# Heritabilities, Age-Age Correlations, and Early Selection in Lodgepole Pine (*Pinus contorta* ssp. *Latifolia*)

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## Abstract

Height, diameter at breast height and stem volume of 610 open-pollinated lodgepole pine families from 42 provenances covering the entire interior range of the species in Canada were measured periodically up to 20 years (age 24 from seed) at a provenance-family plantation in central British Columbia. Genetic variation in growth was large at both provenance and family levels. Provenance effect was always greater than family effect and the difference tended to increase as the test aged. Estimates of heritabilities for provenance means, family means, individual values, and within-family deviations were high, ranging from 0.77 to 0.97, 0.41 to 0.50, 0.28 to 0.42, and 0.22 to 0.35, respectively. Age-age correlations were strong and always positive, varying from 0.85 to 1.00 for provenance means and from 0.51 to 0.98 for additive genetic effects. Genetic age-age correlations demonstrated a strong linear relationship with the natural logarithm of the juvenile-mature age ratio. The expected annual genetic gain was maximised by selection at the earliest assessment ages (i.e., 7 years for height and 14 years for diameter and stem volume) for stem volume at age 24 years, regardless of the selection schemes. Selection based on stem volume was always more efficient than based on height or diameter alone. High heritabilities, strong positive age-age genetic correlations, and early sexual maturity of lodgepole pine suggest a great potential of early selection in this species.

*Key words: Pinus contorta* ssp. *latifolia,* heritability, age-age correlation, early selection, accelerated breeding.

*FDC:* 165.4; 232.11; 174.7 *Pinus contorta.*

## Introduction

Maximising genetic gain per unit time is the ultimate objective of all applied tree improvement programs (Zobel and Talbert, 1984). Forest trees are typical of long rotations and delayed reproductive maturity, and therefore long breeding cycles. In order to speed up breeding progress, the number of years required for each generation of selection and breeding must be reduced. Making selection at early ages is a common practice aiming to shorten breeding cycles in advanced generation tree improvement programs. Besides accelerating breeding progress, selection at early ages may also offer other advantages such as smaller genetic tests, easier measurement, greater adaptability to changing demands, and quicker delivery of genetic gain to the production population (Lambeth, 1980). However, the success of early selection is determined to a large extent by the heritabilities of the juvenile and mature traits and their genetic correlation. The expected increase in genetic gain per unit time through early selection can only be realised if both juvenile and mature traits are heritable and well correlated (Falconer, 1981). Results from previous studies on the efficiency of early selection are either supportive or discouraging. For a sound evaluation of the effectiveness of early selection and a wise choice of the optimum selection ages, a thorough knowledge of the heritabilities of juvenile and mature traits and age-age genetic correlations is of necessity.

Lodgepole pine (*Pinus contorta* ssp. *latifolia*) is one of the most important commercial forest trees in British Columbia. Its annual planting has been increasing steadily since mid 1960s and is expected to exceed 65 million trees by the turn of the century (Albricht, 1993). Genetic improvement of lodgepole pine was not initiated until mid 1970's in the province and the estimated annual production of genetically improved seedlings at year 2000 is only 9 million (Albricht, 1993). Due to the long rotation age of lodgepole pine (Smithers, 1961) and urgent need of genetically improved seed for reforestation, there is a great desire of accelerating the breeding progress of the species. In this study, we use the growth data from a 20-year-old provenance-family plantation located in central British Columbia to estimate the heritabilities and age-age correlations of various growth traits and to evaluate the potential of early selection in this species.

## Materials and Methods

### *Test Materials and Experimantal Design*

A total of 610 open-pollinated families from 42 provenances that cover the entire interior range of lodgepole pine in Canada was used in this study (see Xie and Ying, 1995, for locations of provenance samples). The test plantation was established with 4-years-old seedlings at a low-elevation site near Red Rock, Prince George, British Columbia (lat. 53°46'N, long. 122°42'W. elev. 620 m ) in 1973. Seedlings were planted 3.7 m apart in 2 x 3 rectangular plots (i.e., 6 seedlings per plot) with 3 replications. A compact-family (split-plot) design was employed in which provenances were designated as the main plot and families within provenances as the subplots. Initially, 53 provenances and 15 families per provenance (except for 7 provenances that have 8 to 14 families each) were planted. In this study, 11 provenances demonstrating apparent maladaptation were excluded. Moreover, only those trees survived at age 24 (from seed) were used for the analysis of growth data, including those from earlier assessments.

### *Data Collection and Analysis*

Height (HT) was measured to the nearest cm when seedlings were 7 years and 10 years old, and to the nearest dm at ages 14, 19 and 24. Diameter at breast height (DBH) was measured to the nearest mm when trees were 14, 19 and 24 years old. Stem volume (VOL) was estimated according to Kovats (1977). The traits analysed in the study are referred to as HT7, HT10, HT14, HT19, HT24, DBH14, DBH19, DBH24, VOL14, VOL19, and VOL24, where numbers indicate seedling ages from seed.

Analysis of variance (ANOVA) and covariance (ANCOVA) were conducted for each trait according to the format in *table 1* based on individual values. All effects in the model were assumed to be random. Mean squares and mean cross-products were calculated using the GLM procedure and the type III estimable functions (SAS Institute, 1988). Satterthwaite's (1946) approximate test procedure was used to synthesise appropriate mean squares and mean cross-products for testing the effects in the model.

*Table 1.* – Format of analysis of variance based on individual trees[1]).

| Source of Variation | D.F. | Expected mean squares and mean cross-products[2] |
|---|---|---|
| Replication (r) | 2 | $\sigma_e^2 + k_1\sigma_{rf(p)}^2 + k_2\sigma_{rp}^2 + k_3\sigma_r^2$ |
| Provenance (p) | 41 | $\sigma_e^2 + k_4\sigma_{rf(p)}^2 + k_5\sigma_{rp}^2 + k_6\sigma_{f(p)}^2 + k_7\sigma_p^2$ |
| Replication x Procenance (rp) | 82 | $\sigma_e^2 + k_8\sigma_{rf(p)}^2 + k_9\sigma_{rp}^2$ |
| Family / Provenance (f(p)) | 568 | $\sigma_e^2 + k_{10}\sigma_{rf(p)}^2 + k_{11}\sigma_f^2$ |
| Replication x Family/Provenance (rf(p)) | 913 | $\sigma_e^2 + k_{12}\sigma_{rf(p)}^2$ |
| Error (e) | 5990 | $\sigma_e^2$ |

[1]) all effects are considered as random.

[2]) $k_1 = 3.13$; $k_2 = 35.51$; $k_3 = 1490.90$; $k_4 = 3.45$; $k_5 = 43.42$; $k_6 = 8.98$; $k_7 = 130.23$; $k_8 = 3.53$; $k_9 = 43.05$; $k_{10} = 4.12$; $k_{11} = 10.83$; $k_{12} = 4.44$.

The variance and covariance components for open-pollinated families within provenances were assumed to estimate one-quarter of the additive genetic variance ($\sigma_A^2$) and covariance, respectively. Heritabilities for provenance means ($h_p^2$) were calculated as

$$h_p^2 = \frac{\sigma_p^2}{\sigma_{Prov}^2} = \frac{\sigma_p^2}{(\sigma_e^2 + k_4\sigma_{rf(p)}^2 + k_5\sigma_{rp}^2 + k_6\sigma_{f(p)}^2)/k_7 + \sigma_p^2},$$

while, heritabilities for family means ($h_f^2$), individual values ($h_i^2$) (or narrow-sense heritability), and within-family deviations ($h_w^2$) within provenances were estimated using the following formulas:

$$h_f^2 = \frac{1/4\sigma_A^2}{\sigma_F^2} = \frac{\sigma_{f(p)}^2}{(\sigma_e^2 + k_{10}\sigma_{rf(p)}^2)/k_{11} + \sigma_{f(p)}^2},$$

$$h_i^2 = \frac{\sigma_A^2}{\sigma_I^2} = \frac{4\sigma_{f(p)}^2}{\sigma_e^2 + \sigma_{rf(p)}^2 + \sigma_{f(p)}^2}, \text{ and}$$

$$h_w^2 = \frac{3/4\sigma_A^2}{\sigma_W^2} = \frac{3\sigma_{f(p)}^2}{\sigma_e^2 + \sigma_{rf(p)}^2}.$$

Where, $\sigma_{Prov}^2$, $\sigma_F^2$, $\sigma_I^2$, $\sigma_W^2$, are phenotypic variances of provenance means, family means, individual values, and within-family deviations, respectively (see *Table 1* for other notations). Estimates of $h_f^2$, $h_i^2$, *and* $h_w^2$, were used for calculate expected response from family, individual (or mass), and within-family selection, respectively, made within provenances, and were assumed to be applicable to all provenances.

Genetic correlation between traits at both provenance ($r_p$) and family ($r_A$, additive genetic correlation) levels was estimated as:

$$r_p \text{ or } r_A = \frac{\mathrm{cov}(xy)}{\sigma_x\sigma_y},$$

where, cov($xy$) is the provenance or family covariance component between the juvenile and mature traits $x$ and $y$, and $\sigma_x$ and $\sigma_y$ are the square roots of provenance or family variance components of the two traits, respectively. Estimation of standard errors for heritabilities and genetic correlations was according to BECKER (1975).

The efficiency of early selection ($E$) in terms of gain per year of tree improvement effort was quantified as

$$E = \frac{R_j / T_j}{R_m / T_m}.$$

Where $R_j$ is the predicted response in the mature trait after selection on the juvenile trait and $R_m$ is the predicted response from direct selection on the mature trait (FALCONER, 1981). $T_j$ and $T_m$ are generation time for juvenile and mature selection, respectively. Three years were added to account for breeding time. In this study, juvenile selection based on height, diameter, and stem volume was compared to mature selection at age 24 with gain in stem volume as the goal of selection.

## Results and Discussion

Differences among provenances and among families within provenances were statistically significant for all the traits investigated (*Table 2*). The percentage of variance associated with provenances (or provenance effect) was always greater than that associated with families within provenances (or family effect), and the difference tended to increase as the test aged. The magnitude of provenance effect increased as trees grew, most apparently for height where the percentage of variance associated with provenances at age 24 was over 5 times greater than that at age 7. Age trends in family effect were not consistent among traits. In height, family effect tended to decline as trees grew, while in diameter and stem volume, it tended to increase as test aged (*Table 2*). Steady increase in the percentage of provenance variance and continuous decline in the percentage of family-within-provenance variance seem to be common observations during this juvenile phase of height growth in forest trees. Similar findings have also been reported in Norway spruce (*Picea abies*) (FISHER, 1949), Douglas-fir (*Pseudotsuga menziesii*) (NAMKOONG *et al.*, 1972) and ponderosa pine (*Pinus ponderosa*) (NAMKOONG and CONKLE, 1976).

*Table 2.* – Estimated variance components as percentages of total variance.

| Source | HT7 | HT10 | HT14 | HT19 | HT24 | DBH14 | DBH19 | DBH24 | VOL14 | VOL19 | VOL24 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| $\sigma_r^2$ | $5.07^{d}$ | $0.79^{d}$ | $4.18^{d}$ | $3.18^{d}$ | $1.88^{d}$ | $2.23^{d}$ | $0.43^{b}$ | $0.20^{a}$ | $3.21^{d}$ | $1.06^{d}$ | $0.53^{c}$ |
| $\sigma_p^2$ | $8.45^{d}$ | $14.25^{d}$ | $29.48^{d}$ | $41.49^{d}$ | $45.24^{d}$ | $22.10^{d}$ | $26.99^{d}$ | $26.01^{d}$ | $26.91^{d}$ | $33.62^{d}$ | $34.40^{d}$ |
| $\sigma_{rp}^2$ | $4.11^{d}$ | $5.56^{d}$ | $3.78^{d}$ | $3.13^{d}$ | $2.44^{d}$ | $2.56^{d}$ | $1.42^{d}$ | $1.29^{d}$ | $3.40^{d}$ | $2.06^{d}$ | $1.18^{d}$ |
| $\sigma_{f(p)}^2$ | $7.73^{d}$ | $5.81^{d}$ | $5.85^{d}$ | $5.46^{d}$ | $4.75^{d}$ | $5.08^{d}$ | $5.31^{d}$ | $6.06^{d}$ | $4.92^{d}$ | $5.66^{d}$ | $5.84^{d}$ |
| $\sigma_{rf(p)}^2$ | $6.76^{d}$ | $5.75^{d}$ | $5.73^{d}$ | $5.43^{d}$ | $4.18^{d}$ | $3.61^{d}$ | $2.18^{b}$ | $1.89^{b}$ | $4.98^{d}$ | $2.54^{d}$ | $1.73^{b}$ |
| $\sigma_e^2$ | 67.87 | 63.83 | 50.98 | 41.31 | 41.51 | 64.34 | 63.67 | 64.55 | 56.56 | 55.06 | 56.31 |
| Error Mean Square | 2.81 | 9.99 | 79.04 | 222.35 | 409.50 | 22.67 | 40.88 | 74.25 | 9.31 | 99.55 | 495.37 |

a) b) c) and d) indicate statistical significance at 5%, 1%, 0.1% and 0.01% levels, respectively.

Lodgepole pine at the plantation maintained a steady rate of height increment during the assessment ages, with no sign of growth declining at age 24 (*Figure 1*). Such a linear mode of height increment was also observed across the same ages in ponderosa pine (NAMKOONG and CONKLE, 1976) and shore pine (*Pinus contorta* ssp. *contorta*) (XIE *et al.,* 1995). Evidence from the ponderosa pine study suggests that as trees grow and inter-tree competition becomes more intense, the rate of height increment will decline and family effects will increase (NAMKOONG and CONKLE, 1976). Since diameter growth is more sensitive to intertree competition (SAKAI *et al.*, 1968), its rate of increment may decline earlier and family effects may inflate sooner. Results from the present study seem to support this postulation; declining of diameter increment was signalled at about age 20 (*Figure 1*) and the proportion of family-within-provenance variance increased about 20 % from age 14 to 24 (*Table 2*). The diameter growth curves presented in *figure 1* are quite similar to those observed in shore pine (XIE *et al.*, 1995).

Heritabilities for provenance means were high, varied from 0.77 (HT7) to 0.97 (HT24) (*Table 3*). Heritabilities for family means were much lower, with a maximum of 0.50 (VOL24). Individual heritabilities were lower than family mean heritabilities and, within-family heritabilities were the lowest. The heritability estimates of provenance means, family means and individual values for growth traits derived from this study are similar to those for disease and insect resistance characters estimated at the same plantation (WU and YING, 1995). Compared with most other forest trees, the individual heritabilities of lodgepole pine estimated in this study are among the highest (CORNELIUS, 1994). Besides hereditary differences among species, variation in sampling strategy, experimental design, test site homogeneity, cultural treatment, plantation age, and other factors may also generate different heritability estimates even for the same traits of the same species. In addition, heritabilities derived from a single test tend to be overestimates although the bias may not be large in this species (ILLINGWORTH, 1978; YING *et al.,* 1985). Height demonstrated higher heritabilities than diameter and volume at all ages investigated (*Table 3*), which is coincident with the observations in other forest trees (CORNELIUS, 1994). The heritabilities of family means estimated here are higher than

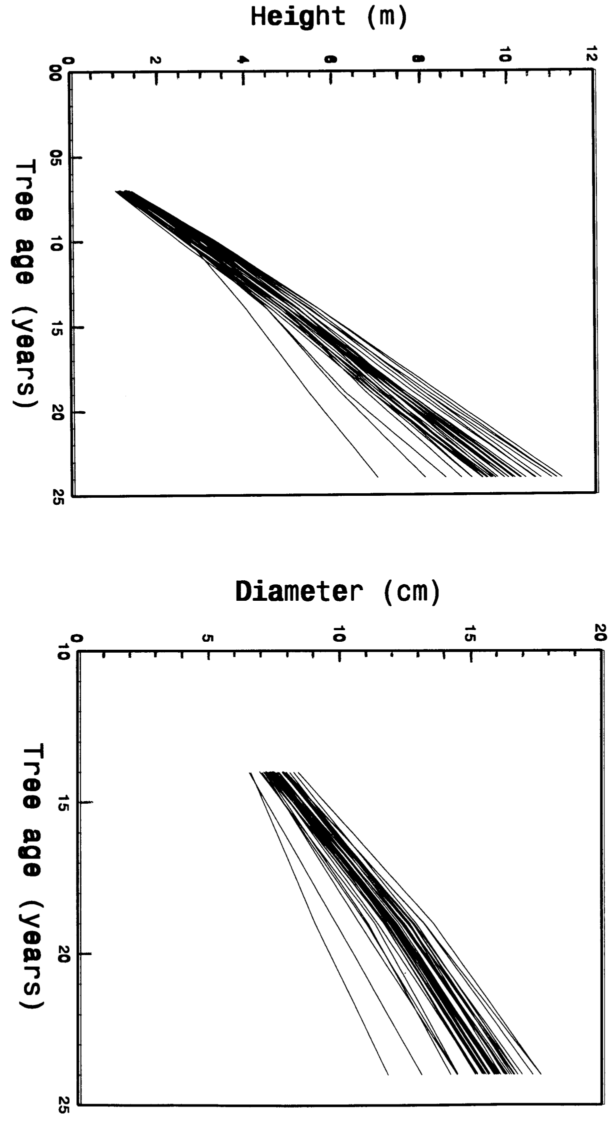

*Figure 1.* – Provenance mean growth curves of height and diameter at breast height.

*Table 3.* – Estimated phenotypic variances, additive genetic variances, and heritabilities.

| Estimates | HT7 | HT10 | HT14 | HT19 | HT24 | DBH14 | DBH19 | DBH24 | VOL14 | VOL19 | VOL24 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| $\sigma_I^2$ | 3.41 | 11.80 | 89.72 | 248.50 | 459.91 | 27.82 | 51.65 | 90.23 | 10.94 | 114.38 | 562.01 |
| $\sigma_{Prov}^2$ | 0.46 | 2.68 | 29.35 | 99.08 | 173.80 | 14.09 | 42.90 | 83.71 | 4.76 | 63.61 | 313.75 |
| $\sigma_F^2$ | 0.69 | 2.18 | 15.23 | 41.96 | 80.81 | 5.66 | 11.22 | 18.20 | 1.98 | 21.18 | 102.97 |
| $\sigma_W^2$ | 3.09 | 10.89 | 83.47 | 229.97 | 421.47 | 25.22 | 46.25 | 81.73 | 10.13 | 104.14 | 510.56 |
| $\sigma_A^2$ | 1.28 | 3.64 | 25.00 | 74.12 | 153.76 | 10.40 | 21.60 | 34.00 | 3.24 | 40.96 | 205.80 |
| $h_i^2$ | 0.38 | 0.31 | 0.37 | 0.42 | 0.38 | 0.28 | 0.30 | 0.33 | 0.30 | 0.36 | 0.37 |
| $s.e.(h_i^2)$ | 0.05 | 0.05 | 0.04 | 0.05 | 0.05 | 0.06 | 0.05 | 0.05 | 0.05 | 0.05 | 0.05 |
| $h_p^2$ | 0.77 | 0.83 | 0.93 | 0.96 | 0.97 | 0.95 | 0.95 | 0.95 | 0.93 | 0.96 | 0.96 |
| $s.e.(h_p^2)$ | 0.22 | 0.22 | 0.22 | 0.22 | 0.22 | 0.22 | 0.22 | 0.22 | 0.22 | 0.22 | 0.22 |
| $h_f^2$ | 0.47 | 0.42 | 0.46 | 0.48 | 0.47 | 0.41 | 0.44 | 0.48 | 0.41 | 0.48 | 0.50 |
| $s.e.(h_f^2)$ | 0.06 | 0.07 | 0.07 | 0.07 | 0.06 | 0.06 | 0.06 | 0.06 | 0.07 | 0.06 | 0.06 |
| $h_w^2$ | 0.31 | 0.25 | 0.31 | 0.35 | 0.31 | 0.22 | 0.24 | 0.27 | 0.24 | 0.30 | 0.30 |
| $s.e.(h_w^2)$ | 0.04 | 0.04 | 0.04 | 0.04 | 0.04 | 0.04 | 0.05 | 0.04 | 0.04 | 0.04 | 0.04 |

those reported for lodgepole pine in Alberta, Canada (average $h^2_f$ = 0.32 ± 0.03 for 9-year height, WU, 1993), slightly lower than that reported in the northern Rocky Mountains of United States ($h^2_f$ = 0.59 ± 0.14 for 6-year height, REHFELDT, 1985) but quite comparable to that from a farm-field test near the plantation ($h^2_f$ = 0.49 for 6-year height) (CARLSON, 1990).

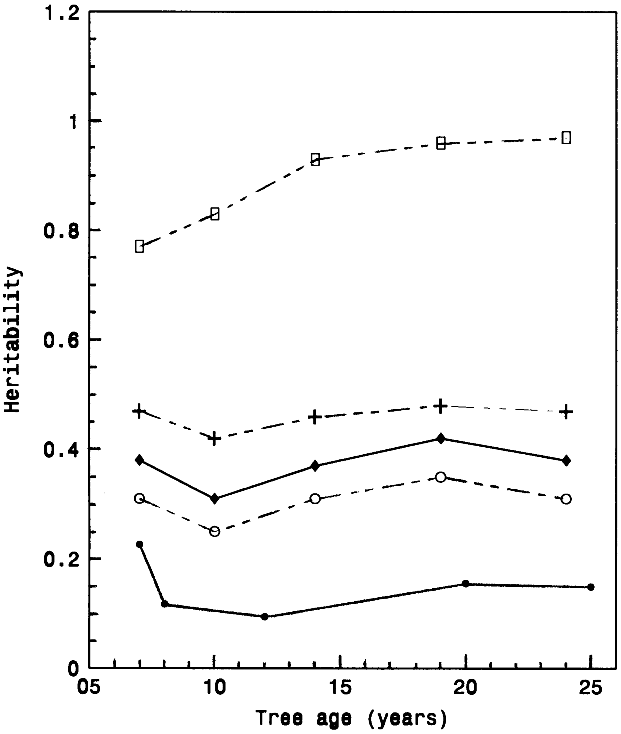

*Figure 2.* – Age trends of provenance (□}, family (+), individual (◆), and within family (○) heritability of height growth in Lodgepole pine in comparison with the individual heritability in ponderose pine (●) (NAMKOONG and CONKLE, 1976).

Heritability of provenance means for all traits tended to increase as test aged. Age trends of heritability for individual values, family means and within-family deviations were parallel. In diameter and volume, all 3 heritabilities increased as test proceeded, while in height, they all decreased from age 7 to 10, peaked at age 19, and declined at age 24 (*Table 3*, *Figure 2*). Given the large standard errors (differences in heritability estimates between ages were generally within one standard error, *Table 2*), one may question the reality of the above age trends of heritabilities. However, the age trend of individual heritability for height detected in this study is remarkably similar to that observed in ponderosa pine (NAMKOONG and CONKLE, 1976) (*Figure 2*), suggesting that those trends are likely realistic estimates.

Age-age correlations were always positive and strong at both provenance and family levels (*Table 4*). Provenance correlations ranged from 0.85 to 1.00 for height, 0.96 to 1.00 for diameter, and 0.97 to 1.00 for stem volume. Provenance correlations between traits (i.e., HT, DBH and VOL) at the same age were almost perfect (the lowest correlation coefficient was 0.98). Age-age correlations at family level (i.e., genetic correlations) varied from 0.51 to 0.98 for height, 0.84 to 0.97 for diameter, and 0.87 to 0.97 for stem volume. Genetic correlations between traits at the same age were also strong, with a minimum correlation coefficient of 0.61. For the same ages, height demonstrated the strongest age-age correlations at both provenance and family levels.

The efficiency of early selection was examined for different selection schemes. To facilitate illustration, a breeding population was presumed to be established using the top 3 % of test trees in the plantation (a total of 7597 trees was tested). The size of the breeding population is, therefore, 228, which is considered reasonable in advanced generation breeding (ZOBLE and TALBERT, 1984). Three selection schemes were considered, each with the same overall selection proportion (3 %). First of all, provenance effect was treated as non-additive and selection was made within provenances using mass selection. The second scheme included selection of individuals from selected

*Table 4.* – Estimates of age-age correlations at provenance (below diagonal) and family (above diagonal) levels (numbers in brackets are standard errors x 1000).

| | **HT7** | **HT10** | **HT14** | **HT19** | **HT24** | **DBH14** | **DBH19** | **DBH24** | **VOL14** | **VOL19** | **VOL24** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **HT7** | | 0.93(15) | 0.75(43) | 0.62(60) | 0.51(73) | 0.54(75) | 0.45(81) | 0.37(84) | 0.67(59) | 0.55(67) | 0.46(75) |
| **HT10** | 0.91(34) | | 0.90(19) | 0.80(37) | 0.67(58) | 0.55(79) | 0.48(83) | 0.41(87) | 0.72(54) | 0.62(64) | 0.52(74) |
| **HT14** | 0.87(45) | 0.95(16) | | 0.96(7) | 0.89(20) | 0.63(65) | 0.65(59) | 0.60(64) | 0.83(33) | 0.80(36) | 0.73(44) |
| **HT19** | 0.85(48) | 0.94(19) | 0.99(3) | | 0.98(4) | 0.61(65) | 0.68(54) | 0.64(56) | 0.81(36) | 0.83(30) | 0.80(34) |
| **HT24** | 0.85(48) | 0.93(22) | 0.99(4) | 1.00(1) | | 0.54(76) | 0.62(63) | 0.61(61) | 0.73(50) | 0.78(38) | 0.78(37) |
| **DBH14** | 0.89(39) | 0.97(11) | 0.98(7) | 0.98(7) | 0.97(10) | | 0.88(24) | 0.84(31) | 0.95(12) | 0.87(25) | 0.81(34) |
| **DBH19** | 0.85(48) | 0.92(26) | 0.97(9) | 0.908(5) | 0.99(5) | 0.98(7) | | 0.97(6) | 0.88(25) | 0.95(9) | 0.93(13) |
| **DBH24** | 0.84(53) | 0.90(33) | 0.97(11) | 0.98(5) | 0.99(3) | 0.96(13) | 1.00(1) | | 0.82(35) | 0.91(16) | 0.94(10) |
| **VOL14** | 0.88(40) | 0.97(11) | 0.99(3) | 0.98(6) | 0.97(10) | 0.99(5) | 0.97(11) | 0.95(15) | | 0.94(11) | 0.87(25) |
| **VOL19** | 0.86(47) | 0.94(21) | 0.98(5) | 0.99(2) | 0.99(4) | 0.99(5) | 0.99(4) | 0.98(5) | 0.99(4) | | 0.97(5) |
| **VOL24** | 0.85(49) | 0.93(24) | 0.98(6) | 1.00(1) | 0.99(2) | 0.97(9) | 0.99(4) | 0.99(4) | 0.97(8) | 1.00(1) | |

families within provenances (i.e., family-plus-within-family selection), still treating provenance effect as non-additive. In mass selection, a selection proportion of 3% (equivalent to a selection intensity (*i*) of 2.252) was applied to each provenance. In family-plus-within-family selection, a selection proportion of 30% ($i = 1.134$) was assigned to family and 10% ($i = 1.585$) to within-family selection to make up a 3% total within-provenance selection proportion. Trees selected from all provenances were pooled to consist of the breeding population. The third scheme treated provenance effect as additive and selection was made both among and within provenances. Since the purpose here is to examine the effect of provenance selection, only mass selection was considered in within-provenance selection. To make up an overall selection proportion of 3%, a selection proportion of 10% ($i = 1.698$) and 30% ($i = 1.152$) was assigned to provenance and within-provenance mass selection, respectively.

The predicted responses in stem volume at age 24 from early selection under the three selection schemes and the corresponding efficiency of selection are presented in *table 5*. The predicted responses from mass selection were always greater than those from family-plus-within-family selection regardless of the traits and ages of selection. High individual heritabilities and large phenotypic variance of individual trees (*Table 3*) should explain this observation. Compared with these 2 selection schemes, the correlated genetic responses through combined provenance and within-provenance selection were more than doubled no matter what the selection ages and traits were (*Table 5*). This observation strongly indicates the importance of incorporating provenance selection in the breeding program. A combination of provenance and within-provenance selection has also been recommended for improving pest resistance in lodgepole pine (Yanchuk *et al.*, 1988).

It should be pointed out, however, that the amount of genetic gain estimated from provenance selection may have been exaggerated because of maladaptation of provenances included in the analysis and incomplete additivity of provenance effect. Altough apparently poorly adapted provenances were excluded from the analysis, some degree of maladaptation may still be expected. Provenances included in the analysis cover most of the province where large regional adaptive differentiation has been observed (Xie and Ying, 1995). Part of the among-provenance genetic variation and the estimated gain is, therefore, not appropriate for operational breeding programs (Land *et al.,* 1987). It is very unlikely that genetic variance among provenances is completely additive. Thus, the estimated genetic gain from provenance selection can only be partially realised when trees selected from different provenances are crossed (Land *et al.*, 1987).

In all the selection schemes, selection at the youngest assessment age (i.e., 7 for height and 14 for diameter and stem volume) resulted in the greatest correlated response per unit time in stem volume at the mature age of 24 (*Table 5*). Moreover, selection based on stem volume was always more efficient than based on height or diameter alone, regardless of the selection schemes and ages (*Table 5*).

Twenty-year test results indicate that early selection is effective in lodgepole pine. An immediate question is whether it is still effective beyond that age, say at age 50 (a possible economic rotation age in well-managed plantations). Although this question can not be answered with the available information, some inference can be drawn. By examining height growth data from several species of *Pinaceae,* Lambeth (1980) found a close relationship between phenotypic age-age correlation and the natural logarithm of juvenile-mature age ratio, i.e., $r_{age.age} = a + b \text{ Ln(juvenile/mature age)}$. By fitting the estimated genetic correlations of height growth in lodgepole pine to Lambeth's model, a strong linear relationship was also derived ($r_A = 1.10 + 0.48 \text{ Ln(juvenile/mature age)}$, $R^2 = 0.98$). Burdon (1989) suggests that in the absence of ulterior information, the Lambeth relationship probably provides the best method for extrapolating age-age genetic correlations to rotation age as a means of projecting gains from early selection for a single trait. Assuming the heritabilities at the juvenile and mature age (50) are equal, the efficiency of early selection in relation to mature selection at age 50 for height can be estimated using the extrapolated age-age genetic correlations based on this relationship. Results indicate that the expected genetic gain per unit time may be maximised by selection at age 16 ($E = 1.55$). Since the extrapolated age-age genetic correlations may be subjected to bias and errors due to their stochastic properties (Magnussen and Yanchuk, 1993) and may change inconsistently with time