Test Designs and Optimum Age for Parental Selection in Advanced-Generation Progeny Tests of Slash Pine[1])

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Abstract

Assuming a half-sib family mating design and a randomized complete block field design with 5 trees per family in each block for advanced-generation progeny tests of slash pine (*Pinus elliottii* var. *elliottii*), this paper: 1) examines optimal numbers of offspring per family and their allocation to varying numbers of blocks and locations and 2) quantifies efficiencies of parental selection at varying ages. Two scenarios of genetic parameter estimates are used, the first being empirical estimates obtained from first-generation progeny tests and the second being a hypothetical scenario reflecting use of better test design, establishment and maintenance methods to reduce experimental error and increase test precision. Using 4 interest rates (0%, 3%, 5% and 8%), discounted selection efficiency (the ratio of discounted gain from early selection to discounted gain from infinite testing at age 15 years) was used to quantify efficiency of parental selection and thereby determine relative efficiencies of various test designs and selection ages.

For a fixed number of progeny per parent (i.e., a fixed amount of effort), a single block per location (therefore using the maximum number of locations) is always optimum if there exists any non-zero genotype x location interaction. However, for both scenarios of parameter estimates, use of 2, 3, or 4 blocks (and therefore fewer locations) was at least 97% as efficient. For a fixed design of 4 blocks per location, testing in more locations always results in more genetic gain. Six to 12 locations (depending on the scenario of parameter estimates) were needed to achieve greater than 95% of the efficiency achieved by 15 locations. Approximately half the number of locations were required to achieve a given level of efficiency under the second scenario of parameter estimates compared to the first scenario.

Optimum age for parental selection is markedly affected by choice of interest rate, but is at or near age 10 for 3 of the 4 interest rates examined. For interest rates of 5% and 8%, the curves have flat, broad peaks indicating that from age 7 to 10 (and probably up to 12), parental selection efficiency will be greater than 95% of the optimum.

Key words: early testing, indirect selection, progeny tests, selection efficiency, *Pinus elliottii*.

Introduction

Progeny testing, defined as the estimation of relative genetic worth of parents based on the performance of their offspring (ALLARD, 1960), is a costly, and yet critical part of tree improvement programs. Once parental rankings or breeding values have been determined, they are used in 2 basic ways: (1) parental or "backward" selection, and (2) offspring or "forward" selection, i. e., in combined family and within family selection on new genotypes. Thus, the potential operational uses of parental rankings are many,

including (BRIDGWATER, et al., 1983; WHITE, 1987; WHITE and HODGE, 1987): (1) to establish and upgrade production populations (such as seed orchards), (2) to formulate deployment strategies that allocate genotypes to appropriate planting sites, (3) to upgrade the breeding population by elimination of inferior genotypes, and (4) to devise complementary mating or best-mate indices (ALLAIRE, 1980).

Each use of parental rankings is a form of parental selection (used here synonymously with family selection) and gain will be maximized if the parental rankings are both precise and accurate. Gains can always be increased by increasing selection intensity (testing more parents) and increasing family heritability (testing more offspring from each parent distributed across more blocks and locations). However, because progeny testing is so expensive, it is critical to develop progeny test designs that both result in precise rankings and are cost-effective. A progeny test design entails 2 components (mating design and field design) and former studies have investigated both components: (1) appropriate mating designs (VAN BUIJTENEN, 1976; LINDGREN, 1977; VAN BUIJTENEN and NAMKOONG, 1973; ZOBEL and TALBERT, 1984; VAN BUIJTENEN and BRIDGWATER, 1986; BURDON and VAN BUIJTENEN, 1990) and (2) optimal field designs including number of offspring and plot configuration (ROBERTSON, 1957; FRANKLIN, 1971; BARNES and SCHWEPPENHAUSER, 1979; LIBBY and COCKRHAM, 1980; BRIDGWATER et al., 1983; COTTERILL and JAMES, 1984; LOO-DINKINS and TAUER, 1987). However, only a few studies (LINDGREN, 1984, 1985) have considered optimal numbers of progeny in the presence of genotype by environment interaction or appropriate allocation of offspring to multiple planting locations.

The relative efficiencies of parental selection at various ages have also been addressed for some situations (BRIDGWATER et al., 1983; COTTERILL and DEAN, 1988; McKEAND, 1988; BALOCCHI, 1990). However, the questions of test designs and selection ages are not separate issues because designs appropriate for older ages may not be those most suited to younger ages; and, fewer studies have examined these issues as a joint optimization problem.

The Cooperative Forest Genetics Research Program (CFGRP) is composed of 14 private and public organizations developing improved slash pine (*Pinus elliottii* ENGELM. var *elliottii*) for the lower coastal plain of the southeastern United States. We have recently made approximately 1000 advanced-generation selections that will form the basis of future generations of breeding (HODGE et al., 1989). For several reasons, we will use complementary mating designs (CMD) that separate the breeding and progeny testing of these selections into distinct phases each with its own design (BURDON and SHELBOURNE, 1971; VAN BUIJTENEN, 1976; VAN BUIJTENEN and LOWE, 1979). Open-pollinated or polymix families are often advocated for the progeny testing phase (VAN BUIJTENEN, 1976) because

this mating design is generally efficient for parental selection (BURDON and VAN BUIJTENEN, 1990).

Thus, for the *a priori* choice of a polymix mating design, this paper presents a general method of using variance component estimates to examine the issue of optimal field designs for progeny tests (e.g., numbers of offspring required, allocation of offspring to various numbers of blocks and test locations). Our specific objectives are (1) to find test designs that result in precise parental rankings and (2) to determine ages of greatest selection efficiency.

Methods

General Approach

We made 4 *a priori* assumptions believed to be appropriate and logistically realistic to the CFGRP situation: (1) the mating design consists of polymix or open-pollinated families assumed to be half-sib families, (2) only randomized complete block designs were considered, (3) only 5-tree plots (5 trees from a given family represent each family in a given block) were considered (LOO- DINKINS and TAUER, 1987), (4) parameter estimates from first-generation progeny tests (and some modifications of these) apply to the next generation of progeny tests.

Within this framework, an existing set of genetic parameter estimates for volume growth of slash pine was used to quantify expected genetic gains from parental selection at various ages. A range of field designs (numbers of blocks

per locations and numbers of locations) were examined at various test ages to see which resulted in optimum allocation of effort. As with all studies of this kind, more effort always results in more gain so "optimum allocation of effort" is taken here to be that point of diminishing returns where addition of more effort results in only a small amount of extra selection efficiency. We quantified selection efficiencies for a range of progeny test ages (4 to 10) to understand which designs were most suited to which ages and also to quantify the relative merit of selection at various ages. This required interpolations of our parameter estimates which were for tree volume at 3 discrete ages (5, 10, and 15 years). Also, as recommended by BURDON (1989) and done by others (PAQUES, 1984; McKEAND, 1988; BALOCCHI, 1990), all designs were examined for 2 different sets of parameter estimates (our empirical estimates and a modification of these) to examine how sensitive the inferences about optimal designs and selection ages are to errors or changes in our parameter estimates.

Selection Efficiency

The target trait used was tree volume at age 15 years, and for each age and test design simulated, selection efficiency of parental selection at a given early age relative to that at age 15 was estimated as a slight modificatio; of that defined by other investigations (PAQUES, 1984; COTTERILL and DEAN, 1988; RIEMENSCHNEIDER, 1988). Using our traits, their definition of selection efficiency per generation, Q_{gen} is:

$$Q_{gen} = \frac{\text{gain in age 15 volume from indirect selection at an early age}}{\text{gain in age 15 volume from direct selection at age 15}}$$

$$= \frac{i_E \, h_E \, h_{15} \, r_g \, \sigma_{P,15}}{i_{15} \, h^2_{15} \, \sigma_{P,15}} \qquad \text{Eq. 1}$$

where i_E and i_{15} are the selection intensities (FALCONER, 1981) on a family mean basis at the early age and age 15, respectively; h^2_E and h^2_{15} are the family heritabilities (defined in Eq. 6) for tree volume at the early age and age 15, respectively; r_g is the additive genetic correlation for volume growth between the 2 ages; and $\sigma_{P,15}$ is the phenotypic standard deviation of family means for volume at age 15.

COTTERILL and DEAN (1988) note that if $i_E = i_{15}$, then

$$Q_{gen} = (h_E \, r_g \, / \, h_{15}). \qquad \text{Eq. 2}$$

Q_{gen} is interpreted as the selection efficiency of indirect selection relative to direct selection for a given test design. We define a new parameter, Q'_{gen}, measuring the selection efficiency of indirect selection for a specific design relative to the theoretical maximum from direct selection, i.e., direct selection based on infinite testing. If each parent is tested by an infinite number of offspring in an infinite number of blocks and locations, then $h^2_{15} = 1$ and

$$Q'_{gen} = h_E \, r_g = \text{Corr}(g,\hat{g}) \qquad \text{Eq. 3}$$

where $\text{Corr}(g,\hat{g})$ is the correlation between predicted and true breeding values, and is calculated as above for this specific case of indirect early selection based on a single trait (WHITE and HODGE, 1991). We find this expression of selection efficiency meaningful for 3 reasons:

(1) It expresses the selection efficiency of finite, early testing relative to infinite testing at age 15, or in other words, for a given selection intensity, the gain relative to the theoretical maximum from direct selection. This allows comparison of different early testing designs (e.g., few versus many locations) and comparison of the same testing design at different ages using the same criterion.

(2) The value $\text{Corr}(g,\hat{g})$ can be interpreted as a standardized gain, i.e., gain per unit of selection intensity and per unit of genetic variance in the target trait (WHITE and HODGE, 1991).

(3) It expresses the correlation between the predicted and true breeding values. Heuristically, with infinite direct testing, the true breeding values, g, would be known without error, while the predicted breeding values, $\hat{g}$, are derived from finite, indirect testing and therefore have error associated with them.

Because there is economic value in realizing gain earlier, we adopted a procedure (similar to McKEAND, 1988, and BALOCCHI, 1990) of discounting the values of the gain from both indirect selection (the numerator of Eq. 1) and direct selection (the denominator of Eq. 1). This entails dividing both gains by a discounting factor, $(1+d)^t$, where d is the real interest rate and t is the time in years (the early age for discounting the numerator and 15 for discounting the denominator). If the previous 2 assumptions (i.e., $i_E = i_{15}$, and infinite progeny testing for the direct

gains) are again adopted, then the ratio of discounted gains from early compared to later selection is:

$$Corr(g,\hat{g})_d = Corr(g,\hat{g}) * [(1+d)^{15}/(1+d)^t]$$

Eq. 4

where $Corr(g,\hat{g})_d$ is the ratio of discounted gains (hereafter called discounted selection efficiency) for a particular interest rate, d, and t is the age of the early selection. An advantage of this approach over some others is that the discounting factor (in square brackets on the right-hand side of equation 3), and hence the discounted selection efficiency, depend only on the difference between the early and later selection ages, but not on the actual number of years to realization of benefits. That is, $[(1+d)^{15+y}/(1+d)^{t+y}]$ is the same for all values of y.

The relative values of early selection at any ages E and E' will be the same whether using Q_{gen} from Eq. 2 or $Q'_{gen} = Corr(g,\hat{g})$ from Eq. 3 as the criterion, since $Q_{gen} = Q'_{gen}$ multiplied by a constant, $1/h_{15}$. Thus, for the purposes of determining the optimum age of selection, the 2 approaches give equivalent answers.

To examine sensitivity of selection efficiency to choice of interest rate, we measured selection efficiency by 4 parameters for each test design and age simulation: $Corr(g,\hat{g})$, $Corr(g,\hat{g})_3$, $Corr(g,\hat{g})_5$, and $Corr(g,\hat{g})_8$. These reflect increasingly larger interest rates (0%, 3%, 5% and 8%).

Table 1. — Genetic parameter estimates for tree volume for slash pine for scenarios 1 (low h²) and 2 (high h²). The variance components σ^2_f, σ^2_{fe}, σ^2_p and σ^2_w are variance due to family effects, family by environment interaction effects, plot effects and within-plot effects, respectively. Variance components are expressed as a fraction of the sum of all 4 components. The values h² and h^2_f are the individual tree and family heritabilities (h^2_f is arbitrarily presented for t=6 and b=4 from equation (6).). The value r_B is the Type B genetic correlation (equation 7) and r_g is the genetic correlation between volume at each age and volume at age 15. Estimates for ages 5, 10 and 15 of scenario 1 are from HODGE and WHITE (1992); the others are modifications of these.

Scenario	Age	Variance Component Estimates				h²	h^2_f	r_B	r_g
		σ^2_f	σ^2_{fe}	σ^2_p	σ^2_w				
1: low h²	4	0.016	0.013	0.145	0.826	0.065	0.518	0.559	0.577
	5	0.020	0.014	0.137	0.829	0.080	0.572	0.590	0.670
	6	0.024	0.015	0.129	0.832	0.095	0.616	0.610	0.746
	7	0.028	0.016	0.120	0.836	0.110	0.652	0.627	0.811
	8	0.031	0.018	0.112	0.839	0.126	0.682	0.641	0.867
	9	0.035	0.019	0.103	0.843	0.141	0.709	0.652	0.916
	10	0.039	0.020	0.095	0.846	0.156	0.731	0.661	0.960
	15	0.041	0.024	0.061	0.874	0.161	0.748	0.630	1.000
2: high h²	4	0.025	0.011	0.000	0.964	0.099	0.715	0.690	0.577
	5	0.030	0.013	0.000	0.958	0.118	0.745	0.700	0.670
	6	0.034	0.014	0.000	0.952	0.137	0.770	0.710	0.746
	7	0.039	0.015	0.000	0.946	0.157	0.790	0.720	0.811
	8	0.044	0.016	0.000	0.936	0.177	0.807	0.730	0.867
	9	0.049	0.017	0.000	0.933	0.197	0.822	0.740	0.916
	10	0.054	0.018	0.000	0.927	0.218	0.835	0.750	0.960

Parameter Estimates from First-Generation Progeny Tests

A basic set of genetic parameter estimates (ages 5, 10 and 15 of scenario 1 in *Table 1*) were used as the foundation to develop the 2 genetic parameter scenarios described in the next section. To ensure that the basic set of parameter estimates were as precisely estimated as possible, data were used from 57 different CFGRP progeny tests containing open-pollinated offspring from 585 different parents and over 70,000 trees. Details of estimation and parameter estimates for a variety of traits are in HODGE and WHITE (1992), but briefly, each progeny test was planted in a randomized complete block design with row-plots of 5 to 10 trees representing each family in each block; the number of blocks and families in a test varied. Measurements of height and diameter at breast height were taken when tests were ages 5, 10 and 15 years old, and used to calculate tree volumes (GODDARD and STRICKLAND, 1968).

Because of imbalance, the data were not well-suited to classical pooled ANOVAs for estimating variance components, and an alternative approach was adopted (see BURDON, 1977; JOHNSON and BURDON, 1990). First, ANOVAs for each location were used to estimate variance components by the method of moments (SAS Type I sum of squares equated to their expectations, MILLIKEN and JOHNSON, 1984), and then Type B correlations from paired site analyses were employed to decompose the family variance component from the single site ANOVAs into the variance portions contributed by average family effects and family by location interaction. An analogous approach was used to estimate covariances. Further details of the advantages and relationship of this approach to the pooled ANOVA approach are in YAMADA (1962) and DICKERSON (1962). Thus, each pair of tests provided estimates of individual tree heritabilities, h^2, age-age genetic correlations, r_g, and Type B genetic correlations for a given age, r_B. Then the estimates from all possible pairs of tests were averaged. The 3 genetic correlations for volume (5 with 10, 5 with 15 and 10 with 15) were modified to obtain an admissible, internally consistent set of correlations (HODGE and WHITE, 1992).

An error variance for each average estimate was calculated using an empirical approach (see HODGE and WHITE, 1992, for details), as opposed to using an approximate formula from a Taylor Series expansion (such as MODE and ROBINSON, 1959; NAMKOONG, 1979, p. 232). This was possible because of the large number of tests and pairs of tests that provided estimates. We believe that these parameter estimates are relatively precise (CVs of 5% to 10% when the standard errors are divided by the estimate).

Two Sets of Genetic Parameter Estimates

To examine sensitivity to genetic parameter estimates, 2 sets of estimates (which will be referred to as "low h^2" and "high h^2" scenarios) were used in the calculation of all selection efficiencies (*Table 1*). In both scenarios, average values for h^2, r_B, and σ^2_w (relative to total variance) were used to calculate σ^2_f, σ^2_{fe}, σ^2_p and σ^2_w (respectively, variance due to average family effects, family by environment interaction effects, plot effects and within-plot effects) according to the following genetic relationships:

$$h^2 = 4\sigma^2_f / (\sigma^2_f + \sigma^2_{fe} + \sigma^2_p + \sigma^2_w), \qquad \textbf{Eq. 5}$$

$$h^2_f = \sigma^2_f / (\sigma^2_f + \sigma^2_{fe}/t + \sigma^2_p/tb + \sigma^2_w/tbn) \text{ and}$$
$$\textbf{Eq. 6}$$

$$r_B = \sigma^2_f / (\sigma^2_f + \sigma^2_{fe}). \qquad \textbf{Eq. 7}$$

The values t, b and n are the number of test locations, blocks and trees per plot (n is always 5 owing to *a priori* assumption number 3), respectively.

Scenario 1, Low h^2: Because tree volume at ages 10 and 15 are nearly identical traits in a genetic sense (similar h^2 and r_g of 0.96 from *Table 1*), we did not examine selection efficiencies beyond age 10. Since parameter estimates were only available at ages 5 and 10, interpolation was necessary to derive estimates for the intervening years 4 through 9 (*Table 1*) as follows. First the log of the age ratio (LAR) approach developed by LAMBETH (1980) and described by BURDON (1989) for smoothing correlation estimates was used to predict the genetic correlation from a fitted line between the 5 to 15 genetic correlation of 0.67 and the 10 to 15 correlation of 0.96: $r_g = 1.1296 + 0.4184$ (LAR). Next, for each age, the variance component estimates were calculated by working backwards starting with a linear interpolation of h^2 values between the 5-year and 10-year values and a relatively smooth progression of r_B values from age 5 to age 10. Thus, for "low h^2" scenario the parameter estimates used for ages 5 and 10 were our actual estimates and those for the other ages were developed to be as internally consistent as possible with these anchor points.

Scenario 2, High h^2: The parameter estimates for scenario 2 (*Table 1*) were obtained from those in scenario 1 using the following 3 assumptions that we believe are realistic. First, the within-block environmental variance can be substantially reduced in advanced-generation tests by choice of more uniform sites, proper field layout, use of smaller block size, vegetation control, and planting of filler trees in poor locations. Thus, for each age we reduced the sum of $\sigma^2_p + \sigma^2_w$ by by 20%. Second, we increased all values of r_B by approximately 0.10. Our empirical genetic parameter estimates indicate higher r_B values when tests are on sites of similar quality (HODGE and WHITE, in Press). Increasing the r_B values refects the assumption that the breeding program could be "regionalized" (JOHNSON and BURDON, 1990), i.e., that progeny testing and seed deployment strategies could be developed to take advantage of predictable genotype x environment interaction (ALLARD and BRADSHAW, 1964). Third, we assumed that use of noncontiguous 5-tree plots within a block (as opposed to the row-plot test data that generated the estimates of scenario 1) would result in σ^2_p values of near zero at all ages (LAMBETH et al., 1983; LOO-DINKINS and TAUER, 1987); thus, at each age the value of σ^2_p was set to zero and σ^2_w increased by the former amount of σ^2_p. From these 3 assumptions, new variance component estimates were calculated for each age, and these basically reflect our belief that precision of new tests could be increased as described. Contrary to this, we have no reason (empirical or theoretical) to believe that the genetic correlations between younger ages and age 15 will be altered by any of these steps to increase test precision. Thus, the genetic correlations for scenario 2 (high h^2) are identical to those of scenario 1 (low h^2).
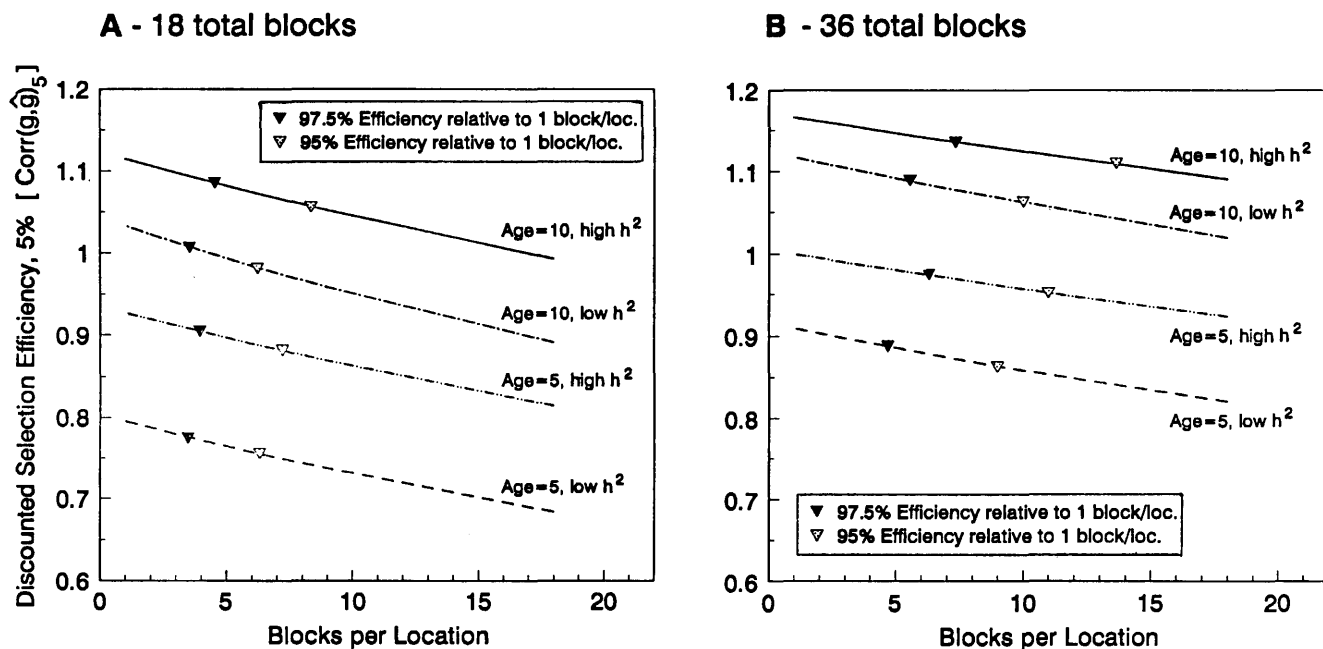
A - 18 total blocks

B - 36 total blocks

Figure 1. — Discounted selection efficiency using a 5% discount rate, Corr(g, $\hat{g}$)$_5$, for ages 5 and 10 and low and high h² scenarios as a function of numbers of blocks per location. Efficiencies are shown for 2 fixed levels of total effort (both assume 5-tree plots): (A) 18 total blocks = 90 progeny per parent and (B) 36 total blocks = 180 progeny per parent.

Results

Numbers of Blocks and Locations

All 4 discounted selection efficiencies, Corr(g,$\hat{g}$)$_d$, showed identical trends and resulted in identical inferences for a given age because all are multiples of Corr(g,$\hat{g}$)$_0$. So, results for determining optimal numbers of blocks and locations are presented for ages 5 and 10 using only the discounted selection efficiency at 5%, Corr(g,$\hat{g}$)$_5$. Given the assumption of 5 trees per family in each block, optimal allocation of a fixed number of blocks across locations was examined for 2 levels of total effort (*Figure 1a* for 18 total blocks, 90 total progeny per family and *Figure 1b* for 36 total blocks, 180 total progeny). In all cases, it is better to sample more locations with fewer blocks per location. In fact, with non-zero family x location interaction ($\sigma^2_{fe} > 0$), 1 block per location (with as many locations as possible) will always result in more efficient parental selection.

Since there may be economic, logistical and operational reasons to place at least a few blocks at a given test location, it is appropriate to consider the relative efficiencies of using more than 1 block per location. The inferences about numbers of blocks per location are very similar for both ages (5 and 10) and both scenarios of parameter estimates. Note that all lines show very similar trends of selection efficiency loss with increasing numbers of blocks per location (*Figure 1*).

The age and particular scenario of parameter estimates have much more impact on selection efficiency than do the number of blocks per location. This is seen in *figure 1* by noting that for a fixed number of blocks per location, the lines for different ages and scenarios are separated by 5% to 10% in selection efficiency; while as many as 6 to 12 blocks per location (depending on the age and scenario) can be 95% as efficient as 1 block per location.

Also, it is more important to use fewer blocks per location when planting fewer total numbers of blocks. In *fig-*

ure 1a with 18 total blocks, all 4 lines have a steeper slope than do those in *figure 1b* with 36 total blocks indicating greater efficiency loss with increasing blocks per location when only 18 total blocks are planted. For all scenarios and both ages the use of up to 4 blocks per location is at least 97% as efficient as use of 1 block per location.

In summary, while use of 1 block per location always results in maximum efficiency for parental selection, for the 2 scenarios employed here, use of 2 to 4 blocks results in near maximum efficiency for all ages, scenarios and total levels of effort. For logistical and analytical reasons the CFGRP will use 4 blocks per location (see Discussion),
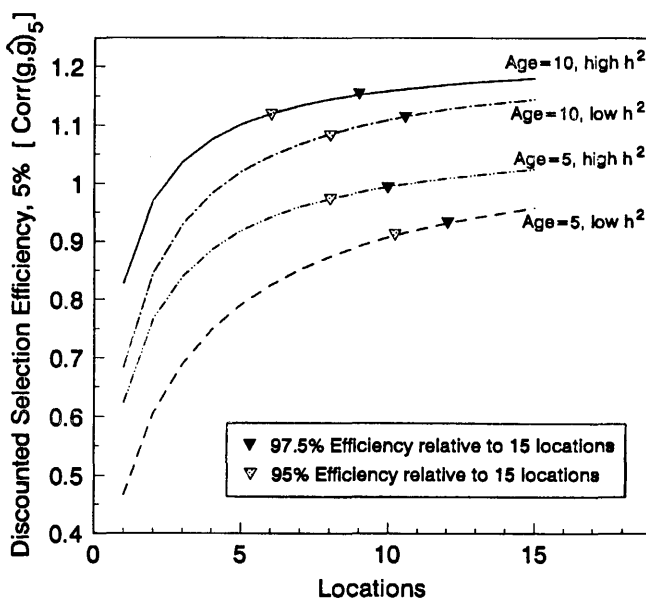

Figure 2. — Discounted selection efficiency using a 5% discount rate, Corr(g,$\hat{g}$)$_5$, for ages 5 and 10 and low and high h² scenarios as a function of the number of locations (assuming 4 blocks per location and 5-tree plots).

and we made this assumption for examination of the next question of how many total locations are needed.

Assuming 4 blocks per location and 5-tree plots, selection efficiency continues to increase with increasing numbers of locations (*Figure 2*), because more locations mean more total progeny planted and hence more precise predictions of parental breeding values. However, the marginal increase in selection efficiency is less as more locations are added. For both ages 5 and 10, the curves for scenario 2 (high h^2) flatten out sooner, indicating less incremental benefit from more locations. In fact, the scenarios (high vs. low h^2) have a large impact on the number of locations needed. For example, with low h^2 and age 5 data, use of 12 locations are required to achieve a $Corr(g,\hat{g})_5 =$

0.93 (*Figure 2*). That same value of discounted selection efficiency is achieved with fewer than 6 locations if the high h^2 scenario is assumed. Thus, the number of locations (and hence total effort expended) can be greatly reduced if each test is as precise as possible.

At 5 years, 8 and 10 locations (high vs. low h^2 scenarios, respectively) are required to achieve 95% of the selection efficiency attained by use of 5-year data from 15 locations, while at age 10, 6 and 8 locations (high vs. low h^2 scenarios, respectively) are required to achieve 95% of the efficiency of using data from 15 10-year-old locations. So, the point of diminishing returns in terms of increased efficiency from adding additional locations is reached sooner at age 10. Depending upon desired efficiencies,
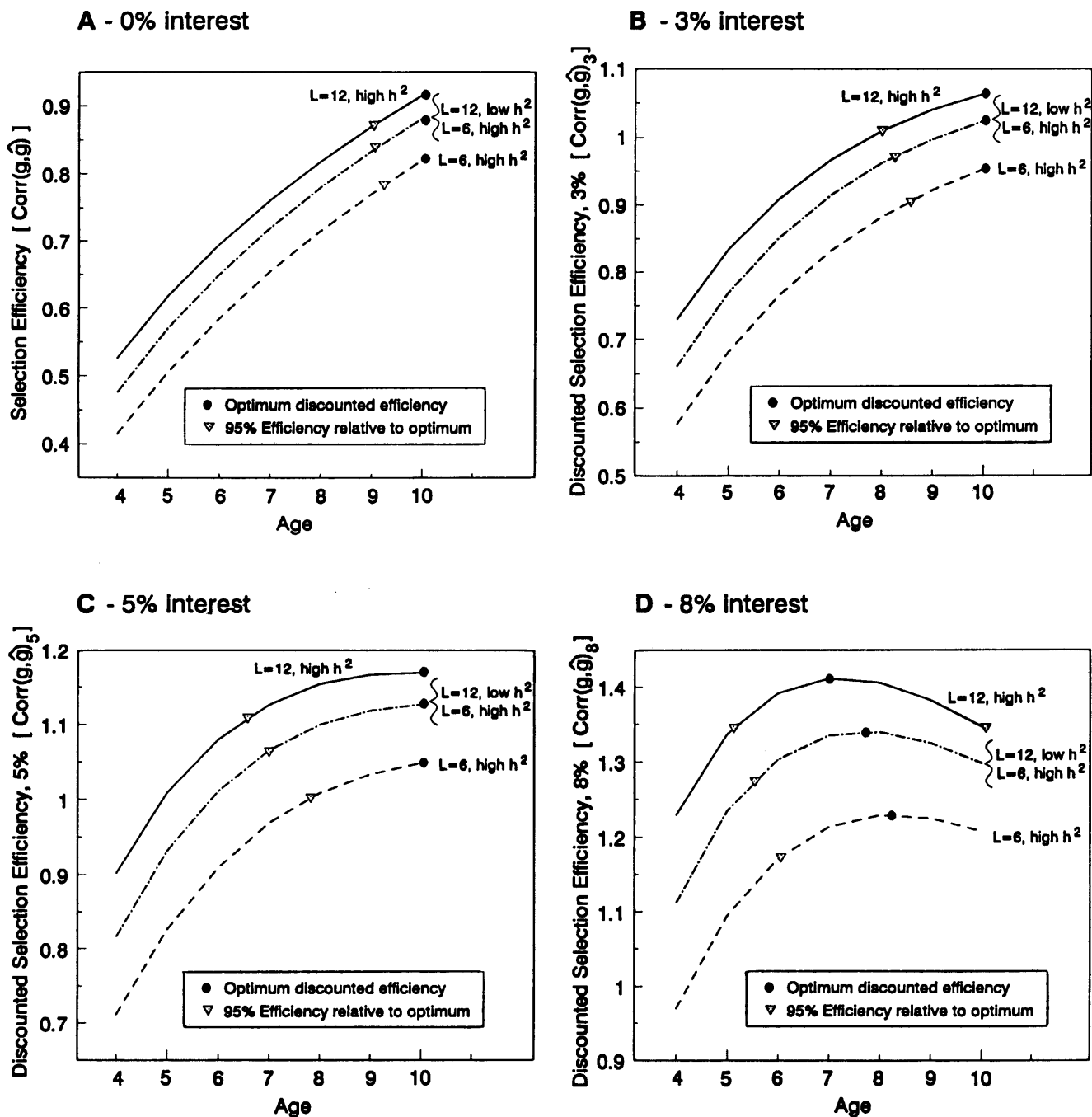

Figure 3. — Discounted selection efficiency, $Corr(g,\hat{g})_d$, for 6 and 12 locations (L) and low and high h^2 scenarios as a function of age for 4 discount rates, d: (A) 0%; (B) 3%; (C) 5%; (D) 8%.

total availability of effort, ages when data will be used, and anticipated operational falldown (partial or total loss of locations), 6 to 12 locations appear to be required to reach the point of diminishing returns where the selection efficiency will be 95% to 97.5% as much as using 15 locations. With 5-tree plots and 4 blocks per test, this amounts to 120 (for 6 locations) to 240 (12 locations) progeny per family.

Selection Efficiencies at Various Ages

Selection efficiencies for ages 4 through 10 were examined for both low and high h^2 scenarios and the extreme numbers of locations found above (6 locations and 12 locations still assuming 4 blocks per location and 5-tree plots). For all cases, efficiency of selection at various ages is affected markedly by the interest rate, d, assumed in calculating the discounted selection efficiencies. However, optimum selection age is at 10 years for 3 of the 4 efficiencies (*Figure 3*). Only for $Corr(g,\hat{g})_8$, which implicitly favors earlier selection because of the high discount rate, is the optimum at 7 or 8 years depending upon the number of locations and parameter estimate scenario.

Because the age of highest selection efficiency is at or near 10 years, it is logical to ask whether older ages might be better (11, 12, etc.). Our parameter estimates do not readily allow interpolation between ages 10 and 15, because the traits appear nearly identical in a genetic sense ($r_g = 0.96$ and similar heritabilities). In addition, the discounted selection efficiencies are very high at age 10 for all 4 interest rates.

Increasing the discount rate, d, broadens the peak and increases the range of ages which are only slightly suboptimal (say 95% as efficient as at the optimal age in *Figure 3*). For example, at 0% interest, 95% efficiency or better (with age 10 as the optimum age) are achieved only at ages 9 or greater (*Figure 3a*). In contrast, at 8% interest, selection at all ages between 5 or 6 years (depending on locations and scenario) and 10 years results in greater than 95% of the optimal efficiency (*Figure 3d*).

Using more locations or data from more precise tests, slightly decreases the optimum and near-optimum selection ages; and this effect is largest at 8% discount rate. For $Corr(g,\hat{g})_8$ (*Figure 3d*), both optimal selection age and the ages that are 95% as efficient as the optimum age are one-half year younger for scenario 2 compared to scenario 1 and for 12 locations compared to 6 locations.

While test designs and scenarios had minimal effects on the pattern of selection efficiency across ages, both of these factors markedly affect the absolute selection efficiencies attainable at all ages. These effects are fairly constant at all ages (nearly parallel curves in *Figure 3a* to b) and most pronounced for higher discount rates (more separation between curves for higher d values in *Figure 3*). In general, efficiency is increased from 4% to 11% either through use of 12 *vs* 6 locations or assuming data from more precise tests (high h^2 *vs* low h^2 scenarios).

The trade-off between more precise tests and use of a larger number of tests is similar at all selection ages and is manifested by the nearly identical curves for low h^2 tests with 12 locations and high h^2 tests with 6 locations. So, the increased test precision implied by the high h^2 scenario increases efficiency the same amount as using 6 additional tests (12 total) with low h^2 (scenario 1) This inference is consistent for all selection ages and discount rates.

Note that all discounted selection efficiencies compare gain expected from parental selection at an early age to that gain expected from selection based on an infinite amount of testing at age 15. For discounted selection efficiencies at 3%, 5% and 8% interest, all values are near or above 1 at age 10 indicating that parental selection at age 10 based on data from either 6 or 12 locations is more efficient than that at age 15 based on infinite testing. In fact, for the 5% and 8% discount rates, early selection can be 20% to 40% more efficient than that at age 15. Even for $Corr(g,\hat{g})_0$ which implicitly assigns no economic benefit from making selections at earlier ages (*Figure 3a*), the lowest selection efficiency at age 10 is 0.82 which occurs for scenario 1 and 6 locations. To convert this to a comparison of parental selection at age 15 based on data from 6 locations (as opposed to the current value of 0.82 which assumes infinite testing at age 15), it is necessary to multiply by the square root of the family heritability of age 15 data based on 6 locations ($h^2_f = 0.748$ from *Table 1*, see text preceding *Equation 3* for details). Thus for this worst case, the efficiency of age 10 selection compared to equal testing at age 15 is $0.95 = 0.82 \times (0.748)^{1/2}$.

Discussion

Progeny Test Designs

Plot configuration and plot size have been the subject of several investigations and it is well-known that small plots are more statistically efficient than large plots (BRIDGWATER et al., 1983; COTTERILL and JAMES, 1984; LOO-DINKINS and TAUER, 1987) and that both single tree and non-contiguous plots are more efficient than row-plots (LIBBY and COCKERHAM, 1980; LAMBETH et al., 1983; LAMBETH, 1986; LOO-DINKINS and TAUER, 1987). On the other hand, optimal numbers of progeny per parent and their allocation to appropriate numbers of blocks and locations have not often been systematically investigated. For several levels of individual tree heritabilities, COTTERILL and JAMES (1984) found that 10 to 20 progeny per parent were sufficient at a given location, but they did not consider genotype x environment interaction or multiple locations. BRIDGWATER et al. (1983) report that 144 progeny per family were to be allocated to 4 locations (6 blocks per location and 6-tree row-plots) for the North Carolina State University-industry Tree Improvement Cooperative diallel tests. With the assumption of certain economic constraints, LINDGREN (1964) concluded that 68 measurable trees per family allocated across 4 sites (17 measurable trees per site) was optimum for Scots pine (*Pinus sylvestris*) in Sweden, but recommended that 5 sites be used operationally.

The methods presented here provide a framework for quantifying selection efficiency and directly comparing various designs at all test ages. In this regard, as long as there is any family x location interaction, selection efficiency is maximized by allocation of a fixed number of progeny per family to as many locations as possible (using fewer progeny per location). This becomes less important as the amount of family x location interaction approaches 0. Our parameter estimates (r_B values of 0.6 to 0.75) indicate a moderate (SHELBOURNE, 1972) amount of interaction in slash pine, and for these levels, use of up to 4 blocks per location achieves greater than 95% of the selection efficiency of the optimum of 1 block per location.

The operational decision of how to allocate a given number of progeny within and across locations is also

influenced by logistical and economic considerations. Although selection efficiency is maximized through use of as many sites as possible, this will most likely not be the economic optimum. LINDGREN (1985) developed an approach to determining the optimum number of locations given the total resources available for genetic testing, and the marginal cost associated with establishing tests in each additional location. This approach results in an objectively determined optimum number of locations, with accuracy dependent on the quality of the cost estimates. Our approach is somewhat more subjective; we implicitly recognize a marginal cost of establishing additional test sites by defining the number of locations which result in 97.5% or 95% of maximum efficiency as optimum.

Analytical issues related to unplanned mortality may also have an impact on the operational decision about number of locations, blocks, and trees. It may be desirable to use enough progeny per location to provide for more stable variances of family means and decrease the probability of missing family plots from blocks and locations.

For our chosen test design of 4 blocks and 5-tree plots, many fewer tests are required (as few as half) to achieve a given level of selection efficiency if the tests can be made more precise as assumed in the high h^2 scenario 2. Scenario 2 assumes that increased test precision is achieved by a 20% decrease in experimental error, slightly less family x location interaction (r_B values were approximately 0.1 higher in scenario 2), and use of non-contiguous plots. Combined, these differences have a substantial impact on the family heritability (e.g., h^2_f values of 0.572 and 0.745 for scenarios 1 and 2, respectively, at age 5 for 6 locations, Table 1), and hence on selection efficiency which is directly proportional to h_f (cf. equations 1 to 3).

It is seemingly worth substantial effort to achieve high test precision, as long as these efforts do not adversely impact the genetic correlation between the trait being measured in the progeny test environment and the target trait performance in operational plantation environments (r_g in equations 1 to 3). This type of g x e might occur if different physiological mechanisms are involved in volume growth in the progeny test environments compared to those of operational plantations. And while some methods for increasing test precision seem quite unlikely to cause this type of g x e (e.g., proper block layout and size, use of filler trees in poor locations, non-contiguous plots), other methods sometimes advocated (e.g., use of old agricultural fields, vegetation control and fertilization) require investigation to quantify effects on r_g. Use of agricultural fields is sometimes advocated for progeny tests because these highly fertile, very uniform sites might increase h^2 and allow genetic differences to be more readily observable (GATES, 1983; TOLIVER, 1983; Anonymous, 1990). However, in both radiata pine (JOHNSON and BURDON, 1990) and slash pine (HODGE and WHITE, 1992), a portion of the family x location interaction is related to family rank changes on locations of different site qualities.

To examine the potential impact of these interactions in slash pine, we calculated (results not shown) discounted selection efficiencies using the parameter estimates from scenario 2 (high h^2) except that r_g values were reduced by a small amount. A 10% reduction in the intercept of the LAR line was assumed (from 1.13 to 1.02, with same slope), so that values were calculated from $r_g = 1.02 + 0.418$ (LAR). Compared to those of scenario 2, this resulted in r_g values at age 5 of 0.56 vs 0.67 and at age 10 of 0.85 vs

0.96. For all ages, numbers of locations and discount rates, these relatively minor reductions in r_g reduced the discounted selection efficiencies to below those of scenario 1 (low test precision). Hence, the gains in selection efficiency can be lost if the increased test precision implied by the parameter estimates of scenario 2 are achieved at the expense of seemingly minor reductions in correlation between performances in the progeny test and the operational environments.

Selection Age

Many factors influence optimum selection age, but our results indicating parental selection ages for volume in slash pine of greater than 8 years for 3 and 5% discount rates and from 6 to 10 years for an 8% rate correspond fairly well with the few investigations of parental selection (as opposed to mass selection or combined family plus within family selection). BALLOCCHI (1990) reported very similar ages for similar discount dates with loblolly pine height growth. Similarly, for basal area growth in radiata pine (using undiscounted selection efficiency), COTTERILL and DEAN (1988) favored age 10 when the target trait age was 16. McKEAND (1988) reported generally younger optimal ages (by 2 or more years) for loblolly pine. In our study, selection ages somewhat above age 10 would also achieve greater than 95% of the optimal selection efficiency for all discount rates (Figure 3). Because of the similarity of parameter estimates between volume at age 10 and 15 (similar h^2 values and $r_g = 0.96$), we did not feel it appropriate to interpolate between ages 10 and 15; however, the 3 smaller discount rates (0%, 3% and 5%) all resulted in optimal selection age of 10 years or greater. So, ages above 10 could be optimal or only slightly suboptimal.

The type of discounted analysis used here (and in McKEAND, 1988; BALOCCHI, 1990) is far from a complete economic analysis because it does not consider (1) costs (e.g., the earlier increased costs associated with earlier selection), (2) tax implications, (3) effects of multiple rotations (early selection would mean earlier harvests of improved material for more than a single rotation), and (4) real rates of stumpage compared to other goods and services. However, this type of analysis is useful because it partially quantifies the economic impact of earlier selection by discounting the expected gains from earlier selection less than those from later selection. Because the choice of discount rates affects both the optimal selection age and the range of ages that are only slightly suboptimal, it is important to ask what is the appropriate rate. For real rates of return (as used here), the United States Forest Service employs 4% nationwide for assessing all forestry-related projects. Private forest industry tends to use higher rates (REDMOND and CUBBAGE, 1985), and real rates of 5% to 6% are often recommended for private forestry investments (Dr. ROBERT ABT, personal communication, Department of Forestry, North Carolina State University, Raleigh, NC). At 5%, we found that selection ages from 7 years to above 10 would all result in greater than 95% of optimal efficiency.

General Discussion and Operational Conclusions

This paper addresses discounted selection efficiency for parental selection based on a single target trait (volume at 15 years), but the methods are readily extendable to selection based on a linear function of any number of target traits. If there are 2 or more target traits, selection index

methods can be used to calculate Corr(g,ĝ) of equation 3 for each trait (WHITE and HODGE, 1989, p. 76) and/or any linear combination of the target traits (WHITE and HODGE, 1989, p. 220). Once Corr(g,ĝ) is estimated, then the discounted selection efficiency is calculated by applying the discounting ratio in equation 3. Further, the selection efficiency can be based on measurements of the target traits and/or any other traits assessed in the progeny tests (WHITE and HODGE, 1991). If multiple traits from the progeny tests are used to predict multiple target traits, then more genetic parameter estimates will be required to estimate selection efficiencies. This may lead to problems in developing an internally consistent and 'optimal' set of parameter estimates which may result in poor estimates of selection efficiency (HILL and THOMPSON, 1978). In these instances it may be appropriate to use only the single most important target trait (as 15-year volume was used herein) and/or to employ many parameter estimate scenarios to try to encompass the range of reasonable sets of relationships.

In addition to the factors considered in any theoretical study, there are operational and logistical issues that influence progeny test designs and selection ages in an applied tree improvement program: (1) operational fall-down due to unplanned mortality, (2) total size of the testing program (number of parents that need to be tested and the required level of precision), (3) availability of short-term tests (such as greenhouse or growth room) and two-stage selection, (4) importance of and special considerations for other traits (e.g., in our CFGRP program testing for rust resistance requires high rust hazard sites that reduce precision for assessing volume), (5) potential of unequal testing for different parents in the selected population (e.g., ancestral information may vary and/or there may be need for more precision on high ranking parents such as those in the nucleus of the breeding population, COTTERILL 1989), (6) ability to use trend or surface analysis to increase test precision and account for differential competitive influence (BONGARTEN and DOWD, 1987, SMITH, 1987), and (7) appropriate block sizes given site heterogeneity.

Some of these factors lend themselves to further quantitative analyses, but taken together the final decisions on progeny test designs and uses of data at various ages will be based on a variety of issues. We believe it is important to have at hand the type of analysis presented here as a critical element when making final operational decisions. Current plans for the CFGRP, based on this analysis, are to use 4 blocks per location with 5-tree non-contiguous plots. Each selection will be tested in 6 to 12 locations, and the actual number may well vary for different selections depending on their ancestral data and predicted genetic quality. Selections with less ancestral data (whose predicted genetic values are therefore less precise) and those that are likely to become part of the production population in the next generation (because their ancestral data indicates high genetic quality) will likely be tested at more locations. This latter is consistent with the general concept of placing more emphasis on material of higher genetic quality (LINDGREN, 1986; COTTERILL, 1989).

Efforts will be made to increase test precision at each location by use of proper test and block layout, non-contiguous plots, smaller block size, vegetation control, and use of filler trees in poor locations within a block (such as near stumps). However, we will not adopt the use of

old agricultural sites or greater than operational levels of fertilization without investigating genotype by environment interactions that might significantly reduce selection efficiency (cf equation 3).

The results indicate that progeny test data from ages 8 and older may be treated as relatively reliable. Operationally, tests will likely be measured once prior to this age (age 4 or 5) to assess fusiform rust infection). Tree volume will also be measured at this time as the parental selection efficiency for volume using these young data will be useful for preliminary decisions. Then, the decision about the exact age to do the second measurement (8, 9 or 10) will be left flexible. If there is no urgent practical need for the date when a test is age 8, the measurement will be delayed.

There appears to be little operational value in maintaining tests past age 10. They become increasingly costly to measure with little incremental genetic benefit. However, the CFGRP may well maintain and measure a subset of the tests until older ages for research purposes, i.e., to allow parameter estimates to be developed for this type of analysis of optimal test designs for the succeeding generation.

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Buchbesprechungen

Genetics of Scots Pine. By M. GIERTYCH and C. MATYAS (Edited). 1991. Elsevier Science Publishers, Amsterdam, Oxford, New York and Tokyo. A copublication with Akademiai Kiado, Budapest, Hungary. 280 pages. Hardcover US $ 137.— / Dfl 240.—.

Scots pine (Pinus sylvestris) is probably the most important conifer forest tree species in Eurasia. It is characterised by a very extensive range, which extends horizontally over a distance of some 14,000 km, and is most extensive of all species of the genus Pinus, and perhaps the whole of the family Pinaceae. It was a good decision by GIERTYCH and MATYAS to discuss the organization of a volume on the Genetics of Scots Pine at the 18th IUFRO World Congress in Ljubljana. Yugoslavia in 1986. There are 21 chapters in this volume contributed by 24 scientists from 9 countries. The following topics are covered in this volume: range of distribution (BORATYNSKI), systematic position within the genus Pinus and intraspecific taxonomy (MOLOTKOV and PATLAJ), karyotypes and cytogenetics (BORZAN), generative reproduction and genetic processes in nature (KOSKI), biochemical polymorphism (PRUS-GLOWACKI), provenance variation in growth and morphology (GIERTYCL), breeding strategies for timber production (HATTEMER), breeding strategies for christmas trees (VAN HAVERBEKE and GERHOLD), seed orchards and plus trees (PIHELGAS), seed orchards

(MATYAS), genetic processes in seed orchards (MÜLLER-STARCK), vegetative propagation (MONTEUUIS and BARNEOUD), regulation of flowering in seed orchards (CHALUPKA), hybridization (KOSINSKI), progeny testing (LINDGREN), inheritance of resistance to biotic factors (STEPHAN), inheritance of resistance to abiotic factors (OLEKSYN), inheritance of wood properties (STAHL and ERICSON), inheritance of tree form (GIERTYCH), the value of early testing (NILSSON), and utilization of improved material: a survey (MIKOLA). The range of topics is extensive. Viewed briefly the volume covers the distribution, systematics, karyology, generative and vegetative reproduction, genetic variability, inheritance of traits, and genetic and breeding strategies for timber and tree improvement. This is a comprehensive treatise on the Genetics of Scots Pine, one of the commercially important species in the Northern Hemisphere. This volume should be of interest to researchers and students of forest tree genetics and breeding. The book is available from Elsevier, P. O. Box 1991, 1000 BZ Amsterdam, The Netherlands, or in North America from Elsevier, P. O. Box 882, Madison Square Station, New York, NY 10159, USA.

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