

GENETIC VARIATION IN TRACHEID LENGTH AND RELATIONSHIPS WITH GROWTH AND WOOD TRAITS IN EASTERN WHITE SPRUCE (*PICEA GLAUCA*)

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ABSTRACT

Wood traits affect the quality of wood products, which is especially true for tracheid length regarding paper quality. While variation in tracheid length in white spruce is well known, estimates of genetic control over that trait as well as its relationships with growth traits and other wood characteristics have not yet been reported. Thus, the objectives of this study were: (1) to determine the extent of the differences in tracheid length among 30-year-old white spruce open-pollinated families; (2) to estimate the narrow sense heritability at both the individual and family levels for tracheid length; and (3) to estimate the phenotypic, genetic, and family mean correlations between height, diameter, volume, and wood specific gravity. We have shown that more than 90% of the variation in tracheid length is due to differences among trees within family plots. Heritabilities at both the family and the individual levels are low, so significant genetic gain could only be obtained from selection and vegetative propagation of the trees with the longest tracheids. Tracheid length in white spruce is negatively correlated to growth traits but appears to be independent of wood specific gravity. Effects of selection for growth traits on tracheid length are discussed.

Keywords: Fiber, *Picea glauca*, progeny, tree improvement.

INTRODUCTION

Geographic variations in white spruce (*Picea glauca* [Moench] Voss) growth and adaptive traits have been thoroughly investigated in the past (Corriveau and Boudoux 1971; Khalil 1985a; Genys 1986); seed zones have been delineated (Li et al. 1997), and heritability and expected genetic gains from selection have been estimated (Holst and Teich 1969; Ying and Morgenstern 1979; Nienstaedt and Riemenschneider 1985; Khalil 1985b; Li et al. 1993). Breeding programs have been implemented in Canadian provinces and the U.S. Lake States (Fowler 1986; Nienstaedt and Kang 1987; Beaulieu 1996), and more attention is now being paid to wood traits because selection for growth could affect them and studies of their genetics showed the potential for their genetic improvement. Indeed, herita-

bility values reported for specific gravity, which is considered to be of key importance in forest product manufacturing (Zobel and van Buijtenen 1989), were quite high (Corriveau et al. 1991; Yanchuk and Kiss 1993), thus indicating the presence of a strong genetic control over that trait.

While wood density provides an excellent means of predicting end-use characteristics of wood such as strength and pulp yield (Jozsa and Middleton 1994), more knowledge on tracheid characteristics is needed because of their influence not only on the yield but also on the quality of pulp produced (Keith 1986; Kennedy 1995). For white spruce, only a few studies have been carried out thus far on tracheid characteristics (Taylor et al. 1982; Wang and Micko 1984; Yang et al. 1988; Antal and Micko 1991; Yang 2002), and no estimates of

heritabilities have yet been reported. Hence, neither the potential for genetic improvement of these traits nor their genetic inter-relationships with growth traits are known. While both tracheid length and coarseness affect paper smoothness and strength, variation in the former is generally investigated because it is easier to obtain good estimates and it has been demonstrated in the past that both were highly correlated (Clark 1962; Sastry and Wellwood 1974).

Progeny tests established in the initial stages of breeding programs are now old enough to provide useful information on the inheritance of traits that are of main importance for pulp quality. Genetic correlations between tracheid characteristics and growth traits must be estimated in order to find out whether progress in pulp quality will follow that in growth traits. The objectives of this study were: 1) to determine the extent of the differences in tracheid length among 30-year-old white spruce open-pollinated families; 2) to estimate the narrow sense heritability at both the individual and family levels for tracheid length; and 3) to estimate the phenotypic, genetic, and family mean correlations between height, diameter, volume and wood specific gravity.

MATERIALS AND METHODS

A progeny test of 39 open-pollinated families from eight populations located within a 60-km radius of the Petawawa Research Forest (PRF), Ontario (lat. 46°00'N, long. 77°26'W, elev. 168 m), was established in the spring of 1969 at the Valcartier Forest Experiment Station (lat. 46°50'N, long. 71°30'W, elev. 150 m). The seedlings were then 4 years old and had been raised in the PRF nursery. The experimental layout was a randomized complete block design with four blocks. The test site has already been described elsewhere (Corriveau et al. 1991).

The first investigations into tracheid lengths and their variation in conifers were carried out by Sanio (1872). His work permitted him to enact a law, which is known as Sanio's law,

according to which the length of tracheids increases from pith to bark. As for wood density, the stem may be divided into two regions for tracheid length. The first one, located near the pith and known as the juvenile phase, is characterized by a rapid increase in tracheid length and changes in cell walls associated with cambial maturation. The second, the mature phase, reflects stabilized functioning of the mature cambium (Panshin and de Zeeuw 1980). Depending on the species, this phase is characterized by a stabilization, a decrease, or an increase in cell length. White spruce belongs to the third group as its tracheid length keeps increasing with age (Taylor et al. 1982). It was also shown in recent studies that tracheid length varies within trees from stump to crown (Wang and Micko 1984) and from earlywood to latewood, with the latter having longer tracheids (Bannan 1965). Hence, tracheid lengths generally are at a minimum within the earlywood zone, increase within the latewood zone, and then decrease at the end of the annual ring.

Despite this variation, samples were collected for this study at breast height for convenience and because this sampling scheme is acceptable (Bannan 1968) for testing differences among families. Hence, 28 growing seasons after planting, an increment core (12 mm diam.) was collected from each of two trees per family plot, for a total of 312 samples. Trees in each plot were randomly chosen among the five sampled for a previous study on the inheritance of wood specific gravity in white spruce 19 years after planting (see Corriveau et al. 1991). Tracheids extracted from the five outer rings, following the method described below, were used to compare trees and families and to estimate genetic parameters. Furthermore, radial variation in tracheid length was examined in a subset of five trees selected on the basis of their outer wood specific gravity, with three of them having the highest and the other two the lowest wood specific gravity among the sampled trees. To do so, increment cores were divided into eight sections with the first five containing two

growth rings, sections six and seven having three growth rings, and the last one including the five outer rings.

For all samples, successive rings were used to lessen the effects of ring-to-ring irregularities in division of cells from year to year on estimates of tracheid length (Bannan 1968). Hence, for most of the trees, tracheid length from rings 17 to 21 was analyzed. Each sample was first softened by heating it at 100°C in distilled water for 5 min and then transferring it into a labelled vial for maceration. A maceration solution of 2:1 30% hydrogen peroxide and glacial acetic acid was added to the vial and kept at 80°C for 3 h. Maceration time varied from sample to sample depending on size and solution volume. The maceration process was considered completed when the sample was whitewashed. Excess maceration solution was then discarded and the sample was stored at 4°C in a vial containing 97% denatured alcohol until tracheid length was measured. Six samples burned during the heating phase and five more were lost for various reasons.

Samples were sent to the Centre spécialisé en pâtes et papiers (Trois-Rivières, Quebec) for analysis using a Kajaani FS-100 Fibre Analyzer. Each delignified sample was first shaken in a disintegrator apparatus to liberate the tracheids, making a suspension of tracheid slurry, hence ensuring good length estimates. To get accurate measurements, a repeatability test was carried out by submitting 20 samples twice to the Kajaani analyzer. On average, the weighted tracheid lengths of the same sample diverged by 1.52% between two consecutive measurements, which is acceptable. Besides the number of tracheids for many classes of length, the analyzer provided three different averages, i.e., the arithmetic tracheid length average, the weight weighted tracheid length average, and the weighted tracheid length average. As recommended by the specialists at the Centre spécialisé en pâtes et papiers, we used the latter to characterize the tracheid length of each sample in order to reduce the effect of small fragments, most of which are

broken tracheids. This weighted average was obtained using the following formula: $WTLA = \sum n_i \cdot l_i^2 / \sum n_i \cdot l_i$.

Relationships of tracheid length with seven other traits were also investigated. Hence, diameters at breast height (D28) for all sampled trees were measured when collecting the increment cores, as was the height in the first block. A second-degree polynomial regression function of height on D28 was developed using Proc Reg (SAS Institute Inc. 1997). Tree height in the three remaining blocks was first estimated with that function and a value between 0 and 1 obtained from a uniform random generator multiplied by the standard error of height, which was added to each height estimate to obtain a more realistic variation in the data. Tree volume was calculated using the general regression model developed for white spruce growing in plantations in Quebec (Bolgari and Bertrand 1984). Outer wood specific gravity (SG) was estimated 9 years earlier (see Corriveau et al. 1991), as well as height (H19), diameter (D19), and pylodin pin penetration (P19).

Before submitting data to other statistical analyses, departure from the normal distribution was tested using statistics provided by Proc UNIVARIATE (SAS Institute Inc. 1997). Tracheid length, volume, and wood specific gravity had to be transformed using the square root transformation in order to normalize their distribution and reduce the heterogeneity of variance. One sample was considered as an outlier and discarded. Data analysis consisted in examining the significance of family variances in all traits and in estimating variance components based on a mixed model, with blocks and provenances being considered as fixed effects. The model used is for the split-plot design although families from a provenance were randomized within a block. Each provenance was treated as being represented by a non-contiguous whole plot within a block (Libby and Cockerham 1980). GLM with MANOVA statement and VARCOMP procedures (SAS Institute Inc. 1997) using the Type 1 method were used to estimate mean squares

and variance components. Estimates of variances of the variance components were obtained using the restricted maximum likelihood method.

The degree of genetic control (heritability) over tracheid length at both the individual and family levels (see Falconer 1981, p. 215) was estimated using the following equations for individuals (1) and families (2):

$$h^2_i = 4\sigma^2_{F(P)} / (\sigma^2_{F(P)} + \sigma^2_{BF(P)} + \sigma^2_w), \quad (1)$$

$$h^2_F = \sigma^2_{F(P)} / [\sigma^2_{F(P)} + (\sigma^2_{BF(P)} / b) + \sigma^2_w / bk], \quad (2)$$

where:

$\sigma^2_{F(P)}$ is family-within-provenance variance, $\sigma^2_{BF(P)}$ plot variance, σ^2_w within-plot variance, b the number of blocks, and k the number of individuals per plot. Approximate standard deviations of heritabilities were calculated following Dickerson's method (Dieters et al. 1995).

Phenotypic correlations among traits for both individual trees and family means were estimated using the CORR procedure (SAS Institute Inc. 1997). Genetic correlations between traits were calculated as:

$$r_{Gxy} = \text{Cov}(F(P)_{xy}) / [\sigma^2_{F(P)x} \cdot \sigma^2_{F(P)y}] \quad (3)$$

where:

$\text{Cov}(F(P)_{xy})$ = covariance due to the cross-product differences of traits x and y at the half-sib family level,

$\sigma^2_{F(P)x}$ = variance due to differences among half-sib families for trait x ,

$\sigma^2_{F(P)y}$ = variance due to differences among half-sib families for trait y .

Standard deviations of genetic correlations were computed using the following formula (Falconer 1981):

$$\sigma(r_A) = [1 - r_A^2 / \sqrt{2}] / \sqrt{[(\sigma h_x^2 \cdot \sigma h_y^2) / h_x^2 \cdot h_y^2]} \quad (4)$$

where:

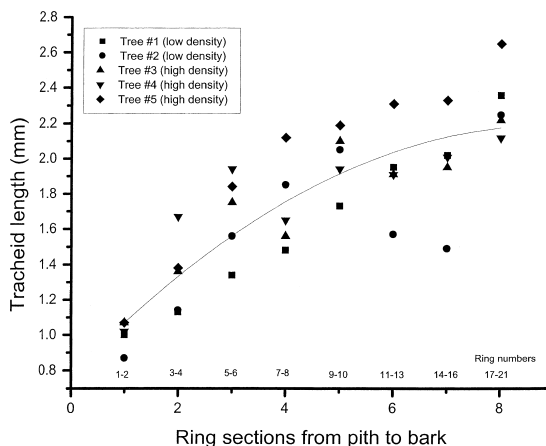


FIG. 1. Tracheid length variation from pith to bark in white spruce.

r_A = estimate of genetic correlation,

h^2_x = heritability estimate of trait x ,

h^2_y = heritability estimate of trait y ,

σh_x^2 = standard deviation of h_x^2 ,

σh_y^2 = standard deviation of h_y^2 .

RESULTS AND DISCUSSION

As expected (see Fujiwara and Yang 2000), tracheids in wood-ring sections closer to the pith were shorter than those close to the bark (Fig. 1), and were of similar length to those of samples collected at a 1.5 m height in white spruce growing in wild stands of the same age (see Taylor et al. 1982 and Wang and Micko 1984). For the five outer rings, family means for tracheid length ranged from 2.13 mm to 2.56 mm, with an overall mean of 2.40 mm. Again, on average, the tracheids measured in this study were similar to those reported by Antal and Micko (1991) and to those of the same age presented by Taylor et al. (1982) and Wang and Micko (1984). These results suggest that despite the tree-to-tree variation in tracheid length, on average, it could be quite stable from site to site for a given age. The overall tracheid length mean was also above the threshold length of about 2 mm needed for

TABLE 1. *Analysis of variance and expected mean squares for tracheid length of white spruce from 30-year-old open-pollinated families.*

Source of variation	Degrees of freedom	Mean squares	F	P-value	Expected mean squares
Blocks [B]	3	0.015596	0.45	0.7180	$\sigma^2_w + 1.8592 \sigma^2_{BF(P)} + 9.2960 \sigma^2_{BP} + Q(B)$
Provenances [P]	7	0.024558	0.61	0.7416	$\sigma^2_w + 1.8580 \sigma^2_{BF(P)} + 9.0386 \sigma^2_{BP} + 7.4321 \sigma^2_{F(P)} + Q(P)$
Families [F(P)]	31	0.029161	1.27	0.1857	$\sigma^2_w + 1.8772 \sigma^2_{BF(P)} + 7.5089 \sigma^2_{F(P)}$
Blocks \times Provenances [BP]	21	0.034184	1.49	0.0974	$\sigma^2_w + 1.8703 \sigma^2_{BF(P)} + 9.0971 \sigma^2_{BP}$
Blocks \times Families [BF(P)]	93	0.022867	0.98	0.5337	$\sigma^2_w + 1.9055 \sigma^2_{BF(P)}$
Within plot [W]	145	0.023294			

making kraft paper with an acceptable tear strength (Zobel and Buijtenen 1989).

No significant effect on tracheid length could be attributed to any tested source of variation at the $\alpha = 0.05$ level (Table 1). An absence of significant differences among white spruce stands was also observed by Taylor et al. (1982) for tracheid length from wood of rings 31 to 35. Of the total variance, families accounted on average for 4.5%, which is about twice the amount of plot variation, and variance among trees within plots accounted for more than 90%. Even though variance due to families was not significantly different from zero at the usual $\alpha = 0.05$ level, we did not consider it equal to zero. Milliken and Johnson (1984, p. 262) recommend removing an effect from an ANOVA model, which is equivalent to assuming that its variance component is equal to zero, only if the p-value is higher than 0.30. The p-value associated with the family effect was about 0.18 (see Table 1), so we decided to use the variance component obtained to estimate the heritabilities for tracheid length, recognizing that these heritabilities would be quite low and imprecise. Hence, the estimates of individual and family narrow sense heritabilities obtained were 0.18 ± 0.19 and 0.27 ± 0.28 , respectively. However, as phenotypic variation is quite high, genetic progress could still be effective. Indeed, from the selection of the best tree out of 100, one would expect a 13% genetic gain (see Falconer 1981 for formula) that would allow the overall tracheid length average to increase by 0.33 mm.

The same selection intensity at the family level would be less impressive with a genetic gain of only 5%. This is not an unexpected result considering the small portion of variation due to differences among families. Phenotypic selection of trees with longer tracheids followed by bulk vegetative propagation of selected trees could provide higher genetic gains. However, it is not possible to calculate expected genetic gains from such breeding strategy with our data set because estimates of total genetic variance, including the non-additive variance, cannot be obtained from open-pollinated families. Moreover, to obtain good estimates for these gains, the average propagation effect must also be known (see Shelbourne 1969, p. 25).

The relationships between tracheid length, growth traits, and wood density were examined by calculating genetic correlations and phenotypic correlations on individual trees and family means (Table 2). Estimated genetic correlations between tracheid length and diameter, volume and wood density were moderate. However, the high standard errors suggest that these estimates are expected to be subject to large sampling errors (Falconer 1981), which is probably due to the limited size of the experimental population. Except for the correlation between height and tracheid length, which was above the theoretical maximum of 1.0, the three types of correlation generally were, for each pair of traits, of the same magnitude and were affected by the same sign. Hence, tracheid length was negatively corre-

TABLE 2. *Estimated individual-tree phenotypic, family means, and genetic correlations between 17-21 rings tracheid length (WTLA) and 28-year height (H28), diameter (D28), and volume (V28) after planting, and 19-year outer wood specific gravity (SG), height (H19), diameter (19), and pylodin penetration (P19) after planting. P-values* for individual-tree phenotypic and family means correlations and standard errors for genetic correlations are in brackets.*

Traits	WTLA		
	Phenotypic	Family mean	Genetic
H28	-0.132 (0.0223)	-0.564 (0.0002)	1.126 (-)
D28	-0.217 (0.0001)	-0.585 (0.0001)	-0.311 (0.509)
V28	-0.214 (0.0002)	-0.590 (0.0001)	-0.227 (0.510)
SG	0.075 (0.1947)	0.200 (0.2213)	0.236 (0.469)
H19	-0.217 (0.0002)	-0.094 (0.5661)	-0.107 (0.563)
D19	-0.145 (0.0120)	-0.476 (0.0022)	0.027 (1.029)
P19	-0.158 (0.0060)	-0.253 (0.1196)	-0.660 (0.240)

* Significant at 0.05 when P -values ≤ 0.0071 after a Bonferroni correction.

lated to growth traits. Based on these estimates, selection for volume growth is expected to have a negative effect on tracheid length in white spruce. However, as tracheids in that species are already long enough for making final products of acceptable quality, the reduction in tracheid length might not have a significant negative effect on the quality of products. Zobel (1997) suggested that wood traits such as tracheid length should be considered as a secondary selection trait to be applied to trees fulfilling the primary demands for fast growth, good form, and good adaptation. This selection strategy could be productive in white spruce, as already indicated for growth traits and wood density (Beaulieu and Corriveau 1985; Corriveau et al. 1987), because the phenotypic variation of its tracheid length seems to be sufficiently large.

On the other hand, with intensive forest management, trees are expected to be harvested at a younger age than in old growth forests; hence, the proportion of wood from the juvenile phase, i.e., with shorter tracheids, relative to that from the mature one, should increase. This will be especially true for fast-growing trees in plantations. Thus, the global impact of selection for growth on the average tracheid length might be more important; genetic improvement of tracheid length in the juvenile phase could hence become essential to maintaining the quality of products. While tracheid length was not measured in juvenile

wood, except for five trees, and the strength of genetic control over them was not estimated in this study, one can nevertheless see in Fig. 1 that extended variation also exists in tracheid length in wood sections near the pith. The presence of this variation seems to indicate that it could be possible to make some progress in selecting trees with longer tracheids, but its pace remains to be demonstrated.

Individual tree as well as family means and genetic correlation coefficients between tracheid length and outer wood specific gravity, estimated 9 years before, were not significantly different from zero at the $\alpha = 0.05$ level. This result is interesting as it shows that selection for high wood specific gravity, whether as a primary or secondary trait, is not expected to affect tracheid length. However, even if there was a slight effect, it seems that it would be positive since all the correlation coefficients were positive. The relationship between tracheid length and pylodin penetration was not as clear as it is for wood specific gravity. The correlation coefficient at the individual-tree level was significantly different from zero, while at the family level, it was not. Furthermore, it seemed to be strongly negative at the genetic level, but the standard error was also quite high. Correlation coefficients similar to those between wood specific gravity and tracheid length, but of a different sign, would have been expected if pylodin penetration had provided precise specific gravity estimates.

While pylodin penetration might be sufficiently effective for indirect selection of families for outer wood specific gravity ($r_A = -0.93$), it may not accurately represent the relationship between tracheid length and specific gravity. In the near future, molecular markers associated with specific gravity will be available to assist white spruce breeders in selecting the best trees. It will then be interesting to see whether there is an association between those markers and tracheid length.

CONCLUSIONS

In this study, we have shown that phenotypic variation in tracheid length is relatively important in white spruce. However, more than 90% of this variation is due to variation among trees within plots, and only 4.5% is due to variation among families. While narrow sense heritabilities at the individual and family levels were low, it would still be possible to make some genetic progress through the selection of families and trees with longer tracheids. However, phenotypic selection followed by mass vegetative propagation seems to be the most promising breeding strategy to improve tracheid length in eastern white spruce. Tracheid length does not appear to be related to wood specific gravity (ages 17 to 21), but is negatively correlated to growth traits. Hence, a selection in favor of volume would cause a decrease in tracheid length. In eastern white spruce, the latter already exceeds the threshold length needed to make good quality products. Thus, we suggest that selection should first be made for growth superiority and then for wood traits. Hundreds of thousands of white spruce rooted cuttings are produced yearly in Quebec. Furthermore, the ministère des Ressources naturelles du Québec, which is responsible for the management of public lands, is presently considering producing half of its needs for the white spruce reforestation program via rooted cuttings (L. Masse, personal communication). This would result in the production of 15 million rooted cuttings each year. This provincial department

is also engaged in the development of somatic embryogenesis (SE) and has already set up facilities to mass produce SE plants. Thus, a strategy based on vegetative propagation of trees having the longest tracheids among those having first been selected for growth, for instance, could be rapidly implemented.

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