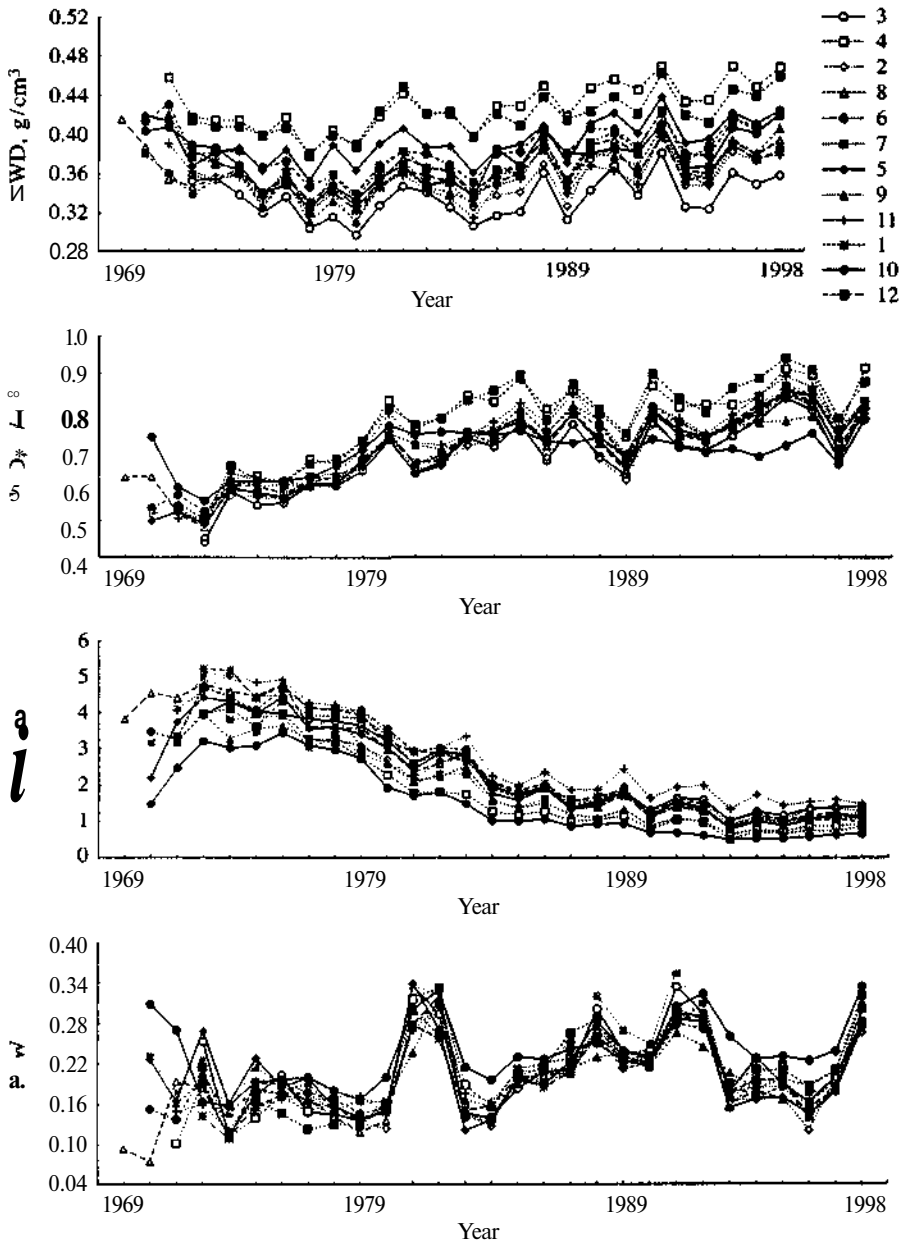
Fig. 1. Raw mean series of early wood density (EWD), latewood density (LWD), tree-ring width (TRW) and a portion of latewood (PLW) for the provenances.

To ascertain to what extent the growth of provenances is influenced by environmental factors we calculated the coefficient of sensitivity (Shiyatov 1986). The coefficient of synchronicity (Shiyatov 1986) and correlation between the local provenance (Kazachinsk) and other provenances revealed the similarity of their growth rhythm. To evaluate quantitatively the similarities and differences between growth characteristics (tree-ring width, latewood and earlywood densities and latewood percentage, $R < 0.85$) of the provenances we calculated Euclidean distances (Ayvazyan et al. 1989).

In previous studies cluster analysis identified two groups (clusters) of the provenances with maximum similarities within each group plus one provenance on its own (Savva et al. 2002b). The first group included the provenances Djida, Tygda, Miass, Sverdlovsk; Kazachinsk; Ulan-Ude; Perm and Boguchany; the second group included Olekma, Leninogorsk and Lensk. The Sangarsk provenance showed an example of a unique provenance from the northern taiga (mixed coniferous forest). However, linkage distances amalgamating the groups are minor. To determine general climatic factors influencing tree-ring characteristics we averaged tree-ring characteristics within the groups, and considered them in relation to the mean monthly data of temperature and precipitation obtained from the weather station located alongside the provenance plantation. We did not take into account the time interval 1969-1972 where replication was less than 100%.

RESULTS

Table 2 shows the mean values of tree-ring widths, maximum density and latewood percentage. The sensitivity coefficients of tree-ring characteristics (Table 3) show that the radial growth chronologies are more sensitive than density chronologies. So we conclude that the latewood formation is more influenced by weather conditions. The range of the sensitivity coefficient among the provenances for the latewood density (0.048-0.095) is higher than that for the earlywood density (0.046-0.066) (Table 3). However tree-ring characteristics of the provenances are not highly sensitive, accord-

Table 2. Mean values for weakly correlated tree-ring characteristics: tree-ring width (TRW), latewood percentage (PLW) and maximum density (MAX).

Provenance	TRW (mm)	PLW	MAX (g/cm3)
Sangarsk	1.50	0.24	0.80
Lensk	1.93	0.20	0.82
Olekma	2.83	0.20	0.85
Boguchany	2.51	0.20	0.82
Perm	2.52	0.20	0.83
Kazachinsk	2.32	0.21	0.80
Sverdlovsk	2.37	0.20	0.80
Miass	2.37	0.21	0.80
Tygda	2.32	0.21	0.90
Ulan-Ude	2.52	0.19	0.81
Dzhida	2.19	0.22	0.82
Leninogorsk	1.92	0.20	0.88

Table 3. Sensitivity coefficients for the index values of tree-ring characteristics to weather conditions. Kazachinsk is the local chronology.

Provenance	Ring widths			Densities				
	TRW	EWW	LWW	PLW	MAX	LWD	MIN	EWD
Sangarsk	0.142	0.136	0.216	0.149	0.049	0.048	0.065	0.046
Lensk	0.176	0.155	0.280	0.169	0.074	0.071	0.068	0.062
Olekma	0.143	0.153	0.271	0.186	0.070	0.073	0.065	0.059
Boguchany	0.165	0.177	0.273	0.197	0.064	0.066	0.064	0.048
Perm	0.132	0.150	0.253	0.211	0.071	0.074	0.048	0.049
Kazachinsk	0.197	0.222	0.313	0.254	0.072	0.073	0.072	0.055
Sverdlovsk	0.186	0.212	0.34,8	0.257	0.083	0.084	0.074	0.066
Miass	0.139	0.163	0.313	0.262	0.085	0.095	0.072	0.065
Tygda	0.138	0.155	0.246	0.209	0.072	0.078	0.043	0.044
Ulan-Ude	0.161	0.177	0.324	0.242	0.075	0.083	0.063	0.057
Dzhida	0.176	0.192	0.290	0.222	0.074	0.079	0.092	0.066
Leninogorsk	0.141	0.150	0.314	0.233	0.077	0.082	0.057	0.047

TRW = mean tree-ring width, EWW = earlywood width, LWW = latewood width, PLW = latewood percentage, MAX = maximum density, LWD = latewood density, MIN = minimum density, EWD = earlywood density.

ing to Ferguson's classification of sensitivity (Shiyatov 1986), with exception for the Kazachinsk, Sverdlovsk, Miass, Ulan-Ude and Leninogorsk provenances. The sensitivity coefficients of latewood width for these provenances are higher than 0.3.

Indexed tree-ring characteristics from all the provenances are highly correlated (with R values above 0.46, p < 0.01) and synchronized with the local Kazachinsk provenance (synchronicity coefficients above 0.84). The correlation and synchronicity coefficients show that the interannual variability of the measured tree-ring characteristics from all provenances reflects the prevailing influence of local weather conditions (Fig. 2). Coefficients of correlation and synchronicity between the local provenance and distant provenances decrease in relation to the increasing latitude of seed origins.

There is a significant negative correlation (p < 0.05) between the sensitivity coefficient and the latitude of seed origin for all the studied latewood characteristics (for maximum density R = -0.60, for latewood density R = -0.71, for latewood width R = -0.51 and for latewood percentage R = -0.65). There is also a significant negative correlation between the sensitivity coefficient and the longitude of seed origin for several latewood characteristics (for maximum density R = -0.60, for latewood density R = -0.56 and for latewood percentage R = -0.66).

Tree-ring widths for all the provenances are highly correlated with the average temperatures in April (Fig. 3a). The correlation decreases for the first four tree rings (juvenile period). For the rest of the period, the years of a growth increase (1981,1982, 1985,1988,1991,1993, etc.) coincide with an abrupt increase in April temperature, and conversely, the years of a growth reduction (1980,1982,1985,1988,1990,1991,1993) coincide with an abrupt decrease in April temperature.
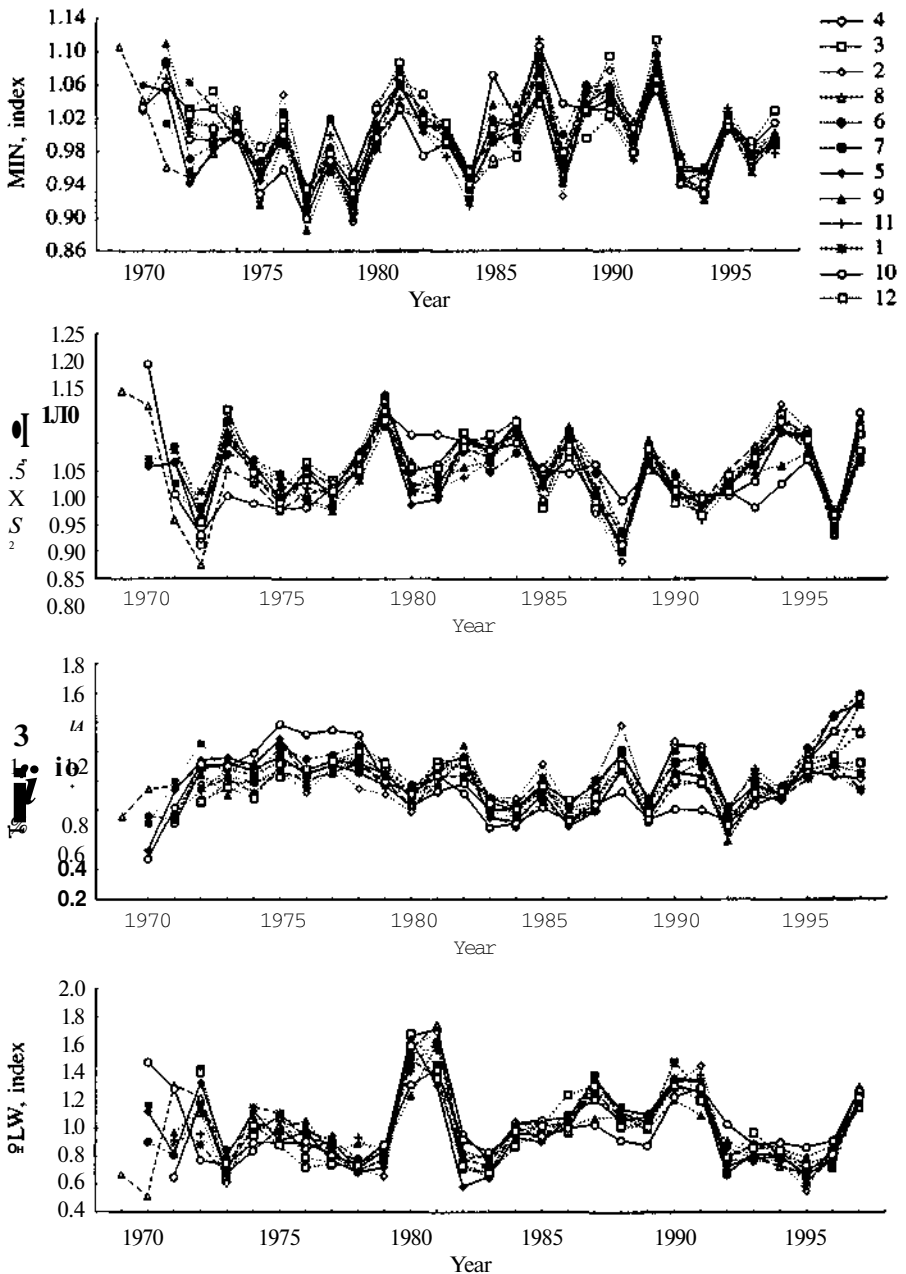
Fig. 2. Indexed curves for minimum density (MIN), maximum density (MAX), tree-ring width (TRW), and latewood percentage (PLW).

Latewood portion series highly conform to the average temperatures in May and average precipitation in July. Figure 3b shows that precipitation in July determines a latewood portion for most of the provenances (cluster 1, cluster 2) and the temperatures in May determine a latewood portion for the most northern provenance (cluster 3).

For all the provenances average precipitation in May negatively influences earlywood density (Fig. 3c). So, the years of abrupt increase in earlywood density coincide with the years of a decrease in average precipitation in May: 1980,1981,1983,1985,1987, etc. Conversely, for all the provenances, earlywood density formed in the years with a wet month of May (1975, 1977, 1982, etc.) is at a minimum. Only the first three tree rings respond differently (positively) to variation in May precipitation.

Increase in summer temperatures positively effects maximum density (Fig. 3d). For northern provenances (cluster 3) the temperature in May mainly influences latewood density, for the rest of the provenances (cluster 1, cluster 2) the June temperature does so. There is no correlation between maximum density and temperature in June within the first four tree rings of the provenances (clusters 1, 2).

The coefficients of correlation and synchronicity of the weakly correlated densito-metric characteristics (tree-ring width, latewood density, earlywood density and late-wood percentage, R values < 0.85) were used to calculate the normalized Euclidean distances between the local provenance (Kazachinsk) and the other provenances. The lowest Euclidean distance ($d_E = 0.11$) connects the Kazachinsk provenance to the provenances from the forest-steppe zone, and southern and middle taiga. The highest Euclidean distance ($d_E = 0.13$) separates the Kazachinsk provenance from the provenances of southern taiga (Sverdlovsk and Perm). Thus the studied provenances differ from the local provenance in interannual variability by no more than 87%.

DISCUSSION

Trees growing under extreme climate conditions at high latitudes are highly sensitive to weather fluctuations (Vaganov & Shiyatov 1998; Nikolaev 1999). The sensitivity coefficient of radial growth decreases from north to south for the native tree population at the Yakutiya (northeast of Russia). For the native population of trees from Sangarsk (Yakutiya) the coefficient of sensitivity to weather changes for tree-ring width is 0.17 (Nikolaev 1999). The same tendency was noticed for seeds moved to another environment. The sensitivity coefficient decreases for the Sangarsk provenance transplanted to the Krasnoyarsk forest-steppe territory to 0.14. We suppose that the more favorable climatic conditions of the Krasnoyarsk forest-steppe promote the decrease of sensitivity of the northern provenance to weather changes.

We have shown that the sensitivity of latewood decreases with increase in the latitude of seed origins. The reason for this behavior is that trees at higher latitudes are adapted to maximally exploit the earliest available heat sum (Mikola 1962; Leikola 1969; Vaganov et al. 1994; Hughes et al. 1999; Vaganov et al. 1999). The climatic conditions of the second half of the growing season therefore have less effect on radial growth characteristics. The southern provenances use the energy resources (heat and light) effectively during the u/hrJ*» m~~~:~~ ~~~~~~. I~ ~ ~~~~^~
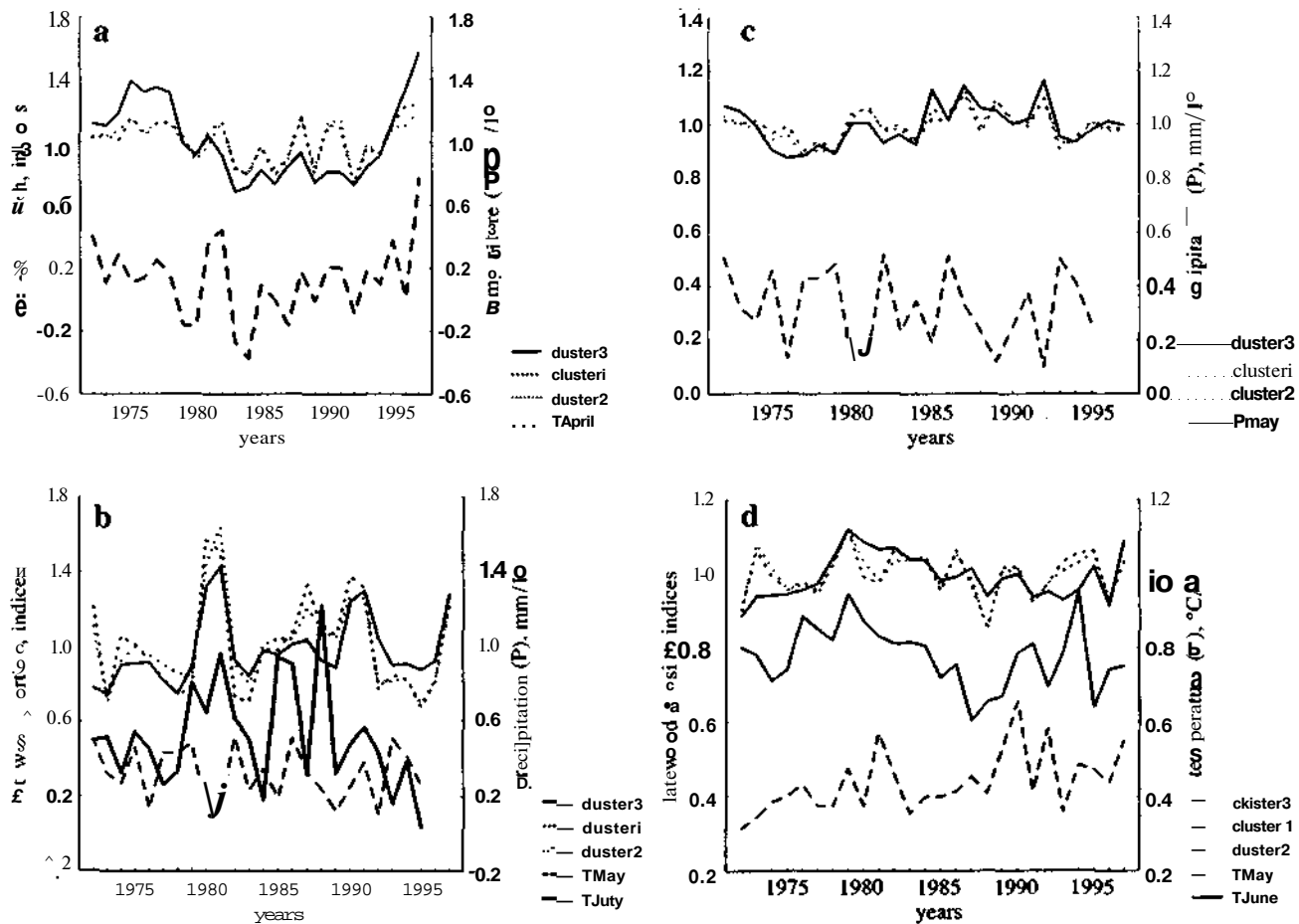
Fig. 3. Overlay (comparison) of tree-ring characteristics and mean monthly data of temperature and precipitation for the test location.

the conditions of the second half of the growing season. Northern provenances show an earlier cessation of growth and transition to dormancy. If these trees are transplanted to the south, they lack the ability to compete with southern provenances which are adapted to use the energy resources over the whole growing season (Table 2). The same tendency of decreasing the sensitivity of latewood characteristics in relation to the increasing latitude of seed origin was recorded for Scots pine provenances planted at a provenance trial in the southern taiga, Central Siberia (Savva et al. 2002a). It seems that the ability of northern provenances to maximally utilize the energy resources of the first half of a growing season is genetically fixed.

Correlation analysis revealed the general factors determining tree-ring characteristics of the provenances planted in Southern Siberia. It was shown that climatic factors influencing tree-ring formation hardly differ between the provenances showing the highly adaptive nature of pine. Climatic characteristics for this region are as follows: appearance of snow cover is 24th October, buildup of steady snow cover 5th November, its thaw 26th March, and final melting 12th April (Zyubina 1974). Positive correlation of tree-ring width and the average temperature in April indicates that the high temperatures of this period accelerate thaw of snow hastening a starting date of cambium initiation for all provenances. The thaw of snow terminates within 8 days. The continental climate is characterized by night frosts during warm summers. Sometimes the temperature of the soil (at a depth of 1.5-2 m) decreases up to -1 °C in June and August (Zyubina 1974). Increased precipitation during a summer compensates (softens) the influence of temporary frosts on radial growth, increasing cell production, i.e. tree-ring width and thus latewood portion, especially for the provenances from the middle and mountain taiga (cluster 2, see Methods; Fig. 3b).

In this region latewood formation begins in June. Increased temperatures in July promote intensive evaporation of moisture from soil. This stimulates suppression of photosynthesis activity that decreases apical growth, therefore cells of small radial size are formed. Latewood density depends on the ratio of radial size and cell wall thickness of latewood tracheids. Therefore the temperature of nearly all summer months influences maximum density positively. D'Arrigo et al. (1992) and Briffa et al. (1991, 1998) obtained the same result for natural northern stands.

Factors influencing tree-ring characteristics in the juvenile phase differ from the factors influencing adult tree-ring characteristics. In our studies, great differences were found between the first four tree rings and the rest of the tree rings, with respect to tree-ring characteristics and weather data. This is because the age of the lateral meristem integrates the influence of internal and external factors differently, in such a way that tracheid length, cell diameter and resin ducts production increase, but tree-ring width and latewood portion decrease in the direction from pith to bark (Wimmer 1994).

In the context of global and regional climatic change these results show that the northern provenances are more conservative by utilizing energy resources of the first half of the growing season effectively. So we suggest that the movement of the northern border of the natural distribution area of *Pinus sylvestris* will not be rapid, especially if other competitive species (e.g. larch) are better adapted to use higher temperatures effectively.

The analysis of the provenance's correlation and synchronicity coefficients and their generally close relationship with the local provenance (Kazachinsk) demonstrates that the local weather conditions mainly influence the interannual variability of tree-ring characteristics. The local weather influence inconsiderably decreases in relation to increasing latitude of seed origin. For example, radial growth of the native population from the Yakutiya (Russia) is mainly influenced by the temperature of June-August (Nikolaev 1999); if northern seed sources are moved southward to the Krasnoyarsk forest-steppe conditions, their vegetation period becomes longer and time of cambial initiation starts earlier. Tree-ring characteristics for all the provenances (even for the northern provenances) planted on the Krasnoyarsk forest-steppe territory reflect the prevailing influence of the local weather conditions.

Significant differences in tree-ring sensitivity were detected between the provenances. These differences prove the existence of genetic control of wood formation. The evaluations of Euclidean distances between the provenances show, however, that the genetic control is not strong. Nevertheless densitometric parameters and their dynamic characteristics such as sensitivity to weather conditions, coefficients of synchronicity and correlation might be used for evaluation of genetic differences between the provenances. They do, however, summarize the influences of climatic conditions and genetic reaction over a long period of time.

CONCLUSIONS

The sensitivity of latewood characteristics decreases with the increase in the latitude of seed origin, showing that the northern provenances retain their ability to utilize only the energy resources (heat and light) of the first half of a growing season effectively.

Factors influencing formation of tree-ring characteristics hardly differ between the provenances. Temperature in April determines the starting day of cambium initiation for all provenances. Precipitation in July determines a latewood portion for most of the provenances, and the temperatures in May determine the latewood portion for northern provenances. Precipitation in May negatively influences earlywood density for all provenances. Increase in summer temperature positively effects latewood density.

The values of the synchronicity and correlation coefficients and the normalized Euclidean distances between the local provenance and the other provenances show that the interannual variability of tree-ring characteristics for all the provenances reflects the prevailing influence of the local weather changes. Even the most remote provenances differ from the local provenance by less than 13%.

ACKNOWLEDGEMENTS

REFERENCES

Ayvazyan, S. A., V.M. Bukhshtaber, I.S. Eniukov & L.D. Meshalkin. 1989. [Applied statistics. A classification and reduction of dimensionality.] Finance and Statistics, Russia. [In Russian].

Barnett, J.R. (ed.). 1981. Xylem cell development. Castle House Publications, Tunbridge Wells.

Briffa, K.R., T.S. Bartholin, D. Eckstein et al. 1991. A 1400-year tree-ring record summer temperatures in Fennoskandia. Nature 346: 434-439.

Briffa, K.R., F.H. Schweingruber, P.D. Jones, T.J. Osborn, I.S. Harris, S.G. Shiyatov, E.A. Vaganov & H. Grudd. 1998. Trees tell of past climates: but are they speaking less clearly today? Phil. Trans. R. Soc, London ??: 65-73.

Cook, E.R., K.R. Briffa, S.G. Shiyatov & VS. Mazepa. 1990. Tree-ring standardization and growth-trend estimation. In: E. R. Cook & L. A. Kairiukstis (eds.), Methods of dendrochronology. Application in the environmental sciences: 104-123. Kluwer Acad. Publ., Dordrecht, Netherlands.

D'Arrigo, D.R., S.G. Jacoby & R.M. Free. 1992. Tree-ring width and maximum latewood density at the North American tree line: parameters of climate change. Can. J. For. Res. 22: 1290-1296.

Ellenberg, H. 1974. Zeigerwerte der Gefasspflanzen Mitteleuropas. Scr. geobot. Goltze, KG. Göttingen.

Ericson, B. 1960. Studies on the genetical wood density variation in Scots pine and Norway spruce. Stat Skogsforskningsinst. Stockholm Rapp. 4: 1-52.

Eschbach, W., P. Nogler, E. Schar & F.H. Schweingruber. 1995. Technical advances in the radiodensitometrical determination of wood density. Dendrochronologia 13: 155-168.

Flanagan, L.B. & J.R. Ehleringer. 1998. Ecosystem-atmosphere CO_2 exchange: interpreting signals of change using stable isotope ratios. Trends in Ecology and Evolution 13: 10-14.

Fritts, H.C. 1987. Tree rings and climate. Methodology of dendrochronology: East/West Approaches. Vol. 1.

Hughes, M.K., E.A. Vaganov, S.G. Shiyatov & R. Touchan. 1999. Twentieth-century summer warmth in northern Yakutia in a 600-year context. The Holocene 9: 603-608.

Iroshnikov, A.I. 1977. [The provenance trials of coniferous wood in southern Siberia]. In: Geographicheskie kul'tury i plantacii hvoynyh v Sibiri: 3-111. Nauka, Novosibirsk, Russia. [In Russian].

Isaeva, L.N. & V.L. Cherepnin. 1988. [Quality of wood of Scots pine provenances at Central Siberia]. Lesovedenie 2: 80-83. Moscow, Russia. [In Russian].

Larson, P.R. 1994. The vascular cambium. Development and structure. Springer-Verlag, Berlin.

Leikola, M. 1969. The influence of environmental factors on the diameter growth of young trees. Acta. For. Fenn. 92: 1-4.

McKimmy, M.D. & D.D. Nicholas. 1971. Genetic differences in wood traits among half-century-old families of Douglas-fir. Wood and Fiber 2: 347-355.

Mikola, P. 1962. Temperature and tree growth near the northern timberline. In: T.T. Kozlowski (ed.), Tree growth: 265-287. Ronald Press, New-York.

Nikolaev, A.N. 1999. [Climatic influence on the spatial-temporal variability of radial growth in coniferous woods from Northern and Central Yakutiy a]. Abstract of PhD 03.00.16, Institute of Forest SB RAS, Krasnoyarsk, Russia: 1- 23 [In Russian].

Rink, G. & E. Thor. 1973. Inheritance and gains of three wood properties in Virginian pine. 12th Southern Forest Tree Improvement Conference, Baton Rouge, LA: 24- 30.

Savidge, R. A. 1996. Xylogenesis, genetic and environmental regulation - A review. IAWA J. 17: 269-310.

Savva, Yu. V., F. H. Schweingruber, N. A. Kuzmina & E. A. Vaganov. 2002a. Sensitivity of diameter growth to annual weather conditions in Scots pine provenances at a Central Siberian location. Silvae Genetica 51(2).

Savva, Yu, E. A. Vaganov & L. Milyutin. 2002b. Ratio of individual and chronological variability in tree-ring series of the Scots pine provenances planted at a forest-steppe location, Southern Siberia. Silvae Fennica (Submitted).

Schweingruber, F.H. 1988. Tree-rings: Basics and applications of dendrochronology. Reidel Publ., Dordrecht, Netherlands.

Shiyatov, S.G. 1986. Dendrochronology of the higher timber line on the Urals. M. Science: 136 pp. [In Russian].

Vaganov, E. A., M. K. Hughes, A. V. Kirdy anov, F. H. Schweingruber & P. Silkin. 1999. Influence of snowfall and melt timing on tree growth in subarctic Eurasia. Nature 400: 149-151.

Vaganov, E. A. & S.G. Shiyatov. 1998. [Dendrochronological methods in studying the climatic history of Siberia] In: [Problems of the reconstruction of climate and environment of Holocene and Pleistocene of Siberia]: 56-63. Edition of Institute of Archaeology and Ethnography SB RAS, Novosibirsk, Russia. [In Russian].

Vaganov, E. A., L. G. Vysotskaya & A. V. Shashkin. 1994. [Seasonal growth and structure of larch annual rings at the northern timberline]. Lesovedeniye 5: 3-15. [In Russian].

Wimmer, R. 1994. Structural, chemical and mechanical trends within coniferous trees. In: P. Spicker & P. Kahle (eds.). Modelling tree-ring development cell structure and environment: 2-11. Freiburg.

Zobel, B. J. & J. P. Van Buijtenen. 1989. Wood variation: its causes and control. Springer-Verlag, Berlin.

Zyubina, V.I. 1974. [Air temperature regime in the Krasnoyarsk forest-steppe and several methodical approaches to study this]. In: Sredoobrazuyuchaya rof lesa: 51-61. Krasnoyarsk, Russia. [In Russian].