Genetic Variation of Wood Properties in Balsam Poplar (*Populus balsamifera* L.)

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Summary

Genetic variation in wood properties among and within 3 provenances of balsam poplar was investigated. Between 1982 and 1984, clonal populations were sampled along the Longitude 90°W in North Wisconsin (Lat. 45°N to 46°N); Thunder Bay, Ontario (Lat. 48°N to 49°N); and Pickle Lake, Ontario (Lat. 50°N to 51°N). Rooted cuttings were planted in a field test near Lakehead University, Thunder Bay. In 1994, 30 clones from each provenance, with 4 ramets per clone, were measured for growth characteristics, and specimen disks were cut at tree base. Ring width, relative density, percent moisture content, fiber length, and vessel element length were determined in the laboratory. Univariate analyses of variance showed significant differences among the 3 provenances in growth rate and cell length. The southern provenance had the fastest growth rate and the longest cells. Provenance differences in relative density and moisture content of the wood were not statistically significant. Canonical multivariate analysis, using growth rate, relative density, and fibre length as dependent variables, showed differences between the southern and northern provenance, with the local source in an intermediate position. Both genetic and environmental variances for a certain trait differed from provenance to provenance. Therefore the estimates of broad sense heritability were different in each provenance. Heritability was more uniform and higher for wood properties than for growth characteristics. Positive phenotypic correlation between growth rate and cell length was found. Genetic correlations and coefficients of genetic prediction showed relative genetic independence of growth characteristics from relative density and moisture content. Results justified selection based on growth characteristics, wood properties, or a combination of these two.

Key words: canonical variate analysis, coefficients of genetic prediction, genetic correlation, heritability, *Populus balsamifera,* provenance test, wood properties.

FDC: 165.3; 165.5; 232.12; 81; 176.1 *Populus balsamifera;* (713).

Introduction

Balsam poplar (*Populus balsamifera* L.) is a transcontinental species, with a wide continuous range across Canada and in the Lake States, USA. The most pronounced trends of variation within the range of the species are in a south-north direction (warm-cold trends). A study of phenotypic variation of wood quality, in natural stands in Ontario, showed that: trees from northern locations had generally slower growth rate than those from the south; relative density had a slight negative correlation with growth rate; trees from the south had longer average fibre length than trees from the north (BALATINECZ and PENG, 1984).

Genetic differentiation among latitudinal provenances has been investigated in several studies of balsam poplar. No significant genetic differences were found among latitudinal provenances in isozyme characteristics (FARMER *et al.,* 1988), rooting ability (FARMER *et al.,* 1989), dormancy (FARMER and REINHOLT, 1985), and spring dehardening (WATSON, 1990). Leaf size was significantly smaller in northern sources (PENFOLD, 1991). The rate of growth cessation in response to short photoperiods was higher in northern sources (CHARRETTE, 1990), which was one of the main reasons for differences in shoot growth and tree height (FARMER, 1993; RIEMENSCHNEIDER and MCMAHON, 1993).

The main objectives of this study were:

– To determine the genetic pattern of wood quality variation in the south-north direction, along longitude 90°, in northern Wisconsin and north-western Ontario;

– To estimate the amount of variation present among clones within provenances, and among individual ramets within clones. By comparing these 2 types of variation, to estimate the broad sense heritability of growth and wood characteristics;

– To examine correlations among growth and wood characteristics, and to determine the degree of genetic association between these characteristics.

Materials and Methods

In 1982 and 1983 balsam poplar populations were sampled on a latitudinal transect that crosses the range of the species between longitudes 89° W and 91° W. Three general locations used for this provenance study were: Rhinelander, northern Wisconsin 45° N to 46° N); Thunder Bay, Ontario (48° N to 49° N); and Pickle Lake, Ontario (50° N to 51° N). Fifty ortets in each provenance were sampled randomly, but, at least 1 kilometre apart, to avoid the possibility of sampling more than 1 tree from a single naturally occurring clone. The vegetatively propagated cuttings were used to establish a long-term clonal test near Lakehead University, Thunder Bay. Square provenance plots were randomly located within blocks (replications), and several clone ramets planted randomly within provenance plots. The design was a nested variation of randomized block design. The design reduced inter-provenance competition, which minimized within block variability for comparison within the set of provenances. Comparisons among provenances were imprecise, however, as main, provenance, plots were large, and the test had fewer degrees of freedom for error. Still, the analysis was appropriate since the clonal variation within provenances was of a greater interest (FINS *et al.,* 1992). In the spring of 1994, 30 randomly chosen clones within each provenance were harvested for the investigation of genetic differences in wood properties. One ramet from each clone was sampled in each of 4 blocks.

To avoid within-tree variation, all wood samples (discs) were taken at the tree base, 30 cm to 50 cm above the ground. For determination of relative density, wood samples were taken at

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the south side of trees, in rings 5, 6, and 7. Only the earlywood portion of the 7th growth ring was used for determination of fibre and vessel element length (ZOBEL and TALBERT, 1984).

Variables Measured

Height of each tree was measured after harvesting, to obtain the mean annual height growth rate (HGR).

After cutting in the field, specimen discs were placed in plastic bags, brought to the laboratory, and processed immediately. Diameter and circumference were measured on each sample disc, to obtain variables mean annual diameter growth rate (DGR), and mean annual circumference growth rate (CGR).

Moisture content (MC%) of the wood (discs without bark) was measured and presented as a percentage of the oven dry weight of the wood.

Mean annual radial growth rate (RGR) was defined as the average width (mm) of the 5th, 6th, and 7th growth ring. It was determined on strips cut through the middle of each sample disc. Cross-sections of the strips were smoothed by fine sand paper, and water applied to the surface to enhance the contrast of the growth rings.

Radial growth rate in the 7th year (RGR7) was measured in order to correlate with cell length, which was determined only for the 7th growth ring.

Relative density (RD)(or specific gravity) was determined by the maximum moisture content method (SMITH, 1954). After measuring ring width, the 5th, 6th, and 7th ring together were cut from the cross-section strips. To determine the maximum weight, these 3-ring pieces were put into distilled water, and placed in a desiccator. To ensure that the wood reached the point of maximum moisture content, they were left submerged until 3 subsequent measurements of weight were the same. Three-ring sections were then dried in the oven for 48 hours, at 105 °C ± 3 °C, to obtain the oven-dry weight. The ratio of maximum to oven-dry weight was calculated to 2 decimal places, and the appropriate value of relative density was found in FOGG's (1967) table.

After measuring RD, the 7th-ring piece was separated, further split into earlywood and latewood splints, and earlywood was used for the cell length determination. Individual earlywood splints were macerated by FRANKLIN's (1945) method. The number of cells to be measured for each growth ring was determined through preliminary sampling, using FREESE's (1986) method. For both, fibre length (FL) and vessel element length (VEL) sample size was rounded to 25 measurements per growth ring. The image of a cell, magnified 100 times, was projected through a microscope onto a HIPAD® digitizer connected to an Apple® microcomputer. Cells were measured from tip to tip so that the "tails" of the vessel elements were included in the length.

Data Analyses

Provenance differences in all above characteristics were analyzed at the first level of univariate analyses of variance (ANOVA-s). Differences among provenance means for each variable were assessed by using the FISCHER's LSD method.

Three most important response variables: radial growth rate (RGR), relative density (RD), and fibre length (FL) were analyzed together in a multivariate analysis of covariance (MANOVA). On the basis of redundancy and linear dependence, only the variable radial growth rate (RGR) was chosen to represent 5 highly correlated growth characteristics. Also, vessel element length (VEL) was eliminated because it was highly correlated with fibre length (FL).

Regardless of the fact that there were 3 variable means per each provenance, they could be defined by a plane, i.e., in a 2 dimensional space. CHATFIELD and COLLINS (1980) explained the process of deriving vectors of linear compounds, which when multiplied by the vectors of provenance means, gave the coordinates of canonical means. The axis which represented the first canonical variate explained the most of the variation that was present in the original variables. The 95% confidence limit was drawn as a circle around the canonical mean of each provenance. Since canonical variates were normalized so that their variance was equal 1, the standard deviation of the means was simply $1/\sqrt{n}$; where n was the number of observations. Therefore, the radius of the circles was $k/\sqrt{n}$; where k was equal to 2, in order to represent 2 standard deviations which gave 95% confidence limits.

Table 1. – Analysis of variance format and expected mean squares for variables: HGR, DGR, CGR, RGR, RGR7, RD, FL, and VEL. (For the variable MC% only 15 clones were sampled within each of only 2 provenances, but the general format is the same.).

Source of variation	df	EMS
Block (B)	3	$\sigma^2 + 90\emptyset_B$
Provenance (P)	2	$\sigma^2 + 120\emptyset_P$
Block X Prov.(BP)(error I)	6	$\sigma^2 + (30\sigma^2_{BP}$ - assumed to be 0)
* This stage of ANOVA was repeated 3 times, once for each provenance .		
Clone/Provenance (C)	29(*3)	$\sigma^2 + 4\sigma^2_C$
Block X Clone (BC)(error II)	87(*3)	$\sigma^2 + (\sigma^2_{BC}$ - assumed to be 0)
Within (ε)	0	σ^2
Total	359	

From the second, clonal, level of ANOVA (*Table 1*) broad sense heritability (H^2) was estimated as the ratio of total genetic variation (σ^2_g) to the phenotypic variation (σ^2_p) (Formula 1):

$$H^2 = \frac{\sigma^2_g}{\sigma^2_p} = \frac{\sigma^2_c}{\sigma^2_c + \sigma^2} \qquad (1)$$

The total genetic variance was represented by the clonal variance component (σ^2_c). The phenotypic variance was represented by the sum of the genetic and environmental variance, i.e., the clonal variance component (σ^2_c) plus the error variance component (σ^2). The standard error of broad-sense heritability was obtained from the formula given by FALCONER (1981) (Formula 2):

$$S_{(H^2)} = \sqrt{\frac{2[1+(n-1)t]^2(1-t)^2}{n(n-1)(N-1)}} \qquad (2)$$

where: t – intraclass correlation (i.e., broad sense heritability – H^2);

n – number of individuals per clone, N – number of clones.

Genetic correlations (NAMKOONG *et al.,* 1988; BECKER, 1984) were estimated as (Formula 3):

$$r_g = \frac{\hat{\sigma}cXY}{\sqrt{\hat{\sigma}^2cY}\ \sqrt{\hat{\sigma}^2cX}} \qquad (3)$$

r_g = genetic correlation
$\hat{\sigma}$cXY = clonal component of covariance for traits X and Y
$\hat{\sigma}^2$cX = clonal component of variance for trait X
$\hat{\sigma}^2$cY = clonal component of variance for trait Y

Genetic correlations were calculated to be zero if the mean square component for clone was of the same sign and of a smaller magnitude than for error. Also, sometimes genetic correlations were greater than ± 1 because of the sampling error and mathematical approximation. However, in such a case they were considered to be ± 1, considering the asymptotic nature of the normal distribution of correlation coefficients (ρ).

Environmental correlation included only the environmental portion of variation and covariation, i.e., error components of variance and covariance (Formula 4):

$$r_e = \frac{\hat{\sigma}XY}{\sqrt{\hat{\sigma}^2X}\ \sqrt{\hat{\sigma}^2Y}} \qquad (4)$$

r_e = environmental correlation
$\hat{\sigma}$XY = error component of covariance for traits X and Y
$\hat{\sigma}^2$X = error component of variance for trait X
$\hat{\sigma}^2$Y = error component of variance for trait Y

Phenotypic correlation was calculated when block source of variation was removed. Phenotypic components of variance and covariance were obtained by adding clone to error components. Phenotypic correlation (r_p) between variables X and Y was estimated from phenotypic values as (Formula 5):

$$r_p = \frac{\hat{\sigma}pXY}{\sqrt{\hat{\sigma}^2pX}\ \sqrt{\hat{\sigma}^2pY}} \qquad (5)$$

r_p = phenotypic correlation
$\hat{\sigma}$pXY = covariance for traits X and Y (i.e. $\hat{\sigma}$cXY + $\hat{\sigma}$XY)
$\hat{\sigma}^2$pX = phenotypic variance of trait X (i.e. $\hat{\sigma}^2$cX + $\hat{\sigma}^2$X)
$\hat{\sigma}^2$pY = phenotypic variance of trait Y (i.e. $\hat{\sigma}^2$cY + $\hat{\sigma}^2$Y)

In addition the coefficient of genetic prediction (CGP) was calculated. This coefficient was used to predict the response of trait Y to selecting for trait X (FINS *et al.*, 1992) (Formula 6).

$$CGP = \frac{\hat{\sigma}cXY}{\sqrt{\hat{\sigma}^2pX}\ \sqrt{\hat{\sigma}^2pY}} \qquad (6)$$

Genetic Gain

The above parameters enabled us to calculate the predicted genetic gain (ΔG). Genetic gain is the function of the phenotypic variation present (σ_p), the amount of genetic variation (H^2), and the intensity of selection (i) (Formula 7):

$$\Delta G = H^2S = i\, H^2\, \sigma_p \qquad (7)$$

where:

S = selection differential, i.e., $\text{mean}_{(\text{selected clones})} - \text{mean}_{(\text{population})}$

The selection differential (S) is not a good indicator of the amount of the selection pressure applied, if we deal with several characteristics at the same time. In that case, it is given in the standardized form, as the selection intensity ($i = S / \sigma_p$). Also, it is often convenient to express the genetic gain as a percentage of the original population mean.

Table 2. – a) The mean squares of the first (provenances) level analyses of variances for the 9 variables; b) provenance means, and ranges of clonal means.

a)		HGR	DGR	CGR	RGR	RGR7	RD	MC%	FL	VEL
Source of variation	[1]df	Mean squares								
Block	3	0,0727	0.0952	0,9139	5.9644	6.5594	0,00150	7774.8	0.00642	0.00196
Provenance	2	**0.0581***	**0.0858***	**0.8057***	**4.5481***	**6.2311^{NS}**	**0.00077^{NS}**	**5587.4^{NS}**	**0.00218***	**0.00144***
Error (B* P)	6	0,0105	0.0128	0,1152	0,8441	1.5409	0,00021	843,8	0.00042	0,00023

b) Provenance	(m)	(cm)	(cm)	Means (range of clonal means) (mm)	(mm)		%	(mm)	(mm)
North Wisconsin	0,574 [2] a (0.827-0,441)	0.723 a (1.000-0.479)	2.309 a (3.156-1.557)	4.515 a (6,317-2,942)	5,011 a (6,875-2,950)	0,343 a (0,380-0.292)	139 a (185-102)	0.638 a (0.710-0,589)	0,349 a (0,413-0,314)
Thunder Bay	0,409 ab (0.559-0.287)	0.540 ab (0.783-0.368)	1.748 ab (2.567-1.324)	2.988 ab (4.417-2.025)	3.282 a (4,875-2,050)	0,357 a (0.408-0.287)	158 a (186-119)	0.632 a (0.707-0,556)	0,334 ab (0,387-0,289)
Pickle Lake	0,340 b (0,477-0,246)	0,433 b (0,575-0,277)	1,421 b (1.912-0,944)	2,462 b (3,392-1,133)	2,587 a (3,600-1.275)	0,371 a (0,399-0,331)	–	0.595 b (0,680-0,530)	0.311 b (0,395-0,266)

Variable abbreviations are presented in the Materials and Methods section
*) Significant at 5% level of probability.
**) Significant at 1% level of probability.
[1]) For the variable MC% degrees of freedom were: Block (1), Provenance (1), Error (B*P) (1).
[2]) Provenance means in a same column, with different letters in the superscript, are significantly different at 5% level of probability.

Results and Discussion

Differences among Provenances

For growth characteristics the provenance test indicated a continuous variation pattern: the rate of growth decreased in a south-north direction. All ANOVA F-tests were significant at 5% level of probability, except for RGR7 (*Table 2*). Since geographic source does not always influence the time of bud break, one of the reasons for the south-north variation pattern could be because northern clones stop their growth earlier in the season (PAULEY and PERRY, 1954; FARMER, 1993).

A decrease in cell length from southern to northern sources was found. On the other hand, wood density (RD) was not significantly different among the 3 provenances. Faster growth rate was generally negatively correlated with wood density. However, when block source of variation was removed, the negative correlation within the provenances was largely reduced. Thus, the faster growth of the southern provenance, in comparison with the other two, was not associated with significant reduction in wood density.

Despite the fact that the MANOVA F-test for RGR, RD, and FL was not significant, canonical multivariate analysis suggested the existence of a variation pattern in the south-north direction. A significant difference between the southern and northern source, and an intermediate position of the local source can be seen from the plot of the first canonical variate (*Figure 1*).

The North Wisconsin provenance exhibited best performance in terms of growth rate and cell length, without a significant loss in density, or a change in moisture of the wood (*Table 2*). This is especially so because no serious frost injuries have been sustained so far by trees from the southernmost provenance.

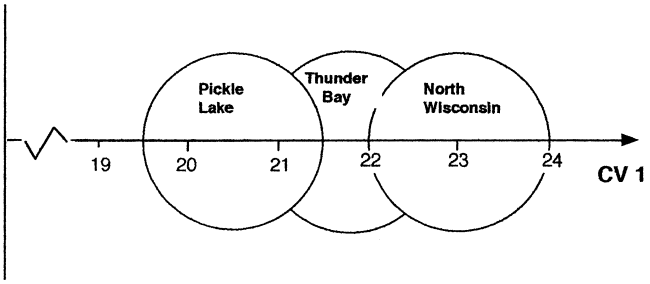

Figure 1. – Canonical means and 95% confidence limits for the 3 provenances projected on the first canonical variate axis.

Heritability of the Traits

At the second level of the analyses of variance precision was greatly improved. This provided a better basis for estimating variance components, and eventually heritability of the traits. Also, it was possible to obtain these estimates for each of the 3 provenances separately. Heritability of the traits differed from provenance to provenance (*Table 3*).

Despite the widespread use of broad sense heritability, SUZUKI *et al.* (1986) pointed out its special and limited meaning: "In general, the heritability of a trait is different in each population and in each set of environments; it cannot be extrapolated from one population and set of environments to another". These considerations proved to be important for this experiment, especially for heritability of growth characteristics. The northern, Pickle Lake, provenance had much higher heritability of growth characteristics than the North Wisconsin and Thunder Bay provenances.

Table 3. – The mean squares of the second (clonal) level analyses of variance and broad sense heritabilities for 9 variables in the 3 provenances.

North Wisconsin		Mean Squares								
Source of variation	^{1}df	HGR	DGR	CGR	RGR	RGR7	RD	MC%	FL	VEL
Block	3	1,84016	2,29043	20,8145	168,880	225.825	0.02968	1748.03	0,07720	0,04249
Clone	29	**0.01998***	**0.06774****	**0.6577***	**3.588***	**4.598***	**0.00229****	**1040.99***	**0.00418***	**0.00231***
Error (B* C)	87	0,01067	0,03503	0,3510	1,897	2,806	0,00052	301,96	0,00257	0,00139
Broad sense heritability		0,18±0,09	0,19±0.10	0,18±0,10	0.18±0.09	0.14±0,09	0,46±0.10	0.55±0.19	0,13±0,09	0.14±0,09
Thunder Bay										
Block	3	0,24952	0,41995	4.1529	21,392	26,909	0,00405	6870.53	0.05597	0.00933
Clone	29	**0.01322^{NS}**	**0.03881^{NS}**	**0.4164^{NS}**	**1.443^{NS}**	**2.596^{NS}**	**0.00360****	**604.03****	**0.00756****	**0.00221^{NS}**
Error (B* C)	87	0,01197	0,03581	0,3736	1,579	2,372	0,00078	83,46	0,00282	0,00148
Broad sense heritability		0.03±0.08	0.00±0.00	0,03±0.08	0.00±0.00	0,02±0.08	0,47±0.10	0.76±0.11	0.30±0,10	0,11±0,09
Pickle Lake										
Block	3	0,72210	0.91236	9,3634	39,962	32.145	0,02331	–	0.08356	0,02111
Clone	29	**0.01171****	**0.02110****	**0.2374***	**0.899***	**0.972^{NS}**	**0.00151****	–	**0.00560****	**0.00288****
Error (B* C)	87	0,00431	0,00972	0,0952	0,451	0,677	0,00040	–	0,00215	0,00091
Broad sense heritability		0,30±0.10	0.24±0.11	0,27±0.10	0.20±0.10	0,10±0.09	0,41±0,10	–	0,29±0,10	0,35±0.10

*) Significant at 5% level of probability.
**) Significant at 1% level of probability.
[1]) For the variable MC% degrees of freedom were: Block (1), Clone (14), Error (B*C) (14).

Heritability of wood properties was generally more uniform among the 3 provenances, as well as higher than that of growth characteristics. In this study, balsam poplar RD had a moderate heritability, which was roughly equal among the 3 provenances. Heritability of MC% was the highest. Cell length heritability was more variable and lower, among the 3 provenances, than heritability of other wood properties.

Correlation among the Traits

Correlations among the traits are presented only for the North Wisconsin provenance, which could possibly be used for selection (*Table 4*). Growth characteristics had highly positive overall, phenotypic, environmental, and genetic correlations among themselves. They also had a general trend of negative relationship with RD. This negative relationship was genetically based only for characteristics of radial growth, but not for the height growth.

Table 4. – Overall, genetic, environmental, and phenotypic correlations calculated for the North Wisconsin provenance.

	HGR	DGR	CGR	RGR	RGR7	RD	MC%	FL	VEL
HGR	1	[a].92** [b].87** [c].80** [d].82**	.91** .85** .81** .82**	.93** .76** .78** .78**	.89** .81** .67** .69**	-.70** -.00 -.50** -.33**	.33 .18 .00 .05	.65** -.98** .56** .32**	.69** -.43** .51** .36**
	DGR	1	.99** 1.00** .99** .99**	.96** .94** .89** .90**	.94** .95** .84** .85**	-.66** -.29** -.37** -.33**	.35* .39* -.04 .06	.60** -.82** .52** .30**	.65** -.29** .47** .34**
		CGR	1	.95** .92** .89** .90**	.93** .89** .84** .84**	-.66** -.26** -.38** -.33**	.33 .39* -.04 .05	.60** -.72** .52** .32**	.66** -.24** .49** .36**
			RGR	1	.97** .98** .91** .92**	-.72** -.41** -.45** -.42**	.41* .44* -.02 .09	.57** -.89** .41** .20**	.65** -.34** .43** .31**
				RGR7	1	-.69** -.45** -.35** -.35**	.28 .32 -.06 .03	.52** -1.00** .30** .13	.60** -.33** .29** .21*
					RD	1	-.41* -.34 -.04 -.09	-.38** .66** .00 .04	-.60** -.06 -.01 -.32**
						MC%	1	.25 .08 .02 .03	.49** .26 .05 .15
							FL	1	.74** .44** .01 .59**
								VEL	1

[a]) Overall correlation
[b]) Genetic correlation
[c]) Environmental correlation
[d]) Phenotypic correlation (block effects excluded)
*) Significant at 5% level of probability;
**) Significant at 1% level of probability

While positive phenotypic correlations of growth characteristics with cell length were found, genetic correlations were significantly negative. This could be explained by the fact that if both characteristics have low heritability, the phenotypic correlation is determined mainly by the environmental correlation; if they have high heritability, then the genetic correlation is more important (FALCONER, 1981).

The genetic correlation of RD with MC% was negative. MC% exhibited a positive overall correlation to VEL, and no correlation to FL. CARLQUIST's (1988) statement that, "Vessel element length always parallels fiber length", was supported again. Moreover, it was found that this kind of relationship had a genetic basis and it was not influenced by the environment.

Coefficients of Genetic Prediction

For the North Wisconsin provenance coefficients of genetic prediction (CGP) were significantly different from 0 only between the diameter growth rate (DGR) and 2 other characteristics of radial growth (*Table 5*). They were not proportional to heritability of any 2 characteristics examined.

Table 5. – Heritabilities and coefficients of genetic prediction for the North Wisconsin provenance.

	HGR	DGR	CGR	RGR	RGR7	RD	MC%	FL	VEL
HGR	[a].18*								
DGR	.16	**.19***							
CGR	.16	.19*	**.18***						
RGR	.14	.18*	.17	**.18***					
RGR7	.13	.15	.15	.15	**.14***				
RD	.00	-.08	-.08	-.12	-.11	**.46****			
MC%	.05	.09	.08	.11	.07	-.06	**.55****		
FL	-.15	-.13	-.12	-.14	-.14	.16	.02	**.13**	
VEL	-.07	-.05	-.04	-.05	-.05	-.01	.13	.06	**.14***

[a]) Values on the diagonal are trait heritabilities
*) Significant at 5% level of probability
**) Significant at 1% level of probability

Genetic Gain and Correlated Response

On the whole, the North Wisconsin provenance was the one with the best performance. The average height growth was 40%, and radial growth over 50% better than in the local Thunder Bay provenance, while relative density was only 4% less (*Table 2*). Hence, if clones from North Wisconsin had been selected so that they had growth rate one standard deviation above the population average, the *genetic gain* would be the standard deviation times appropriate heritability. The *correlated response* in, for example, RD would be one standard deviation in RD times appropriate coefficient of genetic prediction. By using heritabilities and coefficients of genetic prediction (*Table 5*), genetic gain was estimated for selection in some growth and wood characteristics, within the North Wisconsin provenance:

– for selection in height (HGR) or radial growth (RGR) percent genetic gain would be around 8% and 10% of the population mean, respectively,

– for wood density (RD), it would be approximately 6% and for cell length (FL and VEL) less than 2%.

None of the genetic changes caused by above selections would influence genetic potential of other characteristics, since all the CGP were insignificant.

Conclusions

Presently, balsam poplar has a low commercial value. However, there is some interest in the hybrid of this species and eastern cottonwood for intensive plantation establishment in the boreal region. To develop such hybrids, adapted parents with superior shoot growth should be selected. A combination of provenance and individual clone selection before hybridization would be useful (FARMER, 1993). A recent study suggested that multiple-trait selection could increase both tree height and pest resistance (RIEMESCHNEIDER *et al.,* 1992).

Results presented here show that selection for faster growth would not necessarily have a significantly negative genetic influence on relative density or moisture content of the wood. Moreover, selection for growth potential would not affect the highly positive phenotypic correlation between faster growth and cell length.

Combined selection for growth and wood properties is an opportunity for tree improvement. It could simultaneously improve growth rate and relative density (or moisture content) of the wood, without significantly affecting cell length.

Selection concentrated on wood density or moisture content could also give satisfying results.

Even though these conclusions can not be taken as final and general recommendations, further research of balsam poplar genetics is in progress. More reports can be expected (FARMER, 1990). By comparing different studies, from different sites, we will be able to learn more about this native species, whose importance for forestry practice is increasing.

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Growth Rates and Phenology of Fast- and Slow-Growing Families over an Entire Growth Period in *Betula pendula* ROTH

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Abstract

Differences in growth rate and growth rhythm, and their contribution to stem volume were analyzed in fast- and slow-growing full-sib families of silver birch (*Betula pendula*). Observations were made on the basis of a 15-year-old progeny test. Significant differences between fast- and slow-growing family groups were noted for growth rates at almost all development periods over the entire growing season, for growth cessation and for the length of growth period. Growth rates at the middle periods of the growing season and the total length of the growth period were strongly correlated with annual growth or total stem volume. Total stem volume was mainly attributable to growth rates during a certain period in the middle of the growing season, here named "growth efficiency" (GE). It suggests that direct selection for this yield component may be the most efficient way of breeding for high yield.

Key words: Betula pendula, growth rate, growth efficiency, phenology, growth profile.

FDC: 232.11; 181.8; 165.53; 176.1 *Betula pendula.*

Introduction

Selection for high wood production may lead to a prolonged growth period (GP) either through early growth initiation (GI) or late growth cessation (GC) (DIETRICHSON, 1969; CANNELL, 1989; REHFELDT, 1992a and b; WANG and TIGERSTEDT, 1993). However, early budburst or late growth cessation involves increased risks of early or late frost damage, a great concern of tree breeders in Nordic countries. Thus, to achieve genetic gains from tree breeding requires adaptedness to be maintained while economic value is improved. For this purpose, understanding of yield components in morphology, physiology