south Urals, grown in industrially polluted zones, a bigger number of rare alleles was observed compared to populations from ecologically pure habitats (SHIGAPOV et al., 1995; BACHTIYAROVA et al., 1995). In the studied *P. sylvestris* population (A), degrading through untimely death of some plants of long-term (more than thirty years) damaging effects of toxic emissions from chemical plants there does not occur a noticeable change of prevailing alleles frequences (1.00) in any of 18 polymorphic loci compared to the control populations, though the genotypic representation is poorer mainly because of a smaller portion of heterozygotes with rare allele versions. In the population B, significantly damaged by emissions, where the death of plants insignificantly exceeds a natural level there was not observed a noticeable loss of allele and genetic diversity. The decrease of intrapopulation components of genic diversity in the demographically oldest element of the degrading population (A) does not increase the degree of its differentiation compared with the control populations. On the whole these facts may witness that single-directed changes in the genetic structure of the oldest element of degrading populations do not take place. It is not excepted that stochastic change of genes frequences may occur in such populations in case of decrease of emissions effect to the level, which allows natural regeneration in subsequent generations. In will be a result of an incidental genetic drift through the destruction of evolutionary laid bases of their adaptive genetic structure, which occured as a result of the decrease in the number and the lack of regeneration of populations.

Thus, a slightly lower level of genetic diversity was observed in the degrading (through damaging effects of emissions from chemical enterprises of the south-eastern Ukraine) marginal *P. sylvestris* populations, than in the populations, not exposed to the effect of pollutants.

References

BAKHTIYAROVA, R. M., STAROVA, N. V. and YANBAEV, YU. A.: Genetic changes in populations of scotch pine growing under industrial air population conditions. Silvae Genetica **44**: 157–160 (1995). — DAVIS, B. J.: Disc electrophoresis. II. Method and application to human serum proteins. Ann.N.Y. Acad. Sci.**121**: 67–75 (1964). — GEBUREK, TH., SCHOLZ, F., KNABE, W. and VORNWEG, A.: Genetic studies by isozyme gene loci on tolerance and sensitivity in an air polluted *Pinus sylvestris* Field Trial. Silvae Genetica **36**: 49–53 (1987). — GONCHARENKO, G. G., SILIN A. E. and PADUTOV, B. E.: Issledovaniye geneticheskoi structuri i urovnya differentsiatsii u *Pinus sylvestris* L. v tsentralnich i kraevich populyatsiyach vostochnoi Evropi i Sibiri. Genetica **29**: 2019–2038 (1993). — GURIES, R. P. and LEDIG F. T.: Genetic diversity and population structure in pitch pine (*Pinus rigida* Mill.). Evolution **36**: 387–402 (1982). — KOROCHKIN, L. I., SEROV, O. L. and PUDOVKIN, A. I. et al. Genetics of isozymes. Nauca: Moscva, 278 p. (1977). — KORSHIKOV, I. I.: Adaptatsiya rastenii k usloviyam technogenno zagryaznennoi sredi. Nauk. dumka, Kiev. 238 pp. (1996). — KORSHIKOV, I. I., KOTOV, V. S. and MIKHEENKO, I. P. et al..: Vzaimodeistviye rastenii s technogenno zagryaznennoi sredoi. Nauk. dumka, Kiev. 191 pp. (1995). — NEI M.: Molecular population genetics and evolution. Holland Press, Amsterdam. 278 pp. (1975). — NIEBLING, C. R. and CONKLE, M. T.: Diversity of washoe pine and comparisons with allozymes of ponderosa pine races. Can. J. Forest Res. **20**: 298–308 (1990). — PLASSAS, M. E. and STRANSS, S. H.: Allozyme differentiation among populations, stands, and cohorts in Monterey pine. Canad. J. Forest Res. **16**: 1155–1164 (1986). — PRUS-GLOWACKI, W., NOWAK-BZOWY, R.: Demographic processes in *Pinus sylvestris* L. populations from regions under strong and weak anthropogenous pressure. Silvae genetica **38**: 55–62 (1989). — PRUS-GLOWACKI, W. and NOWAK-BZOWY, R.: Genetic structure of a naturally regenerating Scotch pine population tolerant for high pollution near zinc smelter. Water, Air and Soil. Pollut. **62**: 249–259 (1992). — PRUS-GLOWACKI, W. and GODZIK, ST.: Changes induced by zinc smelter pollution in the genetic structure of pine (*Pinus sylvestris* L.) seedling populations. Silvae genetica **40**: 184–188 (1991). — SCHOLZ, F. and VENNE, H.: Structure and first results of a research program on ecological-genetics of air pollution effects in Norway spruce // Genetic effects of air pollutants in forest tree populations. Springer-Verlag, Berlin; Heidelberg: 39–54 (1989). — SCHULTZE U.: Erhaltung forstlicher Genressourcen wichtiger denn je. Österr. Forstztg. **101**: 43–44 (1990). — SHIGAPOV, Z. X., BACHTIYAROVA, R. M. and YANBAEV, YU. A.: Geneticheskaya izmenchivost i differentsiatsia prirodnich populyatsii sosni obiknovennoy (*Pinus sylvestris* L.). Genetica. **31**: 1386–1393 (1995). — SMIT, Y. X.: Forest and atmosphere interrelations between forest ecosystems and and mixtures of air.- Moscva: Progress, 429 p.(1985). — YEH, F. C., KHALIL, M. A., EL-KASSABY, G. A. and TRUST, D. C.: Allozyme variation of *Picea mariana* from New Foundland: genetic diversity, population structure and analysis of differentiation. Can. J. Forest Res.**16**: 713–720 (1986). — YEH, F. C. and EL-KASSABY, G. A.: Enzyme variation in natural populations of Sitka spruce (Picea sitchensis (Bong.) Carr.). I. Genetic variation patterns in ten IUFRO provenances. Canad. J. Forest Res. **10**: 415–422 (1986).

Sensitivity of Diameter Growth to Annual Weather Conditions in Scots Pine Provenances at a Central Siberian Location

By Y. V. SAVVA[1]), F. H. SCHWEINGRUBER[2]), N. A. KUZMINA[1]) and E. A. VAGANOV[1])

(Received 28th July 2000)

Summary

Eight tree-ring characteristics (tree ring width, latewood and earlywood widths and densities, maximum and minimum densities and latewood percentage) were measured densitometrically in 16 Scots pine provenances in the southern taiga, Central Siberia. Age trends were excluded by standardization. It was found that the sensitivity coefficient of latewood width, latewood and maximum densities and latewood percentage has a tendency to decrease in relation to the increasing latitude of seed sources. Northern provenances utilise only the energy resources (heat and light) during the first half of the growing season effectively. The correlation of tree ring series between the local provenance and the other provenances decreases in relation to the increasing latitude difference between seed origins. As a whole, the values of the normalized Euclidean distance, correlation and synchronicity coefficients between the local provenance and the other provenances prove that, for most of the provenances, the interannual variability of the chosen tree ring characteristics reflects the prevailing

---

[1]) Institute of Forests, Siberian Branch of the Russian Academy of Sciences, Akademgorodok, Krasnoyarsk, Russia; e-mail: Institute@forest.akadem.ru, fax: +7 3912 433686

[2]) Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland; e-mail: schweingruber@wsl.ch; fax: +41 1 7392215

influence of weather conditions (even for the populations from the northern taiga and forest-tundra zone). The variability of weather conditions determines up to 85% the variability of radial growth and wood density.

Key words: annual ring, weather sensitivity, climate tolerance, latitudinal transfer, environmental change.

Introduction

Several general models of global climate change predict very rapid warming due to an increase in atmospheric concentrations of CO_2 and other greenhouse gases (Briffa *et al.,* 1998; Flanagan *et al.,* 1998) and it is believed that the effects of global warming could have a substantial impact on tree species distribution (Joyce *et al.,* 1990; Roberts, 1989). However, there are no sure answers to the general question: how will global and regional climate changes affect trees; their growth rates; their survival in natural ecosystems; and their succession processes? (Beuker, 1994; Stettler *et al.,* 1994). Kauppi and Posch (1988) have predicted increases in larch productivity in northern boreal forests in response to climatic warming. Their model assumes that the trees will adapt to the new climate. Estimates of the effects of climate change on tree growth are important because trees, with their long life spans, are least able to respond in a short time by migration or genetic selection (e.g. Davis, 1990; Davis and Zabinski, 1992; Nance *et al.,* 1993; Matyas, 1994). Matyas (1992) proposed that one effective way to reveal the ability of trees to adapt genetically and to document the response of a tree species to climatic change would be the analysis of provenance trials.

The results of provenance trials have shown that if seed sources are moved slightly northwards, populations out perform local sources. However, if seed sources are moved too far to the north, trees suffer cold damage and may not perform as well as those from the original source. If moved to the south, trees also may not perform as well because of heightened sensitivity to disease (Wells and Wakeley, 1966; Wright, 1978). Several authors have also noted that there is a reduction in tree growth, if northern seed sources are moved too far south (Iroshnikov, 1977, Shutyaev *et al.,* 1990; Kuzmina, 1999).

Vaganov *et al.* (1994) have found that tree ring data can supply comprehensive information on weather influences during the growing season. Cook *et al.* (1990) have proposed that the densitometric method provides an appropriate analytical tool for comparing the response of tree growth to different climatic conditions.

The objective of this study is to evaluate the response to annual weather conditions of Scots pine (*Pinus sylvestris* L.) through testing sixteen provenances in the southern taiga, Central Siberia using densitometry measurements of tree rings.

Material

In the years 1974 to 1976 throughout the former USSR, a series of provenance trials on Scots pine were established by the state Forestry Committee (Shutyaev *et al.,* 1998) with 113 provenances planted on over 33 planting sites. The program was prepared by the late Ye.P. Prokazin from the Forest Seed Laboratory of the All-Union Forest Research Institute (VNIILM), Pushkino, near Moscow. The present paper is based on the study of Scots pine trees from one of the provenance trial, which was included in this program and was established in the Krasnoyarsk region (Boguchany), Central Siberia (58° 23'N, 97° 26'E). The Laboratory of Forest Genetics and Plant Breeding of the Institute of Forests (A.I. Iroshnikov, L.I. Milyutin, N.A. Kuzmina) raised seedlings in 1974 and a field trial of 3 year-old plants was established in 1977. Details of the establishment and design of the test has been described more recently by N. Kuzmina (1999). A total of 405 increment cores from 16 pine provenances were collected from the Boguchany test site. The area is classified as southern taiga and sub-taiga, zone of pine and larch forests (Korotkov, 1994). The Boguchany plantation lies on a large flat area of 9 hectares, on the site of a former open pine forest with dark grey forest soil. The climate is typically continental, with a cold winter (average January temperature is –20 °C to –21 °C), summer temperatures average +23 °C in July. The average annual temperature is between –2.3 °C to –3.6 °C. More than 50% of the annual precipitation falls in the three summer months, with spring usually being the driest season. Average annual precipitation is about 350 mm to 400 mm. The locations of all the seed sources and their forest types are given in *table 1.*

Table 1. – Data of the 1974 Scots pine provenance trial. Provenances are listed in order of decreasing latitude of origin.

Provenance	Latitude [^{0}N]	Longitude [^{0}E]	Number of trees analysed	Forest type
Pechenga	69° 40'	31° 17'	20	Forest-tundra ecotone
Turukhansk	65° 51'	88° 04'	20	Northern taiga
Yakutsk	62° 11'	129° 37'	22	Middle taiga
Pryazha	61° 45'	33° 40'	19	Middle taiga
Severo-Yeniseisk	60° 27'	93° 04'	21	Middle taiga
Boguchany	58° 23'	97° 26'	15	Southern taiga
Revda	56° 47'	58° 54'	20	Southern taiga
Ayan	56° 26'	138° 13'	22	Northern taiga
Kurovskoye	55° 35'	38° 55'	23	Pine forests
Minusinsk	53° 43'	91° 45'	17	Forest-steppe
Nikol'sk	53° 42'	46° 04'	18	Hardwood-coniferous mixed forests
Avzyan	53° 35'	57° 32'	20	Northern steppe
Zaudinskii	51° 45'	108° 50'	19	Forest-steppe
Svobodnyi	51° 28'	128° 04'	21	Light-coniferous taiga
Balgazyn	50° 58'	95° 10'	22	Steppe
Kyakhta	50° 28'	106° 30'	20	Forest-steppe

The seed sources are distributed across a wide climatical range, between approximately 50°N to 70°N and 31°E to 129°E, and distributed along four meridional transects including: European, Urals, East Siberian and Far Eastern transects. For each provenance, 20 to 25 trees were sampled (*Table 1*). We selected the widest trees in the plots. Cores were taken in two directions at approximately 50 cm above ground to avoid mechanical influences at the stem base. This height above the base represents a loss of about 8 years growth in relation to total tree age. Analysis was carried out on tree rings formed in the age period from 8 to 22 years.

Methods

Cores were analysed densitometrically with a DENDRO-2003 densitometer. (Schweingruber, 1988; Eschbach *et al.,* 1995; Kirdyanov, 1999). Tree ring width, earlywood width, latewood width (radial growth chronologies), minimum and maximum densities, density of early and latewood (density chronologies) and percentage latewood were measured and crossdated (Kirdyanov, 1999; Savva *et al.,* in press). Chronologies of all these eight tree ring parameters were obtained for each tree (and for each provenance by averaging the individual chronologies) showing interannual weather related reactions and age trends. In studies of ring-width variability associated with climate, it is usually most convenient to estimate the systematic changes in ring width associated with age and to remove them from the measurement (FRITTS, 1987). The indices generally have no linear trend; (their mean value is one); and the large variability in ring-width of a provenance would be comparable to the lower variability in the ring-width of the another provenance. In a previous study of the provenances it was found that the individual variability of all tree ring parameters was one to four times greater than the chronological variability due to weather (SAVVA, *et al.,* in press). To exclude age trends and differences within the provenance, the radial growth, minimum and earlywood density chronologies were standardized using a 3rd degree polynomial function (*Figure 1A*). Linear functions were used for standardising the latewood and maximum density chronologies (*Figure 1B*); and a 2nd degree polynomial function was used for standardising the latewood percentage chronologies. Then indices (*Figure 1,* curve 3) were calculated by dividing the measured parameter (*Figure 1,* curve 2) by the expected value obtained from the fitted curve (*Figure 1,* curve 1) (COOK *et al.,* 1990). The interannual variability due to weather influence can be determined from the indices curves, with a mean of 1.0 and a relatively constant variance.

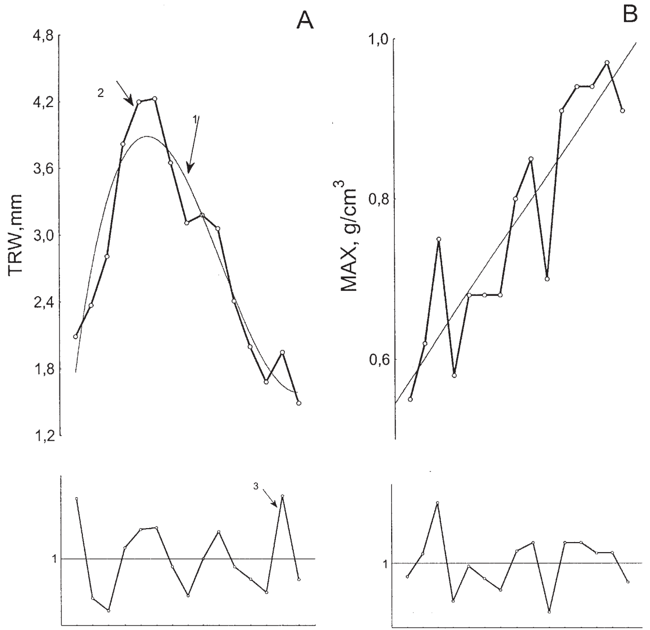

Fig. 1. – Examples of excluding the age trend in tree-ring characteristics (for Avzyan provenance): A) TRW – tree ring width; B) MAX – maximum density (1 – calculated curve, 2 – measured data, 3 – index curve).

The coefficient of sensitivity was calculated to evaluate the radial growth variations quantitatively. Once the sensitivities had been calculated it was possible to ascertain to what extent the growth of population was influenced by weather conditions (SCHWEINGRUBER, 1988). The following formula was used to calculate the coefficient of sensitivity:

$$K_r = \frac{1}{n-1}\sum_{t=1}^{n-1}\left|\frac{2(x_{t+1} - x_t)}{x_{t+1} + x_t}\right|,$$

there x_t is the relative index in year *t*, and *n* is the number of observations (SHIYATOV, 1986).

The coefficient of synchronicity (K_c) (HUBER, 1943) was calculated to evaluate the conformity between the local, Boguchany, and the other provenances' dendrochronological curves. The degree of synchronicity reveals the similarity of growth rhythm of two populations (SHIYATOV, 1986). This is expressed as:

$$K_c = \frac{n^+ \cdot 100}{n-1},$$

where n^+ is the number of segments from radial growth curves having the same directional tendency and n is the length of the compared period (in years).

To estimate the similarities in interannual variability between the local (Boguchany) and the other provenances, the normalised Euclidean distances were calculated (AIVAZYAN *et al.,* 1987). We chose statistically independent parameters of radial growth and density (coefficient of correlation between them <0,85): tree-ring width, latewood and earlywood densities and latewood percentage (SAVVA *et al.,* in press). The Euclidean distance is expressed as:

$$d_{Ei}(X_i X_j) = \frac{1}{p}\sqrt{(x_i^{(1)} - x_j^{(1)})^2 + (x_i^{(2)} - x_j^{(2)})^2 + \ldots + (x_i^{(p)} - x_j^{(p)})^2},$$

where $x_i^{(1)},\ldots, x_i^{(4)}$ are the coefficients of synchronicity between the local provenance and the i-th transformed provenance (i = 1–16) for the: (1) tree-ring width, (2) earlywood density, (3) latewood density, (4) latewood percentage; $x_i^{(5)},\ldots,x_i^{(8)}$ are the coefficients of correlation between the local provenance and the i-th provenance for the same tree ring characteristics; $x_j^{(1)},\ldots, x_j^{(8)}$ are the coefficients of synchronicity and correlation between the local provenance and the j-th provenance (where j-th provenance is the local provenance (Boguchany)), with being equal 1 correspondingly. According to this, p = 8.

Results

Table 2 demonstrates the mean values of tree ring width and latewood portion. It was found that the values of tree ring width decrease, but the values of latewood portion increase in relation to increasing latitude of seed origins.

Age influences and individual differences among the provenances were excluded by standardisation. Now we can evaluate and compare the reaction of the provenances to weather changes. The sensitivity coefficients of radial growth and density

Table 2. – Mean values of tree ring width and latewood ratio.

Provenance	Tree ring width, mm	Latewood ratio
Pechenga	2,38	0,215
Turukhansk	2,72	0,206
Yakutsk	2,91	0,180
Pryazha	3,69	0,198
Severo-Yeniseisk	3,50	0,192
Boguchany	3,55	0,170
Revda	3,54	0,164
Ayan	3,17	0,176
Kurovskoye	3,87	0,174
Minusinsk	3,33	0,175
Nikol'sk	3,72	0,173
Avzyan	2,80	0,185
Zaudinskii	3,74	0,165
Svobodnyi	3,87	0,169
Balgazyn	2,93	0,182
Kyakhta	3,12	0,175

given in *Table 3* show that radial growth chronologies are more sensitive than density chronologies.

- The sensitivity coefficient of latewood width is higher (0.20 to 0.36) than that for earlywood width (0.09 to 0.17), showing that latewood formation is more influenced by weather conditions.
- Range of variation of the sensitivity coefficient for latewood density (0.05 to 0.10) are higher, than for earlywood density (0.03 to 0.04).
- However, tree ring characteristics are not highly sensitive, according to S.G. Shiyatov's (1985) classification of sensitivity, with one exception from the Svobodnyi provenance (Amurskaya obl.) where the sensitivity coefficient for latewood width is 0.36.

Table 3. – Sensitivity coefficients of the tree ring characteristics for different provenances (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,).

	RING-WIDTHS				DENSITY			
Provenance	TRW	EWW	LWW	PLW	MAX	LWD	MIN	EWD
Pechenga	0,17	0,17	0,20	0.12	0,04	0,05	0,04	0,03
Turukhansk	0,13	0,12	0,19	0,15	0,04	0,05	0,04	0,03
Yakutsk	0,10	0,08	0,20	0.13	0,07	0,07	0,03	0,03
Pryazha	0,10	0,09	0,25	0,23	0,07	0,07	0,05	0,03
Severo-Yeniseisk	0,13	0,12	0,22	0.16	0,05	0,05	0,05	0,03
Boguchany	0,12	0,09	0,25	0.17	0,07	0,08	0,07	0,04
Revda	0,11	0,09	0,25	0.17	0,09	0,09	0,05	0,03
Ayan	0,13	0,12	0,20	0.14	0,06	0,07	0,03	0,03
Kurovskoye	0,08	0,06	0,23	0.18	0,07	0,08	0,07	0,04
Minusinsk	0,14	0,12	0,28	0.22	0,09	0,09	0,06	0,04
Nikol'sk	0,11	0,11	0,22	0.19	0,09	0,09	0,05	0,03
Avzyan	0,12	0,12	0,26	0.21	0,10	0,10	0,04	0,04
Zaudinskii	0,12	0,10	0,24	0.19	0,08	0,08	0,06	0,03
Svobodnyi	0,16	0,13	0,36	0.26	0,07	0,06	0,05	0,04
Balgazyn	0,12	0,10	0,30	0.22	0,10	0,10	0,06	0,04
Kyakhta	0,14	0,14	0,25	0.20	0,07	0,07	0,04	0,03

Table 3 shows the conformity in interannual variability between the local Boguchany and other provenances expressed by correlation and synchronicity coefficients. Except for latewood percentage, tree ring parameters from all the provenances from Revda and southward are highly correlated with Boguchany (with R values mostly between 0.7 to 0.9), with the notable exception of R = 0.45 for Svobodnyi. The correlation coefficients are a little lower for the northern provenances, with exceptionally low correlations for Pechenga (forest-tundra) provenance, with R = 0.34 for latewood density, and in the Severo-Yeniseisk and Turukhansk provenances with R = 0.44 and 0.37 respectively for tree ring widths. The synchronicity coefficients for the latewood percentages for about half of the provenances are below 0.7 and the earlywood densities for five out of the 16 provenances are also low.

As a whole, the values of the correlation and synchronicity coefficients show that, for most of the provenances, the interannual variability of the chosen tree-ring characteristics reflects the prevailing weather conditions, with the variability of conditions mainly determining the variability in radial growth and wood density. The analysis of the parameters interannual variability shows that the directional response to weather changes is the same in most provenances (*Figure 2*). The synchronicity coefficient for tree ring width indices is >0.71 and for latewood density it is >0.54. For example, *Figure 2A* shows that the years of maximum and minimum radial growth coincide in all the provenances, with an especially abrupt marked decrease in maximum density in 1991 (*Figure 2B*).

The sensitivity of tree ring characteristics was also considered in relation to seed origin. There is a significant negative correlation (p <0.05) between the sensitivity coefficient and the latitude of seed origin for all latewood parameters (for maximum density and for latewood percentage R= –0.68, for latewood density R= –0.65 and for latewood width R= –0.65).

The correlation and synchronicity coefficients of the independent dendrochronological characteristics were used to compare the radial growth parameters of Boguchany with the other provenances. The lowest Euclidean distance (d_E = 0.06) connects Boguchany to Revda provenance (southern taiga), its nearest neighbour. The Euclidean distance increases for the northern taiga provenances (*Figure 4*). The highest Euclidean distance (d_E = 0.15) separates Boguchany from its most remote northern provenance, Pechenga (forest-tundra).

Discussion

The analysis of the provenances correlation and synchronicity coefficients and their generally close relationship with Boguchany provenance demonstrates that the local weather conditions mainly influence the interannual variability of the tree ring characteristics. The influence of the local weather conditions decreases with the increase in the distance from the seed origin (*Figure 4*). Trees growing in subarctic and high latitude regions are highly sensitive to summer temperature variations (Vaganov *et al.,* 1999). However, if northern seed sources are moved southward, their tree ring parameters do not exhibit as high a sensitivity as in their native environmental conditions.

The main environmental parameters determining growth response differences among provenances are heat sum, precipitation and photoperiod (latitude). In the subarctic regions of Siberia (forest-tundra and the northernmost parts of the northern taiga) the temperature of the two summer months: June and July is the main limiting factor. In the middle taiga, interannual growth variability depends on the June-July temperature and winter precipitation (Vaganov *et al.,* 1996, Kir-

Table 4. – The correlation and synchronicity coefficients of the tree ring width and density chronologies between the local (Boguchany) and the other provenances.

Provenance	**Correlation coefficient (R)**				**Synchronicity coefficient (K_c)**				**R**	**K_c**
	EWD	**LWD**	**TRW**	**PLW**	**EWD**	**LWD**	**TRW**	**PLW**	**mean**	**mean**
Pechenga	0,66	0,34*	0,77	0,52	0,75	0.79	0.88	0.50*	0,57	0,73
Turukhansk	0,54	0,64	0,37*	0,69	0,63*	0.58*	0.79	0.83	0,56	0,71
Yakutsk	0,47*	0,89	0,90	0,53	0,83	0.79	0.79	0.58*	0,70	0,75
Pryazha	0,74	0,94	0,46*	0,71	0,67*	0.71	0.71	0.75	0,71	0,71
Severo-Yeniseisk	0,65	0,90	0,44*	0,64	0,75	0.79	0.79	0.83	0,66	0,79
Revda	0,75	0,89	0,89	0,86	0,88	0.75	0.88	0.83	0,85	0,84
Ayan	0,96	0,75	0,91	0,49*	0,71	0.79	0.88	0.58*	0,78	0,74
Kurovskoye	0,63	0,93	0,52	0,66	0,67*	0.88	0.75	0.67*	0,69	0,74
Minusinsk	0,80	0,91	0,8	0,84	0,83	0.79	0.88	0.75	0,84	0,81
Nikol'sk	0,61	0,81	0,87	0,52	0,75	0.54*	0.71	0.50*	0,70	0,63
Avzyan	0,70	0,90	0,81	0,80	0,67*	0.79	0.92	0.67*	0,80	0,76
Zaudinskii	0,95	0,92	0,82	0,68	0,79	0.88	0.92	0.83	0,84	0,86
Svobodnyi	0,45*	0,82	0,89	0,41*	0,63*	0.67*	0.75	0.67*	0,64	0,68
Balgazyn	0,90	0,91	0,77	0,73	0,88	0.79	0.71	0.75	0,83	0,78
Kyakhta	0,89	0,94	0,79	0,55	0,88	0.71	0.96	0.67*	0,79	0,81

(* the lowest correlation and synchronicity coefficients, p< 0,05)

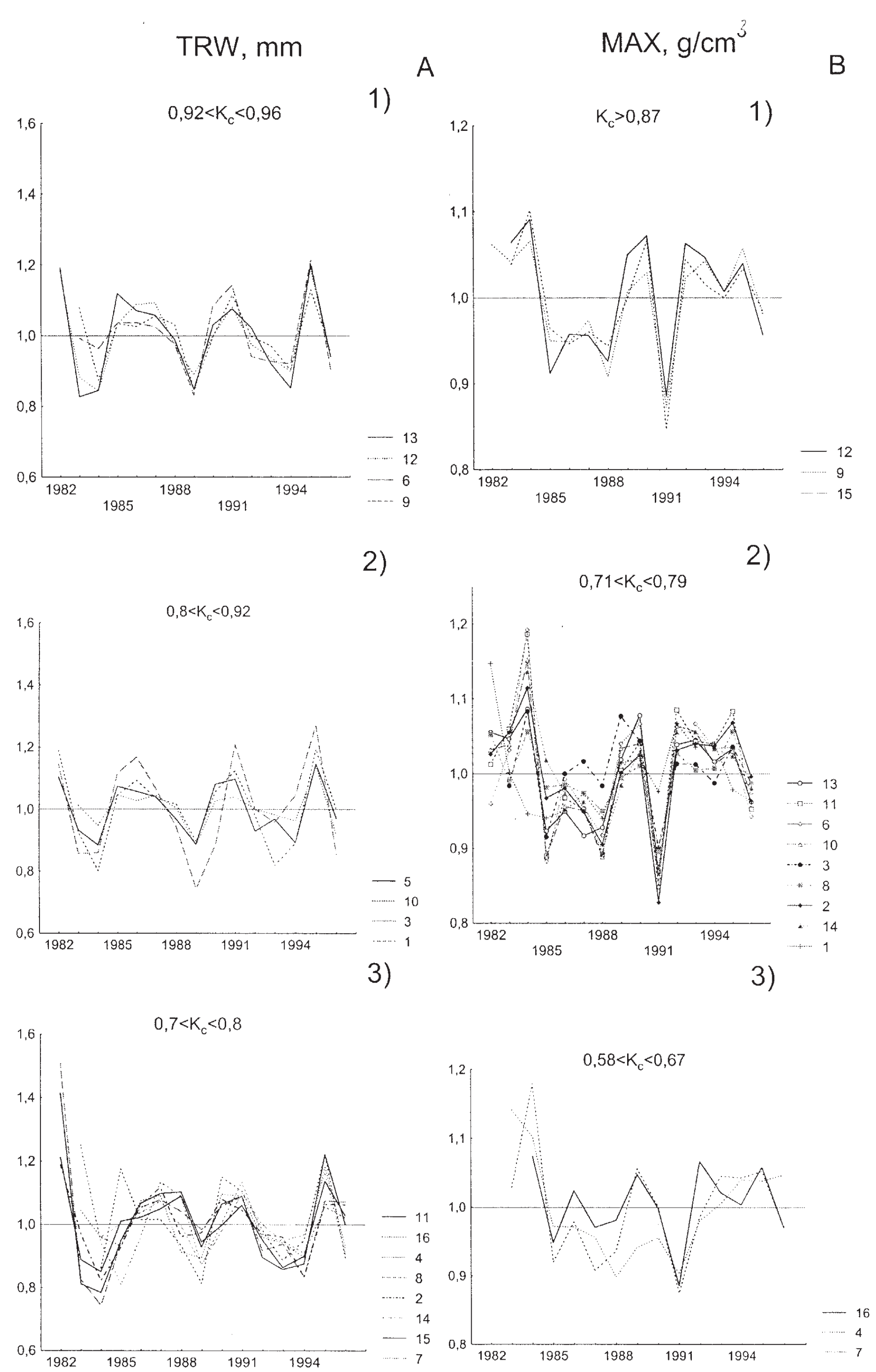

Fig. 2. – Index curves for: A) tree ring width (TRW); B) maximum density (MAX).The provenances are grouped by the value of K_c, the synchronicity coefficient. Provenances are numbered as in *Fig. 4*.

DYANOV *et al.,* 1996) and in the forest-steppe the major factors are April to June temperatures and June to July precipitation (VAGANOV, 1989).

The growth limiting factors for the studied provenances from the forest-tundra and northern taiga that were transplanted to the southern taiga differ greatly, while those for seedlings transplanted from the forest-steppe and steppe differ much less. This is due to the increase of the heat sum which is used by the northern provenances and to the decrease of the heat sum for the steppe and forest-steppe provenances planted in the conditions of the southern taiga.

We have shown that the sensitivity of latewood decreases with increases in the latitude of seed origins. This is because trees at higher latitudes have adapted to maximally exploit the earliest available heat sum (MIKOLA, 1962; LEIKOLA, 1969; VAGANOV *et al.,* 1994; HUGHES *et al.,* 1999). The 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 whole growing season. Latewood formation mainly depends on 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

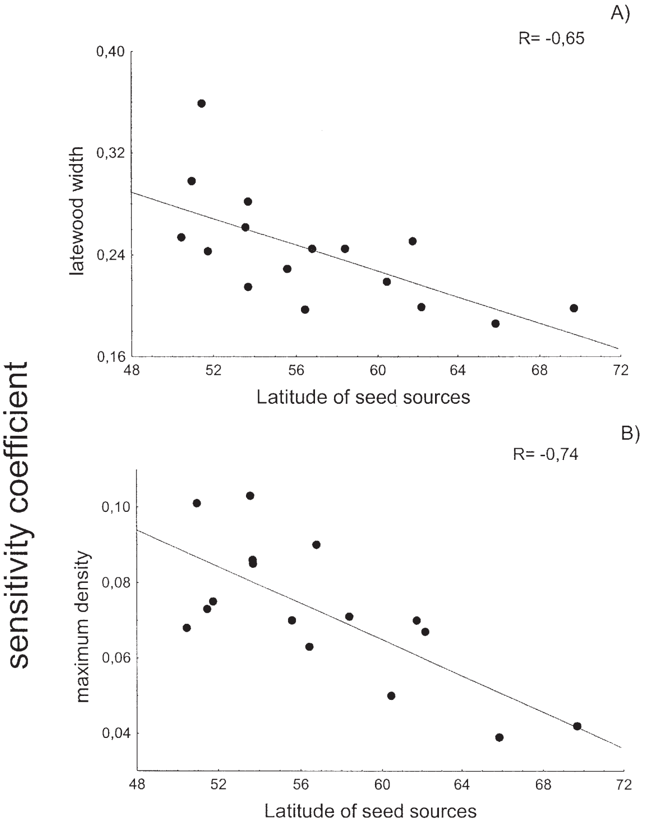

Fig. 3. – Sensitivity coefficients of tree ring characteristics in relation to the geographical location of seed origin.

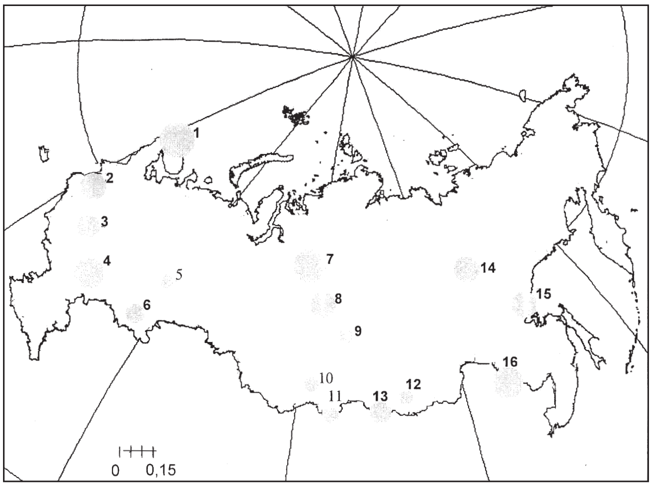

Fig. 4. – A map of the seed origin locations sampled in the Scots pine provenance test in Boguchany (1. Pechenga, 2. Pryazha, 3. Kurovskoye, 4. Nikol'sk, 5. Revda, 6. Avzyan, 7. Turukhansk, 8. Severo-Yeniseisk, 9. Boguchany, 10. Minusinsk, 11. Balgazyn, 12. Zaudinskii, 13.Kyakhta, 14.Yakutsk, 15. Ayan, 16. Svobodnyi). Diameter of the circles is proportional to the Euclidean distance for TRW, PLW, MAX, MIN between the local (Boguchany) provenance and the other provenances.

south, they lack the ability to compete with southern provenances which are adapted to use the energy resources across the whole growing season (*Table 2*).

The values given by the normalised Euclidean distance show that the differences between tree-ring parameters from the northern provenances and those from the southern taiga provenances differ by less than 15%, while the provenances from the middle taiga and forest-steppe zone differ by 6% to 11%. The larger part (85%) of the variability in tree ring characteristics is due to differences in current local weather conditions even in the northern provenances.

Tree ring characteristics of different provenances integrates the complex processes of wood formation such as cell division, radial extension and cell wall deposition (Larson, 1994). On the one hand this is controlled by the genetical program of xylem differentiation, while on the other hand environmental factors influence these processes (directly or indirectly) (Xylem, 1981; Savidge, 1996). The analysis of densitometrical tree ring characteristics might be considered as a tool to evaluate genetical control of xylem differentiation under current environmental conditions. Significant differences in tree rings sensitivity were detected between the provenances. These differences prove the existence of genetical control of wood formation if trees moved to new environment. The evaluation of Euclidean distances between the provenances show that the genetical control is not strong. Nevertheless densitometrical parameters and their dynamic characteristics such as sensitivity to weather conditions might be used for evaluation of genetical differences between the provenances. They do, however, summarize the influences of climatic conditions over a long period of time.

In the context of global and regional climatic changes the results show that the northern provenances are more conservative by utilizing only the energy resources of the first half of the growing season effectively. Moving of the northern border of the *Pinus sylvestris's* natural habitat will not be very rapid, especially if the other competitive species (for example, larch) turn out to be more adaptive to use heat effectively.

Conclusions

1. Northern provenances, planted in the southern taiga, retain their ability to use only the energy resources (heat and light) of the first half of the growing season effectively.
2. Latewood is more sensitive to weather conditions than earlywood.
3. Including the northern provenances, large part (up to 85%) of the variability in tree ring characteristics is due to local weather conditions.

Acknowledgements

The authors express gratitude to Dr. V. Winchester and Prof. C. Matyas for helpful discussions. The research was conducted with financial support from the Russian Fund of Fundamental Research. Grant 99-04-48678.

References

Aivazyan, S. A., Bukhshtaber, V. M., Eniukov, I. S. and Meshalkin, L.D.: Prikladnaya statistica. [Applied statistics. A classification and reduction of dimensionality.]. Moscow: Finance and Statistics (In Russian), 608 p. (1989). — Beuker, E.: Long-term effects of temperature on the wood production of *Pinus sylvestris* L. and *Picea abies* (L.) Karst. in old provenance experiments. Scand. J. Res. **9**: 34–45 (1994). — Briffa, K. R., Schweingruber, F. H., Jones, P. D., Osborn, T. J., Harris, I. C., Shiyatov, S. G., Vaganov, E. A. and Grudd, H.: Trees tell of past climates: but they are speaking less clearly today? Physiological transactions of the Royal Society of London. Series B., Biological Sciences **353** (1365): 65–73 (1998). — Cook, E. R., Briffa, K. R., Shiyatov, S. G. and Mazepa, V. S.: Tree-ring standardization and growth-trend estimation. In: Methods of Dendrochronology. Application in the Environmental Sciences. Eds. E. R. Cook and L. A. Kairiukstis. Dordrecht, Netherlands: Kluwer Acad. Publ. pp. 104–123 (1990). — Davis, M. B.: Climate change and the survival of forest species. In: The Earth Transition: Patterns and Processes of Biotic Improverishment. Ed. G. M. Woodwell. Cambridge Univ. Press, Cambridge, pp. 99–110 (1990). — Davis, M. B. and Zabinski, C.: Changes in geographical range resulting from greenhouse warming-effects on biodiversity in forests. In: Global Warming and Biological Diversity. Eds. R. L. Peters and T. E. Lovejoy. Yale University Press, New Haven. pp. 297–308 (1992). — Eschbach, W., Nogler, P., Schär, E. and Schweingruber, F. H.: Technical advances in the radiodensitometrical determination of wood density. Dendrochronologia **13**: 155–168 (1995). — Flanagan, L. B. and Ehleringer, J. R.: Ecosystem-atmosphere CO_2 exchange: interpreting signals of change using stable isotope ratios. Trends in Ecology and Evolution **13** (1): 10–14 (1998). — Fritts, H. C.: Tree Rings and Climate. Methodology of Dendrochronology: East/ West Approaches. Volume one. 245 p. (1987). — Huber, B.: Über die Sicherheit Jahrring – chronologischer Datierung. Holz als Roh- und Werkst. **6**(10/12): 263–268 (1943). — Hughes, M. K., Vaganov, E. A., Shiyatov, S. and Touchan, R.: Twentieth-century summer warmth in northern Yakutia in a 600-year context. The Holocene **9**, (5) 603–608 (1999). — Iroshnikov, A. I.: [Provenances trials and plantations of conifers in Siberia.] Novosibirsk: Nauka. (In Russian). 167 p. (1977). — Joyce, L. A., Fosberg, M. A. and Comanor, J. M.: Climate change and America's forests. USDA For. Gen. Tech. Rep. RM-187 (1990). — Kauppi, P. and Posch, M.: A case study of the effects of CO_2-induced climatic warming on forest growth and the forest sector: A. Productivity reactions of northern boreal forests. In: Impact of Climatic Variations on Agriculture. Vol.1. Assessment in Cool Temperate Regions. Eds. M. L. Parry, T. R. Carter and N. T. Konijn. Kluwer Academic Publishers, Dordrecht. pp. 183–194 (1988). — Kirdyanov, A. V.: [Usage of the density characteristics of wood in dendroclimatological studies.] Sibirskiy Ekologicheskiy Zhurnal **2**: 193–203, (In Russian) (1999). — Kirdyanov, A. V. and Zaharjevsky, D. V.: Dendroclimatological study on tree-ring width and maximum density chronologies from *Picea obovata* and *Larix sibirica* from the north of Krasnoyarsk region (In Russian). Dendrochronologia **14**: 227–236. (1996). — Korotkov, I. A.: [The forest-plant zoning of Russia and republics of former USSR. Carbon in forest ecosystems and bogs of Russia.] Krasnoyarsk, pp. 29–47. (In Russian) (1994). — Kuzmina, N. A.: [Growth characteristics of the Scots pine provenances in Priangar'ye.] Lesovedeniye **4**: 23–29. (In Russian) (1999). — Larson, P. R.: The vascular cambium. Development and structure. – Berlin: Springer-Verlag. 725 p. (1994). — Leikola, M.: The influence of environmental factors on the diameter growth of young trees. Acta.For.Fenn. **92**: 1–4 (1969). — Matyas, C. and Yeatman, C. W.: Effect of geographical transfer on growth and survival of jack pine (*Pinus banksiana* Lamb.) populations. Silvae Genetica **43**(6), 370–376 (1992). — Matyas, C.: Modelling climate change effects with provenance test data. Tree Physiol. **14**: 797–804 (1994). — Mikola, P.: Temperature and tree growth near the northern timberline. In: Tree Growth (T. T. Kozlowski, ed.). Ronald Press, New-York. pp. 265–287 (1962). — Nance, W. L., Cook, E. R. and Eckert, R. T.: Assessing the genetic sensitivity of loblolly pine (*Pinus taeda* L.) to climate events: as approach based on tree-ring analysis. In: Ecophisiology and Genetics of Trees and Forest in a Changing Environment. Eds. G. Scarascia-Mugnozza and R. Valentini. Convengo Internazionale, Viterbo, Italy. 73 pp. (1993). — Roberts, L.: How fast can trees migrate? Science (Washington, D.C.) **243**: 735–737 (1989). — Savidge, R. A.: Xylogenesis, genetic and environmental regulation. JAWA **17**(3): 269–310 (1996). — Savva, Y., Schweingruber, F., Milyutin, L. I. and Vaganov, E. A.: Genetical and environmental signals in tree rings from different provenances of *Pinus sylvestris* L. planted in the Southern taiga, Central Siberia. In: Trees. Structure and Functions. Springer-Verlag, Berlin, Heidelberg. (in press). — Schweingruber, F. H.: Tree Rings: Basics and Applications of Dendrochronology. Dordrecht: Reidel Publ. 276 p. (1988). — Shiyatov, S. G.: [Dendrochronology of the higher timber line on the Urals.] M.: Nauka. (In Russian). 136 p. (1986). — Shutyaev, A. M. and Giertych, M.: Height growth variation in a comprehensive Eurasian provenance experiment of (*Pinus sylvestris* L.). Silvae Genetica **46**(6): 332–349 (1998). — Shutyaev, A. M. and Veresin, M. M.: [Productivity of the Scots pine populations.] Lesnoye hozyaistvo **11**: 36–38. (In Russian) (1990). — Stettler, R. F. and Bradshaw, H. D., Jr.: The choice of genetic material for mechanistic studies of adaptation in forest trees. Tree physiology **14**: 781–796 (1994). — Vaganov, E. A.: [technique of the grain productivity forecast with dendrochronological data.] Ekologiya **3**: 15–23 (In Russian) (1989). — Vaganov, E. A., Arbatskaya, M. K. and Shashkin, E. A.: [Climate history and fire frequency in the Central part of the Krasnoyarsk region. I. Climate conditions of growing season and frequency of fires.] Sibirskiy Ecologicheskiy Zhurnal **3** (1), 9–18 (1996) (In Russian). — Vaganov, E. A., Hughes, M. K., Kirdyanov, A. V., Schweingruber, F. H. and Silkin, P. P.: Influence of snowfall and melt timing on tree growth in subarctic Eurasia. Nature **400**: 149–151 (1999). — Vaganov, E. A., Shiyatov, S. G. and Mazepa, V. S.: [Dendroclimatic Studies in the Urals-Siberia subarctic]. Novosibirsk: Nauka. (In Russian). 246 p. (1996). — Vaganov, E. A., Vysotskaya, L. G. and Shashkin, A. V.: [Seasonal growth and structure of larch annual rings at the northern timberline]. Lesovedeniye **5**: 3–15. (In Russian) (1994). — Wells, O. O. and Wakeley, P. C.: Geographic variation in survival, growth, and fusiform rust infection of planted loblolly pine. For. Sci. Monogr. **11**. 40 p. (1966). — Wright, J.: [Introduction to forest genetics]. Moskva: Lesnaya promyshlennost' (In Russian), 469 p. (1978). — Xylem cell development. Ed. J. R. Barnett, Tunbridge Wells, Kent. Castle House Publications. 307 p. (1981).

A Study of Population Variation and Inheritance in Sitka Spruce

II. Age Trends in Genetic Parameters for Vigour Traits and Optimum Selection Ages

By S. J. Lee[1], J. Woolliams[2], C. J. A. Samuel[1] and D. C. Malcolm[3]

(Received 10th October 2000)

Abstract

This study represents the second in a series investigating the additive genetic variance operating within an unselected population of Sitka spruce trees of known single origin. The first study presented by Samuel and Johnstone (1979) looked at height between 1 and 6 years from planting. This study looks at the additive genetic control of growth traits at just one site up to 23 years from planting. Basic genetic statistics for each individual trait are presented along with the genetic relationship between each trait and the optimum ages of selection relative to mature ages of 23 years and 40 years. Analysis was carried out at both the individual tree and family-mean level.

The optimum individual tree and family mean selection ages in terms of generation efficiency were 9 year height and 23 year diameter respectively. When selection was based on genetic gain per year, the optimum ages were again 9 year height at the individual tree level, but fell to 5-year height at the family-mean level.

There was very little difference in optimum selection ages depending on the age of the mature trait. Efficiencies could be improved and selection ages reduced if the delay necessary to bring juvenile selections to flower could be reduced to just 3 years or 5 years.

Key words: Picea sitchensis, genetic correlations, phenotypic correlations, heritability, indirect selection.

---

[1] Forestry Commission Research Agency, Northern Research Station, Roslin, Midlothian, EH25 9SY, Scotland

[2] Roslin Institute, Roslin, Midlothian, EH25 9PS, Scotland

[3] Institute of Ecology and Resource Management, Darwin Building, The King's Buildings, Mayfield Road, Edinburgh, EH9 3JU, Scotland