

It is clear from *table 4* that selection for improved growth in Douglas-fir will lead to increased FSF even when change in forking score is limited, unless change in FSF itself is somehow constrained. Since limiting change in FSF will significantly limit the potential for juvenile growth improvement, the need for including FSF in selection programs needs to be carefully considered. The main concern is the extent to which increasing FSF increases susceptibility of improved varieties to damage from late season drought or early fall frost. Although the timing of SF was not observed in this study, it was recorded recently in a farm field trial in France involving seedling families from mother trees in western Washington (C. BASTIEN, INRA, Centre de recherches d'Orleans). A large proportion of individuals in this test second-flushed shortly after initial budset in late June, but many also had 1 or more second-flushes in August. The extent to which families with late-season SF are among the fastest growers, and the degree to which late final budset influences stem hardening and resistance to cold or drought are unclear, but are important topics for future research.

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Optimum Age for Selection in *Pinus radiata* Using Basal Area under Bark for Age:Age Correlations

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Abstract

Age-related changes in the inheritance of stem diameter in *radiata* pine were studied using discs cut at 1.3 m above ground in trees from a progeny test. Measurements of cross-sectional area enclosed within annual growth rings

yielded annual estimates of basal area. The progeny test was a diallel cross which enabled estimation of genetic parameters such as heritability and genetic correlations between measurements at different ages. The greatest gain per generation would have been obtained through selec-

tion at age 14, but gain per year was greatest at age 10. Additive genetic variance generally increased with time, but non-additive variance was a maximum at age 4, declining to negligible levels by age 9.

Age-age correlations generally improved the closer the 2 ages involved were. However, these correlations were not linearly related to the logarithm of the age ratio.

Key words: age-age correlation, early selection, *Pinus radiata*.

FDC: 165.4; 165.62; 174.7 *Pinus radiata*.

Introduction

Genetic control of quantitative traits can differ depending on stage in the life cycle at which measurements are made. For example, traits depending on sexual maturity will not be present in immature individuals, juvenile traits will not be present in adults. Genetic control of growth is likely to be different in mature populations in which growth has essentially ceased (such as human populations), than in immature ones in which growth is close to its maximum. Tree species do not cease growing when they reach maturity and so changes in genetic control of growth with increasing age may occur. Age-related changes in genetic control occur in Douglas-fir (*Pseudotsuga menziesii*; NAMKOONG et al., 1972), loblolly pine (*Pinus taeda*; FOSTER, 1986), sycamore (*Platanus occidentalis*; ROUSSEAU, 1989), Norway spruce (*Picea abies*; BENTZER et al., 1989) and *Pinus radiata* (COTTERILL and DEAN, 1988). These changes have sometimes been linked to stand development phases originally developed by FRANKLIN (1979).

Selection for growth rate in tree breeding programs usually takes place long before harvest; it takes place commonly at about 10 to 12 years of age in southern Australia during a rotation of around 30 to 35 years for *P. radiata*. It is possible to delay selection until just before harvest-time in plantations, but this holds back the breeding program by up to two decades in a species like *P. radiata*. It is also possible to make selections very early, but family performance for growth when the trees are young is rarely the same as family performance when trees are older (LOWE and VAN BUIJTENEN, 1989; MATHESON et al., 1994). Somewhere between these 2 extremes gains made by making more accurate selection will be outweighed by delays in the breeding program. It seems likely there is an optimum where the genetic gains per unit time are maximised.

Relative growth rates are not the only characteristics of a population which change during a plantation's life; genetic parameters change too. Optimum time for selection is not simply the time when family rankings for growth cease to change because measured family performance must accurately reflect family genetic potential, i. e. heritability must be high. Moreover, optimum time for selection is not necessarily the time when heritability is greatest, i.e. when expression of family performance is greatest relative to other sources of variation. This is because selections made early may not be the same as those made later. Optimum age for selection is the time when genetic gain in the harvested crop per unit time is at a maximum and may be different for different traits. In this paper, we are concerned with selection for growth rate as expressed by stem cross-sectional area under bark.

The correlation between growth at different ages is probably not linear and asymptotically approaches unity as the 2 ages become closer. LAMBETH (1980) proposed that

the relationship between "juvenile-mature" (phenotypic) correlation and the logarithm of the age ratio was approximately linear, i.e.

$$r_{\text{age,age}} = 1.02 + 0.38 \text{ LAR} \quad (1)$$

where LAR is the logarithm of the ratio of the younger age to the older age, provided the younger age was greater than 1 year. S. MAGNUSSEN (1989) used a simulation approach to predict from empirical growth models heritabilities and age:age correlations and hence the optimum selection age, finding it to be less than one-sixth of rotation age. He obtained a continuous, non-linear function relating age:age correlation with age. COTTERILL and DEAN (1988) obtained point estimates of additive genetic correlations for height growth and basal area between ages 2½, 6½, 10½ and 16 years. Correlations with age 16 data were low to negative for age 2½ year data, and over 0.7 by age 6½ years for both traits. The optimum age for selection in this case was presumably somewhere between 2½ and 6½ years. Most experimental estimates of age:age correlations suffer from the same problem as those of COTTERILL and DEAN (1988), namely too few points. A method of estimating the correlations annually would be an advantage in finding the optimum age for selection.

The objective of this project was to estimate the optimum age for selection and measurement in a *P. radiata* progeny test using measurements representing all years of growth to age 14 years (about half rotation age).

Materials and Methods

Discs of wood were taken from trees thinned systematically from a progeny test. Cross-sectional areas enclosed by annual rings in each disc were measured and annual growth in basal area estimated from these measurements.

An experimental progeny test (PT53) planted in 1972 in the Buccleuch State Forest New South Wales was selected for this study. The experiment was an incomplete 5 x 5 diallel cross (controls plus 16 full-sib families including reciprocals) involving first-generation selected parents arranged in 10 randomised complete blocks of 5-tree row plots. Spacing was 2.4 m x 2.4 m. The small number of parents in the diallel mean that genetic parameters must be interpreted with caution. Thinning was carried out in December 1986 and involved removing 2nd and 4th trees in each 5-tree plot. For this study, the 2nd tree was used except where missing, in which case the 4th tree was sampled instead; 11 plots had both 2nd and 4th trees missing and so were not sampled at all. Each tree to be sampled was felled just above ground level and a disc of wood cut 1.3 m above the cut surface. Discs were planed flat and photocopied while still fresh so that shrinkage of discs would not bias results. A total of 169 discs was treated in this way. Cross-sectional areas for each year of growth were measured using a light pen and digitising graphics tablet connected to a computer.

The computer program DIALL (SCHAFER and USANIS, 1968) was used to analyse the results. This program treats all effects as random and mean squares are equated to their expectations for variance component estimation. The model fitted included terms for replicates, general and specific combining ability (GRIFFING, 1956). Reciprocal effects were generally small and were treated as part of specific combining ability. Heritabilities and additive genetic correlations for different years' cross-sectional areas were calculated from estimates of genetic variances and covariances as follows (FALCONER, 1989; BECKER, 1984):

$$h^2 = \frac{V_A}{V_P} \quad (2)$$

where $V_A = 4V_{GCA}$
 $V_P = V_A + V_D + V_E$
 and $V_A =$ additive variance
 $V_P =$ phenotypic variance
 $V_{GCA} =$ general combining ability variance component
 and $V_D =$ non-additive variance
 $V_E =$ environmental variance
 $=$ residual variance $-(3 \cdot V_{GCA}) - (3 \cdot V_{SCA})$
 $V_D = 4V_{SCA}$

where $V_{SCA} =$ specific combining ability variance
 Additive genetic correlations were calculated using GCA covariance components from analyses of cross products.

Gain from selection in a trait measured at maturity is (LAMBETH, 1980):

$$G_M = i_M h^2_M \sigma_{P_M} \quad (3)$$

where $G_M =$ gain at maturity
 $i_M =$ selection intensity at maturity
 $h^2_M =$ heritability of the trait at maturity $= \frac{\sigma_{G_M}^2}{\sigma_{P_M}^2}$
 $\sigma_{G_M} =$ genetic standard deviation
 $\sigma_{P_M} =$ phenotypic standard deviation

Most measurements of genetic experiments are carried out before maturity (defined as harvest time), so the gain estimated at maturity based on selection before maturity (when the trees are 'juvenile') is (FALCONER, 1989):

$$CG_M = i_J h_J h_M r_{AJM} \sigma_{P_M} \quad (4)$$

where subscripts M, J, A and P represent mature, juvenile, additive genetic and phenotypic respectively; and:
 $CG =$ correlated gain
 $h =$ square root of heritability
 $r_{AJM} =$ additive genetic correlation between juvenile and mature trait.

In this context, 'juvenile' means young and 'mature' means older (probably harvest age); there is no implication of sexual maturity.

Gain per year was also calculated assuming that crosses take 2 years from pollination to seed collection and that seedlings grow for 1 year in the nursery between sowing and planting out.

Results from diameter measurements at breast-height over bark (DBHOB) taken in 1976 (at age 4), 1981 (at age 9) and 1986 (at age 14) were available for comparison. Genetic correlations were obtained as above, using data from corresponding trees.

Diameters under bark in 1986 were measured directly on photocopies of discs. The diameter of each disc was measured on both the north-south axis and at right angles to it. The mean of these 2 values was used for comparison with disc areas to test the assumption that discs are circular and to test whether increment cores would give similar results.

Results

Phenotypic variance for cross-sectional area of each growth ring was partitioned into additive, non-additive and environmental components. The changes taking place for these components with time are presented in figure 1.

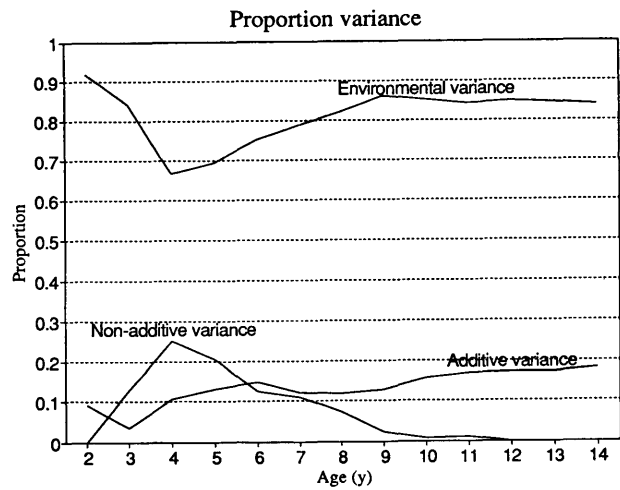


Figure 1. — Components of variance expressed as a proportion of the total phenotypic variance at different ages.

Additive variance began at a low level but increased until about age 6, declined slightly before increasing again, reaching a maximum of over 18 % by age 14. Non-additive variance also began at a low level, increased to a maximum of more than twice the additive variance at age 4 then declined slowly to negligible levels by age 9 to 12. Environmental variance began at a very high level, declined to age 4 then increased to about 83 % by age 8 at which level it remained.

Heritability for cross-sectional area was low early in the experiment (only 4 % at age 3 — Table 1, Figure 2) but rose to 14 % at age 6, declined slightly before rising to a maximum (18.3 %) at age 14. The change in heritability with age was due to increase in additive variance in the face of increasing environmental variance (Table 1, Figure 1); after age 6 they increased at about the same rate.

Genetic correlations between cross-sectional areas for each year and 1986 cross-sectional area at age 14 are presented in table 1. In general, apart from pith diameter (not presented) with genetic correlation of 0.40 with age 14 cross-sectional area, genetic correlations were low and sometimes unfavourable between early growth and growth at age 14. They increased fairly steadily, reaching 0.5 by age 6 and 0.95 by age 10 (Fig. 2).

Additive correlation between all years' measurements were plotted against log(age ratio) (LAR) (Fig. 3). In gen-

Table 1. — Heritabilities (h^2) and additive genetic correlations (r_{AJM}) between cross-sectional areas of rings for various years and cross-sectional area in 1986 at age 14.

Year	Age	r_{AJM}	h^2	SE(h^2)
1974	2	-0.53	0.09	0.10
1975	3	-0.43	0.03	0.08
1976	4	0.10	0.11	0.10
1977	5	0.35	0.13	0.11
1978	6	0.53	0.15	0.11
1979	7	0.69	0.12	0.11
1980	8	0.81	0.12	0.11
1981	9	0.89	0.13	0.11
1982	10	0.96	0.16	0.12
1983	11	0.98	0.17	0.12
1984	12	0.99	0.17	0.12
1985	13	1.00	0.17	0.12
1986	14	-	0.18	0.12

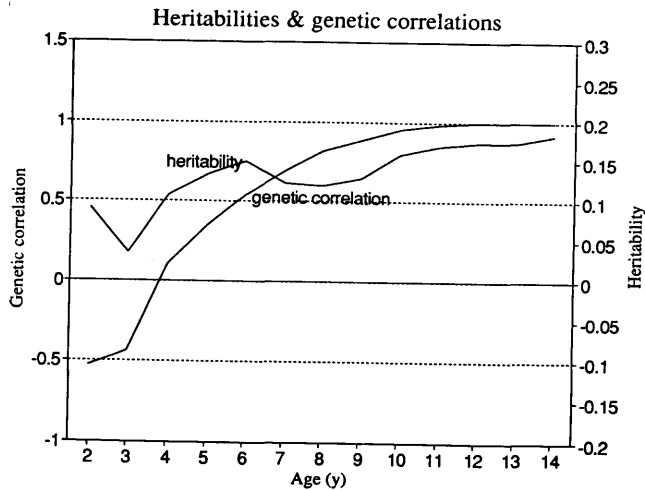


Figure 2. — Heritabilities at different ages and genetic correlations between results at different ages and age 14 cross-sectional area

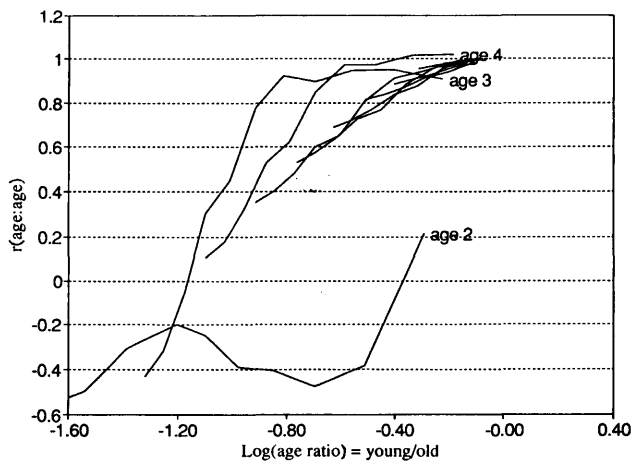


Figure 3. — Relationships between age:age correlations and log (age ratio) for cross-sectional areas of different ages.

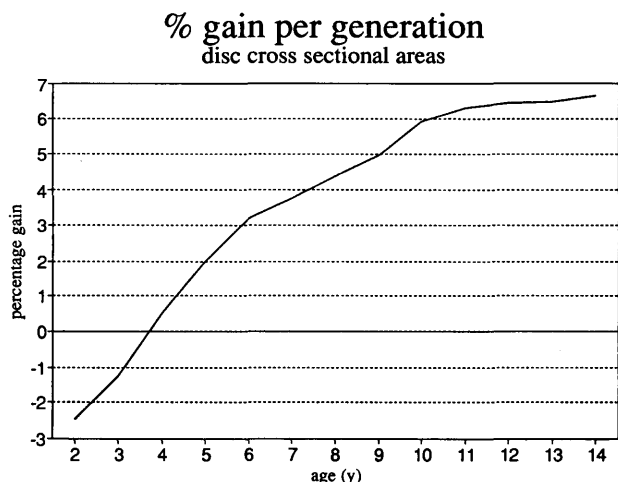


Figure 4. — Gain per generation for selection at different ages.

eral, the closer 2 measurements are in time, the better is the genetic correlation; partly due to autocorrelation — consecutive measurements on the same material. Correlations involving age 2 with all other ages showed a rather different pattern than that shown by correlations in-

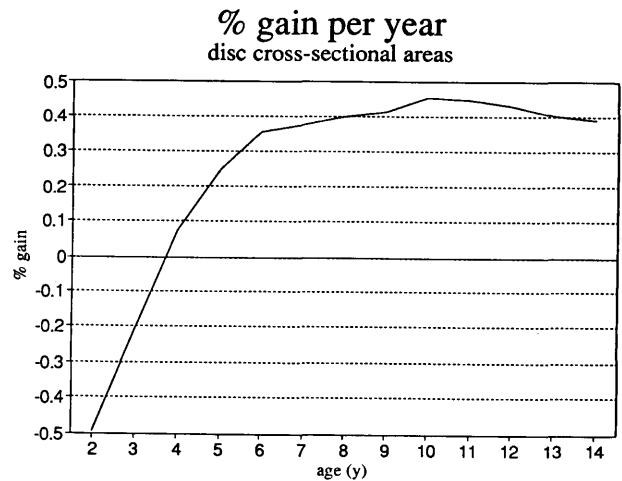


Figure 5. — Gain per year assuming 3 years from measurement to seed collection.

Table 2. — Additive genetic correlations between Disc cross-sectional areas (CSA) and standing tree diameters measured at 1.3 m above ground over bark (DBHOB).

CSA Year	Age	Standing tree trait		
		DBHOB	DBHOB	DBHOB
		1976	1981	1986
1974	2	-0.74	-0.18	-0.38
1975	3	1.25	1.08	-0.03
1976	4	1.70	0.97	0.32
1977	5	1.94	0.92	0.51
1978	6	1.84	0.95	0.64
1979	7	1.59	0.98	0.76
1980	8	1.36	0.98	0.85
1981	9	1.06	0.98	0.93
1982	10	0.49	0.94	0.99
1983	11	0.21	0.90	1.00
1984	12	-0.35	0.82	1.00
1985	13	-0.75	0.76	0.99
1986	14	-0.89	0.73	0.99
Heritability		0.08	0.25	0.32

volving later ages. Age 3 correlations were high with ages between 4 and 8 and then dropped sharply, to become negative with age 14. This pattern was followed by all other ages with the slope of the curve becoming more consistent as the young part of each age-age correlation became older.

Genetic gain per generation also increased from a negative figure at ages 2 and 3 years to 6.3% at age 10 and 7.4 % at age 14 (Fig. 4). This may seem small, but the selection intensity used in the calculations was low. More interesting is the genetic gain per year which followed a similar pattern except that it reached a maximum of 0.48 % per year at age 10 before declining slightly (Fig. 5). The figures from years 8 (0.40 %) to 14 (0.43 %) are probably not significantly different. Figures 4 and 5 were produced assuming an intensity of selection of 1.271 (i.e. 4 in 18 BECKER, 1984).

Genetic correlations between results obtained from disc data and data collected on standing trees in 1976 and 1981 were generally very high (Table 2). Correlations for standing tree diameter at breast height over bark (DBHOB) in 1976 increased rapidly, reaching a maximum with disc cross-sectional area in 1977 then decreasing again. Correla-

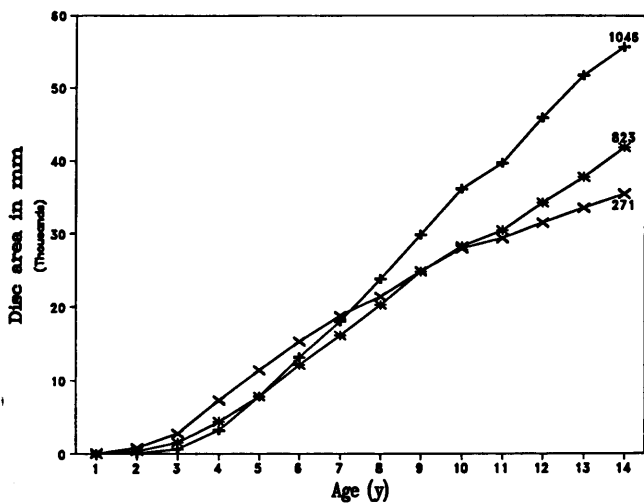


Figure 6. — Cross-sectional area of discs from 3 trees, plotted against age.

tions for DBHOB in 1981 were high with cross-sectional area in 1975, remaining high before decreasing after 1982. Correlations for DBHOB in 1986 showed a steady increase to a maximum in 1983 to 1984.

Low genetic correlation between disc cross-sectional area at young age and later means that wrong selections would be made at the earlier time. This is illustrated in figure 6 in which growth in 3 individual trees is plotted against time. Ranking at age 4 is exactly the opposite of ranking at age 14 for the 3 discs plotted. Final ranking was not achieved until age 11.

Tree 1046 started growing slowly but ended up much larger than the other 2. On the other hand, tree 271 started growing much faster but ended up smaller than the other 2. Tree 823 is intermediate, starting slowly, becoming the smallest, but ending up between trees 1046 and 271 in size at age 14.

Genetic correlation between diameter calculated from cross-sectional area in 1986 measured using the light pen and estimated by measuring under-bark diameter with a ruler (simulating an increment core) was very high (0.9996), implying that selection using one method would give almost exactly the same gain as selection using the other. The actual values of estimates reported here relate to this experiment and, because of the small number of parents, may not be general. However, the trends from year-to-year are more likely to have general validity.

Discussion

Changes in genetic parameters with time were studied using measurements of cross-sectional areas for each annual ring in trees systematically thinned from a diallel cross experiment. Although it is possible to study such changes using external measurements of trees, it is not usual to measure diameters of trees less than 3 or 4 years old nor to make annual measurements.

This experiment represents a very small sample of possible available parents at the time the crosses were carried out. For this reason, the actual values obtained here for variance components and heritabilities may not be very close to true population values. However, present estimates are generally only slightly smaller than previously-published values (COTTERILL and ZED, 1980; MATHESON and RAYMOND, 1986) and the purpose of this paper is to report

on age-related changes in genetic parameters rather than actual values themselves.

The age at which the proportion of additive variance is highest is about 11 years in this experiment although ages 10 to 16 probably do not differ. This means that the most accurate selection of trees for the next generation would have been made at 11 years. Some gain each generation can be sacrificed in order to turn over generations more quickly. Assuming it takes two years for pollinations and one year for seedlings to grow in the nursery before outplanting in progeny trials, the maximum gain per year in this experiment would be obtained by selecting at age 8 although ages 6 to 10 are probably not significantly different. At present, *Pinus radiata* takes about 6 to 8 years from seed to flower in any case so pollinations earlier than 6 years are probably not practicable yet. It would seem, in this experiment, that any time from 6 to 10 years would be appropriate for selection for stem diameter, depending on the pollination potential, in general agreement with COTTERILL and DEAN (1988). However, little, if any gain would be lost by waiting until trees are 8 to 9 years old to ensure all selections are flowering and that all desired crosses to produce the next generation are possible.

Selection based on over-bark diameters measured in standing trees may follow a similar pattern. Selection in this experiment for cross-sectional area in 1986 (at age 14) based on DBHOB in 1976 would be unsuccessful because of the negative additive genetic correlation between the traits at these ages. Selection based on DBHOB in 1981 would be better ($r_{AJM} = 0.73$).

Non-additive variance in this experiment included variance caused by maternal effects which are expected to persist only a few years. Although larger than additive variance at age 4, non-additive variance was only one quarter of the additive variance two years later and by age 9 it had disappeared. Non-additive variance also includes variance caused by non-genetic effects related to family such as nursery effects (if the nursery was non-randomised) and reciprocal effects (usually rare).

Age:age correlations have proved not to be linearly related to the log of the age ratio (LAR) in this experiment. LAMBETH (1980) proposed a linear function linking phenotypic correlations to LAR. Results here agree with LAMBETH's in that age 2 results differ in quality rather than quantity from other age results. In this experiment, regularity of results was not obtained until age 3 and linearity was not obtained at all. LAMBETH's function (1) does not fit data from this experiment. There was some regularity in correlations for large age differences, but the relationship was not linear. A cubic equation was fitted to the correlations for the largest age differences for each age. It agreed closely with the data within the ages studied here. It was

$$r_{\text{age, age}} = -0.28 + 0.275(\text{LAR} + 1.7) + 1.15(\text{LAR} + 1.7)^2 + 0.515(\text{LAR} + 1.7)^3 \quad (4)$$

This is an unwieldy relationship, not generally recommended, but it does illustrate that the relationship is not linear.

Conclusion

Maximum gain in cross-sectional area per year in this experiment would have been obtained by selecting when trees were between 6 and 10 years. The expression of genetic

variance had a local maximum at about 6 years of age and increased only slightly after that time.

Non-additive variance for cross-sectional area in this experiment was unimportant after about 6 years of age.

The assumption that trees are generally circular in cross-section would not lead to appreciable inaccuracy in selection in this experiment.

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Genetic Parameters for Bole Volume in Longleaf Pine: Large Sample Estimates and Influences of Test Characteristics¹⁾

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Abstract

Data from 17 progeny test/seedling seed orchard sites of longleaf pine (*Pinus palustris* MILL.) containing a total of 901 open-pollinated families and 40,801 trees were analyzed to obtain precise genetic parameter estimates for bole volume at age 8, to evaluate genetic gains in seedling seed orchards, and to determine relationships between genetic parameter estimates and the test characteristics of survival, site productivity, and statistical precision. Estimates of bole volume heritability based on individual-test analyses (biased heritability) averaged 0.311 (range 0.143 to 0.570 across the 17 tests). Thirty-four pairwise combinations of tests were also analyzed to estimate unbiased heritabilities and Type B genetic correlations (r_B). The mean estimates for these parameters were 0.205 and 0.675, respectively. In most cases, genetic parameter estimates were not significantly related to characteristics of the tests. Type B genetic correlations, however, were significantly larger (indicating less genotype x environment interaction) when test pairs were in the same geographical planting

zone ($r_B = 0.747$), than when they were in different (east vs. west) zones ($r_B = 0.610$). Planting zone x family interaction will need to be considered in future selection and seed deployment decisions. Nevertheless, even if this interaction is ignored, genetic gain in eight-year volume from low intensity (50%) roguing of families and individuals in the seedling seed orchards is expected to average around 11%. Gain in a 1.5 generation clonal seed orchard containing the best individual in each of the top 25 (2.8%) of the families is expected to exceed 35%.

Key words: Heritability, Type B genetic correlation, genotype x environment interaction, seedling seed orchard, *Pinus palustris* MILL.

FDC: 165.3; 232.11; 232.311.3; 174.7 *Pinus palustris*.

Introduction

Longleaf pine (*Pinus palustris* MILL.) is a high quality timber tree known for straight, well-formed stems, high bolewood density, and resistance to fusiform rust (SNYDER et al., 1977; BOYER, 1990). Despite these attributes, longleaf pine is a low priority choice relative to slash (*Pinus elliotii* ENGELM.) or loblolly (*Pinus taeda* L.) pines, for planting within the longleaf native range in the southeastern United States. The main reason historically for this low priority status has been the difficulty experienced in adequately establishing longleaf pine plantations. In addition to low seedling survival, young longleaf pine typically

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