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# Age Trends in Douglas-fir Genetic Parameters and Implications for Optimum Selection Age

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## Abstract

Trends in genetic variation were examined over 51 progeny test sites throughout western Oregon. Narrow sense heritabilities for height and diameter showed an increasing trend to age 25, the oldest age examined. Before age 10, height heritabilities were relatively unstable. Type B site-site genetic correlations increased slowly with age for height and remained relatively stable for diameter. Age-age correlations were used to develop an equation to predict age-age correlations by using the log of the age ratios (LAR). Optimum selection age was calculated for a 60-year rotation by using two measures of efficiency: gain per year and discounted gain. The optimum selection age for height tended to be 2 to 3 years earlier than for diameter. Gain per year was maximized at age 10 for height and age 13 for diameter.

*Key words*: heritability, age-age correlations, Type B genetic correlation, gain efficiency, *Pseudotsuga menziesii* (Mirb.) Franco.

*FDC*: 165.3; 165.6; 181.65; 181.79; 232.19; 174.7 *Pseudotsuga menziesii*; (795).

## Introduction

Tree improvement activities started in the Pacific Northwest (USA and Canada) in the 1950's, with large-scale operational breeding programs for coastal Douglas-fir beginning in Oregon and Washington in the 1960's. Many of these programs are entering the second generation, and organizations are developing or revising tree improvement strategies. Accurate genetic information is needed to make optimal decisions during design of the second generation programs. Such information includes estimates of heritability and their trends with time, patterns of genetic variability over the landscape, the partitioning of genetic variation into additive and nonadditive components, and age-age correlations. A number of studies have documented this information for young trials (CAMPBELL *et al.*, 1985; KING *et al.;* 1988; MAGNUSSEN and YANCHUK, 1994; NAMKOONG *et al.*, 1972; ST.CLAIR, 1994; STONECYPHER *et al.*, 1996; WOODS *et al.,* 1995), but very little information is available for older ages. NAMKOONG *et al.* (1972) report on a 53-year-old study and MAGNUSSEN and YANCHUK (1994) report age-24 data. STONECYPHER *et al.* (1996) reported extensively on data before age 12. Although these studies provide important information, two do not have sufficient number of sites or families to thoroughly address the trends, and one (STONECYPHER *et al.*, 1996) reports only on data to age 11, except for age-age correlations to age 17.

The Northwest Tree Improvement Cooperative (NWTIC) has open-pollinated progeny tests covering a range of environments, for which growth data ranging from age 5 to 25 are available. The number, size, and age of these tests allow for a more thorough examination of genetic time trends in the Pacific Northwest than has been reported to date. The objectives of this study were to use these data to document the trends in heritability and Type B genetic correlations over time, establish age-age correlations, and determine optimum age of selection for NWTIC programs.

## Materials and Methods

The study used data from six local Oregon breeding zones, which are part of the NWTIC. These zones were chosen because all had age-15 or older assessment data. The philosophy of the NWTIC breeding programs is described in SILEN and WHEAT (1979). In each breeding zone, 300 to 1,200 parent trees were chosen from natural stands. Parent trees were tested only within their own breeding zone by using open-pollinated seed. Therefore, each breeding zone represents a separate and unique breeding program. The field trials for these programs were established in a "reps-in-sets" design and established on 6 to 12 sites (*Table 1*). In such a design, the open-pollinated families were assigned to sets of 25 to 50 families. At each test site three to five replications of each set were planted together. This can be viewed as planting a number of separate progeny trials at each location. Families were established as two- to four-tree noncontiguous plots. Test details are shown in *table 1*.

In four of the breeding zones, three sets were "randomly" chosen for analysis. In some cases sets were excluded because of severe mortality or injury from animal browse. The analyses were limited to three sets for Vernonia, Umpqua Coast, and Burnt Woods because only three sets had information after age 15. Medford only had four sets, of which three were chosen. In the remaining two breeding zones (Snow Peak and Gold Beach), six sets were chosen, representing both high and low heritability sets.

### Genetic Calculations

Narrow sense heritabilities were determined for each progeny test site by using the formula:

$$h^2 = (4\ \sigma^2_{family}) / (\sigma^2_{family} + \sigma^2_{within\ family})$$

This formula assumes that the open-pollinated families were truly half-sibs, such that $\sigma^2_{family}$ = ¼ the additive genetic

*Table 1.* – Progeny test and assessment information.

| Breeding Zone | No. of Progeny Trials | Families/ Set | Reps / site | plot size | Assessment Ages[z] | |
|---|---|---|---|---|---|---|
| | | | | | Height | Diameter[y] |
| Vernonia | 12 | 50 | 5[x] | 2 | 7[w], 10, 15, 20, 25 | 7[v], 15, 20, 25 |
| Umpqua Coast | 7 | 30 | 4 | 4 | 7, 10, 15, 20 | 7, 15, 20 |
| Burnt Woods | 7 | 30 | 4 | 4 | 7, 10, 15, 20 | 7, 15, 20 |
| Snow Peak High | 9 | 30 | 3 | 4 | 5, 10, 15 | |
| Gold Beach | 10 | 30 | 3 | 4 | 5, 10, 15 | |
| Medford – Grants Pass | 6 | 30 | 5 | 4 | 5, 10, 15 | |
| **TOTAL** | **51** | **600** | | | | |

z) Age is age from seed, not plantation age. Plantation age is one year less for Snow Peak and Gold Beach, 2 years less for the other breeding zones.
y) Age-7 is diameter above the root collar, all other ages is diameter at breast height (DBH; 4.5 ft).
x) 3 sites had only 2 replications.
w) Age-7 height on 5 of 12 sites.
v) Age-7 diameter on 9 of 12 sites.

variance ($\sigma^2_a$) and ignores bias from genotype-environment interaction (to be discussed later). Variance components were obtained by using SAS Varcomp procedure (SAS, 1990) from the following model:

$$y_{ijkl} = \mu + \text{set}_i + \text{rep}_{ij} + \text{family}_{ik} + \text{error}_{ijkl}$$

where, $y_{ijkl}$ is l$^{th}$ tree in the k$^{th}$ family in the j$^{th}$ rep in the i$^{th}$ set,

$\mu$ is the population mean,

set$_i$ is the effect of the i$^{th}$ set,

rep$_{ij}$ is the effect of the j$^{th}$ replication in the i$^{th}$ set,

family$_{ik}$ is the effect of the k$^{th}$ family in the i$^{th}$ set,

error$_{ijkl}$ is the pooled effect of the replication-by-family interaction for the j$^{th}$ replication and k$^{th}$ family in the i$^{th}$ set, and the effect of the ijkl$^{th}$ tree, ie. the within plot variation. The rep · family component was included in the error term because there was no evidence of rep · family interactions.

The REML option (SAS, 1990) was used to estimate the variance components because maximum likelihood procedures, such as REML, are reported to be superior to ANOVA-based estimators when data are unbalanced (Searle *et al.*, 1992; Swallow and Monahan, 1984). The individual tree data all had some degree of imbalance as a result of mortality.

Heritability trends over time were examined by using relative heritabilities for each site. Relative heritabilities were constructed by setting the age-15 h$^2$ for each site to the overall average (0.195 for height, 0.203 for DBH) and determining the heritabilities for other ages according to the ratio of assessment-age h$^2$ to age-15 h$^2$:

$$\text{relative } h^2_{\text{age-x}} = (h^2_{\text{age-x}} / h^2_{\text{age-15}}) \cdot 0.195 \text{ for height } (0.203 \text{ for DBH}).$$

The relative h$^2$ estimates were pooled over all sites to compare the time trends from this study with those found in prior studies.

The single-site approach used in the above equations gives biased estimates of heritabilities, because any genotype-environmental interaction is confounded in the estimate of the family variance component (Comstock and Moll, 1963). Genotype-environment interaction was examined in a separate set of analyses using Type B genetic correlations (Burdon, 1977). The Type B genetic correlation represents the site-to-site genetic correlation. By examining each pair-wise combination, it was possible to obtain an average Type B genetic correlation for each breeding zone and a standard deviation based on the multiple estimates.

Type B genetic correlations were computed for all pairs of tests within a breeding zone using the equation:

$$r_b = (\sigma^2_{\text{family}}) / (\sigma^2_{\text{family}} + \sigma^2_{\text{family} \cdot \text{site}}) \qquad (\text{Burdon, 1977})$$

Variance components were obtained by using plot means which had been standardized by subtracting the site mean and dividing by the site's phenotypic standard deviation. The model used was:

$$y_{ijkm} = \mu + \text{set}_i + \text{site}_{im} + \text{rep}_{imj} + \text{family}_{ik} + \text{family} \cdot \text{site}_{imk} + \text{error}_{jkm}$$

where, $y_{ijkm}$ is plot mean for the k$^{th}$ family in the j$^{th}$ rep in the i$^{th}$ set at the m$^{th}$ site

$\mu$ is the population mean,

set$_i$ is the effect of the i$^{th}$ set,

site$_{im}$ is the effect of the m$^{th}$ site in the i$^{th}$ set,

rep$_{imj}$ is the effect of the j$^{th}$ replication at the m$^{th}$ site in the i$^{th}$ set,

family$_{ik}$ is the effect of the k$^{th}$ family in the i$^{th}$ set,

family · site$_{imk}$ is the interaction between the k$^{th}$ family and the m$^{th}$ site in the i$^{th}$ set, and

error$_{ijkm}$ is the effect of the three-way interaction in the i$^{th}$ set, which for plot means, is the overall error term.

Age-age genetic correlations were estimated for each breeding zone using the formula:

$$r_g = \sigma_{\text{family(younger age, older age)}} / (\sigma^2_{\text{family (younger age)}} \cdot \sigma^2_{\text{family (older age)}})^{0.5}$$

where, $r_g$ is the genetic correlation between the younger and older age,

$\sigma_{\text{family(younger age, older age)}}$ is the family covariance between two ages,

$\sigma^2_{\text{family (younger age)}}$ is the family variance for the younger age,

$\sigma^2_{\text{family (older age)}}$ is the family variance for the older age.

Variance and covariance components were estimated with adjusted plot-means and used the SAS Varcomp procedure TYPE1 option (SAS, 1990). These ANOVA-based estimators were selected because computer limitations did not allow for use of the REML option. The data were relatively balanced because the analyses used plot means. ANOVA-based estimators are of minimum variance (like maximum likelihood estimates) when data are balanced (Read, 1961). The analyses were performed over all sites within a breeding zone and were done individually for each of the three sets by using the model:

$$y_{jkm} = \mu + \text{site}_m + \text{rep(site)}_{mj} + \text{family}_k + \text{family} \cdot \text{site}_{mk} + \text{error}_{jkm}$$

This model provided three estimates of age-age correlations for four zones and six estimates for two zones (corresponding to the number of sets). Having a minimum of three zones for each age-age correlation provided a minimum of nine (maximum of 24) estimates from which the standard deviation was calculated. In calculating means and standard deviations, the Snow Peak and Gold Beach data were given a weight of 0.5 in order to have equal representation among breeding zones.

Namkoong and Kang (1990) and Kang (1991) demonstrated that the age-age correlation is a function of the variance of the younger measurements relative to the older measurements and the correlation of the early measurement with the subsequent growth. The components of the age-age correlation as reported in Kang (1991) were derived as follows. $X_i$ is a measurement at time t for tree i, and $X'_i$ is a measurement at time t + $\triangle$t. $S_i$ and $S'_i$ are X and X' variables standardized by the standard deviation of X' ($S_i = X_i / \sigma_{x'i}$). $D_i$ is the difference between $S_i$ and $S'_i$ ($D_i = S'_i - S_i$). From these variables Kang shows that the correlation between the two measurements is:

$$r_{SS'} = \sigma_S + (\sigma_{SD} / \sigma_S)$$

Family means from the three breeding zones with age-20 height data were used to examine the standardized variances at each age and the correlation of height growth with subsequent growth to age 20.

Multiple regression was run on the age-age genetic correlation estimates to develop a equation to estimate age-age correlations based on the natural log of the age ratio (LAR = ln (younger age / older age)) as developed by Lambeth (1980):

$r_{g(\text{younger age, older age})} = \hat{a} + b \cdot \text{LAR}$. Again, information from Gold Beach and Snow Peak was given weights of 0.5 so that each breeding zone had equal weight. Equations were developed for height and diameter but not volume. Volume estimates were available only for two ages in two breeding zones and three in a third, thereby limiting the number of data points available for developing an equation. The resulting equations were used to estimate age-age genetic correlations with rotation age. The estimated genetic correlation with rotation age was used to estimate the genetic gain (△G) from family selection for each selection age from the equation for indirect selection (FALCONER, 1989):

$$\triangle G = i\, r_g\, h_{\text{selection age}} h_{\text{rotation age}}\, \sigma_{P\,\text{rotation age}}$$

where, i is selection intensity,

$r_g$ is the estimated age-age correlation between selection age and rotation,

$h_{\text{selection age}}$ is the square root of family mean heritability at selection age,

$h_{\text{rotation age}}$ is the square root of family mean heritability at rotation.

$\sigma^2_{P\ \text{rotation age}}$ is the phenotypic variance at rotation age.

To adjust for genotype-environmental interaction and obtain unbiased estimates of heritability, the selection age heritability was multiplied by the Type B genetic correlation, which yielded the following equation:

$$\triangle G = i\, r_g\, (r_b\, h^2_{\text{selection age}})^{0.5}\, h_{\text{rotation age}}\, \sigma_{P\,\text{rotation age}}$$

Gain efficiency (GE) is defined as the amount of gain per year and is simply:

$$GE = \triangle G\ /\ (\text{selection age} + \text{number of years to breed})$$

Because selection ages are compared relative to the same rotation age, the equation can be simplified for comparison purposes to:

$$GE = r_g (r_b h^2_{\text{selection age}})^{0.5} / (\text{selection age} + \text{number of years to breed})$$

The number of years to breed is the time from making selections until the first progeny tests are sown. The growth efficiency (GE) of family selection was examined for height and DBH at specific ages by using the above equation. A 5-year crossing period was assumed for calculating the GE. Family mean heritabilities were calculated from narrow sense heritabilities to represent family mean heritabilities for progeny trials with 30 individuals per family (n) by using the equation:

$$h^2_{\text{family mean}} = [1 + {}^1\!/\!_4\,(n-1)]h^2 / [1 + {}^1\!/\!_4\,(n-1)h^2] \quad \text{(FALCONER, 1989)}$$

Age-age correlations were extrapolated to a rotation age of 60 by using the results of the regression of age-age correlation on LAR. This required extrapolation of the data rather than interpolation. This we felt was justified because the LAMBETH relationship is to a large degree a function of the early growth being a component of the total growth at rotation (NAMKOONG and KANG, 1990; KANG, 1991). This part of the age-age correlation holds regardless of age. It should also be noted that the trait of most interest is volume at rotation, not 25-year volume which is a minor component of overall gain.

For ease in comparisons, GEs were changed to relative efficiencies (Q), which for this paper are the ratio of a GE at a given age divided by the GE for age 10.

Relative efficiency (Q') also was calculated in a method similar to the one described by WHITE and HODGE (1992). Instead of gain per year, WHITE and HODGE examined discounted gains relative to discounted gains at a specific selection age. We discounted gains for each selection age by using the equation:

$$\text{discounted gain} = r_g\, (r_b\, h^2_{\text{ selection age}})^{0.5} / (1 + d)^t$$

where d is the discount rate and t the selection age. Q' was then calculated as discounted gain for a selection age divided by discounted gain for selection at age 10. Discount rates of 4%, 6%, and 8% were examined.

## Results and Discussion

Narrow sense heritabilities ($h^2$) for each of the 51 progeny trials are shown in *tables 2a* and *2b*. In general there is an increasing trend in heritability with time. An exception is for height during the period before age 10. Four breeding zones (Umpqua Coast, Burnt Woods, Snow Peak, and Medford) showed a decrease in heritability from the youngest measurement to the age-10 measurements; the other two zones showed the opposite trend. Heritability decreased from the youngest age to age 10 at 23 of 44 sites. In contrast, all six breeding zones showed an increase in heritability from age 10 to 15; only 12 of 51 progeny trials showed a decrease in heritability (not tested statistically). It seems that at very young ages, the trend in heritability is relatively unstable, but a relatively stable trend exists for increasing heritability after age 10. Regression analyses performed on adjusted heritabilities indicated a statistically significant increase in heritability with age for both diameter and height. The dip in age-10 height heritability was statistically significant as indicated by a significant age-squared component. This dip in heritability conforms to the model proposod by FRANKLIN (1979), where the dip comes at a point when progeny tests move from the juvenile genotypic phase to the mature genotypic phase. The increasing trend in heritability was more profound for diameter than height as indicated by a higher $r^2$. The final equations including only significant effects were:

$$h^2_{\text{height}} = 0.238 - (0.0115 \cdot \text{age}) + (0.00058 \cdot \text{age}^2) \qquad r^2 = 0.094$$

$$h^2_{\text{DBH}} = 0.077 + (0.0083 \cdot \text{age}) \qquad r^2 = 0.344$$

The trend for increasing heritability is similar to that found in other Douglas-fir studies that examined traditional progeny tests (ie. not farm field trials) (*Figure 1*). All the studies in *figure 1* show an increasing trend between the ages of 12 and 23. Before age 12, the pattern is mixed, similar to the results found among the progeny trials in this study. A dip in heritability similar to that shown here was found in NAMKOONG *et al.* (1972) (*Figure 1*). A reason for the later dip in heritability for the NAMKOONG *et al.* study could be that its growth rate was significantly slower than those examined in this study, and stand development therefore would progress slower.

The Type B site-to-site genetic correlations were relatively strong, usually averaging over 0.65 (*Table 3*). There was a statistically significant trend of an increase in Type B correlations with age for height (Type B = 0.571 + 0.010 age, $\alpha = 0.0174$, $r^2 = 0.25$), but not for DBH (*Table 3*). Breeding zone influenced the intercept of the line, but not the slope. Although

*Table 2a.* – Heritabilities for height over 6 breeding zones.

| Breeding zone | Site | Age of assessment (years)<br>5 | 7 | 10 | 15 | 20 | 25 |
|---|---|---|---|---|---|---|---|
| **Vernonia** | 1 | | 0.16 | 0.25 | 0.20 | 0.11 | 0.16 |
| | 2 | | 0.14 | 0.13 | 0.33 | 0.37 | 0.37 |
| | 3 | | 0.22 | 0.25 | 0.23 | 0.23 | 0.24 |
| | 4 | | 0.16 | 0.20 | 0.20 | 0.19 | 0.13 |
| | 5 | | 0.05 | 0.07 | 0.07 | 0.25 | 0.09 |
| | 6 | | | 0.12 | 0.12 | 0.16 | 0.21 |
| | 7 | | | 0.08 | 0.16 | 0.11 | 0.15 |
| | 8 | | | 0.17 | 0.09 | 0.06 | 0.15 |
| | 9 | | | 0.14 | 0.14 | 0.04 | 0.11 |
| | 10 | | | 0.06 | 0.08 | 0.13 | 0.17 |
| | 11 | | | 0.05 | 0.06 | 0.16 | 0.28 |
| | 12 | | | 0.00 | 0.00 | 0.00 | 0.02 |
| | Mean | | **0.15** | **0.13 (0.18)**[z] | **0.14 (0.21)** | **0.15 (0.23)** | **0.17 (0.20)** |
| **Umpqua Coast** | 1 | | 0.34 | 0.22 | 0.23 | 0.26 | |
| | 2 | | 0.28 | 0.20 | 0.18 | 0.28 | |
| | 3 | | 0.19 | 0.19 | 0.24 | 0.24 | |
| | 4 | | 0.14 | 0.12 | 0.09 | 0.14 | |
| | 5 | | 0.13 | 0.21 | 0.25 | 0.22 | |
| | 6 | | 0.24 | 0.25 | 0.29 | 0.32 | |
| | 7 | | 0.19 | 0.23 | 0.22 | 0.30 | |
| | Mean | | **0.22** | **0.20** | **0.22** | **0.25** | |
| **Burnt Woods** | 1 | | 0.40 | 0.25 | 0.20 | 0.13 | |
| | 2 | | 0.34 | 0.24 | 0.20 | 0.17 | |
| | 3 | | 0.42 | 0.30 | 0.39 | 0.37 | |
| | 4 | | 0.15 | 0.00 | 0.05 | 0.18 | |
| | 5 | | 0.19 | 0.21 | 0.20 | 0.16 | |
| | 6 | | 0.19 | 0.16 | 0.23 | 0.29 | |
| | 7 | | 0.07 | 0.08 | 0.06 | 0.07 | |
| | Mean | | **0.25** | **0.18** | **0.19** | **0.20** | |
| **Snow Peak** | 1 | 0.36 | | 0.32 | 0.38 | | |
| | 2 | 0.43 | | 0.38 | 0.44 | | |
| | 3 | 0.26 | | 0.20 | 0.24 | | |
| | 4 | 0.17 | | 0.16 | 0.19 | | |
| | 5 | 0.24 | | 0.26 | 0.31 | | |
| | 6 | 0.65 | | 0.23 | 0.38 | | |
| | 7 | 0.27 | | 0.10 | 0.22 | | |
| | 8 | 0.32 | | 0.22 | 0.22 | | |
| | 9 | 0.01 | | 0.12 | 0.24 | | |
| | Mean | **0.30** | | **0.22** | **0.24** | | |
| **Gold Beach** | 1 | 0.18 | | 0.32 | 0.41 | | |
| | 2 | 0.28 | | 0.27 | 0.25 | | |
| | 3 | 0.16 | | 0.19 | 0.17 | | |
| | 4 | 0.02 | | 0.06 | 0.12 | | |
| | 5 | 0.08 | | 0.03 | 0.09 | | |
| | 6 | 0.02 | | 0.08 | 0.12 | | |
| | 7 | 0.20 | | 0.29 | 0.32 | | |
| | 8 | 0.11 | | 0.19 | 0.26 | | |
| | 9 | 0.24 | | 0.05 | 0.09 | | |
| | 10 | 0.16 | | 0.17 | 0.19 | | |
| | Mean | **0.14** | | **0.17** | **0.20** | | |
| **Medford - G.P.** | 1 | 0.15 | | 0.05 | 0.11 | | |
| | 2 | 0.12 | | 0.07 | 0.07 | | |
| | 3 | 0.14 | | 0.12 | 0.15 | | |
| | 4 | 0.18 | | 0.20 | 0.17 | | |
| | 5 | 0.10 | | 0.08 | 0.11 | | |
| | 6 | 0.07 | | 0.12 | 0.18 | | |
| | Mean | **0.13** | | **0.11** | **0.13** | | |

[z] Means in parenthesis are of the progeny sites that are common to the sites with age-7 data for Veronia

the increase is slight, it appears that older ages yield higher Type B correlations. Similar trends have been shown in slash pine; with one study showing a slight increase in Type B correlations with age (DIETERS *et al.,* 1995) and another showing a relatively constant level (HODGE and WHITE, 1992).

Age-age genetic correlations were relatively strong (*Table 4*). As expected, as time between assessment ages decreased, the genetic correlation between the assessments increased. More variation was evident in correlations using the early assessments, as can be seen by the larger standard deviations for correlations involving age-5 height and age-7 diameter. Further examination showed that the Medford breeding zone had lower than average age-age correlations, which both lowered the mean age-age correlation and substantially added to the

*Table 2b.* – Heritabilities of diameter over 3 breeding zones.

| | | Assessment age (years) | | | |
|---|---|---|---|---|---|
| **Breeding zone** | Site | 7 | 15 | 20 | 25 |
| **Vernonia** | 1 | 0.12 | 0.26 | 0.26 | 0.29 |
| | 2 | 0.11 | 0.15 | 0.28 | 0.30 |
| | 3 | 0.15 | 0.18 | 0.33 | 0.30 |
| | 4 | 0.03 | 0.15 | 0.19 | 0.26 |
| | 5 | 0.20 | 0.19 | 0.19 | 0.23 |
| | 6 | 0.00 | 0.00 | 0.00 | 0.00 |
| | 7 | 0.05 | 0.08 | 0.13 | 0.13 |
| | 8 | 0.00 | 0.22 | 0.20 | 0.26 |
| | 9 | 0.19 | 0.11 | 0.07 | 0.06 |
| | 10 | | 0.30 | 0.25 | 0.34 |
| | 11 | | 0.14 | 0.14 | 0.14 |
| | 12 | | 0.04 | 0.07 | 0.09 |
| | Mean | **0.09** | **0.15** | **0.18** | **0.20** |
| **Umpqua Coast** | 1 | 0.30 | 0.36 | 0.33 | |
| | 2 | 0.28 | 0.26 | 0.31 | |
| | 3 | 0.18 | 0.20 | 0.26 | |
| | 4 | 0.12 | 0.17 | 0.15 | |
| | 5 | 0.00 | 0.18 | 0.22 | |
| | 6 | 0.22 | 0.32 | 0.34 | |
| | 7 | 0.13 | 0.21 | 0.22 | |
| | Mean | **0.18** | **0.24** | **0.26** | |
| **Burnt Woods** | 1 | 0.32 | 0.25 | 0.23 | |
| | 2 | 0.15 | 0.33 | 0.33 | |
| | 3 | 0.37 | 0.41 | 0.48 | |
| | 4 | 0.01 | 0.09 | 0.11 | |
| | 5 | 0.26 | 0.26 | 0.24 | |
| | 6 | 0.13 | 0.31 | 0.37 | |
| | 7 | 0.00 | 0.10 | 0.22 | |
| | Mean | **0.18** | **0.25** | **0.28** | |

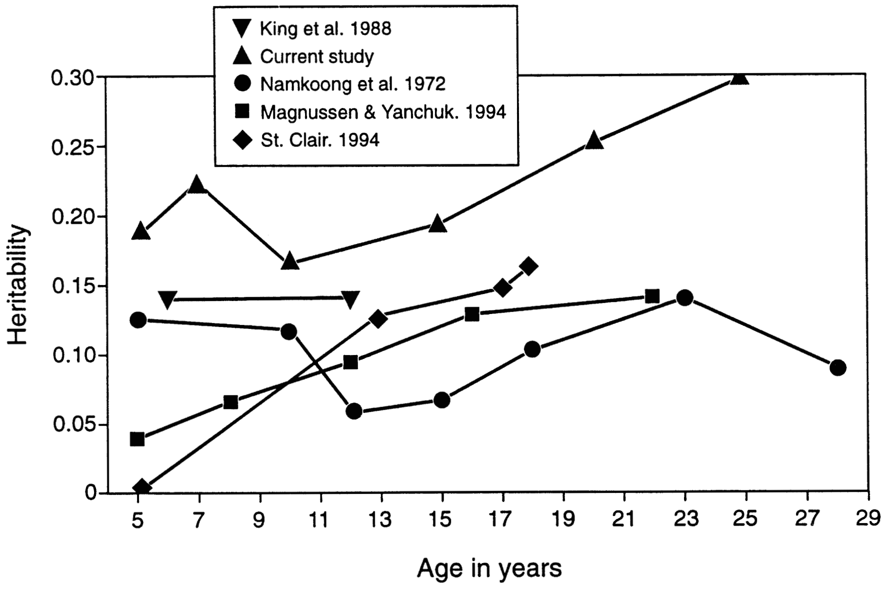

*Figure 1.* – Narrow sense height heritability trends for plantation grown Coastel Douglas-fir.

*Table 3.* – Type B, site-to-site genetic correlations averaged over each breeding zone for the traits height and diameter.

| Age | Breeding zone<br>Vernonia | Umpqua Coast | Burnt Woods | Snow Peak | Gold Beach | Medford - G.P. | Mean<br>All | Mean<br>Vernonia Ump.Coa. B. Woods |
|---|---|---|---|---|---|---|---|---|
| **Height** | | | | | | | | |
| 5 / 7 | 0.615 | 0.742 | 0.673 | 0.555 | 0.708 | 0.604 | 0.649 | 0.677 |
| 10 | 0.761 | 0.802 | 0.632 | 0.651 | 0.698 | 0.423 | 0.661 | 0.731 |
| 15 | 0.785 | 0.839 | 0.698 | 0.776 | 0.700 | 0.508 | 0.718 | 0.774 |
| 20 | 0.828 | 0.756 | 0.769 | | | | | 0.784 |
| 25 | 0.803 | | | | | | | |
| **Diameter** | | | | | | | | |
| 7 | 0.706 | 0.735 | 0.674 | | | | | 0.705 |
| 15 | 0.609 | 0.743 | 0.697 | | | | | 0.683 |
| 20 | 0.582 | 0.742 | 0.653 | | | | | 0.659 |
| 25 | 0.591 | | | | | | | |

standard deviation estimate. Removal of the Medford data resulted in age-age correlations of 0.82 and 0.72 for the correlations of age 5 with 10 and 15, respectively. Respective standard deviations were 0.05 and 0.13.

The age-20 family mean height data shows that as ages become closer, the overriding factor affecting the age-age correlation is the standard deviation (variance) of the earlier measurement rather than the correlation of the earlier measurement with the additional growth (*Table 5*). The correlation with the additional growth decreases, but the age-age correlation continues to increase due to the increased variance of the earlier measurement.

The relation among site index (height at age 15), heritability of age-15 height, site survival, and the age 10 to 15 genetic correlation was examined for the 51 progeny tests. The only significant correlation found was between site heritability and survival ($r = 0.36$, $\alpha = 0.01$). A similar relation was found in loblolly pine (NCSU-ICTIP, 1995). No other significant correlations were found, thereby implying that site index did not affect the genetic components of the trials. In similar analyses with slash pine, no significant correlation between site class and heritability was found (DIETERS et al., 1995; HODGE and WHITE, 1992). Other factors should be examined in the future to determine the key environmental components affecting heritability.

*Table 4.* – Age-age genetic correlations averaged over 6 breeding zones, with standard deviation of the estimates in parenthesis for the traits height and diameter.

| Younger age | Older age (years)<br>10 | 15 | 20 | 25 |
|---|---|---|---|---|
| **Height** | | | | |
| 5 | 0.69 (0.17) | 0.63 (0.16) | | |
| 7 | 0.97 (0.08) | 0.85 (0.07) | 0.79 (0.09) | 0.64 (0.21) |
| 10 | | 0.94 (0.04) | 0.90 (0.09) | 0.74 (0.05) |
| 15 | | | 0.99 (0.03) | 0.93 (0.04) |
| 20 | | | | 0.97 (0.03) |
| **Diameter** | | | | |
| 7 | | 0.83 (0.16) | 0.74 (0.14) | 0.56 (0.21) |
| 15 | | | 0.98 (0.02) | 0.87 (0.02) |
| 20 | | | | 0.95 (0.03) |

The regression of height age-age correlations on LAR using all six breeding zones resulted in a statistically significant relation ($\alpha = 0.0001$), but with a relatively poor $r^2$:

$$r = 1.086 + 0.359\ \mathrm{LAR} \qquad (r^2 = 0.438)$$

There was a significant zone-by-LAR interaction. The model $r^2$ increased to 0.706 when the interaction was added. The significant interaction implies that not any single equation would suffice for the Pacific Northwest. This is in contrast to LAMBETH's (1980) results, which indicated one equation was broadly applicable. Further examination of our data showed the interaction was a result of the Medford data. When the regressions were run without Medford, the zone-by-LAR interaction dropped out of the model and resulted in the following equation:

$$r = 1.077 + 0.309\ \mathrm{LAR} \qquad (r^2 = 0.541)$$

The above equation was used to estimate the genetic correlation of assessment age with rotation (age 60) for calculating relative efficiency.

The equation for the diameter assessments of three breeding zones was very similar to that of height:

$$r = 1.064 + 0.329\ \mathrm{LAR} \qquad (r^2 = 0.487)$$

Relative efficiency (Q) for height using the previously mentioned equations for heritability and age-age correlations

*Table 5.* – Family mean age-age correlation, correlations with additional growth to age 20, and the standard deviation of standardized family means (s) for 3 ages.

| | Correlation with age-20 height | | | Correlation with additional growth to age 20 | | | Standardized standard deviation | | |
|---|---|---|---|---|---|---|---|---|---|
| Breeding Unit | age-7 | age-10 | age-15 | age-7 | age-10 | age-15 | age-7 | age-10 | age-15 |
| Vernonia - set 1 | 0.514 | 0.742 | 0.942 | 0.986 | 0.921 | 0.661 | 0.175 | 0.421 | 0.805 |
| Vernonia - set 2 | 0.688 | 0.856 | 0.950 | 0.986 | 0.936 | 0.721 | 0.206 | 0.456 | 0.789 |
| Vernonia - set 3 | 0.589 | 0.660 | 0.908 | 0.985 | 0.903 | 0.643 | 0.191 | 0.418 | 0.794 |
| Ump. Coast - set 1 | 0.692 | 0.879 | 0.959 | 0.513 | 0.323 | -0.060 | 0.890 | 0.960 | 1.061 |
| Ump. Coast - set 2 | 0.767 | 0.884 | 0.959 | 0.272 | 0.319 | 0.456 | 1.054 | 0.960 | 0.906 |
| Ump. Coast - set 3 | 0.727 | 0.896 | 0.943 | 0.653 | 0.546 | 0.446 | 0.758 | 0.844 | 0.901 |
| Burnt Woods - set 1 | 0.678 | 0.879 | 0.948 | 0.964 | 0.952 | 0.848 | 0.299 | 0.424 | 0.686 |
| Burnt Woods - set 2 | 0.716 | 0.815 | 0.945 | 0.952 | 0.909 | 0.766 | 0.345 | 0.480 | 0.749 |
| Burnt Woods - set 3 | 0.791 | 0.884 | 0.977 | 0.973 | 0.944 | 0.870 | 0.295 | 0.451 | 0.741 |
| Mean | 0.685 | 0.833 | 0.948 | 0.809 | 0.750 | 0.595 | 0.468 | 0.601 | 0.826 |

over time is shown in *figure 2*. Height Q (i.e., gain per year) was maximized by selecting at age 10. Relative efficiencies were very similar for ages 8 through 14, implying that little would be lost if selection occurred within this range. Altering the equation for height to include the Medford data shifted the height curve to the right, because the Medford data implied that early selections were poorly correlated with older selections. Increasing rotation age also shifted the curves so that older ages became more efficient. As expected, earlier rotation ages gave earlier maximums, age 9 maximized Q for 50-year rotations, and age 7 for 40-year rotations. When Q' (discounted gain) was examined, the optimum selection age ranged from age 9 (discount rate = 8%) to age 18 (discount rate = 4%) (*Figure 2*). Although the Q' maximums were similar to the Q maximum for discount rates of 6% and 8% (age 9 and 11, respectively), the Q' lines for these discount rates showed a very limited range of ages having values close to the maximum. Efficiencies dropped off quickly after the curve peaked, unlike the curve for Q, which had a broad range of near optimum selection ages.

The Q for diameter selection was maximized at a later age than that for height (age 13 vs. age 10) and also had a broad range of selection ages that gave close to optimal REs (*Figure 3*). It is reasonable for DBH to have an older maximum than height, because DBH cannot be measured accurately in young stands just passing breast height in total height.

The Q' maximums for DBH also were larger than the Q' maximums for height when using 6% and 8% discount rates (ages 9 and 11, respectively). The 4% DBH Q' maximum was less than that for height (age 16 vs age 18).

These results, especially the gain per year calculations (Q), are similar to recommendations made by STONECYPHER *et al.* (1996); based on results from numerous Douglas-fir studies, they state that "early growth measurements (8 to 15-years) provide a reliable basis for ranking families and/or sources for performance and stability."

The optimum selection ages fall within the range of our data, therefore the estimates of heritability are probably reliable. The estimated correlation with age-60 cannot be verified since

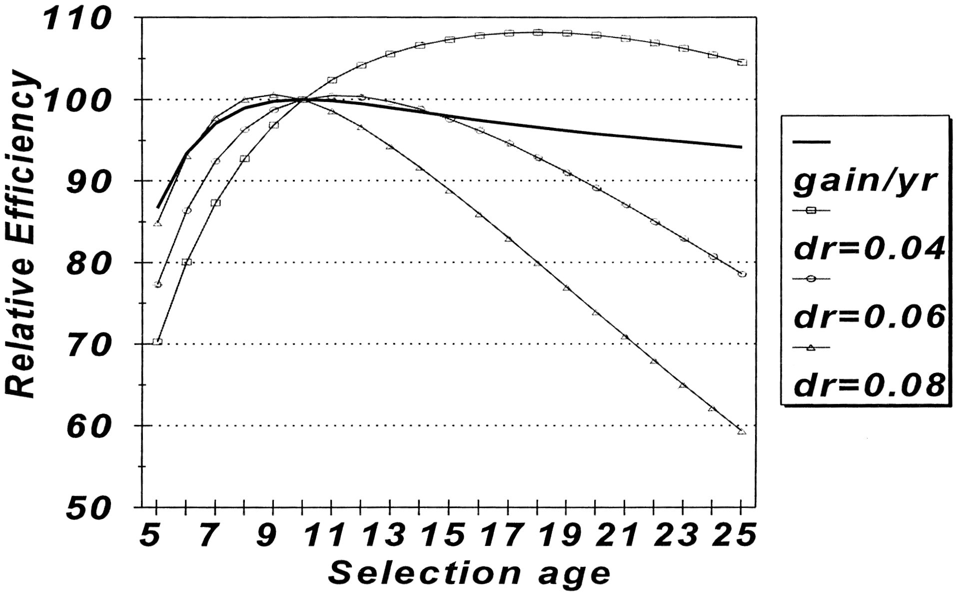

*Figure 2.* – Relative efficiencies for selecting height at different ages using gain per vear (Q), and discounted gain (Q') using discount rates of 0.04, 0.06 and 0.08 (standardized to age-10 efficiency = 100).

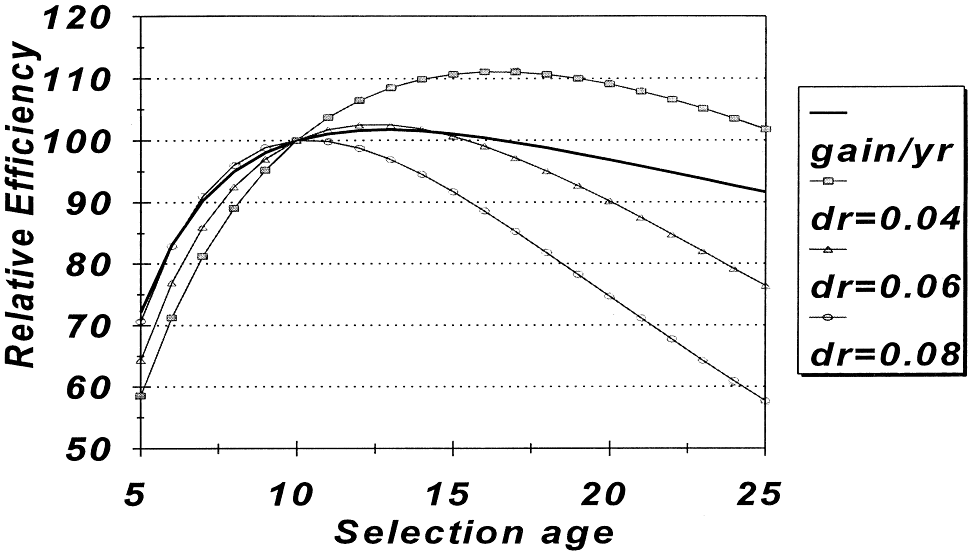

*Figure 3.* – Relative efficiencies for selecting DBH at different ages, using gain per year (Q), and discounted gain (Q') using discount rates of 0.04, 0.06 and 0.08 (standardized to gain from age-10 selection).

it is outside the range of our data. Data to age 53 was available from Namkoong *et al.* (1972) and was used to examine the impact of using data younger than rotation age. Using their correlations of deviations in plot error (their *table 6*), LAR equations were developed for all data and for only data less than age-25. The equation for all the data was:

Age-age correlation = 1.0035 + (0.4010 · LAR) $(r^2 = 0.7587, \alpha = 0.0001)$

The equation for using only the data less than age-25 was:

Age-age correlation = 1.0315 + (0.6034 · LAR) $(r^2 = 0.7716, \alpha = 0.0001)$

Both equations accounted for about the same amount of variation, but the equation using only the younger data yielded significantly smaller correlations than the equation using all the data. This single example (with a limited statistical design) suggests that the estimated correlations with age-60 may be low. If this were the case, then the theoretical optimum selection ages would be younger than what was previously stated.

It should also be noted that the equations developed in this paper with the NWTIC data yield larger age-age correlations than even the equation using all the Namkoong *et al.* (1973) data. Data was also available on provenance DBHs from another test site of the series investigated by Namkoong *et al.* (1973) (Silen, unpublished data). The ages available were 29, 41, 51, 61, 71, and 81. Analysis of the age-age correlations of provenance means resulted in the following equation:

Age-age correlation = 1.0133 + (0.2617 · LAR) $(r^2 = 0.7565, \alpha = 0.0001)$

This equation is not statistically different from the one developed in this paper with NWTIC data.

From a growth perspective, breeding programs should be increasing volume, not only height or diameter. Genetic correlations of height and diameter with age-20 volume averaged over three sets for three breeding zones are shown in *table 6*. Correlations became relatively stable after age 10 for height and age 15 for diameter. Calculation of REs for these genetic correlations using heritabilities previously calculated show that the most efficient age for these points is age 7. Two points should be made: (1) this early optimum considers "rotation age" to be 20 years, which is unrealistic; and (2) even though the averages may imply this to be an optimum selection age, the relatively unstable heritabilities and age-age correlations for the younger ages imply that risks may be too great. Magnussen and Yanchuk (1993) point out that optimum selection age tends to be older than that calculated with averages when one considers risks in their calculations.

*Table 6.* – Genetic correlations of height and diameter with age-20 volume. Correlations are means of 3 sets from 3 breeding cooperatives. Standard deviations are in parenthesis.

| Trait | Assessment age (years) | | | |
|---|---|---|---|---|
| | 7 | 10 | 15 | 20 |
| Height | 0.781<br>(0.071) | 0.828<br>(0.094) | 0.843<br>(0.104) | 0.854<br>(0.087) |
| Diameter | 0.685<br>(0.148) | | 0.959<br>(0.015) | 0.992<br>(0.011) |

Previous studies have shown that optimum age for family selection is earlier than that for within family selection when dealing with traditional progeny tests (Lambeth *et al.*, 1983; Magnussen and Yanchuk, 1993). It therefore appears that the optimum age for within family selection couid be later than the optimums calculated above for family selection. Use of two-stage selection is a logical alternative. Because several years are needed to develop breeding orchards after selections are made, one could select a number of individuals within the best families at the optimum age for family selection (age 10 for height) and then rogue the breeding orchard based on later assessments. Later assessments would provide trees large enough to give reasonable heritabilities for DBH and allow for thorough assessment of candidate trees for form and health.

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# Optimum Selection Age for Height in *Pinus taeda* L. in Zimbabwe

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## Summary

Four progeny tests of *P. taeda* L. planted in the Eastern Highlands of Zimbabwe were assessed for height at 1.5, 9.5, 13.5, and 22.5 years. Age-age genetic correlations were all positive and high (0.76 to 0.97), with low to moderate standard errors (0.01 to 0.10). Genetic correlations were always higher than corresponding phenotypic correlations. Two linear models were fitted, by regressing genetic correlation on (1) the natural logarithm of the ratio of the younger age to the older age (LAR), and on (2) age difference. The age difference model fitted the data better than LAR model, indicating that the commonly used logarithm models are not necessarily the most appropriate. Predictions of genetic correlations by models based on genetic correlation were more accurate than those estimated using the common model based on phenotypic correlation. Where flowering age was assumed to be 10 years, either genetic or phenotypic models predicted annual genetic gain to be greatest at 10 years. However, the phenotypic model underestimated genetic gain at all ages-particularly at very young ages, for which the potential gain was less than a quarter of that predicted by the other models. When flowering age was reducing to 3 years, optimum selection age under the phenotypic model was 6 years, but was reduced to 3 years using the genetic models. Reducing flowering age to 3 years increased annual genetic gain by 100%, indicating the potential of artificially inducing flowering for enhancing genetic progress with *P. taeda* in Zimbabwe.

*Key words*: Genetic correlation, phenotypic correlation, genetic gain, optimum selection age, *Pinus taeda*.

*FDC*: 165.3; 165.6; 174.7 *Pinus taeda*; (689.1).

## Introduction

*Pinus taeda* Linnaeus is a major exotic plantation species in Zimbabwe and other southern African countries. Breeding of *P. taeda* in Zimbabwe began in 1958 (Barret and Mullin, 1968) and the most comprehensive progeny tests were established in the 1970s.

Forest trees have long generation intervals. Early selection is preferred, as it results in an increased gain per unit of time through reduced generation intervals and may lead to reduced testing costs (Magnussen, 1988). Such early selection is necessarily indirect and offers the means for quicker incorporation of gains into production as parents to be used for multiplication can be selected early and seed orchards or propagation hedges can be culled early.

Optimum selection age is usually defined as the age at which annual genetic gain of breeding cycle is maximized and it is critical to the efficiency of any tree breeding program. Thus, identification of the optimum age for early indirect selection has been of major interest to tree breeders (e.g. Ballochi *et al.*, 1993; King and Burdon, 1991; McKeand, 1988; Riemen-

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