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GENETIC PARAMETERS OF HEIGHT AND DIAMETER OF INTERIOR SPRUCE IN BRITISH COLUMBIA

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ABSTRACT

Data from 406 open-pollinated interior spruce families selected from 3 selection units located in the East Kootenay, Prince George and Prince Rupert region of British Columbia (BC), Canada were used to estimate genetic parameters for cumulative height and diameter (DBH) at plantation ages up to 20 years. Variation among families in both traits was highly significant in all selection units and at all assessment ages, but the levels of genetic variability varied greatly among them. The estimates of individual, family, and within-family heritability for 15-year height ranged from 0.15 to 0.34, 0.61 to 0.84, and 0.12 to 0.28, respectively, among selection units. The corresponding estimates for 20-year DBH varied from 0.10 to 0.23, 0.50 to 0.81, and 0.08 to 0.18, respectively. In all three selection units, temporal variation in individual, family and within-family heritabilities of height displayed parallel patterns and they all started at the highest values at age 3, decreased to the lowest at about age 10, and raised at age 15. Genetic correlation between height and diameter was always positive and impressively strong (>0.87 at age 15). The estimated coefficients of age-age genetic correlation in height fit the logarithmic relationships (r_A = a + b (*LAR*) and r_A = a + b (*LAR*^{2})) very well ($R^2 > 0.94$) in all selection units but the prediction models of age-age genetic correlation developed in the Prince Rupert selection unit were apparently different from the others. The optimum plantation ages for early selection were calculated to be 15 and 16 years for Prince Rupert selection unit using the *LAR* and *LAR*^{2} prediction model, respectively, and 7 years for both the East Kootenay and Prince George selection units using both models. Overall, the Lambeth model (r_A = 1.02 + 0.308 (*LAR*)) developed based on phenotypic correlation of height in *Pinaceae* tends to underestimate the age-age genetic correlation in interior spruce in BC. Type-b genetic correlation between sites within East Kootenay and Prince George selection units was always positive and strong, but weak positive and even negative correlation was observed between sites in the Prince Rupert selection unit. This observation suggests that the first two selection units may need expansion while the third requires more regionalization for proper breeding and seed planning.

Key words: Interior spruce, *Picea glauca, Picea englemannii*, open-pollinated progeny test, heritability, genetic correlation, early selection, genotype x environment interaction

INTRODUCTION

White (*Picea glauca* (Moench) Voss) and Engelmann spruce (*P. engelmannii* Parry ex Engelm) form a complex of sympatric and allopatric populations covering a large portion of interior British Columbia (BC). Due to intensive introgressive hybridization, these two species share nearly identical characteristics ranging from morphology to wood property, and their woods are used interchangeably (Barton & Gardner 1957, Roche 1970). For management convenience, this white-Engelmann spruce complex is referred to as interior spruce in BC.

In the late 1960's, little was known about the genetics of interior spruce other than preliminary genecological information provided by Roche (1969). However, it was clear that spruce reforestation programs were going to expand considerably in the province, and that high quality artificial regeneration would be necessary (Kiss 1968). Accordingly, the need surfaced for a comprehensive breeding program aimed at producing sufficient quantities of genetically improved seeds to meet the anticipated regeneration demand. With the limited resources available at that time, it was impossible to initiate a breeding program that covers the entire natural range of the species. Meanwhile, it would be risky, or at least not efficient, to do so since there was such little genetic information on the species. Considering these problems, it was decided to divide the area into smaller, more manageable units and commence with the breeding program on a smaller scale (Kiss 1968). In 1968, the BC Forest Services Research Branch designated three selection units (or populations), that is, East Kootenay (EKSU), Prince George (PGSU), and Prince Ruport (PRSU) selection unit, across the entire interior spruce distribution in BC (Figure 1) and formed the primary spruce selection and testing series. Although the delineation was not based on a solid scientific basis, these populations were believed to cover the major genetic landscape of the species in the province. In addition, environmental conditions within the region covered by each selection unit were considered to be relatively homogeneous so that selected materials would not be subject to maladaptation.

In British Columbia, the main focus of the interior spruce genetic improvement program is growth potential. Therefore, the main objective of this study is to estimate the genetic parameters of height and diameter (at breast height) within the three selection units. The genetic parameters studied in this paper include the coefficient of additive genetic variation, individual, family, and within-family heritability, and additive genetic correlation between the two traits, between two ages of each trait and between two sites. Estimates of these genetic parameters are deemed crucial for 1) developing appropriate breeding and commercial propagation strategies (Namkoong *et al.* 1988, p.45; White 1987); 2) choosing proper selection methods and projecting the expected genetic improvement (NYQUIST 1991; ZOBEL & TALBERT 1984, p.136); 3) determining optimum selection age and target trait; 4) delineating seed planning (or breeding) zones (JOHNSON & BURDON 1990); and 5) predicting the breeding values of the tested materials.

Spruce breeding in BC has come to the stage of the second generation testing and selection. Old seed planning zones are being modified, producing seed orchards are subject to further rouging, and orchard seedlot rating has become mandatory. It is, therefore, timely to report the test results of these experiments which should provide a scientific basis for making sound decisions in tree breeding and other genetic resources management activities of interior spruce in the province.

MATERIALS AND METHODS

As illustrated in Figure 1, East Kootenay selection unit is located in the dry belt of the southeast corner of BC. The population is mostly high elevation Engemann spruce, with some influence of white spruce at lower elevations. One hundred and thirty-two plus-trees were selected in 1969 from latitudes 49°00' to 50°45'N and longitudes 114°30' to 116°30'W. Prince George selection unit is located in the Prince George area in the central interior region of the province. It is composed mostly of white spruce and possibly some small hybrid swarms of white and Engelmann spruce. A total of 178 plus-trees were selected in 1968, covering an area between latitudes 52°47' to 54°06' N and longitudes 121°26' to 122°38' W. Prince Rupert selection unit is situated in the northwest interior region of the province and is composed mostly of white spruce with introgression from Sitka spruce (*Picea sitchensis* (Bong) Carr.). Plus-tree selection was accomplished in 1970 and a total of 134 trees were selected from an area between latitudes 53°42' to 55°23' N and longitudes 124°55' to 127°59' W. Visual size (height and diameter) was the primary selection criterion, while form and branching traits were the secondary criteria (KISS 1976).

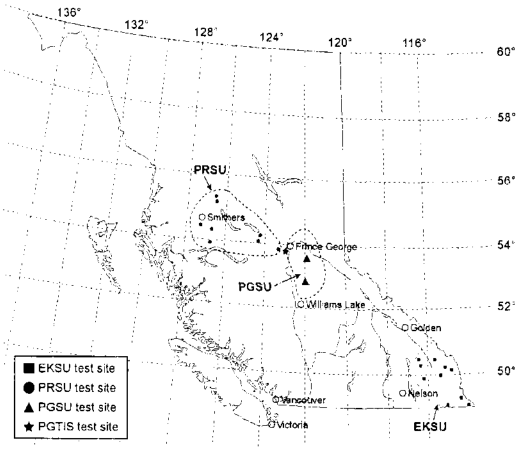

Figure 1. Locations of selection units and test sites.

Open-pollinated progeny test trials were established at 14, 2, and 22 local sites for EKSU, PGSU and PRSU selections, respectively. Trees from all the three selection units were also tested at a common site located at the Prince George Tree Improvement Station (PGTIS) near Prince George. All the tests were established using 2+1 bare root seedlings and a randomized complete block design. The number of blocks planted at each site ranged from 2–4 in EKSU, 10 in PGSU, and 1–8 in PRSU. Ten-tree row plots with an initial spacing of 2.5 x 2.5 m were applied at all the test sites. Due to lack of sufficient seedlings, only 110, 168 and 128 families were tested in EKSU, PGSU and PRSU, respectively.

Height (*HT*) was measured to the nearest centimeter from the ground to the tip of the tree after 3, 6, 10, 15 and 20 years of planting in EKSU and PRSU, while in PGSU the 20-year height measurements were not taken. In the absence of a leader, measurement was made to the height of the tip of the lateral branch furthest above the ground. Diameter at breast height (*DBH*) was measured to the nearest millimeter at 15 and 20 years of plantation age in all three selection units. The traits analyzed in the study are referred to as *HT3*, *HT6*, *HT10*, *HT15*, *HT20*, *DBH15*, *DBH20*, where numbers represent plantation ages.

Because of unfavorable environmental conditions following planting and heavy grass competition, initial survival at four sites in EKSU was very poor. Those four trials were considered failures and were excluded from analysis. For PRSU testing, the 20-year measurements were conducted only at the best 20 replications according to the 15-year height ranking due to lack of funding. Those 20 replications were distributed at 9 sites including PGTIS and were the only ones included in this study. Besides the 134 plus-trees, there are 17 trees that were selected from PRSU based on characters other than size. They were excluded from genetic parameter estimation since our present interest in genetic improvement is timber productivity (i.e. size). There are also 22 families selected from various eastern Canadian sources and tested at some sites in PRSU. Their performance was compared with that of the local PRSU families but they were not included in genetic parameter estimation since they are not from the population of interest.

Analysis of variance (ANOVA) for each variable and analysis of covariance (ANCOVA) for each pair of variables were performed in each selection unit using plot means and according to the format in Table 1. The mean squares and mean cross-products were calculated using SAS GLM MANOVA procedure and the type III estimable functions (SAS Institute 1988). SATTERTHWAITE's (1946) approximate test procedure was used to synthesize mean squares and mean cross-products for testing the effects in the model. All the effects in the model were assumed random. Variance and covariance components were estimated by equating the observed mean squares and mean cross-products to those expected and solving the ensuing equations. Open-pollinated families were assumed to be truly half-sibs, and therefore, family variance and covariance components were assumed to estimate one quarter of the additive genetic variance and covariance, respectively. Heritabilities for individuals (h_i^2), family means (h_f^2) and within-family deviations (h_w^2) were estimated using the following formulas:

$$h_i^2 = \frac{\sigma_A^2}{\sigma_I^2} = \frac{4\sigma_f^2}{\sigma_{wp}^2 + \sigma_p^2 + \sigma_{fs}^2 + \sigma_f^2},$$

$$h_f^2 = \frac{0.25\sigma_A^2}{\sigma_F^2} = \frac{\sigma_f^2}{(\sigma_e^2 + k_5\sigma_{fs}^2)/k_6 + \sigma_f^2}, \text{ and}$$

$$h_w^2 = \frac{0.75\sigma_A^2}{\sigma_F^2} = \frac{3\sigma_f^2}{\sigma_{wp}^2 + \sigma_p^2 + \sigma_{fs}^2}.$$

Where, σ_A^2 is the additive genetic variance, and σ_I^2, σ_F^2, σ_W^2 are the individual, family, and within-family phenotypic variances, respectively. σ_{wp}^2 is the within-plot mean square calculated separately. σ_p^2 is the plot variance component calculated as $\sigma_e^2 - (\sigma_{wp}^2/H)$, H is the harmonic mean of number of trees per plot (see Table 1 for other notations).

Type-a genetic correlation, genetic correlation between two traits measured on the same individuals (BURDON 1977), was estimated as

$$r_A = \frac{cov(xy)}{\sqrt{\sigma_x^2\sigma_y^2}}.$$

Where, *cov*(*xy*) is the family covariance component

Table 1. Format of analysis of variance and covariance based on plot means in each selection unit (all effects are assumed to be random).

Source of variation	Degrees of freedom	Expected mean squares and cross-products
Site	$(l-1)$	$\sigma_e^2 + k_1\sigma_{fs}^2 + k_2\sigma_{r/s}^2 + k_3\sigma_s^2$
Replication / site	$l(r-1)$	$\sigma_e^2 + k_4\sigma_{r/s}^2$
Family	$(f-1) - n_{mf}$	$\sigma_e^2 + k_5\sigma_{fs}^2 + k_6\sigma_f^2$
Family x site	$(r-1)(f-1) - n_{m(fs)}$	$\sigma_e^2 + k_7\sigma_{fs}^2$
Error	$l(r-1) - n_{mp}$	σ_e^2

where, l, r, f, n_{mf}, $n_{mf(s)}$, and n_{mp} are the members of test sites, replications at each site, families, missing families, missing family-by-site cells, and missing plots, respectively.

between traits x and y, and $\sigma^2_x$and σ^2_y are the family variance components of the two traits, respectively. Estimation of standard errors for heritabilities and genetic correlation was according to BECKER (1975).

Estimated age-age genetic correlation coefficients of height were used to fit the Lambeth model (LAMBETH 1980):

$$r_{A_{jm}} = a + b(LAR).$$

Where, LAR = natural log of age j over age m ($j < m$). Recently, LAMBETH and DILL (2001) found that LAR^2 was a better predictive independent variable than LAR in their study of loblolly pine LAR^2 was also used in this study.

Assuming both the selection intensities and heritabilities are the same at the juvenile and mature ages, the efficiency of early selection (E) in terms of expected gain per year of tree improvement effort could be quantified as

$$E = r_{A_{jm}} \frac{T_m}{T_j}.$$

Where, T_j and T_m are the generation time for juvenile and mature selection, respectively ($T_j = 10$ when $j \leq 7$ or $= j + 3$ when $j > 7$. T_m = rotation age + 3 = 83).

Burdon's Type-b genetic correlation (i.e., genetic correlation between performance of the same trait in two environments, BURDON 1977) was employed to quantify the extent of true family-by-site (G´E) interaction (i.e., lack of perfect positive correlation of family ranking between test sites). It was estimated using the following formula (BURDON 1991):

$$r_{gij} = \frac{Cov_{gij}}{\sqrt{MS - \sigma^2_{ei}/h_i)(MS_j - \sigma^2_{ej}/k_j)}}.$$

Where, Cov_{gij} = covariance between the means of families common to both sites (family means were - calculated using "the mean of plot means" method), MS_i and MS_j = the mean squares for the inputted means of the common families at the respective sites, $\sigma^2_{ei}$and σ^2_{ej}= the error variances for testing family effects in ANOVA using all families represented at the respective sites, and k_i and k_j = the coefficients for family variance components in the expected mean squares for families in the ANOVA at the respective sites.

RESULTS AND DISCUSSION

Both height and diameter growth tended to increase across the three selection units from southeast to northwest. The overall 15-year mean height was 215 cm, 244 cm and 306 cm, and the 20-year mean diameter was 51 mm, 56 mm and 70 mm in the East Kootenay (XIE *et al.* 1997), Prince George, and Prince Rupert Selection Unit (Table 2), respectively. This growth pattern has a strong genetic basis as evidenced at Prince George Tree Improvement Station (PGTIS) near Prince George, where progeny from all the three selection units were tested and the environmental conditions and silviculture treatments were similar. At PGTIS, 15-year mean height was 250 cm, 273 cm and 331 cm, and the 20-year mean diameter was 71 mm, 66 mm and 77 mm for progeny from EKSU (XIE *et al.* 1997), PGSU, and PRSU, respectively. Progeny from the eastern Canadian sources survived equally well as those from the local population of PRSU (data not presented) but grew significantly ($p < 0.05$) faster (506 cm vs. 472 cm in 20-year height and 74 mm vs. 70 mm in 20-year diameter).

Variation among sites in both height and diameter were highly significant within all selection units and accounted for the largest proportions of total variation among the non-error variation sources (except *HT15* in PGSU) (Table 2). It was evidenced in all the three selection units that site conditions had greater effect on growth than on survival.

Significant among-site differences in the most recent measurements of height and diameter were detected for 87 % and 84 % of the tested families in EKSU (Xie *et al.* 1997), 80 % and 90 % in PGSU and 33 % and 37 % in PRSU. However, only 74 %, 40 %, and 25 % of the families in the respective selection units demonstrated significant among-site differences in survival at the plantation age of 20 years (data not presented). In addition, faster growing families tended to have lower levels of across-site variability in all the traits investigated and growth and survival were positively correlated (after the family with the poorest survival in PRSU was removed). These observations suggest that superior families not only grew faster and survived better but also performed more uniformly across different site environments.

Among-family variation in both height and diameter were statistically highly significant ($p < 0.0001$) at all the assessment ages in all the selection units. It accounted for about 3 to 6 % and 2 to 4 % of the total variation in the most recent measurements of height and diameter, respectively (Table 2). Compared with the other two selection units, PRSU demonstrated the lowest additive genetic variability at all assessment ages as measured by the coefficients of additive genetic variation (CV_A) (Figure 2). In all the three selection units, CV_A for height declined to the lowest level at plantation age 10, raised to age 15 and declined again thereafter. CV_A for DBH also demonstrated declining trends from age 15 to 20 (Figure 2). The estimates of

Table 2. Estimates of the means, variance components (as a percent of total variance), and heritabilities of *HT20* (or *HT15*) and *DBH20* (numbers in brackets are probabilities of statistical significance).

Estimation of Parameters	East Kootenay Selection Unit			Prince George Selection Unit			Prince Rupert Selection Unit		
	d.f.	*HT20* (cm)	DBH20 (mm)	d.f.	*HT15* (cm)	DBH20 (mm)	d.f.	*HT20* (cm)	DBH20 (mm)
Mean		354	51		215	56		472	70
Variance component									
σ_s^2	9	30.6 (0.0001)	29.0 (0.0001)	22	14.5 (0.0001)	21.9 (0.0001)	8	15.9 (0.0001)	15.6 (0.0001)
$\sigma_{r/s}^2$	13	2.1 (0.0001)	2.0 (0.0001)	27	4.1 (0.0001)	3.5 (0.0001)	11	6.7 (0.0001)	5.4 (0.0001)
σ_f^2	109	5.5 (0.0001)	2.8 (0.0001)	167	6.3 (0.0001)	4.3 (0.0001)	126	3.1 (0.0001)	2.0 (0.0001)
σ_{fs}^2	954	0.0 (0.8257)	0.0 (0.5222)	329	0.8 (0.0002)	0.7 (0.0005)	831	0.3 (0.3446)	0.0 (0.9732)
σ_p^2	1294	12.9 (0.0001)	12.4 (0.0001)	4170	18.4 (0.0001)	15.5 (0.0001)	1128	12.8 (0.0001)	13.5 (0.0001)
σ_{wp}^2	12943	48.9	53.8	38120	55.9	54.2	35912	61.2	63.5
Heritability									
h_i^2		0.32	0.16		0.31	0.23		0.16	0.10
h_f^2		0.81	0.68		0.84	0.81		0.62	0.50
h_w^2		0.26	0.13		0.25	0.18		0.13	0.08

CV_A in interior spruce were higher than those reported for many other forest tree species (CORNELIUS 1994).

As indicated by the estimates of individual heritability (Table 2), additive genetic variation accounted for 32 % and 16 % of the total phenotypic variation of individual trees in *HT20* and *DBH20* in EKSU (h_i^2 = 0.32 and 0.16), while 31 % and 23 % (h_i^2 = 0.31 and 0.23 for *HT15* and *DBH20*, respectively) in PGSU. Prince Rupert selection unit demonstrated the lowest heritabilities for both height and diameter at all levels (i.e., individual, family and within family) and at all assessment ages as compared to the other two selection units (Table 2, Figure 3). Temporal variation in individual, family and within-family heritabilities of height displayed parallel patterns that are similar in all selection units. The general trends were that all the heritabilities started at the highest values at age 3, decreased to the lowest at about age 10, and raised at age 15. Slight declines from age 15 to 20 were observed in EKSU while the opposite trends were evidenced in PRSU. The age trends of heritabilities detected in interior spruce in the present study were very similar to those observed in other conifers such as interior lodgepole pine (XIE & YING 1996), ponderosa pine (FRANKLIN 1979) and white spruce in east Canada (MAGNUS-

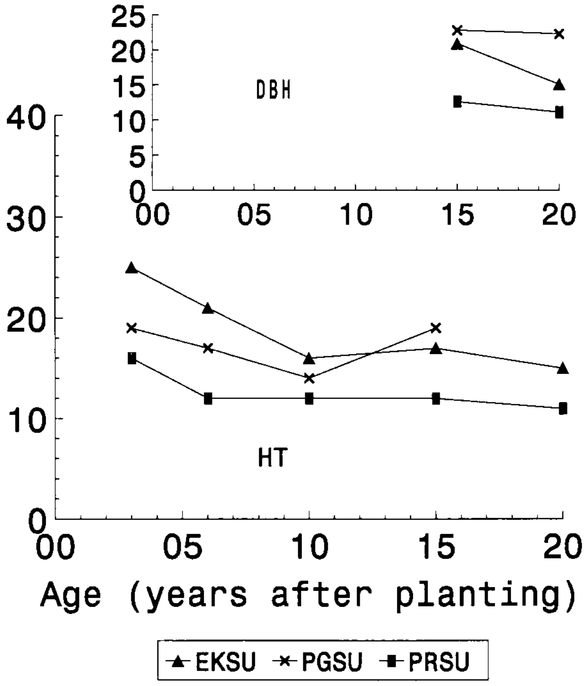

Figure 2. Age trends in the coefficients of additive genetic variation (CV_A %) in height and diameter. Coefficients of additive genetic variation were calculated as $\sqrt{4\sigma_f^2}/\bar{x}\times 100$, where $\bar{x}$ is the test mean across all sites in the selection unit.

Table 3. Estimates of Type-a genetic correlation coefficients between traits (numbers below the diagonal are standard errors).

Trait	East Kootenay Selection Unit						
	HT3	*HT6*	*HT10*	*HT15*	*HT20*	*DBH15*	*DBH20*
HT3		0.96	0.92	0.89	0.84	0.90	0.82
HT6	0.0006		0.98	0.97	0.93	0.95	0.87
HT10	0.0013	0.0004		0.99	0.97	0.96	0.90
HT15	0.0016	0.0005	0.0002		0.99	0.96	0.91
HT20	0.0024	0.0012	0.0006	0.0002		0.96	0.92
DBH15	0.0018	0.0010	0.0008	0.0008	0.0009		0.97
DBH20	0.0031	0.0025	0.0022	0.0019	0.0017	0.0008	

Trait	Prince George Selection Unit						
	HT3	*HT6*	*HT10*	*HT15*	*HT20*	*DBH15*	*DBH20*
HT3		0.95	0.88	0.81	–	0.84	0.82
HT6	0.008		0.98	0.92	–	0.93	0.91
HT10	0.020	0.004		0.98	–	0.96	0.96
HT15	0.031	0.013	0.003		–	0.94	0.97
HT20	–	–	–	–		–	–
DBH15	0.027	0.013	0.007	0.010	–		0.98
DBH20	0.029	0.016	0.007	0.005	–	0.003	

Trait	Prince Rupert Selection Unit						
	HT3	*HT6*	*HT10*	*HT15*	*HT20*	*DBH15*	*DBH20*
HT3		0.89	0.64	0.47	0.36	0.49	0.28
HT6	0.027		0.89	0.83	0.68	0.78	0.62
HT10	0.077	0.031		0.96	0.89	0.87	0.75
HT15	0.098	0.046	0.012		0.99	0.87	0.81
HT20	0.110	0.076	0.031	0.003		0.82	0.81
DBH15	0.111	0.066	0.041	0.040	0.055		0.94
DBH20	0.127	0.096	0.071	0.054	0.054	0.023	

SEN 1993).

Genetic correlation between height and diameter and between ages (i.e., Type-a genetic correlation) was always positive and impressively strong in EKSU and PGSU but much weaker in PRSU (Table 3). In all the three selection units, the estimated coefficients of age-age genetic correlation of height fit the logarithmic relationships very well but both the intercept (*a*) and the regression slope (*b*) varied considerably among selection units (Table 4). Large site to site, test series to test series and population to population variation in both parameters of the prediction models of age-age genetic correlation has also been reported in other studies (GWAZE *et al.* 2000; LAMBETH & DILL 2001). While the prediction models of age-age genetic correlation for the EKSU and PGSU populations were similar, they were apparently different from that of PRSU population. Besides other possible reasons, there might be a genetic basis for this observation. Due to intensive introgressive hybridization with Sitka spruce as mentioned earlier, PRSU population may have genetically differentiated from those of EKSU and PGSU, and therefore, has different structure of age-age genetic correlation. Overall, the estimated age-age genetic correlation in interior spruce is much stronger than those of other species reported for similar ages, such as loblolly pine (0.58 between 5 and 15 year height, FOSTER 1986), interior lodgepole pine (0.51 between 7 and 24 year heights, XIE & YING 1996), and slash pine (0.79 between 5 and 15 year heights, HODGE & WHITE 1992). From the parameters of the prediction model for the combined data of the three selection units (Table 4), one also can see that the LAMBETH (1980) model developed based on phenotypic correlation of height in *Pinaceae* (i.e., $r_A = 1.02 + 0.308\,LAR$) tends to underestimate the age-age genetic correlation in interior spruce in BC. Similar results have also been reported in other species such as jack pine (RIEMENSCHNEIDER 1988),

Table 4. Intercepts (*a*), slopes (*b*) and the coefficients of determination (R^2) of linear regression models for predicting age-age genetic correlations of height in interior spruce in BC.

Selection Unit	Independent variable					
	LAR			LAR^2		
	a	*b*	R^2	*a*	*b*	R^2
EKSU	1.03	0.090	0.94	0.99	–0.042	0.98
PGSU	1.05	0.144	0.99	0.99	–0.072	0.99
PRSU	1.14	0.400	0.98	0.97	–0.182	0.97
Selection units combined	1.08	0.230	0.50	0.99	–0.107	0.51

*) $LAR = \log_e\left(\frac{Age_j}{Age_m}\right)$, where, $j < m$

Table 5. Estimates of type-b genetic correlation coefficients for height (above diagonal) and diameter (below diagonal).

Site	East Kootenay Selection Unit *(HT20 & DBH20)*										
	BC	LC	LP	JC	HC	WC	PC	EWR	GC	RC	RR
BC		0.89	0.90	0.89	0.87	0.84	0.70	0.88	0.79	0.44	0.85
LC	0.90		0.89	0.88	0.72	0.79	0.53	0.99	0.77	0.10	0.93
LP	0.63	0.73		0.94	0.75	0.82	0.79	0.95	0.84	0.33	0.85
JC	0.84	0.96	0.94		0.89	0.71	0.61	0.92	0.87	0.62	0.91
HC	0.88	0.65	0.62	0.85		0.73	0.67	0.64	0.57	0.45	0.74
WC	0.76	0.85	0.96	0.82	0.75		0.68	0.70	0.79	0.34	0.80
PC	0.54	0.39	0.85	0.32	0.32	0.52		0.64	0.57	0.74	0.73
EWR	0.80	1.10	0.97	0.92	0.52	0.71	0.60		0.88	0.42	0.92
GC	0.72	0.77	0.68	0.87	0.47	0.79	0.48	0.79		0.42	0.78
RC	0.50	0.07	0.26	0.87	0.27	0.15	0.76	0.19	0.52		0.14
RR	0.81	1.04	1.03	0.96	0.64	0.86	0.73	0.98	0.85	0.07	

Site	Prince George Selection Unit *(HT15 & DBH20)*		
	BL	QL	RR
BL		0.90	0.88
QL	0.82		0.91
RR	0.91	0.88	

Site	Prince Rupert Selection Unit *(HT20 & DBH20)*								
	RR	SL	DC	CL	TR	Q	NL	TL	AL
RR		0.54	0.48	0.25	0.13	0.58	0.40	0.38	0.57
SL	0.58		0.38	0.02	0.19	0.30	0.30	0.27	0.39
DC	0.38	0.26		0.15	0.16	0.09	0.55	0.26	0.70
CL	0.34	0.08	–0.02		0.03	0.30	0.32	0.17	0.62
TR	0.13	0.11	0.07	0.46		0.33	0.18	0.03	0.43
Q	0.36	0.24	0.03	0.21	0.16		0.46	0.51	0.41
NL	0.50	0.35	0.89	0.39	0.24	0.47		0.35	0.61
TL	0.28	0.17	0.28	0.04	–0.07	–0.52	0.18		0.38
AL	0.94	0.35	0.63	0.67	0.49	0.55	1.06	0.17	

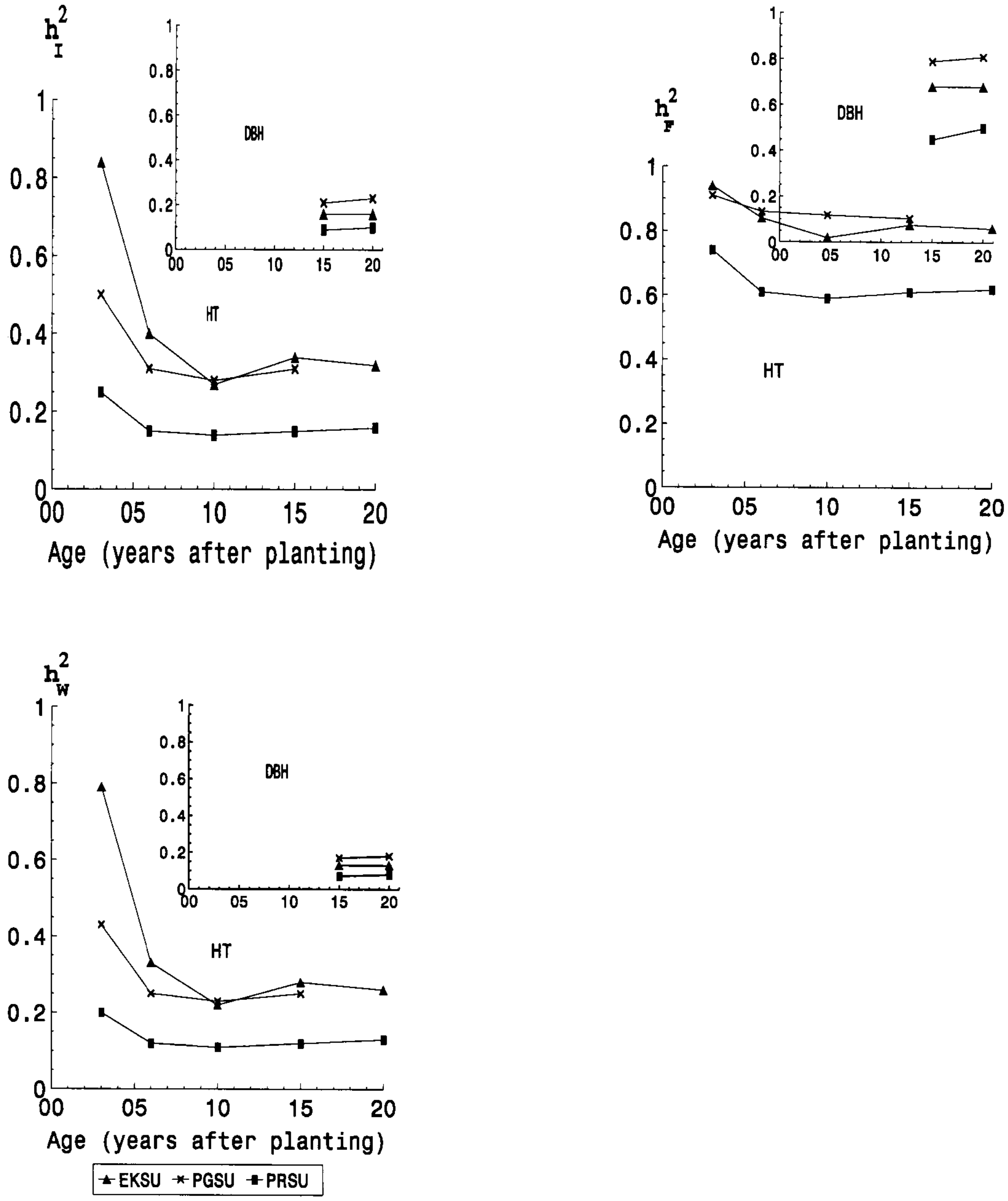

Figure 3. Age trends in individual (h_i^2), family (h_f^2) and within-family (h_w^2) heritabilities of height (*HT*) and diameter (*DBH*).

slash pine (HODGE & WHITE 1992) and lodgepole pine (XIE & YING 1996).

In their recent study of loblolly pine, LAMBETH and DILL (2001) found that using LAR^2 as the independent variable in the regression yielded a consistently better fit than using *LAR*. In the present study, however, such observation cannot be confirmed (Table 4). The optimum plantation ages of early selection predicted from both models for each of the three selection units were either exactly the same (7 years for EKSU and PGSU) or very similar (15 and 16 years for PRSU) (Figure 4). The current practice of making selection at plantation age 10 years seems to be conservative in EKSU and PGSU but a little too early in PRSU. Thus, it is particularly important to rogue the seed orchards that target the Prince Rupert selection unit based on older test information.

GxE interaction appears to be weak in the East Kootenay selection unit. No negative type-b genetic correlation was detected between any pairs of sites at any assessment ages. Although the coefficients of type-b genetic correlation for height declined as tests aged

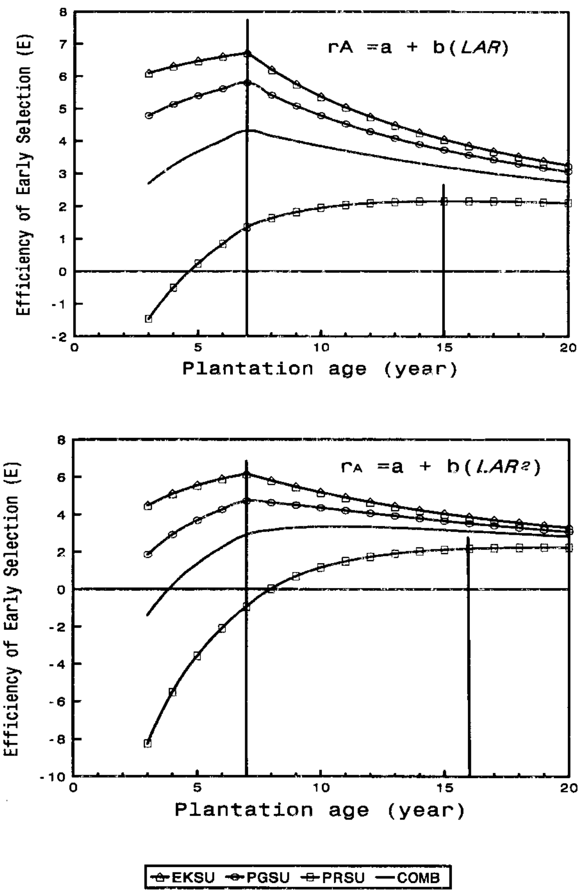

Figure 4. Expected genetic gain per year by selection at early ages relative to that at the mature age of 80 years.

($\bar{r}_{A_{ij}}$ =1.05, 1.00, 0.78, 0.76, and 0.72 at age 3, 6, 10, 15 and 20, respectively), they were generally high even at age 20 (Table 5). By excluding Roche Creek where the additive genetic variance vanished, the average coefficients of type-b genetic correlation for *HT* and *DBH* at age 20 elevated to 0.79 and 0.76, respectively. There was no evidence of any strong GxE interactions between sites located in the old East Kootenay Acidic and Calcareous zones (see XIE *et al.* 1997 for the assignment of sites to different zones). The average type-b genetic correlation coefficients between sites located in the two zones were 0.84 for both 20-year height and diameter. GxE interaction was very weak even between the test site at PGTIS, near Prince George, and those within the East Kootenay selection unit. The average type-b genetic correlation of the same families planted at PGTIS and East Kootenay sites was 0.82 for 20-year height and 0.88 for 20-year diameter. Those observations suggest that it is not only unnecessary to manage the old Acidic and Calcareous zones separately, but EKSU could be combined with neighboring areas to form a larger breeding zone (or seed planning zone). Minimum GxE interactions were also observed between sites in the Prince George selection unit, with an average coefficient of type-b genetic correlation of 0.90 in *HT15* and 0.87 in *DBH20* (Table 5). Comparing to EKSU and PGSU, Prince Rupert selection unit demonstrated much stronger GxE interactions (Table 5). The average coefficients of type-b genetic correlation were 0.34 and 0.32 in *HT20* and *DBH20*, respectively. The nine test sites are distributed in five old seed planning zones (ILLINGWORTH & SZIKLAI 1993), and therefore, the stronger GxE interactions are expected.

CONCLUSIONS

In all the three selection units studied, interior spruce demonstrated higher levels of additive genetic variability and similar heritabilities in both height and diameter compared with other conifer species. This indicates that the ongoing breeding (focus on general combining abilities) and production (open-pollinating seed orchards) programs in British Columbia are appropriate and the expected gain in timber production is promising. The observed outstanding performance of east Canadian white spruce as compared to the local interior spruce in the province suggests that extra gain may be achieved by infusing genes from superior east Canadian sources into the interior spruce breeding program in BC.

Positive and strong genetic correlation between height and diameter and between ages suggests that there is great potential to increase volume gain per unit time by making selection based on height at an early age. It is particularly beneficial that faster growing trees are better survivors and perform more uniformly across different site environments.

The current practice of evaluating test materials at plantation age of 10 years tends to be conservative in the East Kootenay and Price George selection units but a little too early in the Prince Rupert selection unit.

GxE interaction results indicate that certain extent of expansion of the East Kootenay and Prince George selection units is biologically justifiable. While, more regionalization may be needed in the Prince Rupert selection unit for proper breeding and seed planning.

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