production in these two years. The rank correlation between good (1991) and poor (1990) as well as between moderate (1989) and poor (1990) years, were found insignificant and very low, with values 0.12, and 0.24 respectively, indicating that the changes in ranking of clones in these years are significant. The results show that year to year correlations in cone production are not significant between consecutive years (1989 x 1990, 1990 x 1991), while it is highly significant between biennial years (1989 x 1991), indicating the presence of carry over-effect.

Variance Components and Heritability Estimates

The variance components and the broad sense heritability estimates have been presented in *table 2*. The estimates of clone variances from single years are larger from the value estimated from the combined-over-years analysis. This is due to year x clone interaction component of variance, which, in the single analyses by year, is confounded with the genetic component of variance. The clone by year interaction component of variance could arise for 2 reasons, namely differing overall clone means and components of variance in the 3 years and changes of clone rankings over the 3 years. In examining the estimates of variances (*Table 2*), it is apparent that the estimates are higher in year 1991, followed by year 1989 and 1990. These differences suggest that the variances are not independent of the means and that scaling effect is present, besides the transformation made.

Broad sense heritability values on individual tree bases were ranked from 0.61 (1990) to 0.71 (1969), while the values on clone mean basis were, as expected, higher ($H = 0.82$ for 1990, and $H = 0.88$ for 1989). The values estimated from the combined over years analyses were 0.28 and 0.75 on single tree and clone mean basis respectively.

The higher heritability values from the single year analyses were expected, because the clone x year interaction component of variance is confounded with the clone variance (BECKER, 1984). The high heritability values indicate that cone production in black pine is under strong genetic control. Heritability values estimated in slash pine (VARNELL *et al.*, 1967) were much lower, suggesting that this parameter is a property of the species age and siting of the material to which it may referred.

Conclusions

From a study of cone production in a black pine clonal seed orchard, over three successive years, 11, 12 and 13 years, the following conclusions were drawn:

1. There is a significant amount of genetic (clonal) variation in cone production. The clones do not contribute equally to the next generation since more of the cones are produced by only a few clones; 25% of the clones produced 43%, 51% and 40% of the total cones in moderate, poor and good cone years respectively.

2. Crop size influences the degree of parental balance (equal contribution of all clones), with the good cone crop years being closer to the ideal situation.

3. Year to year clone mean correlations in number of cones per tree are positive and very strong between good and moderate cone years and insignificant between good X poor and moderate X poor cone years.

4. Cone production is under strong genetic control, indicating that considerable gain can be expected from roguing or by selecting good cone producing clones and establishing new clonal seed orchards.

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Genetic Variation in Growth and Wood Specific Gravity and its Utility in the Improvement of Interior Spruce in British Columbia

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Summary

Juvenile wood specific gravity (SG) from increment cores was assessed by the maximum-moisture content

(MMC) method in 40 open-pollinated families of interior spruce from two 15-year-old progeny test sites in north-central British Columbia to examine: (1) the magnitude of family differences of SG and growth traits; (2) phenotypic, genetic and family mean correlations among traits, and; (3) to develop an approach for using these parameters for the prediction of parental breeding values. Differences among the 40 families for mean SG were large (range 0.38 to 0.44), as indicated by high individual ($h^2_i = 0.47 \pm 0.03$) and family mean ($h^2_f = 0.67 \pm 0.11$) heritabilities. Genetic correlations between both height and diameter growth and SG were near zero, whereas phenotypic correlations were significant ($P<0.05$) at —0.40 and —0.46, respectively. Family differences using the Pilodyn (PIN) apparatus, as an indirect measure of SG, were significant ($P<0.05$) and exhibited a moderate family heritability (0.48 ± 0.25). The genetic correlation between PIN and SG, as assessed by the MMC method, was -0.80 ± 0.10. Family selection for SG using PIN data was expected to be 68% as efficient as direct family selection for SG based on the MMC values. Parental breeding value predictions for height growth and SG, based on height and PIN data at age 15, indicate that height may be improved by approximately 11% without a substantial change in SG. The development of slight negative genetic correlations between SG and growth traits in the last few growth rings, as suggested by the PIN data, might have two consequences. First, gains in both SG and growth will be more difficult to attain if the negative trend continues. Second, the ability to successfully select for SG at early ages (less than 15 years) will be problematic.

Key words: White spruce, Engelmann spruce, wood specific gravity, height growth, diameter growth, heritability, Pilodyn.

Introduction

The objective of most tree breeding programs has been to increase stem volume through genetic selection for increased height and diameter growth. More recently, however, interest in incorporating wood quality traits into tree breeding has occurred, and according to Kellogg (1982) and van Buijtenen (1982 and 1986) should be an essential consideration. In multiple-trait improvement the magnitude of genetic variances and covariances among traits will greatly influence potential genetic gains, and will directly affect the strategies for improving production and breeding populations. Moreover, estimates of genetic variances and covariances are necessary for predicting breeding values. Once predicted values have been derived, expected genetic gain can be easily determined for individual traits, or for correlated traits, by averaging the breeding values of the parents or progeny retained (White and Hodge, 1989).

While estimates of heritability for height growth of interior spruce (*Picea glauca* (Moench) Voss, *P. engelmannii* Parry and their hybrids) have been reported previously (Kiss and Yeh, 1988), little is known about the genetic relationships between growth traits and wood specific gravity (SG) of interior spruce. Micko *et al.* (1982) reported a moderate to strong negative phenotypic correlation between ring width and wood density in the outer rings of mature (40 to 60 year old) white spruce trees (*P. glauca* (Moench) Voss). Corriveau *et al* (1990). reported similar results in white spruce from eastern Canada. Taylor *et al.* (1982) found that this relationship was either negative or not different from 0 in wood samples from individual white spruce trees in the wild. Recently, Petty *et al.* (1990) reconfirmed the strong negative phenotypic correlation between ring width and ring density in Sitka spruce (*Picea sitchensis* (Bong.) Carr.); however, in the same study, this relationship was rather weak in Norway spruce (*Picea abies* (L) Karst.). These phenotypic relationships, along with the negative genetic correlations reported by Birot and Nepveu (1979) and Worral (1975) in Norway spruce, might suggest that the genetic relationship between growth and SG in interior spruce may also be negative. However, as stated by Falconer (1981), the magnitude and the sign of a genetic correlation cannot necessarily be determined from the corresponding phenotypic correlation.

The objectives of this study were: (1) to estimate the magnitude of the differences in wood SG among 15-year-old open-pollinated families of interior spruce; (2) to estimate the phenotypic, genetic and family mean correlations between height and diameter growth and wood SG, and; (3) to examine the utility of these genetic parameters in the prediction of parental breeding values for growth and wood SG.

Materials and Methods

Detailed descriptions of the 2 test sites used in this study have been reported elsewhere (Kiss and Yeh, 1988; Kiss and Yanchuk, 1991). Briefly, the tests are open-pollinated progeny tests of 167 families that were established in 1973 using 2+1 planting stock. Parent-tree selections were part of the genetic improvement program of interior spruce in the Prince George Selection Unit and details regarding parent-tree locations are given in *figure 1* of Kiss and Yeh (1988). No meaningful stand structure was present among parent trees to group them as a "provenance" effect in the analysis. Thus, additive genetic variance estimates in this study will be biased upwards if provenance effects are not wholly additive.

Three test sites are present in the complete experiment and the experimental design at each site is 10 replications and 10-tree row plots in a randomized block design. Due to sampling constrains of time and expense, only two of the sites (Red Rock and Quesnel) and 40 randomly chosen families were used in this study. Trees were 15-years in the field at the time of sampling (18 years-old from seed). Two trees per plot, in the first 7 replications at each site, had measurements made of height (HT), diameter (DIA) and specific gravity (SG). Due to the relatively small size of some of the trees, only the first 2 trees large enough to provide cores (i. e., typically trees with diameters greater than 20 mm at breast height) were sampled in each row plot. The number of trees with a diameter smaller than 20 mm was not large (approximately 25 trees with diameters slightly less than 20 mm were still included in the data set); therefore, any bias should be minimal (discussed later). HT in cm was measured to the tip of the leader. DIA measurements were recorded in mm at breast height (1.5 m above ground). A 5 mm diameter increment core from bark-to-bark through the pith was taken approximately 30 cm above the ground from the same cardinal direction on each of the two sample trees per plot. Specific gravity measurements of whole cores were obtained using the maximum-moisture-content method (MMC) (Smith, 1954). Pilodyn (6 J Forest Model, 2.5 mm pin diameter) pin pentration measurements (PIN) were also made through the bark on the sample trees adjacent to where the core was extracted (in wood that appeared knot free), but far enough away from the increment bore hole to avoid wood that may have had its ultrastructure altered by the coring

process (typically 5 cm to 10 cm above and below the core hole). The average of 2 readings was used as the PIN score for each tree.

The PROC VARCOMP (Method = Type 1) routine of SAS Institute INC. (1988) was used to estimate variance and covariance components. Negative variance component estimates were set to 0. Heritability estimates were calculated as shown in KISS and YEH (1988) and their standard errors estimated as shown by BECKER (1975). Covariances were calculated as described by KEMPTHORNE (1968) and genetic correlations and their standard errors were estimated as shown by FALCONER (1981). Phenotypic correlations, both on individual trees and on family means, were obtained using PROC CORR (SAS Institute, 1988). No true error term was available in the expected mean squares for "site" effects; therefore, this term was not tested for significance with an F statistic. Instead "site" differences are discussed in relation to the size of the variance component. Family effects (or general combining ability, GCA) were calculated as family mean deviations pooled across both sites. Statistically, this makes "sites" a fixed effect, which has been considered appropriate for the calculation of parental breeding values (WHITE and HODGE, 1989).

The prediction of parental breeding values (BV%) for a single trait can be calculated from;

$$BV\% = 2 \cdot \text{GCA effect (\%)} \cdot h^2_f \qquad [1]$$

where GCA effect (%) is the family mean deviation expressed as a percentage of the grand mean and h^2_f is the heritability based on family means (WHITE and HODGE, 1989, p. 97). For a 2 trait situation, where an expected response is required for only one trait (e. g., SG, through the use of the correlated trait, such as PIN), an expected correlated breeding value CBV_{SG} can be calculated for each parent by; ·

[2]

$$CBV_{SG} = 2 \cdot \frac{GCA_{PIN}}{S.D._{fam.\ PIN}} \cdot CGP \cdot S.D._{fam.SG}$$

where, GCA_{PIN} is a GCA effect (i. e., a family mean deviation) for PIN, CGP is the Coefficient of Genetic Prediction (BARADAT, 1982), $S.D._{fam.\ PIN}$ is the phenotypic standard deviation among family means for PIN, and $S.D._{fam.\ SG}$ is the phenotypic standard deviation among family means for SG. The division of GCA_{PIN} by $S.D._{fam.\ PIN}$ in [2] standardizes the GCA effect (or creates a standardized

Table 1. — Estimated variance components and heritabilities (h^2 ± standard errors) for wood specific gravity (SG), 15-year height (HT) and diameter (DIA) growth and Pilodyn pin penetration (PIN) based on 40 interior spruce open-pollinated families in British Colombia. Values in parentheses are components expressed as a percentage of the total variance.

SOURCE	DF	SG(%)	HT(%)	DIA(%)	PIN(%)
Sites(S)[1]	1	0 (0)	20.4(0)	45.6(19)	2.03(25)
Block/S[1]	12	13.9(2)	326.0(6)	12.4(5)	0.26(3)
Family (F)	39	111.3(12)*	413.9(7)*	5.1(2)	0.32(3)*
S x F	39	24.7(3)	192.7(3)	10.0(4)*	0.14(2)
B/S x F	448	266.4(28)*	770.4(30)*	62.8(26)*	1.56(19)*
Error	475	541.4(57)	3216.0(54)	109.5(45)	3.97(48)
h^2_{family}		0.67±.26	0.54±.24	0.26±.28	0.48±.25
$h^2_{within\ family}$		0.41±.21	0.25±.11	0.09±.09	0.18±.09
$h^2_{individual}$		0.47±.16	0.30±.14	0.11±.11	0.22±.11

[1]) indicates that no true error term was present or approximated.
*) indicates significant at $P<0.05$.

Table 2. — Estimated genetic correlations (top diagonal) and individual-tree phenotypic and family mean correlations (below diagonal — phenotypic, top value and family mean, bottom value) among 15-year height (HT), diameter (DIA), specific gravity (SC) and Pilodyn pin penetration (PIN). Standard errors of genetic correlations are in brackets.

	SG	HT	DIA	PIN
SG		0.00(0.28)	0.08(0.41)	-0.80(0.10)
HT	-0.40* -0.26		0.94(0.06)	0.20(0.33)
DIA	-0.46* -0.28	0.85* 0.87*		0.35(0.44)
PIN	-0.61* -0.72*	0.44* 0.36*	0.63* 0.56*	

*) indicates correlation significant at $P<0.05$.

selection differential for a family for PIN) so that once it is multiplied by the $S.D._{\cdot fam.\ SG}$, the correlated response is in the units of SG. The CBV_{SG} can easily be expressed as a percentage by replacing $S.D._{\cdot fam.\ SG}$ with the coefficient of variation. The CGP is the product of the genetic correlation multiplied by the square root of the 2 family heritabilities, and is in essence a standardized genetic regression coefficient of the two traits (Baradat, 1982). Eq. [2] is similar to the correlated response as given by Falconer (1981) except in this form it can be used for individual families. Both Eq. [1] and [2] are useful in the sense that they make it possible to derive and compare the distribution of BV's for parents for the same trait, one from direct selection (i.e., BV's from Eq. [1]), the other from indirect selection (i. e., CBV's from Eq. [2].

Because it is likely that PIN information will be collected as a surrogate for SG in many operational breeding programs, it may be necessary to predict parental BV% for a measure of growth (e.g., height, diameter or volume) along with SG, using the PIN data as a surrogate for SG. Equation 2, then, would not be useful in this situation because it cannot incorporate more than 2 traits. (Eq. [2] will not be specifically used in this study, but has been presented for the sake of completeness and aid in understanding the matrix solutions which follow.) The appropriate genetic and phenotypic variances and covariances are now arranged as elements of matrices to predict breeding values of parents for growth and SG based on phenotypic observations of growth and PIN. Due to the low heritability of DIA (*Table 1*) and the high genetic correlation of HT with DIA (*Table 2*) in this study, HT was considered the only important growth trait for selection in the remainder of this analysis. In other words, BV's for HT will be predicted directly, while BV's for SG will be predicted indirectly, from PIN measurements. The BV predictions for both traits can be simultaneously obtained from:

$$\mathbf{g_i = C'V^{-1}p_i} \qquad [3]$$

where,

g_i = predicted genetic values of the ith parent for height and SG,

C = 2 x 2 matrix of genetic variances and covariances among HT, SG and PIN,

V = 2 x 2 matrix of phenotypic variance and covariances among family means for HT and PIN, and;

p_i = 2 x 1 column vector of phenotypic family mean effects for HT and PIN for the ith family.

The construction of the C and V matrices is as follows:

$$\mathbf{C} = \begin{bmatrix} 1/2\ Var_{a(HT)} & 1/2\ Cov_{a(HT,SG)} \\ 1/2\ Cov_{a(PIN,HT)} & 1/2\ Cov_{a(PIN,SG)} \end{bmatrix},$$

$$\mathbf{V} = \begin{bmatrix} Var_{P(HT)} & Cov_{P(HT,PIN)} \\ Cov_{P(PIN,HT)} & Var_{P(PIN)} \end{bmatrix},$$

where, Var_a and Cov_a terms are additive genetic variances and covariances, respectively, and Var_P and Cov_P are phenotypic variances and covariances among family means. Elements in the C matrix are equivalent to two times the family variances and covariances (e. g. $1/2\ Var_a = 2 \cdot Var_{Family}$) because selection occurs on both males and females (Namkoong, 1979).

Results

Mean SG across both test sites was 0.407 (CV = 7.6%). Family effects for SG were significant and accounted for 12% of the variance *(Table 1)*. Family means pooled across test sites for SG ranged from 0.383 to 0.443. Heritability estimates for SG were 0.67 (±0.23) when based on family means, 0.47 (±0.16) when based on individuals irrespective of family identification (i. e., mass selection heritability), and 0.41 (±0.21) when based on differences among individuals within families. The site by family interaction was small and non-significant (3% of total variance) (*Table 1*).

Although better estimates of heritability for height (HT) and diameter (DIA) growth would be obtained by including data from all 174 open-pollinated families in the tests, heritability estimates presented here for HT and DIA are based, for comparison purposes, on the same 40 families that were sampled for SG. Family means combined across sites for HT ranged from 269 cm to 373 cm, were significantly different ($P<0.05$), and had a heritability of 0.54±0.24 (*Table 1*). Family means combined across sites for DIA ranged from 35.4 mm to 54.6 mm and were not significantly different, which is also reflected by the lower heritability (0.26 ± 0.28).

The relationships between SG and growth traits (HT, DIA) were examined in three ways: (1) genetic correlations, (2) phenotypic correlations among family means, and; (3) phenotypic correlations on individual trees. Estimated genetic correlations between SG and HT and DIA were both near 0 (*Table 2*). These correlations suggest, that at this age, no linear genetic dependency exists between SG and stem growth. Although low and non-significant, the negative family mean correlations between growth traits and SG (*Table 2*) suggest that a negative relationship between stem growth and SG may be

developing. This suggestion is proposed for three reasons. First, probability levels for both family-mean correlations (HT vs SG and DIA vs SG) were close to $P = 0.10$. Second, family mean correlations may reflect the underlying distribution of breeding values better for this relatively small population sample. Genetic correlation estimates are usually subject to large sampling errors unless the experimental population is rather large (FALCONER, 1981; BURDON, 1989). MOREOVER, family-mean correlations are expected to be lower than genetic correlations because they contain non-genetic effects (WHITE and HODGE, 1990), but this was not the case (*Table 2*). Third, the genetic correlations between PIN and HT and DIA were significant and positive (*Table 2*), suggesting that a negative genetic relationship may exist between growth rate and SG in the last 2 or 3 growth rings (where the PIN is expected to sample). Nevertheless, the overall relationship between PIN and SG and growth rate does not appear to be strong at this age.

Individual-tree (phenotypic) correlations between HT and DIA and SG were moderate and significant, which corroborates results from wild-tree studies mentioned earlier. At the family level, correlations between the 2 growth traits and PIN were significant, as were the phenotypic correlations (*Table 2*). Family effects were significant for PIN (*Table 1*), but more importantly, genetic and family-mean correlations were high and negative between SG and PIN (—0.80 and —0.72, respectively); however, the phenotypic correlation was somewhat lower at 0.61. While site effects were negligible for SG, variations due to site differences for PIN were rather large (25%) (Table 1). The reason for this discrepancy is not obvious, but will be discussed later.

Discussion

Heritabilities and Correlations

Our heritability estimates for SG in interior spruce are comparable to those reported for other conifers in that the individual-tree heritability was close to 0.5 (as suggested by ZOBEL and TALBERT, 1984).

The non-significant family effect for diameter may be explained by: (1) the sampling bias introduced by choosing trees above a minimum diameter of 20 mm; (2) a genetic sampling "error" of the 40 families, or; (3) an actual low level of family variation in diameter at this age. From this data it is not possible to determine which of the three reasons is valid. However, from an additional analysis (not shown) where all progeny from the 167 families were included, family effects for diameter were significant and the estimated family heritability for diameter was more than twice that indicated in *table 1*. Moreover, when all trees with diameters smaller than 20 mm were dropped (from a second analysis of all 167 families), the family heritability for diameter decreased by only 0.01. This, along with the strong family-mean correlation and genetic correlation between height and diameter growth (*Table 2*), suggest that the practical impact of the sampling bias was not particularly large. Therefore, it appears that any bias is primarily due to the effects of random sampling of these 40 families.

Although the non-significant effect for diameter may negate our original intention of obtaining good correlation estimates between both height and diameter growth with SG, height differences were significant in our study. Therefore, the estimated genetic correlation between height and SG (which was near 0) is probably quite valid. In support of our findings, BIROT and NEPVEU (1979) reported a non-significant correlation between wood density and height in a clonal Norway spruce test, but interestingly, the correlation of wood density with diameter became more negative as the test matured. Similarly, ZOBEL and VAN BUIJTENEN (1989), in their review of this general topic, suggest that it is not too uncommon to find a negative genetic correlation between diameter and SG and near zero genetic correlations between height and SG. For example, studies in various pine species by SHELLBOURNE *et al.* (1969), ERNST *et al.* (1983) and MAGNUSSEN and KEITH (1990) found genetic correlations of similar magnitude to those in *table 2.* For tree breeders these situations of genetic correlations being in and around 0 between growth and SG are quite fortunate, as it seems more the norm that adverse genetic correlations are present between both height and diameter and wood density (e.g., ZOBEL and VAN BUIJTENEN, 1989; KING *et al.*, 1988; YANCHUK, 1986).

TAYLOR *et al.* (1982) found, for mature wild-stand individuals of white spruce, that wood density near the pith is very high and decreases rapidly until approximately age 10 to 15 where it then remains relatively constant or increases slightly. CORRIVEAU *et al.* (1990) also showed that in a spruce provenance trial, wood density decreased to age's 10 to 15; although, in their even-aged plantation environment the decrease was not as sharp as that reportet by TAYLOR *et al.* (1982). This transition point in the SG profile at age 10 to 15 is thought to be where change to "mature" wood occurs. In this study, typically only 12 growth rings were present in each core sample. Therefore, our results only pertain to wood that could be classified as exhibiting "juvenile" characteristics.

The large variance between sites for PIN (*Table 1*) may be because the Pilodyn apparatus only samples the last few growth rings of individual trees. Since no site-to-site variation was detected for SG itself (*Table 1*), one site may have experienced a large change in the type of wood produced in the last few years. This was apparently not detectable in the whole-core samples. Differences in bark thickness between sites could have been a factor as well, although this was not directly determined. Also of interest, given the large variance among sites, was the non-significant family x site interaction for PIN (*Table 1*).

High correlations of SG with PIN data suggest that the PIN measurement may be adequate for ranking families for SG, as has been suggested for Douglas-fir (KING *et al.*, 1988). SPRAGUE *et al.* (1983) estimated that for loblolly pine, the relative efficiency (i. e., the ratio of correlated gain over the gain expected from direct selection) of mass selection for SG based on PIN measurement was 77%. The genetic correlation of -0.80 ± 0.10 between PIN score and SG in this study suggests that the Pilodyn may also be quite effective for indirect selection of families for SG in spruce. Estimated relative efficiencies (as determined by $h_{f(PIN)} r_{g(SG,PIN)} / h_{f(SG)}$, where r_g is the genetic correlation between SG and PIN and h_f is the square root of the appropriate heritability) in this study were 68% for family selection, 55% for mass selection and 53% for within-family selection. Therefore, the Pilodyn may also be adequate as a general indicator for selecting individual trees within families.

Table 3. — Family mean effects for height at age 15 (HT), specific gravity (SG) and Pilodyn score (PIN), and predicted breeding values for HT (BV_{HT}%) and SG (BV_{SG}%), for the 10 top and bottom ranked families (out of 40) based on HT. Family mean effects are deviations from the grand mean of 2 sites[a]).

Family rank[b]	Family code	Family mean HT (cm)	Family mean SG[c]	Family mean PIN	BV_{HT}%	BV_{SG}%
1	87	53.7	-16	1.57	15.8	-8.3
2	161	47.6	-5	0.76	15.4	-2.1
3	6	33.6	22	-0.99	14.2	11.2
4	143	25.9	-1	-1.09	11.7	11.3
5	16	30.5	-14	0.57	9.7	-2.1
6	84	24.9	4	-0.26	9.5	4.3
7	17	34.3	-12	1.37	9.3	-8.4
8	40	26.1	1	0.41	8.5	-1.1
9	9	21.7	-2	-0.19	8.2	3.5
10	22	30.1	-24	1.20	8.1	-7.3
Average of top 10 =		32.9	-5	0.33	11.0	0.1
31	104	-30.3	36	-1.64	-7.3	11.0
32	36	-30.2	-9	-0.82	-9.0	4.2
33	82	-18.6	-17	1.39	-9.7	-13.2
34	90	-50.0	31	-2.19	-13.1	13.8
35	106	-32.9	-13	0.68	-13.3	-8.5
36	149	-45.5	6	-1.09	-13.9	5.1
37	41	-44.0	10	-0.64	-14.4	1.5
38	168	-38.9	-16	0.81	-15.7	-10.1
39	153	-39.3	-1	0.78	-15.8	-9.9
40	156	-42.9	4	0.39	-16.3	-7.0
Average of bottom 10 =		-35.6	3	-0.24	-12.2	-1.1

[a]) Predicted breeding values were derived from phenotypic effects on HT and PIN (see equation 3).
[b]) Family ranking based on descending family mean height HT effects.
[c]) SG effects (x1000).

Breeding Value Determinations

In most applied breeding programs it is unlikely that the breeder will be able to practice culling following some strict theoretical selection intensity. Other factors can determine whether or not an individual is worthy of inclusion in a seed orchard or breeding population (e.g., fecundity, graft incompatibility, number of ramets, and other non-quantitative traits), and this subsequent culling will directly affect estimated gain calculations for a seed production population. White and Hodge (1989) discussed the advantages of calculating BV's for individual parents (or individual trees within families). An important attribute is that expected gain can be calculated by simply averaging the predicted BV's of the selected population. These BV's for height and SG (from Eq. [3]), for simplicity, are expressed as percentages of the grand mean for height and SG and are now denoted as BV_{HT}% and BV_{SG}%, respectively (*Table 3*). If, for example, the "top" 10 parents in this study were selected based on BV_{HT}%, expected gain would be 11% for height and 0.1% for SG (*Table 3*). Any gain in SG is an indirect response due to the covariance structure among HT, SG and PIN.

The calculation of BV's (from direct or indirect measures of traits of interest) is attractive because it allows the breeder flexibility to (1) choose among high BV parents for a combination of traits, and (2) avoid the use of a theoretically based i values (i.e., selection intensity tables), which may not reflect the exact distribution of the data. *Figure 1* presents the relationship between the predicted BV_{SG}% using PIN data in the index with HT (i.e., BV_{SG}%'s derived from Eq. [3], and that of BV of SG directly (i.e., BV_{SG}%'s derived from Eq. [1] using family mean SG effects). The less than perfect relationship reflects both the "errors" in using the PIN to predict BV for SG, plus the impact of a genetic covariance with HT (even though the genetic correlation of SG with HT was near zero [*Table 2*]). Low and high wood density families are predicted well, and only a few families are outliers in this regards (e. g., family #143, #1, #3, #103, #156, and #153) (*Figure 1*).

For index selection of HT and SG, the next step would be to multiply the g_i values (i. e., BV%'s from Eq. [3] [*Table 3*]) by some economic or technical weighting for each trait. The sum of the 2 products would provide an index score for each parent. These scores are unitless but would allow a comparison of families for multiple-trait improvement, assuming the technical weightings have some meaning to the breeder.

Conclusions

In these relatively young interior spruce trees apparently only small correlations exist between growth traits and SG at the phenotypic family level (zero at the genetic), but are moderate at the individual phenotypic tree level. It will be important to continue to assess these relationships in interior spruce to monitor possible changes in correlations as more "mature-type" wood is produced on the stems. It would also seem appropriate to increase the number of families sampled to overcome the effects of random genetic sampling and to reduce the standard errors of genetic correlation estimates among growth traits and SG. Nevertheless, if these near zero correlation estimates between growth and SG persist, or become slightly negative, it will still be possible (although more

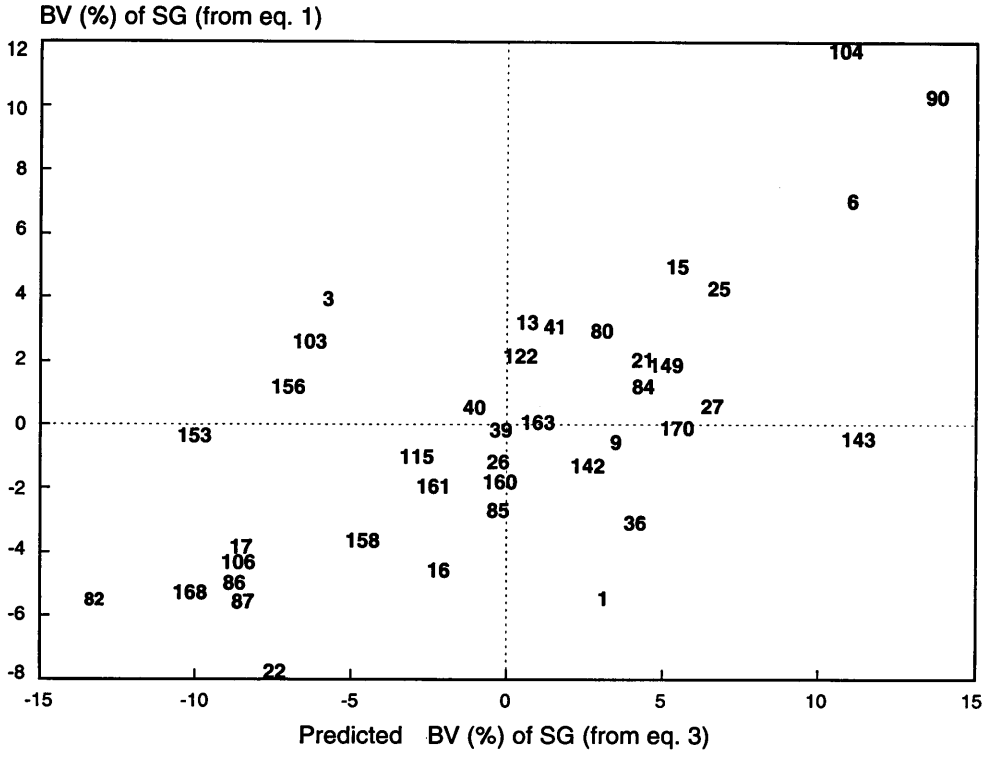

Figure 1. — Relationship between parental predicted breeding values for wood specific gravity (BV% of SG) from Eq. [1] and predicted breeding value of specific gravity using equation [3] (i. e., expected BV% of SG from PIN data with height in the index) for 40 open-pollinated interior spruce families in British Columbia. Values in graph are family code numbers from all 40 families, of which 20 (top and bottom 10 ranked families) are listed in *table 3.*

difficult) to achieve gains in both growth traits and wood SG in interior spruce by selecting parents that appear to "break" the correlations. Also, if correlations drastically change (i. e., become negative) after age 15 or greater, then any type of early selection for SG may prove quite ineffective. The decision, then, whether or not to include SG as a trait for selection before age 15 must be carefully considered. Follow-up investigations, using older material with a larger number of families, will be carried out to address these questions.

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Latitudinal Variation in Height and Phenology of Balsam Poplar

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Summary

Fifty clones from each of 4 provenances (Lat. 45° N to 53° N at Long. 90° W) were grown in 2 common garden tests at Lat. 48° N for 7 years and 5 years respectively. Provenance differences in height were mainly related to the period of shoot elongation, with the most southerly provenance (Lat. 45° N to 46° N) continuing elongation later and growing taller than northerly provenances. Clonal variation within provenances was also statistically significant, and broad-sense heritability estimates for height ranged from 0.04 to 0.19, depending upon degree of microsite variation within provenance blocks. Variation in spring bud break was mostly attributable to differences among clones within provenances, was under moderate genetic control (h^2 = 0.21 to 0.47), and generally was not related to the amount of height growth.

Key words: Shoot elongation, bud break, genetic variance.

Introduction

Balsam poplar (*Populus balsamifera* L.) is a wide ranging, predominantly boreal species. In previous work with the species we have noted low genetic differentiation among latitudinal provenances (northern Wisconsin to Hudson's Bay) with respect to isozyme characteristics (FARMER et al., 1988a), preformed root primordia (FARMER et al., 1989), dormancy relations (FARMER and REINHOLT, 1985), relative growth rate and net assimilation rate (SCHNEKENBURGER and FARMER, 1989) and spring dehardening (WATSON, 1990). Most variation in stomatal density and transpiration rate is accounted for by clones within provenances, but leaf size decreases with an increase in latitude (PENFOLD, 1991). On the other hand, CHARRETTE (1990) observed a south-north increase in the rate of shoot growth cessation in response to short photoperiods. In most of the above characteristics there is substantial genetic variation within provenances. Here we report on the pattern of genetic variation in juvenile growth in the first phase of a long-term common garden experiment. In it we test the hypotheses that: (1) there is major latitudinal variation in shoot growth which is mainly due to provenance differences in photoperiodic response, (2) provenances from south of the test site will grow over a longer period at the test site than local or more northern material and (3) within-population genetic variance in growth will be as large as inter-population variance.

Methods

In 1982 and 1983, stem cuttings from approximately 50 juvenile trees (genets) were collected in each of the following areas between Longitude 90° W and 91° W: northern Wisconsin (Lat. 45° N to 46° N), Thunder Bay, Ont. (48° N to 49° N), Pickle Lake, Ont. (50° N to 51° N), and the upper Severn River near Bearskin Lake (53° N to 54° N). Genets were selected at least 1 km apart to reduce the possibility of sampling more than 1 plant from a natural clone. Selection was thus not random, but neither was it biased with respect to observable tree characteristics. Cuttings were rooted in a greenhouse, then established in a nursery where several ramets of the resulting 50 clones per provenance were grown for 1 season.

In the spring of 1984 (year 1, the year of propagation), cuttings from these clones were rooted and grown in 750 ml SPENCER-LE-MAIRE containers filled with a peat-vermiculite mix. In July, they were transplanted in a field test the design for which is outlined in *table 1* as test. I. The test site is an imperfectly drained 2.8 ha area in Thunder Bay (48° N) which prior to test establishment was occupied by a stand containing balsam poplar, willows (*Salix* sp.), aspen (*Populus tremuloides* MICHX.), black spruce (*Picea mariana* (DU ROI) K. KOCH) and paper birch (*Betula papyrifera* MARSH.). Growth of natural balsam poplar and a lush ground cover of herbaceous species indicated that it was a suitable test site. The soil is loam to clay loam (20 cm to 30 cm) underlain by sands. Variation in elevation within the site is about 1 m.

The trees and shrubs were sheared in the winter of 1983 to 1984, and all debris was removed from the site. After regrowth was well underway in June 1984, the site was sprayed with glyphosate (12l/ha). Planting began about one month after treatment.

Each of the six replications in test I was a rectangle about 25 m x 100 m; 4 square provenance blocks were randomly located in each replication with the exception of 1 replication which contained only the 3 most southerly provenances. Three ramets of each of the 50 clones were randomly located within provenance blocks. Square spacing was 2 m x 2 m. After planting, vegetative competition (mostly grasses and sedges) was reduced for 3 years using hand equipment. Mortality was over 75% in some portions of 5 replications due to vegetative competition and poor drainage. These areas were deleted from the test; however no provenances were deleted from any replication and no clones were deleted from the test.

Total height was recorded annually for each plant from 1985 (year 2) to 1990. During the summers of 1986, 1987 and 1988, shoot elongation in a 10-clone sample from each provenance was observed. Measurements of terminal shoot length were made weekly on 2 ramets in each of 3 replications. These data were used to compute periodic rates (mm/day) for (1) the grand period of elongation in late

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