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Genetic Variation in Height, Branch and Needle Lengths of *Pinus sylvestris* L. from Siberia Tested in Alberta, Canada[1]

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(Received 4th April 2002)

Summary

We performed the analysis of variance and covariance on height, branch length, height to branch length ratio, and needle length measurements from thirty open-pollinated families of *Pinus sylvestris* L. from Siberia, Russia. This progeny trial was replicated on three sites in central Alberta, Canada. At six years from seeds, there was statistically significant variation for height, branch length to height ratio and needle length. On individual test sites, values of individual-tree heritability for height ranged from 0.20 to 0.35, whereas values of heritability for family means ranged from 0.41 to 0.59. These low to moderate heritabilities suggest that a combination of family and within-family selection would be effective in improving height growth for this population on individual sites. Across sites, values of individual-tree heritability for height ranged from 0.03 to 0.06, whereas values for heritability of family means ranged from 0.17 to 0.29. These low heritabilities across sites were due to high genotype by environment (GE) interaction. Analysis showed that 87% to 99% of the GE interaction was due to lack of genetic correlation among sites. Heterogeneity of the genetic variance among test sites contributed 1% to 13% of the GE interaction. This shows that families in this population of Scots pine are not broadly adapted and are therefore suitable only for a site-specific breeding programme. The paper also presents and discusses results of other traits with emphasis to breeding Scots pine for production of Christmas trees, which is the main use of this species in North America.

Key words: Pinus sylvestris, genetic variation, heritability, genetic correlation, Siberia.

Introduction

Scots pine (*Pinus sylvestris* L.) is an important Christmas tree species in parts of Canada and the United States (WRIGHT and BULL, 1963; GIERTYCH, 1991; VAN HARVERBEKE and GERHOLD, 1991). A feasibility study in Alberta showed that Scots pine and white pine were the most valued and preferred Christmas tree species in the province (NEEDHAM et al., 1991). An economic feasibility study by KNOPF and WALL (1992) in Saskatchewan showed that Christmas tree production was a risky business, because of strong market competition and a short marketing period. However, the risk would be less by reducing the time required to raise the trees to marketable size. Thus, KNOPF and WALL (1992) concluded that because of its fast growth, Scots pine would make a better Christmas tree investment than balsam fir, white spruce and white pine, the three other species considered in the study.

A good Christmas tree is one with short internodes and a dense crown that does not expose the main stem (HAWBOLDT, 1958). This, however, may apply in places where Scots pine produces more than one internode per growing season. Where it produces only one internode per growing season, short internodes may be equated with slow growth, thus delaying return on investment relative to alternative species. In this case, longer internodes may be desirable to accelerate growth with quality characteristics being met through selection for crown characteristics such as many branches per whorl, acute branch angle, more and longer needles. Therefore, we need to develop progenies of Scots pine that combine both adequate growth to ensure early return on investment, and good qualities of Christmas trees.

Previous studies showed that Scots pine provenances from Russia were more adapted to Canadian environment than provenances from other areas (KASPER and SZABO, 1969; SOOS and BROWN, 1970; KLEIN, 1971; TEICH and HOLST, 1970). Russian provenances survived and grew better than jack pine (KASPER and SZABO, 1969; TEICH and HOLST, 1970), ponderosa pine (KASPER and SZABO, 1969), and lodgepole pine (DHIR et al., 1989). Better adaptation of Russian provenances in the Canadian Prairies can be attributed to climatic similarities between central Russia and the Canadian Prairie Provinces (GIERTYCH, 1991).

In 1988, the Alberta Forest Service initiated a progeny study of Russian Scots pine. The objective was to develop a regionally adapted Scots pine for Christmas trees and possibly timber

[1] Based on the Master of Science thesis submitted to the University of Alberta by the first author.

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production. The study was restricted to materials from a narrow area in west central Siberia; a region identified by previous studies as a source of potentially adapted populations for Alberta. Our objective in this paper is to present and discuss the results of this study for height, branch length and needle length. The null hypothesis tested was that of the absence of the genetic variance ($H_0: \sigma^2 = 0$), against the alternative hypothesis of the presence of the genetic variance ($H_1: \sigma^2 > 0$). We give emphasis to levels of genetic variability, heritability, genotype by environment interactions, and genetic and phenotypic correlations, and their implications to selection and breeding of Scots pine in Alberta. Our discussion focuses exclusively to breeding Scots pine for Christmas tree production, since this is the main use of Scots pine in North America.

Materials and Methods

1. Description of the Test Material

The study involved 30 open-pollinated families that were randomly sampled from five locations in the region between latitudes 54° 00' and 55° 08' N, and longitudes 81° 15' and 86° 20' E. This region is within the Kemgrovo and Novosibirsk administrative provinces. The number of families per location was between 4 and 10. The Alberta Forest Service obtained seeds from the Petawawa National Forestry Institute. Since information on climate and soil conditions of the seed origin was not available, we have attempted to describe the region using information obtained from the literature. Based on information obtained from NUTTONSON (1950) and LYDOLPH (1977), the sampled area is within the West Siberian Lowland climatic region. The region is characterized by low elevation and flat terrain. Mean monthly temperature range from –19°C in January to 19°C in July. However, individual days can have winter temperatures as low as –55°C and summer temperatures as high as 38°C. Mean annual precipitation is between 380 mm and 500 mm, 65–80% of it falling in the period between May and October. July is the peak of the rain season.

2. Seedling Production, Field Testing and Assessment

Seeds were cold stratified for four weeks in January 1990 and sown in Spencer-Lemaire Tinus (350cc) containers using a 3:1 peat to vermiculite potting mixture. Seedlings were raised in the greenhouse at Pine Ridge Genetics and Tree Improvement Centre, using 18-hour photoperiod and approximately 25°/18°C day/night temperatures. In June 1990, seedlings were hardened and moved to a shade frame and later to heel-in beds for overwintering. In the summer of 1991, seedlings were transferred and planted in the field on three study sites in central Alberta, Canada (*Table 1*).

Throughout this paper, each experimental site will be represented by the letter (A, B, C) as shown in the parentheses. Similarly, combination of sites will be represented by a combination of letters. Sites A and C lie within the Lower Foothills Subregion of Alberta. This region is characterized by organic poorly drained soils. Site B is located in the Central Parkland Subregion with poor sandy soils (ANONYMOUS, 1994).

A randomised complete block experimental design with five blocks, and five-tree row plots was used on each site. At sites A and C, a 2.5 x 2.5m spacing was used, whereas at site B a 3 x 3m spacing was used. A wider spacing at site B was used to facilitate mechanical weeding. To ensure adequate survival at a sandy and drier site B, seedlings were watered in the first two years of field growth and fertilised in the third year. Neither watering nor fertilization was done at sites A and C.

We conducted field assessment in the fall of 1995, after budset has taken place. Traits assessed included height, branch length, needle length, and the number of surviving trees in each plot. The following symbols will be used throughout the paper:

H4 – height at age four, i.e., tree height up to the second whorl from top of the tree,

H5 – height at age five, i.e., tree height up to the first whorl from top of the tree,

H6 – height at age six, i.e., total tree height,

BL – branch length, i.e., the mean of the three longest branches in the second whorl,

CS – crown size, i.e., BL ÷ H6,

NL – needle length, i.e., the mean of three needles randomly sampled from the eastern side of the second whorl. The longest needle was measured in each fascicle.

Height and branch lengths were measured to the nearest centimetre (cm) whereas needle length was measured to the nearest millimetre (mm).

3. Data Analysis

Before being analysed, the data were checked for conformity to the normality and homogeneity of variance assumptions that underlies the analysis of variance. Except for CS, all traits met these assumptions and were therefore analysed without transformation. To stabilise the variance, the data for CS were square root-transformed ($\sqrt{CS + 0.5}$) as described by STEEL and TORRIE (1980). Early analyses showed that the five populations did not differ significantly in the traits assessed (RWEYONGEZA, 1997). Therefore, the population structure was ignored in the present analyses. On individual sites, the following random-effects model was used:

Table 1. – Description of the sites used in progeny testing of Scots pine in Alberta.

Site	Latitude (N)	Longitude (W)	Elevation (m)	Mean Monthly Temperature (°C)		Mean Annual Precipitation
				January	July	(mm)
Whitecourt (A)	54°03'	115°47'	823	-16.60	15.10	552.50
Pine Ridge (B)	54°04'	112°12'	610	-19.50	15.40	487.20
Swartz Creek (C)	53°23'	116°30'	990	-14.40	15.00	572.00

$$Y_{ijn} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \omega_{ijn}$$

where,

Y_{ijn} = observation on the n-th tree in the j-th family planted in the i-th replication,

μ = general mean,

α_i = effect due to the i-th replication, IND (0, σ^2_α),

β_i = effect due to the j-th family, IND (0, σ^2_β),

$\alpha\beta_{ij}$ = effect due to replication by family interaction, IND (0, $\sigma^2_{\alpha\beta}$),

ω_{ijn} = within-family effect, an error associated with an observation on the n-th tree in the j-th family planted in the i-th replication, IND (0, σ^2_ω).

Except for the general mean, all effects on the right-hand side of the model were considered random, additive, independent, and normally distributed with zero mean and their respective variances (in parentheses). ANOVA for this model is shown in *Table 2*.

For combined-sites analysis, the following random effects-model was used:

$$Y_{kijn} = \mu + \gamma_k + \alpha_{i(k)} + \beta_j + \gamma\beta_{kj} + \varepsilon_{ji(k)} + \omega_{i(k)jn} \ ,$$

where,

Y_{kijn} = observation on the n-th tree in the j-th family planted in the i-th replication within the k-th test site,

μ = general mean,

γ_k = effect due to the k-th test site, IND (0, σ^2_γ),

$\alpha_{i(k)}$ = effect due to the i-th replication within the k-th test site, IND (0, σ^2_α),

β_i = effect due to the j-th family, IND (0, σ^2_β),

$\gamma\beta_{ij}$ = effect due to site by family interaction, (0, $\sigma^2_{\gamma\beta}$),

$\varepsilon_{ji(k)}$ = residual, an effect due to replication-within-site by family interaction, IND (0, σ^2_ε)

$\omega_{i(k)jn}$ = within-family, an error associated with an observation on n-th tree in the j-th family planted in the i-th replication within the k-th test site.

The assumptions made for the single-sites model hold for the combined-site model. ANOVA for the combined-sites model is shown in *Table 2*. Differences in spacing between site B and the other two sites were ignored, since at the time of measurement trees were still far apart.

We analysed the variances and covariances using the general linear model procedure (SAS INST., 1994) because the data were unbalanced. Since two cells were missing, one at site B and one at site C, we used Type IV sum of squares to generate expected mean squares. Type IV sums of squares are the appropriate sums of squares for testing hypotheses when the design has missing cells (SAS INST., 1994). Single-site heritabilities were estimated using the following formulae:

$$h_i^2 = \frac{4\sigma^2_\beta}{\sigma^2_\omega + \sigma^2_{\alpha\beta} + \sigma^2_\beta} \quad \text{and} \quad h_f^2 = \frac{\sigma^2_\beta}{\frac{1}{k_4}\sigma^2_\omega + \frac{k_5}{k_4}\sigma^2_{\alpha\beta} + \sigma^2_\beta}$$

where h_i^2 and h_f^2 refer to heritabilities for individual tree and family means, respectively.

Similarly, heritabilities for combined sites were estimated using the following formulae:

$$h_i^2 = \frac{4\sigma^2_\beta}{\sigma^2_\omega + \sigma^2_\varepsilon + \sigma^2_{\gamma\beta} + \sigma^2_\beta} \quad \text{and} \quad h_f^2 = \frac{\sigma^2_\beta}{\frac{1}{k_9}\sigma^2_\omega + \frac{k_{10}}{k_9}\sigma^2_\varepsilon + \frac{k_{11}}{k_9}\sigma^2_{\gamma\beta} + \sigma^2_\beta}$$

Standard errors of individual tree heritabilities were computed as described in BECKER (1975), whereas standard errors of heritabilities for family means were computed according to WRIGHT (1976).

Genetic and phenotypic correlation coefficients between traits were estimated from covariances and variances of respective traits as expressed in the following formulae:

$$r_{A_{XY}} = \frac{\sigma_{\beta_{XY}}}{\sigma_{\beta_X} \times \sigma_{\beta_Y}} \quad \text{and} \quad r_{P_{XY}} = \frac{\sigma_{P_{XY}}}{\sigma_{P_X} \times \sigma_{P_Y}}, \quad \text{where,}$$

$r_{A_{XY}}$ and $r_{P_{XY}}$ are, respectively, the genetic and phenotypic correlation coefficients between any two traits; $\sigma_{\beta_{XY}}$ and $\sigma_{P_{XY}}$ are, respectively, the genetic and phenotypic covariances between any two traits; and $\sigma_{\beta X}$, $\sigma_{\beta Y}$, σ_{P_X} and σ_{P_X} are the genetic and phenotypic standard deviations of individual traits. Standard errors of correlation coefficients were estimated according to ROBERTSON (1959).

As will be shown in the results section, the analysis of variance showed a highly statistically significant family by site

Table 2. – Analysis of variance table for the single-site and combined-site models.

Source	df[1]	df[2]	EMS[1]	EMS[2]
Site		γ-1		$\sigma^2_\omega + k_1\sigma^2_\varepsilon + k_2\sigma^2_{\gamma\beta} + k_3\sigma^2_\alpha + k_4\sigma^2_\gamma$
*Replication/Site	α-1	γ(α-1)	$\sigma^2_\omega + k_1\sigma^2_{\alpha\beta} + k_2\sigma^2_\alpha$	$\sigma^2_\omega + k_5\sigma^2_\varepsilon + k_6\sigma^2_\alpha$
Family	β-1	β-1	$\sigma^2_\omega + k_3\sigma^2_{\alpha\beta} + k_4\sigma^2_\beta$	$\sigma^2_\omega + k_7\sigma^2_\varepsilon + k_8\sigma^2_{\gamma\beta} + k_9\sigma^2_\beta$
Site x Family		(γ-1)(β-1)		$\sigma^2_\omega + k_{10}\sigma^2_\varepsilon + k_{11}\sigma^2_{\gamma\beta}$
**Replication/Site x Family	(α-1)(β-1)	γ(α-1)(β-1)	$\sigma^2_\omega + k_5\sigma^2_{\alpha\beta}$	$\sigma^2_\omega + k_{12}\sigma^2_\varepsilon$
Within-family	αβn-1	γαβn-1	σ^2_ω	σ^2_ω

* Nesting on the replication applies for the combined-sites model only; ** Residual component for the combined-sites model df[1] and df[2]-degrees of freedom for the single-site and combined-sites model, respectively; EMS[1] and EMS[2]-expected mean squares for single-site and combined-sites model, respectively.

interaction for height, which is a form of genotype by environment (GE) interaction. To explore the magnitude of GE interaction, we computed the Type B genetic correlation for site pairs (FALCONER, 1981), using the mean squares from the combined-site analysis of variances as described by ROBERTSON (1959). In addition to the genetic correlation between pairs of test sites, we partitioned the GE interaction into components attributable the heterogeneity of the genetic variance and lack of correlation among test sites. This was done using equation 9 of COOPER and DELACY (1994), which is described as follows:

$$\sigma^2_{ge} = \frac{\sum[(\sigma_{g_i} - \sigma_{g_j})^2 + 2\sigma_{g_i}\sigma_{g_j}(1 - r_{g_{ij}})]}{n_e(n_e - 1)} \quad (1)$$

where σ^2_{ge} is genotype by environment interaction variance, σ_{gi} and σ_{gj} are square roots of the genotypic variance components expressed in environment i and j, respectively, r_{gij} is the genetic correlation (Type B) between environment i and j, n_e is number of test environments. Equation 1 has the following parts:

$$\frac{\sum(\sigma_{g_i} - \sigma_{g_j})^2}{n_e(n_e - 1)} \times 100$$

is the percentage of the GE interaction that is attributable to the heterogeneity of the genotypic variance among test environments, and

$$\frac{\sum[2\sigma_{g_i}\sigma_{g_j}(1 - r_{g_{ij}})]}{n_e(n_e - 1)} \times 100,$$

is the percentage of the GE interaction attributable to lack of genetic correlation (different ranking of genotypes) among test environments.

The pooled genetic correlation for all three sites was computed as the intraclass correlation among genotypes, which is adjusted for heterogeneity of the genotypic variance among test environments. This method is described by equation 14 in COOPER and DELACY (1994) as follows:

$$r_g = \frac{\sigma^2_g}{\sigma^2_g + \sigma^2_{ge} - A} \quad (2)$$

where, r_g is the pooled genetic correlation across all test sites, σ^2_g is the genotypic variance across test sites, and

$$A = \frac{\sum(\sigma_{g_i} - \sigma_{g_j})^2}{n_e(n_e - 1)},$$

where all terms are as previously defined.

Results

1. Survival

Percentage survivals were 98.1%, 92.9% and 87.2% at site A, B and C, respectively. The lowest surviving family at site A was 2926 with 84% survival. All other families had greater than 90% survival. Except for families 2908 and 2927 with 64% survival each, all families at site B had greater than 80% survival. At site C, families with the lowest survival were 2902 and 2909 with 68% survival each. Survival rates of all the remaining families were greater than 75%. The Chi-square test showed no significant differences in survival rates among families (RWEYONGEZA, 1997).

2. Height Growth

Six years from the seeds (H6), the mean height was 153.1cm, 144.0cm and 123.7cm at site A, B and C, respectively. The shortest and tallest families were, respectively, 14.5% and 15.2% below and above the mean at site A, 15.8% and 12.7% below and above the mean at site B, and 16% and 13.8% below and above the mean at site C. When the three sites were considered jointly, the shortest and tallest families for H6 were 6.4% and 10.6% below and above the general mean, respectively.

The family variances were statistically significant for H4 through H6 at all test sites (*Table 3*). They were, however, not

Table 3. – Site wise percentages of the variance components and heritability estimates for height growth.

Trait	Site	Percentages of Variance Components							Heritability	
		σ^2_γ	σ^2_α	σ^2_β	$\sigma^2_{\alpha\beta}$	$\sigma^2_{\gamma\beta}$	σ^2_ε	σ^2_ω	h^2_i	h^2_f
H4	A		1.76*	5.66*	17.31***			75.27	0.23±0.10	0.46±0.12
	B		1.32	8.68***	11.92***			78.08	0.35±0.13	0.59±0.15
	C		3.79	5.69**	10.90**			79.61	0.24±0.11	0.46±0.12
	Across	24.36***	1.97***	0.60		3.60**	10.72***	58.74	0.03±0.02	0.17±0.05
H5	A		2.79**	6.11**	15.67***			75.43	0.25±0.10	0.49±0.13
	B		1.68	6.36**	15.40***			76.56	0.26±0.11	0.49±0.13
	C		4.52	6.05**	12.10***			77.32	0.25±0.11	0.48±0.13
	Across	6.50**	3.00***	1.36		3.63**	13.02***	72.48	0.06±0.03	0.29±0.06
H6	A		3.95**	6.79**	15.68***			73.59	0.28±0.11	0.52±0.13
	B		2.19*	4.91*	16.98***			75.92	0.20±0.10	0.41±0.11
	C		4.70	4.84*	13.25***			77.20	0.20±0.10	0.42±0.11
	Across	19.10***	3.19***	1.08		3.17**	11.84***	61.63	0.06±0.03	0.27±0.06

* (P<0.05); ** (P<0.01); *** (P<0.001); Variance components are as follows: σ^2_γ - site, σ^2_α - replication, σ^2_β - family, $\sigma^2_{\alpha\beta}$ - replication x family, $\sigma^2_{\gamma\beta}$ - site x family, σ^2_ε - residual, σ^2_ω - within-family; h^2_i - individual tree heritability, $h^{2\gamma}_f$ - heritability for family means; H4, H5, H6 - total tree height at age four, five and six, respectively; A, B, C - Whitecourt, Pine Ridge, and Swart Creek, respectively.

Table 4. – Site wise percentages of the variance components and heritability estimates for branch and needle characteristics.

Trait	Site	Percentages of Variance Components							Heritability	
		σ^2_γ	σ^2_α	σ^2_β	$\sigma^2_{\alpha\beta}$	$\sigma^2_{\gamma\beta}$	σ^2_ε	σ^2_ω	h^2_i	h^2_f
BL	A		6.96***	3.28*	5.47*			76.15	0.25±0.11	0.52±0.13
	B		5.14**	0.51	20.75***			73.60	0.02±0.06	0.06±0.07
	C		1.82	2.27	11.91***			84.00	0.09±0.08	0.23±0.09
	Across	47.56***	2.74***	0.63		0.87	7.42***	40.77	0.05±0.03	0.30±0.06
CS	A		3.65***	3.28*	5.47*			87.59	0.14±0.08	0.40±0.10
	B		7.69***	3.08*	7.69**			81.54	0.13±0.08	0.36±0.09
	C		0.55	2.40	6.97*			90.08	0.10±0.09	0.26±0.09
	Across	54.05***	2.03***	0.47		0.68*	2.70**	35.81	0.05±0.03	0.32±0.06
NL	A		3.27***	6.64**	14.76***			75.30	0.27±0.11	0.52±0.13
	B		9.98***	3.81*	8.90*			77.32	0.17±0.09	0.42±0.11
	C		12.51***	3.55*	4.24			79.70	0.16±0.09	0.42±0.10
	Across	16.62**	6.90***	3.30***		0.00	7.81***	65.37	0.17±0.06	0.79±0.12

* (P<0.05); ** (P<0.01); *** (P<0.001); Variance components are as follows: σ^2_γ - site, σ^2_α - replication, σ^2_β - family, $\sigma^2_{\alpha\beta}$ - replication x family, $\sigma^2_{\gamma\beta}$ - site x family, σ^2_ε - residual, σ^2_ω - within-family; h^2_i - individual tree heritability, h^2_f - heritability for family means; BL - branch length, CS - BL÷H6, NL - needle length; A, B, C - Whitecourt, Pine Ridge, and Swart Creek, respectively.

significant across sites. At site A, the family variance increased from 5.66% of the total variance for H4 to 6.79% for H6. Contrary, the family variance declined from 8.68% for H4 to 4.91% for H6 at site B. The family variance did not show a clear trend at site C. Here, the variance increased from 5.69% for H4 to 6.05% for H5 and then declined to 4.84% for H6. Across sites, the family variance increased from 0.6% of the total variance for H4 to 1.36% for H5 and then declined to 1.08% for H6.

Heritability estimates for height showed trends similar to those of the family variance (*Table 3*). At site A, heritability increased with tree age, whereas heritability declined with tree age at site B. For site C, heritability increased between ages four and five, but then declined between ages five and six. Across sites, heritability for individual tree height increased between ages four and five and remained constant between age five and six. On the other hand, heritability for family means increased between ages four and five and then declined between ages five and six. Generally, except for H4 at site B ($h^2_i = 0.35$), the heritability for individual tree height was less than 0.30, whereas the heritability for family means was less than 0.6. At all test sites and across sites, the standard errors of individual tree heritability estimates for height were less than or equal to 50% of the heritability estimates. Standard errors of heritability estimates for family means were less than 25% of heritability estimates.

3. Branch and Needle Characteristics

The average branch length (BL) was 40.4cm, 46.7cm and 27.8cm at site A, B and C, respectively. The family variance for BL was statistically significant only at site A (*Table 4*). At this site, the family variance was 5.71% of the total variance. Compared to site A, site B and C exhibited high family by replication interaction for BL. At site A, the standard error of individual-tree heritability was 50% of the heritability value, whereas at site B and C the standard error was equal or greater than the heritability value.

Site averages for the ratio of branch length (BL) to total tree height (H6), here called crown size (CS) were 0.26, 0.33, and 0.22 for sites A, B and C, respectively. The family variance for CS was statistically significant only at sites A and B. Family variances were 3.28%, 3.08% and 2.40% of the total variance for CS for site A, B and C, respectively. Generally, heritability estimates for individual tree CS were less than 0.15, and those of family means did not exceed 0.40 (*Table 4*). Standard errors of heritabilities for individual tree CS at sites A and B were slightly greater than 50% of heritability estimates. Contrary, the standard error was almost equal to the heritability estimate at site C.

Needle lengths (NL) averaged 55.8mm, 60.7mm and 51.6mm at site A. B and C, respectively. Family variance for NL was statistically significant at all sites and across sites (*Table 4*). At site A, the family variance was 6.64% of the total variance. Elsewhere, it was between 3.3% and 3.81% of the total variances for NL. Individual tree heritability estimates for NL were between 0.16 and 0.27, whereas those of family means were between 0.42 and 0.79 (*Table 4*).

4. Genotype by Environment Interaction

The analysis of variance showed that GE interaction was statistically significant for H4 through H6, and CS (*Table 3* and *4*). It was not statistically significant for BL and NL. Generally, the GE interaction variance decreased from approximately 3.6% of the total variance for H4 and H5 to 3.1% for H6. Genetic correlations between sites (Type B) were very low with standard errors that were higher than the correlations themselves (*Table 5*). Very low PEARSON's correlation coefficients for family means (Table 5) also indicate the existence of high GE interaction between pairs of test sites. Pooled genetic correlations for the three sites (*Table 5*) ranged from 0.149 (H4) to 0.317 (H6). *Table 5* also shows that 86.9% to 99% of the GE interaction was due to lack of correlation among test sites and that only 1% to 13.1% of the GE interaction could be attributed to heterogeneity of the genetic variance among test sites.

5. Genetic and Phenotypic Correlations

Age-to-age genetic and phenotypic correlations for height were between 0.84 and 0.99 on individual sites, and 0.74 to 0.99 across sites. At all three sites and across sites, genetic correlations were slightly greater than the corresponding phenotypic correlations (*Table 6*). On individual sites and across sites, genetic and phenotypic correlations between height and branch length were between 0.44 and 1.00. With few exceptions, genetic correlations between height and branch length were greater than the corresponding phenotypic correlations (*Table 6*). At site A, needle length was negatively correlated genetically with height ($r_{A_{XY}}$ = –0.56 to –0.71) and branch length ($r_{A_{XY}}$ = –0.47). The phenotypic correlations for needle length with height and branch length at this site were positive but weak. Considering the size of the standard errors, needle length had no genetic and phenotypic relationship with height and branch length at both sites B and C (*Table 6*). Across sites, needle length was not correlated genetically and phenotypically with height, but was negatively correlated genetically with branch length.

Discussion

1. Performance on Individual and Across Sites

Overall, site A had the best height growth whereas site B had the longest branches and needles. Because of long branches, site B had also the highest branch-height ratio. Greater lateral growth compared to height growth at site B can be attributed to intensive tending of this site, which included watering, fertilisation, and adequate weed control. Trees at sites A and C were neither watered nor fertilised, and weed control was much less intensive than that of site B. It is known that ade-

Table 5. – Quantification and partitioning of the genotype by environment interaction for height.

Trait	Site A and B		Site A and C		Site B and C	
	r_b	r_f	r_b	r_f	r_b	r_f
H4	0.032±0.406	0.03	0.421±0.351	0.310	-0.127±0.288	-0.116
H5	0.337±0.350	0.235	0.363±0.332	0.231	-0.001±0.306	-0.032
H6	0.224±0.332	0.161	0.261±0.332	0.141	0.192±0.375	0.119

Traits	r_{pl}	V_{het}	L_{cor}
ABCH4	0.149	13.1	86.9
ABCH5	0.310	8.7	91.3
ABCH6	0.317	1.0	99.0

r_b - Type B genetic correlation, r_f - PEARSON's correlation for family means, r_{pl} - pooled genetic correlation, H4, H5, H6 total height at age four, five and six, respectively, A, B, C - Whitecourt, Pine Ridge and Swartz Creek, respectively, ABC - all three sites considered together, ABCH4 to ABCH6 - all sites considered together for H4, H5 and H6, V_{het} and L_{cor} percentage of GE interaction due to heterogeneity of the genetic variance and lack of genetic correlation among test sites, respectively.

Table 6. – Site wise genetic (r_A) and phenotypic (r_P) correlations between traits.

Traits	Site A		Site B		Site C		Across Sites	
	r_A	r_P	r_A	r_P	r_A	r_P	r_A	r_P
H4&H5	0.99±0.01	0.95	0.93±0.04	0.92	0.99±0.01	0.95	0.99±0.01	0. 93
H4&H6	0.92±0.04	0.88	0.88±0.07	0.85	0.95±0.03	0.84	0.74±0.18	0.85
H5&H6	0.96±0.02	0.93	0.97±0.02	0.95	0.96±0.03	0.93	0.92±0.05	0.94
H4&BL	0.72±0.15	0.67	0.45±0.60	0.60	0.80±0.16	0.44	0.56±0.31	0.57
H5&BL	0.79±0.11	0.76	1.00±0.00	0.75	0.84±0.13	0.58	0.84±0.11	0.72
H6&BL	0.88±0.07	0.81	0.87±0.21	0.79	0.75±0.21	0.65	0.77±0.16	0.77
H4&NL	-0.66±0.17	0.15	0.23±0.30	0.16	0.02±0.36	0.01	-0.25±0.32	0.12
H5&NL	-0.71±0.14	0.19	0.14±0.33	0.22	0.15±0.34	0.07	-0.09±0.29	0.17
H6&NL	-0.56±0.19	0.27	0.11±0.36	0.27	0.16±0.37	0.13	0.05±0.30	0.24
BL&NL	-0.47±0.22	0.28	NA	0.28	NA	0.12	-0.52±0.24	0.24

H4, H5, H6 - total tree height at age four, five and six, respectively; BL - branch length, CS - BL÷H6, NL - needle length; A, B, C - Whitecourt, Pine Ridge, and Swart Creek, respectively; NA - values much greater than –1.0.

quate moisture, nutrients, and lack of competition promote more lateral growth than tree height (FORD, 1976). Even in natural stands of Scots pine, solitary trees have larger branches and wider canopies than trees in closed stands (PRZYBYLSKI, 1975). Therefore, greater lateral growth at site B was not unexpected.

At all sites, there was a significantly large family by replication interaction for height, branch length, branch-height ratio, and needle length. High family by replication interaction was also reflected in significantly large residual variances across sites. This high family by replication interaction might be the result of within-site heterogeneity in soil and moisture, and their influence on microclimate of the trees (YEH and RASMUSSEN, 1985).

In this study, all traits on individual sites and H5, H6, and NL across sites showed high within-family variability as reflected by the high percentages of within-family variance. This high variability among trees in open-pollinated families might be an indicator of many effective pollen parents (YEH and RASMUSSEN, 1985).

2. Implications of Genotype by Environment Interaction

This study showed that GE interaction was a significant source of variation across test sites and that the interaction was almost entirely due to lack of correlation among test sites. This is evident from low Type B genetic correlations, person's correlations for family means and the partitioning of the GE interaction into components due to heterogeneity of the genetic variance and lack of genetic correlation across sites (*Table 5*). *Table 5* shows that in most cases the standard errors of the genetic correlations were greater that the correlations themselves. Hence, the genetic correlations in *Table 5* may not be far from zero.

Table 5 also shows that the pooled genetic correlation increased as the percentage of the GE interaction attributable to lack of genetic correlation among test sites increased. This is rather a misnomer, since the genetic correlation should decline as the percentage of the GE interaction attributable to lack of correlation among test sites increases. The most likely explanation for this anomaly is that the pooled genetic correlation is also in great errors similar to those computed for site-pair correlations. Otherwise the increase with tree age of the percentage of the GE interaction attributable to the lack of correlation among sites is consistent with the decline with age of the site-pair Type B genetic correlations.

Lack of correlations among test sites implies that most of the tested families ranked differently on the three sites. It can be shown that out of the thirty families tested, only six (2904, 2906, 2910, 2912, 2925, and 2926) were above the mean for H4 through H6 at all sites. All the remaining families did well on some sites and poorly on other sites. The following examples illustrates the extent of rank changes for total height at age six (H6): family 2903 was 12.1% below the mean (fifth shortest) at site C, 9.8% above the mean at site B (third tallest), and 1.6% below the mean at site A. Family 2915 was 12.8% above the mean (third tallest) at site C, and just around the mean at sites A (1.7%) and B (1.0%). Family 2920 was 12.4% below the mean (second shortest) at site C and just around the mean at sites A (1.4%) and B (1.3%). Family 2922 was 15.8% below the mean (the shortest) at site B, and 4.6% and 8.1% above the mean at sites A and C, respectively. Family 2928 was 16% below the mean (the shortest) at site C, 9.4% below the mean at site B (one of the shortest), but 2.2% above the mean at site A. These rank changes are extreme, and generally show that some of the best families are not suitable for planting on a wide range of environments. They must be carefully matched with sites where they do well.

The GE interaction observed in this study has two major implications. First, the cause of the GE interaction is almost entirely due to rank changes across sites. This is the form of GE interaction that is detrimental to plant breeding, since it implies that genotypes selected for better performance on some sites cannot be deployed on other sites without losing the genetic gain (COOPER and DELACY, 1994). Secondly, high GE interaction affects the estimates of single-site heritabilities. When analysis of variance is performed on single-site basis, the family and family by site interaction variances are confounded, leading to overestimation of single-site heritabilities (NYQUIST, 1991). Thus, because of high GE interaction, single-site heritabilities in this study are biased upward.

Previous studies of Scots pine revealed the existence of the GE interaction in growth traits, especially height (KING, 1965a, 1965b; GIERTYCH, 1979, 1991; GULLBERG and VEGERFORS, 1987). According to MERGEN et al. (1974), GE interaction occurs more in genotypes from the periphery than from the centre of the species' natural range, and in genotypes from areas of low growth potential than those from areas of high growth potential. Early provenance studies elsewhere showed that Scots pine from Siberia ranked below average in growth when compared with Scots pine from other areas (GIERTYCH, 1991). Furthermore, the families used in this study originated from a region outside the main distribution of Scots pine in central Asia. Thus, the families used in this study can be expected to show strong GE interaction by virtue of their origin.

3. Heritabilities and their Implications

With one exception, individual tree heritabilities estimated in this study were less than 0.3 and heritabilities for family means were less than 0.6 for all traits. Therefore, our heritability values especially for individual trees were on the lower side. Nevertheless, heritabilities estimated in this study were within the range of those estimated in other studies of Scots pine. For example, except for two cases where heritabilities of 0.6 and 0.85 were estimated, KRUSCHE et al. (1980) found that heritabilities for individual tree height did not exceed 0.4. Other reported heritability values for height in Scots pine include 0.41 and 0.65 (EHRENBERG, 1963), 0.32 and 0.95 (POYKKO, 1982; HAAPANEN and POYKKO, 1993), and 0.816 and 0.803 (WRIGHT, 1963). Low values of individual tree heritability in this study might be attributed to large family by replication interaction and within-family variances, compared with the family variances. Likewise, large values of family by site interaction, residual, and within-family variances especially for height reduced individual tree heritabilities across sites.

Heritabilities estimated in this study also compare well with those reported for other *Pinus* species. For example, the following heritabilities for height have been reported: 0.314–0.80 and 0.56–0.88 in *Pinus patula* (LADRACH and Lambeth, 1991), 0.078–0.128 in *Pinus eliotii* (HODGE and WHITE, 1992), 0.36 and 0.54 in *Pinus monticola* (BOWER and YEH, 1988), and 0.29 in *Pinus caribaea* var. *hondurensis* (DEAN et al., 1986). Therefore, heritabilities observed in this study were also within range of what we would expect for a *Pinus* species.

4. Implications of Genetic Correlations

High age-to-age genetic correlations between heights at age four and six suggest that selection for fast growing trees can be done at the early ages of trees. However, the interval between age four and six is too short a time to realise significant changes in family ranks with tree age for the tested families. Therefore, caution should be taken when interpreting such genetic correlations, since they might be low when longer inter-

vals are involved. For example, in a study with Scots pine, KRUSCHE et al. (1980) found that the genetic correlations between 6- and 11-year heights on two sites were 0.91 and 0.95. The corresponding values between 3- and 11-year heights were 0.68 and 0.34. The sharp decline of a genetic correlations from 0.95 between age 6 and 11-years to 0.34 between age 3 and 11-years shows that ranking of genotypes at 3 years of age was different from ranking of the same genotypes at 11-years of age. In one case, however, WRIGHT and BALDWIN (1957) observed a correlation of 0.93 between heights at a nursery stage and 17-years of field growth. Age-to-age genetic correlation is important in early selection and should, therefore, be monitored in future assessments of these progeny tests.

The high positive genetic correlations between height and branch length suggest that selection for fast height growth would result in trees with long and possibly thick branches. For Christmas trees, this might be partly favourable, since thicker branches are needed to hold ornaments (HAWBOLDT, 1958). On the other hand, long branches that are not proportional to the height of the tree might result in poor crown shape, a characteristic of a poor Christmas tree. The strong association between tree height and branch length means that one cannot select for shorter branches to improve the shape of the tree crown without suppressing height growth. Thus, one way of improving the shape of the tree crown would be to select for a desired value of branch to height ratio (CS) rather than selection for branch length (BL).

In this study, needle length was negatively genetically correlated with height and branch length at site A. Considering the size of the standard errors the positive genetic correlations for NL with height and branch length at site B, C and across sites were negligible (*Table 6*). On the other hand, the phenotypic correlations cast a universal picture of the relationship of NL to height and branch length. At all three sites and across sites, phenotypic correlations show that needle length had low positive correlations with height and branch length. This supports the argument by RUBY and WRIGHT (1976) that needle length in Scots pine has no causal relationship with growth-related traits.

5. Time Factor and Genetic Parameters

For Christmas tree production in the Canadian Prairies, Scots pine can be expected to have an average rotation age of six years (KNOPF and WALL, 1992). Irrespective of species, height for a good Christmas tree is between 1.7 m and 2.4 m (STIELL and STANTON, 1974). At six years from seeds, only family 2904 and 2914 at site A had reached the minimum height for a standard Christmas tree. None of the families had reached the minimum height at both sites B and C. Nevertheless, there were individual trees in different families at all sites that had reached the required height for Christmas tree. We predict that the rotation age for Christmas tree production on these sites and other similar sites may be between eight and ten years. The genetic parameters reported in this paper are likely to change by the time trees are eight to ten years old. However, for Christmas tree production, these trees have already passed half the rotation age recommended by ZOBEL and TALBERT (1984) for making meaningful genetic decisions in forest tree breeding. Therefore, our genetic parameter estimates can be used with certainty in making decisions regarding selection and breeding for better Christmas trees in Alberta.

Conclusions

From the foregoing discussions on the genetic parameters of Scots pine, we can make the following general conclusions:

1. Heritability values for height were low on individual sites and much lower across sites. Thus, to realise sufficient genetic gain in height growth, a combination of family and within-family selection would be required.

2. Height exhibited high GE interaction and the source of this interaction was almost entirely due to different ranking of families across sites. Hence, breeding Siberian populations of Scots pine for better height growth in central Alberta would require development of site-specific genotypes as opposed to regionally adapted ones.

3. There were high positive genetic correlations between tree height and branch length suggesting that breeding to increase height would increase the length and possibly the thickness of branches. For a Christmas tree, a high positive correlation between height and branch length is favourable, since strong branches are needed to hold decorations. However, if timber production becomes an option for these Scots pine populations, thick branches would lead to reduction in timber quality due to large knots.

4. The length of Scots pine needles was not correlated genetically and phenotypically with growth-related traits such as height and branch length. In addition, needle length had the least GE interaction of the assessed traits. Hence, needle length appeared to have no causal relationship with growth-related traits.

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Genetic Diversity of *Pinus massoniana* Revealed by RAPD Markers

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(Received 24th June 2002)

Abstract

Random amplified polymorphic DNA (RAPD) markers were used to measure genetic diversity within and among *Pinus massoniana* populations, a multipurpose economic tree species in China. Concordant with previous studies based on allozymes, we also detected high genetic diversity within and low genetic differentiation among populations. Unexpected UPMGA clustering results indicated genetic uniformity throughout South China caused probably by large-scale artificial afforestation. The significant positive correlations between population genetic diversity and its elevation suggested the populations at lower elevation harbor less genetic diversity than those at higher elevation.

Key words: AMOVA; Genetic differentiation; Genetic diversity; *Pinus massoniana*; RAPD.

Introduction

Knowledge on genetic variation of forest tree populations is fundamental for sustainable forest management. However, information on genetic diversity of tree species in China is limited only to few studies.

Pinus massoniana, a conifer native to China, is widely distributed from 21°41' to 33°56' degree latitude and from 102°10' to 123°14' degree longitude, including 17 provinces, growing at elevation up to 1500-1650m. Being one of the most economically important forest trees (e.g., for timber and pulp production), it has been widely used for plantations and afforestation (MEN and LUO, 1987). In order to improve its economic value, many studies have been carried out on quantitative genetic variation of the rate of growth, height, biomass and other characters (LAI and WANG, 1997; WANG, 1993), and high diversity within geographic provenances has been found. The studies on the genetic diversity of *P. massoniana* using allozyme markers also demonstrated high genetic diversity within and low genetic differentiation among populations (GE et al., 1988; HUANG and ZHANG, 2000), however indicating greater differentiation along latitude than altitude gradients (RONG and ZHOU, 1989).

However, allozymes can detect only a limited number of coding regions of genome and its expression might be affected by environmental conditions and different stages of plant development. In contrast, DNA-based markers, such as RAPD (random amplified polymorphic DNA), overcome these disadvantages and are proved to be more powerful than allozyme markers when used to reveal genetic structure and diversity of populations (SZMIDT et al., 1996; WU et al., 1999). In addition, once established, RAPD has the advantage of being quick and easy,