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# Selection system efficiencies for computer simulated progeny test field designs in loblolly pine

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**Summary.** Six simulated progeny test field designs in combination with three within-family selection systems were tested on three loblolly pine (*Pinus taeda* L.) progeny test sites in southeastern Oklahoma and southwestern Arkansas, to compare genetic gains for the single trait, height. Residual deviations obtained by subtraction of family and plantation mean effects for each plantation were combined with simulated genetic effects with known family variance structure. The simulated genetic populations, arranged in the following progeny test field designs – large square or almost square plots, five- and ten-tree row plots, five-tree noncontiguous plots, two-tree row plots, and single-tree plots – were superimposed on the residual data for each plantation. Within-family selection methods based on deviations from block means, deviations from neighborhood means and deviations from plot means were built into the model. Realized genetic gain attained by each design – selection system combination was compared with the genetic gain theoretically possible if selection accuracy were perfect, and with expected gain estimated using the general linear model. In general, average realized genetic gain compared well with expected gain. Differences between designs with large versus small plots were generally lower than expected, although the single-tree plot design always yielded highest realized gain. Realized gain was generally higher than expected when within-family selection was based on deviations from block or neighborhood means, but equal to or lower than expected when selection was based on deviations from plot means.

**Key words:** Progeny testing – Within-family selection – Modeling – Genetic gain – Selection accuracy

## Introduction

Loblolly pine (*Pinus taeda* L.) is the most important commerical forest species in southeastern Oklahoma and southern Arkansas. The species is often planted on highly heterogeneous sites, with the heterogeneity appearing as random microsite variability, as patchiness due to such factors as soil moisture, texture or depth, or as a gradient.

An important purpose of progeny testing is to evaluate family performance to choose parents for commercial seedling production. Progeny tests must sample a range of commercial planting sites to predict performance on such sites. As the size and purpose of progeny testing do not allow avoidance of much of the variability, the test sites may be highly variable. A secondary, but equally important, function of many progeny tests is to provide a base for selection of the next generation of parents. Thus, in addition to accurate estimation of family means, which depends primarily on the test design, a within-family selection system to optimize gain for a given field design and environmental variation pattern is also important.

The phenotypic variance of family means is largely determined by the relative sizes of among- and within-plot variances (Barnes and Schweppenhauser 1979). The among-plot variance can be substantially altered by changing the plot size and number of blocks. Given a fixed plantation size and number of families tested, plot size will be inversely related to number of blocks. In addition, the number of trees per family varies inversely with the number of families that can be tested.

The theoretical value of small plot size is well known (Conkle 1963; Libby and Cockerham 1980; Cotterill and James 1984). Single-tree plots maximize the number of microsites sampled and minimize size, while maximizing number of blocks (Wright 1973). Possible confounding of environmental and genetic covariances among members of a genetic unit is virtually eliminated. A noncontiguous plot design, with each plot consisting of a number of trees randomly located throughout a block, would have most of the advantages of the single-tree plot design. In addition, the probability of a given family becoming absent from one or more blocks is much lower (Lambeth et al. 1983, Libby and Cockerham 1980). Lambeth et al. (1983) compared a test design consisting of five-tree noncontiguous plots with a five-tree row plot design and found that the number of blocks required to obtain a given level of precision was lower for noncontiguous plots than for row plots.

A four- to six-tree row plot design has probably been used more frequently than any other test design in past and present progeny tests. This design allows sib comparison for within-family selection, field layout and silvicultural thinning by family are relatively easy and plots are large enough to allow analysis on a plot means basis, often correcting much of the imbalance due to unplanned mortality. Larger row plots and square, or rectangular, plots have also been frequently used in the past, in part because early tree improvement workers were concerned about possible non-normality of among- or within-plot effects with small plot size (Evans et al. 1961; Barnes and Schweppenhauser 1979). Franklin (1971) noted that the environmental effect is always sufficiently large relative to the genetic values to validate the assumption of normality. In addition, genetic values themselves are usually normally distributed (Falconer 1981). The large block plots may be valuable for growth and yield studies on a per area basis and for within-family selection, as they allow for most efficient sib-comparison, although this design is not ideal for progeny testing on a variable site.

Loo-Dinkins and Tauer (1987) compared the theoretical efficiencies of six progeny test field designs on three site types with respect to variance associated with family mean estimation. They found that the relative efficiency of designs varied with the site type, but that single-tree, two-tree row and five-tree noncontiguous plot designs resulted in lower sampling variance associated with family means than larger row or square, or almost square, plots, for the tested sites. Their results indicated that, on a relatively uniform site, 30 trees per family, arranged in noncontiguous or single-tree plots, may provide as accurate estimates of family means as would 60 trees per family arranged in five-tree row plots.

Expressions for expected genetic gain have been derived and are well known for the traditional selection systems (Shellbourne 1969; Namkoong 1979). Some combination of among and within-family selection, depending upon the heritability of the trait, is usually utilized in advanced generation selection from progeny tests. In practice, the relative intensities of within-and among-family selection are also influenced by inbreeding considerations as well as by size of the test. Frequently, the best families are identified and one or two individuals within each family are selected. The optimum selection method of individuals within families may vary with the test design and pattern of site variability.

Current within-family selection methods include use of deviations from family plot means, as practiced by the Western Gulf Forest Tree Improvement Program, and deviations from block means, as utilized by the North Carolina State Cooperative Tree Improvement Program. These procedures are applied in the initial stages, to identify trees worthy of a field assessment.

The optimum size and shape of a comparison area for selection may fall between the size of a family plot and a block. Gardner (1961) described a method to reduce the environmental variance within the selection area for corn by superimposing a grid on the test area and by selecting a set number of individuals from within each square. A similar procedure applicable to selection of forest trees would be to superimpose a grid on a plantation, creating "neighbourhoods", and to select individuals on the basis of their deviations from these neighbourhood means. The neighbourhoods should be small enough that, on average, the environmental correlations between trees would be greater than zero, but the size and shape of optimum neighbourhoods would probably vary with site type.

The theory of progeny test field design efficiency has been previously examined (Conkle 1963; Lambeth et al. 1983; Wright 1973), but not in combination with different within-family selection methods. Modeling may be the only way to compare combinations of progeny test field designs and within-family selection methods on a given site. This can be done by using "real" estimated environmental data combined with simulated genetic populations with known variance structure. This allows "realized" genetic gain to be compared both with the gain theoretically possible if selection accuracy were perfect, and with expected gain derived using the appropriate environmental and genetic variances. Results of a simulation model are based on a large number of trials, thus "realized" gain represents an average devoid of the sampling error attendant upon any single gain evaluation. Comparison of average realized gain with expected gain tests the robustness of the expected gain theory with respect to adequacy of the linear model in describing the partitioning of variances in sites with very different patterns of variation. If the expected gain theory is sufficiently robust, the "realized" gains attained by various within-family selection methods should be distributed about the expected gain estimate.

The objectives of this study were to compare the genetic gains attained using various progeny test field designs in combination with three within-family selection

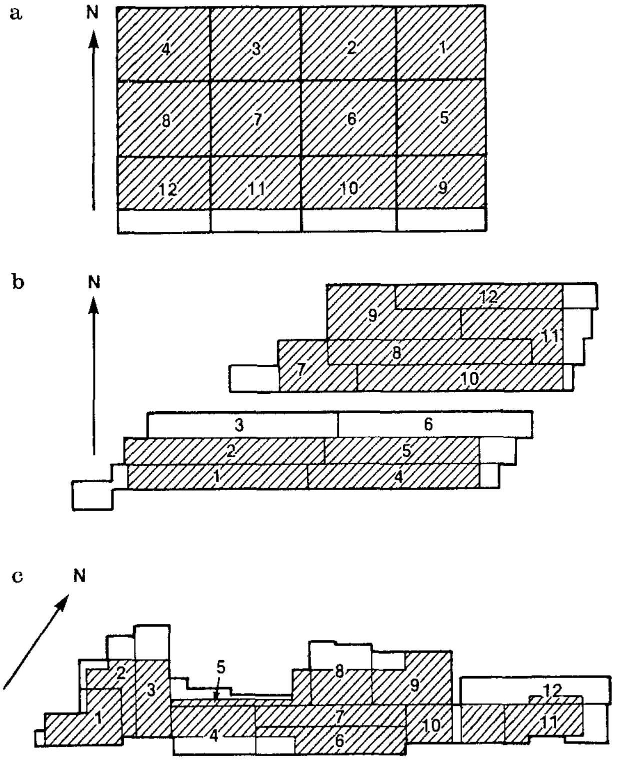

**Fig. 1a–c.** Plantations used in field test design – within-family selection combinations: **a** – Dierks, **b** – Cloudy and **c** – Hempwallace. The *shaded areas* represent the area used in simulations

methods for height in loblolly pine, and to compare these results with expected gains. The genetic gains attained using various combinations were compared using an environmental data base obtained from three distinctly different progeny test sites, combined with genetic populations generated by Monte Carlo type simulation.

## Materials and methods

Height data from three Weyerhaeuser Company loblolly pine progeny tests occupying distinctly different site types in southeastern Oklahoma and southwestern Arkansas were used to approximate environmental values. The shape and the area of each plantation used in the study are shown in Fig. 1. The Dierks plantation is a half-sib progeny test, planted in 1975, located near Dierks, Arkansas. The site is rectangular in shape and is relatively uniform with apparently random site variability. The Cloudy and Hempwallace plantations are full-sib progeny tests planted in 1980, located near Cloudy, Oklahoma, and Hempwallace, Arkansas, respectively. The Cloudy test site contains a strong gradient as it straddles a ridge, with east-west orientation. The Hempwallace site is relatively wet, causing a pattern of patchy variability. Filler trees were planted extensively on microsites judged to be anomalous in both plantations and the plantation shapes are highly irregular (Fig. 1). Eight-year height data were used from the Dierks plantation and 5-year data were used from the other two plantations. Survival in the three plantations ranged from 85% to 95%.

Analyses of variance were conducted on each data set using the following model with the General Linear Models Procedure of SAS (SAS Institute Inc. 1982a):

$$\text{Height} = \text{Family} + \text{Residual} \qquad (1)$$

The residual values, thus obtained, included within-family genetic effects, representing one-half or three-quarters of the average additive variance in full- and half-sib tests, respectively. The environmental effects were assumed to be sufficiently larger than the remaining genetic effects, however, to allow each residual value to primarily reflect a measure of microsite quality, as suggested by Franklin (1971). For example, if individual tree heritability is 0.20, almost 90% of the residual values (consisting of one-half the genetic variance and all of the environmental variance) in a full-sib progeny test would be due to nonadditive genetic and environmental causes.

The residual values provided the basis for an environmental map for each plantation. Each position was given a row and column number and filler trees were indicated. As filler trees were not measured in the plantations, they appeared as missing data in the mapped residual data sets. Values were approximated for filler trees using a random function of SAS (SAS Institute Inc. 1982b) to avoid treating the filler positions as empty due to mortality. For each filler tree, a value was chosen at random from a normal distribution using the mean and variance of the surrounding 24 trees. A grid pattern was superimposed on each mapped data set to establish 5 × 5-tree neighbourhoods for selection based on comparison with surrounding trees.

Six simulated field designs were tested with each environmental data set with a relatively low number of families (30, 38 or 48) and a high number of trees per family (50 or 60). Square, or almost square, plots, 5 × 6 trees on the Dierks plantation, and 5 × 5 trees on the other two plantations, were arranged in two blocks. These large plots could not be tested when the number of families was increased (50, 63 or 96) and number of trees per family was reduced to 30. The remaining five designs were tested under both sets of conditions. Ten-tree row plots, five-tree row plots, five-tree noncontiguous plots, two-tree plots, and single-tree plots were arranged in the appropriate number of blocks for each data set. The number of usable positions varied among plantations because for a given plantation, each design had to fit in the same area in such a way that blocking was effective, to allow valid comparisons among design-selection system combinations (Fig. 1). The within-family selection systems included selection based on deviations from block means, deviations from plot means and deviations from neighbourhood means.

A model was constructed using SAS Macro Language (SAS Institute Inc. 1982b) to generate genetic populations with known among- and within-family genetic variance structure and to superimpose each genetic population, arranged in each of the designs on the environmental data sets. The among- and within-family variances were chosen using the residual variance from Eq. (1) as follows:

$$h^2 = \frac{k^*(\sigma_f^2)}{\sigma_r^2 + \sigma_f^2} \qquad (2)$$

where $h^2$ = individual-tree heritability, $k = 2$, if full-sib and 4, if half-sib families, $\sigma_f^2$ = among-family variance estimated to correspond to $h^2 = 0.20$ or 0.30, and $\sigma_r^2$ = residual variance. The residual variance included the block variance component, which is not usually considered part of the phenotypic variance in a heritability estimate. In this case, however, it did not seem valid to remove the original block variance, as block size was variable in the simulations. In addition, owing to the difficulty in fitting all designs in the same area on an irregularly shaped test site, only about two-thirds of the Cloudy site area was utilized in the simulations. In generating the residuals and estimating the appropriate family variances, however, all data were used. Thus, realized heritabilities could be expected to be larger than the initial heritabilities set at 0.20 and 0.30, with the difference depending, in part, on the blocking efficiency of each design. The within- was equal to the among-family variance for simulated full-sibs and was three times as large as the among-family variance for half-sibs. The original residual variances were 1.032, 0.287 and 0.510 m for the Dierks, Hempwallace and Cloudy plantations, respectively. The among-family variances used were 0.064, 0.032 and 0.057 m for $h^2 = 0.20$ and 0.110, 0.051 and 0.090 m for $h^2 = 0.30$. The residual variances, partitioned into block, among- and within-plot components were presented by Loo-Dinkins and Tauer (1987).

Approximate plantation means (7.5 m for Dierks, and 3.7 m for Cloudy and Hempwallace) were added to the additive genetic and residual values for each design, to result in simulated height values corresponding to each position as follows:

$$\text{Height} = \mu + \text{GF} + \text{GI} + \text{R} \tag{3}$$

where $\mu$ = the plantation mean, GF = simulated family genetic value, GI = simulated individual tree genetic value and R = residual value. The ten best families were chosen based on ranking of family means, and the within-family selection methods, based on ranking of deviations from block, plot or neighborhood means, were applied to choose two phenotypes from each of the chosen families. Regardless of selection method or design, a total of 20 trees was selected, thus selection intensity, both among and within families, was constant for a given plantation and number of families tested.

Results for each set of conditions were the average of 100 trials. The two heritability levels were modeled at a high and a low number of families for each of the three data sets. The design-selection system combinations were compared using three criteria: the genetic gain in height of the 20 selected trees expressed as a percentage of the planation mean, the accuracy of selection, expressed as a percentage of the gain theoretically possible and the ratio of realized to expected gain. Expected gain was estimated as:

$$G = i_F * \frac{\sigma^2_{GF}}{\sqrt{\{\sigma^2_{GF} + (\sigma^2_P/b) + (\sigma^2_W/n\,b)\}}} + i_I * \frac{\sigma^2_{GI}}{\sqrt{\{\sigma^2_{GI} + \sigma^2_P + \sigma^2_W\}}} \tag{4}$$

where $i_F$ and $i_I$ are among- and within-family selection intensities in standard deviation units, $\sigma^2_{GF}$ and $\sigma^2_{GI}$ are known family and individual genetic variances, $\sigma^2_P$ and $\sigma^2_W$ are among- and within-plot variances estimated from the residual data sets for each test design, using a general linear model, reported by Loo-Dinkins and Tauer (1987) and b and n are the number of blocks and trees per plot, respectively. The block variance was not considered to be a component of the phenotypic variance, implying a correction for blocks in the selection process. This is the usual expression for genetic gain prediction whether or not selections are adjusted for block effects.

Realized gains provide a useful measure for comparison among design-selection system combinations within a plantation, but they cannot be compared among plantations because they reflect the absolute size of the genetic variance as well as the selection intensity, both of which vary among plantations. Genetic gain in its simplest form, ignoring the among- and within-family levels of selection, can be expressed as $i\,h\,\sigma_A$, where i is the selection intensity, h is the square root of heritability, which may be considered a measure of selection accuracy and $\sigma_A$ is the square root of the additive genetic variance. The gain theoretically possible, if selection accuracy were perfect, would equal $i \cdot \sigma_A$. Thus, the percentage of the maximum genetic gain attained by each combination is a measure of the accuracy acheived in a given field design by a given selection system. These selection accuracies may be more readily compared among test sites. The ratio of the realized to expected gain provides a measure of the adequacy of the general linear model in accounting for the distribution of among- and within-plot variances.

## Results and discussion

Heritabilities for each design-site-family variance combination were estimated as;

$$h^2 = \frac{k \cdot \sigma^2_{GF}}{(\sigma^2_{GF} + \sigma^2_P + \sigma^2_W)} \tag{5}$$

The estimated heritabilities were all higher than the originally intended heritability values because of the effect of blocking. For a given selection intensity, the degree to which estimated heritabilities exceed initial ones reflects, in part, the blocking efficiency of the various designs. The estimated heritabilities, selection accuracy, realized gains and the ratio of realized to expected gains are presented in Tables 1–3. The mean selection accuracy was consistently between 47% and 75%, regardless of test design, selection system, site or initial heritability. These percentages represent realized heritabilities of approximately 0.22–0.56. The standard errors associated with mean accuracy for 100 trials were consistently small, ranging from 0.50 to 0.95. Differences among designs, among selection systems and among design-selection system combinations were found to be highly significant using analysis of variance.

Percent gains for a given plantation and set of conditions (input genetic variance and number of families) differed among design-selection systems by approximately 2% for the lower genetic variances and by 3% for the higher genetic variances. The percent gains attained in the half-sib Dierks plantation (Table 1) were comparable to those attained in the full-sib plantations, Hempwallace (Table 2) and Cloudy (Table 3), because the Dierks plantation was larger, allowing considerably higher selection intensities. In addition, the site variability, relative to the size of the plantation mean, was greater at both the Dierks and Cloudy plantations than at the Hempwallace plantation. The relatively high variability at the Dierks site was attributable to older trees in this plantation (8 versus 5 years). Thus, the simulated genetic variances were higher for the Dierks and Cloudy sites than for the Hempwallace site, resulting in lower potential gain at the latter site.

The large square, or almost square, plot designs consistently resulted in lower gains in comparison with the other designs, regardless of the selection system. Differences among the other designs were slight in most cases, but a trend for higher gains with small plots than for larger plots was apparent under each set of conditions for

**Table 1.** Realized genetic gain ($G_R$), accuracy of selection (ACC) and ratio of realized to expected gain ($G_R/G_E$) for two estimated heritabilities ($h^2$) for each of six field test designs and three within-family selection systems for the Dierks plantation

| Design | Selection system[a] | 48 families | | | | 96 families | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | $h^2$ | $G_R$ | ACC | $G_R/G_E$ | $h^2$ | $G_R$ | ACC | $G_R/G_E$ |
| 30-tree rectangular plots | B | 0.22 | 9.56 | 53.9 | 1.13 | | | | |
| | | 0.34 | 14.40 | 62.0 | 1.08 | | | | |
| | N | 0.22 | 9.96 | 56.2 | 1.17 | | | | |
| | | 0.34 | 14.88 | 64.1 | 1.11 | | | | |
| | P | 0.22 | 9.31 | 52.5 | 1.10 | | | | |
| | | 0.34 | 14.16 | 61.0 | 1.06 | | | | |
| 10-tree row plots | B | 0.23 | 10.57 | 59.6 | 1.16 | 0.23 | 10.61 | 55.3 | 1.23 |
| | | 0.35 | 15.30 | 65.9 | 1.09 | 0.35 | 15.11 | 67.0 | 1.12 |
| | N | 0.23 | 10.58 | 59.7 | 1.16 | 0.23 | 10.89 | 56.8 | 1.26 |
| | | 0.35 | 15.23 | 65.6 | 1.08 | 0.35 | 14.80 | 65.6 | 1.10 |
| | P | 0.23 | 10.04 | 56.6 | 1.10 | 0.23 | 10.32 | 53.8 | 1.19 |
| | | 0.35 | 15.33 | 62.6 | 1.09 | 0.35 | 14.46 | 64.1 | 1.07 |
| 5-tree row plots | B | 0.23 | 10.58 | 59.7 | 1.13 | 0.23 | 11.09 | 57.8 | 1.23 |
| | | 0.36 | 15.44 | 66.5 | 1.08 | 0.36 | 15.36 | 68.1 | 1.10 |
| | N | 0.23 | 10.55 | 59.5 | 1.13 | 0.23 | 11.18 | 58.3 | 1.24 |
| | | 0.36 | 15.39 | 66.3 | 1.08 | 0.36 | 15.70 | 69.6 | 1.13 |
| | P | 0.23 | 9.45 | 53.3 | 1.01 | 0.23 | 10.36 | 54.0 | 1.15 |
| | | 0.36 | 13.91 | 59.9 | 0.97 | 0.36 | 14.37 | 63.7 | 1.03 |
| 5-tree noncontiguous plots | B | 0.23 | 10.57 | 59.6 | 1.09 | 0.23 | 11.68 | 60.9 | 1.22 |
| | | 0.36 | 15.72 | 67.7 | 1.08 | 0.35 | 15.25 | 67.6 | 1.05 |
| | N | 0.23 | 10.74 | 60.6 | 1.11 | 0.23 | 11.85 | 61.8 | 1.23 |
| | | 0.36 | 16.09 | 69.3 | 1.10 | 0.35 | 15.66 | 69.4 | 1.08 |
| | P | 0.23 | 9.56 | 53.9 | 0.99 | 0.23 | 11.03 | 57.5 | 1.15 |
| | | 0.36 | 14.07 | 60.6 | 0.96 | 0.35 | 14.35 | 63.6 | 0.99 |
| 2-tree row plots | B | 0.24 | 10.85 | 61.2 | 1.12 | 0.25 | 11.68 | 60.9 | 1.22 |
| | | 0.36 | 15.86 | 68.3 | 1.08 | 0.37 | 15.79 | 70.0 | 1.09 |
| | N | 0.24 | 10.73 | 60.5 | 1.11 | 0.25 | 11.95 | 62.3 | 1.25 |
| | | 0.36 | 15.67 | 67.5 | 1.07 | 0.37 | 15.93 | 70.6 | 1.09 |
| | P | 0.24 | 8.37 | 47.2 | 0.86 | 0.25 | 9.88 | 51.5 | 1.03 |
| | | 0.36 | 12.42 | 53.5 | 0.85 | 0.37 | 13.67 | 60.6 | 0.94 |
| Single-tree plots | B | 0.24 | 10.99 | 62.0 | 1.12 | 0.25 | 11.93 | 62.2 | 1.21 |
| | | 0.37 | 16.21 | 69.8 | 1.10 | 0.38 | 15.68 | 69.5 | 1.06 |
| | N | 0.24 | 10.66 | 60.1 | 1.09 | 0.25 | 12.12 | 63.2 | 1.23 |
| | | 0.37 | 15.90 | 68.5 | 1.08 | 0.38 | 15.97 | 70.8 | 1.08 |

[a] Selection systems based on: B – deviations from block means, N – deviations from neighborhood means and P – deviations from plot means

each site. The trend was strongest when the lower number of trees per family with the higher number of families was tested. The genetic gain generally increased by about 1% from least to most efficient design, regardless of site, when selection was based on deviations from block means.

Selection based on deviations from plot means consistently resulted in poorer accuracy and lower gains than either of the other selection systems, and differences were greatest when plot size was five trees or less. The selection system based on deviations from plot means performed particularly poorly in combination with the two-tree plot design, probably because, for this design, the sample being compared for selection was very small. Selection based on deviations from block means generally improved as plot size, and consequently, block size decreased. Selection based on deviations from neighborhood means was always better than deviations from plot means and generally slightly better than selection based on deviations from block means when the plot size was five trees or greater.

The realized genetic gains for the three sites attained by the five-tree non contiguous plot design were very close to the two-tree plot results when the block and neighborhood deviation selection systems were applied with 30 trees per family. Results for noncontiguous plots were similar to those for five-tree row plots with either number of families when selection was based on deviations from plot means. Loo-Dinkins and Tauer (1987)

**Table 2.** Realized genetic gain ($G_R$), accuracy of selection (ACC) and ratio of realized to expected gain ($G_R/G_E$) for two estimated heritabilities ($h^2$) for each of six field test designs and three within-family selection systems for the Hempwallace plantation

| Design | Selection system[a] | 38 families | | | | 63 families | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | $h^2$ | $G_R$ | ACC | $G_R/G_E$ | $h^2$ | $G_R$ | ACC | $G_R/G_E$ |
| 25-tree square plots | B | 0.28 | 8.99 | 54.8 | 1.06 | | | | |
| | | 0.42 | 13.14 | 63.4 | 1.07 | | | | |
| | N | 0.28 | 9.19 | 56.0 | 1.09 | | | | |
| | | 0.42 | 13.38 | 64.6 | 1.09 | | | | |
| | P | 0.28 | 9.19 | 56.0 | 1.09 | | | | |
| | | 0.42 | 13.38 | 64.6 | 1.09 | | | | |
| 10-tree row plots | B | 0.30 | 10.07 | 61.4 | 1.06 | 0.29 | 11.60 | 60.4 | 1.19 |
| | | 0.45 | 13.99 | 67.5 | 1.05 | 0.43 | 14.33 | 67.8 | 1.04 |
| | N | 0.30 | 10.19 | 62.1 | 1.07 | 0.29 | 11.73 | 61.1 | 1.20 |
| | | 0.45 | 14.11 | 68.5 | 1.06 | 0.43 | 14.58 | 69.0 | 1.06 |
| | P | 0.30 | 9.70 | 59.1 | 1.02 | 0.29 | 11.40 | 59.4 | 1.17 |
| | | 0.45 | 13.41 | 64.1 | 1.01 | 0.43 | 14.33 | 67.8 | 1.04 |
| 5-tree row plots | B | 0.32 | 10.01 | 61.0 | 1.03 | 0.30 | 12.06 | 62.8 | 1.19 |
| | | 0.46 | 13.82 | 66.7 | 1.02 | 0.44 | 14.79 | 70.0 | 1.05 |
| | N | 0.32 | 10.14 | 61.8 | 1.04 | 0.30 | 12.38 | 64.5 | 1.22 |
| | | 0.46 | 13.90 | 67.1 | 1.03 | 0.44 | 15.00 | 71.0 | 1.06 |
| | P | 0.32 | 9.52 | 58.0 | 0.98 | 0.30 | 11.83 | 61.6 | 1.16 |
| | | 0.46 | 12.97 | 62.6 | 0.96 | 0.44 | 14.20 | 67.2 | 1.01 |
| 5-tree noncontiguous plots | B | 0.31 | 10.26 | 62.5 | 1.04 | 0.30 | 12.38 | 64.5 | 1.19 |
| | | 0.45 | 13.88 | 67.0 | 1.02 | 0.44 | 14.77 | 69.9 | 1.03 |
| | N | 0.31 | 10.37 | 63.2 | 1.05 | 0.30 | 12.46 | 64.9 | 1.20 |
| | | 0.45 | 13.96 | 67.4 | 1.02 | 0.44 | 15.00 | 71.0 | 1.05 |
| | P | 0.31 | 9.52 | 58.0 | 0.97 | 0.30 | 11.71 | 61.0 | 1.12 |
| | | 0.45 | 12.72 | 61.4 | 0.93 | 0.44 | 14.03 | 66.4 | 0.98 |
| 2-tree row plots | B | 0.30 | 10.21 | 62.2 | 1.05 | 0.29 | 12.40 | 64.6 | 1.21 |
| | | 0.44 | 13.80 | 66.6 | 1.02 | 0.43 | 15.42 | 73.0 | 1.09 |
| | N | 0.30 | 10.29 | 62.7 | 1.06 | 0.29 | 12.46 | 64.9 | 1.22 |
| | | 0.44 | 13.80 | 66.6 | 1.02 | 0.43 | 15.36 | 72.7 | 1.08 |
| | P | 0.30 | 8.53 | 52.0 | 0.88 | 0.29 | 10.77 | 56.1 | 1.05 |
| | | 0.44 | 11.71 | 56.5 | 0.87 | 0.43 | 13.27 | 62.8 | 0.94 |
| Single-tree plots | B | 0.32 | 10.22 | 62.3 | 1.03 | 0.32 | 12.44 | 64.8 | 1.18 |
| | | 0.47 | 14.01 | 67.6 | 1.02 | 0.47 | 15.06 | 71.3 | 1.03 |
| | N | 0.32 | 10.35 | 63.1 | 1.04 | 0.32 | 12.58 | 65.5 | 1.19 |
| | | 0.47 | 14.09 | 68.0 | 1.03 | 0.47 | 15.19 | 71.9 | 1.04 |

[a] Selection systems based on: B – deviations from block means, N – deviations from neighborhood means and P – deviations from plot means

reported lower error variance associated with family means for five-tree noncontiguous plots than for five-tree row plots, implying more accurate family selection with noncontiguous plots. Within-family selection would be expected to be more accurate with the row plots, however, as within-plot uniformity is usually higher for contiguous than for noncontiguous plots. Consequently, the greater efficiency of family mean estimation with the noncontiguous plots may be offset by the improved within-family selection accuracy provided by row plots, if within-family selection is based on deviations from plot means. The proportion of gain attributable to among-versus within-family selection depends upon heritability and selection intensities at each level. The greater accuracy of among-family selection with noncontiguous plots would be expected to become more important with declining heritability.

When the number of families was increased at the expense of the number of trees per family, differences between the designs were greater. It appeared that given 50 or 60 trees per family, and 30–48 families, the design was less important than when the number of trees per family was reduced to 30. In particular, the difference between five- and ten-tree row plot designs was apparent only when 30 trees per family were tested with a high number of families. In some cases, the row plot designs performed slightly worse, but the five-tree noncontiguous, single-tree and two-tree plot designs generally result-

**Table 3.** Realized genetic gain ($G_R$), accuracy of selection (ACC) and ratio of realized to expected gain ($G_R/G_E$) for two estimated heritabilities ($h^2$) for each of six field test designs and three within-family selection systems for the Cloudy plantation

| Design | Selection system[a] | 48 families | | | | 96 families | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | $h^2$ | $G_R$ | ACC | $G_R/G_E$ | $h^2$ | $G_R$ | ACC | $G_R/G_E$ |
| 25 tree square plots | B | 0.32 | 11.54 | 55.1 | 1.08 | | | | |
| | | 0.46 | 17.40 | 64.3 | 1.12 | | | | |
| | N | 0.32 | 11.64 | 55.6 | 1.09 | | | | |
| | | 0.46 | 17.56 | 64.9 | 1.13 | | | | |
| | P | 0.32 | 11.47 | 54.8 | 1.07 | | | | |
| | | 0.46 | 17.13 | 63.3 | 1.01 | | | | |
| 10-tree row plots | B | 0.37 | 12.98 | 62.0 | 1.03 | 0.36 | 14.11 | 65.5 | 1.06 |
| | | 0.53 | 18.35 | 67.8 | 1.05 | 0.51 | 19.16 | 70.8 | 1.04 |
| | N | 0.37 | 13.23 | 63.2 | 1.05 | 0.36 | 14.15 | 65.7 | 1.06 |
| | | 0.53 | 18.78 | 69.4 | 1.07 | 0.51 | 19.24 | 71.1 | 1.04 |
| | P | 0.37 | 12.21 | 58.3 | 0.97 | 0.36 | 13.51 | 62.7 | 1.01 |
| | | 0.53 | 17.16 | 63.4 | 0.98 | 0.51 | 18.16 | 67.1 | 0.98 |
| 5-tree row plots | B | 0.41 | 13.32 | 63.6 | 1.02 | 0.38 | 14.13 | 65.6 | 1.03 |
| | | 0.58 | 19.10 | 70.6 | 1.06 | 0.55 | 19.67 | 72.7 | 1.04 |
| | N | 0.41 | 13.13 | 62.7 | 1.01 | 0.38 | 14.09 | 65.4 | 1.02 |
| | | 0.58 | 18.83 | 69.6 | 1.05 | 0.55 | 19.40 | 71.7 | 1.03 |
| | P | 0.41 | 12.10 | 57.8 | 0.93 | 0.38 | 13.20 | 61.3 | 0.96 |
| | | 0.58 | 17.05 | 63.0 | 0.95 | 0.55 | 18.10 | 66.9 | 0.96 |
| 5-tree noncontiguous plots | B | 0.41 | 13.21 | 63.1 | 1.01 | 0.38 | 14.56 | 67.6 | 1.04 |
| | | 0.57 | 19.32 | 71.4 | 1.08 | 0.54 | 20.00 | 73.9 | 1.05 |
| | N | 0.41 | 13.04 | 62.3 | 1.00 | 0.38 | 14.50 | 67.3 | 1.04 |
| | | 0.57 | 19.13 | 70.7 | 1.06 | 0.54 | 19.78 | 73.1 | 1.04 |
| | P | 0.41 | 11.68 | 55.8 | 0.90 | 0.38 | 13.03 | 60.5 | 0.94 |
| | | 0.57 | 17.07 | 63.1 | 0.95 | 0.54 | 18.10 | 66.9 | 0.95 |
| 2-tree row plots | B | 0.51 | 13.84 | 66.1 | 1.00 | 0.45 | 14.54 | 67.5 | 1.01 |
| | | 0.70 | 19.48 | 72.0 | 1.03 | 0.62 | 19.83 | 73.3 | 1.01 |
| | N | 0.51 | 13.46 | 64.3 | 0.97 | 0.45 | 14.34 | 66.6 | 1.00 |
| | | 0.70 | 18.83 | 69.6 | 0.99 | 0.62 | 19.81 | 73.2 | 1.01 |
| | P | 0.51 | 11.37 | 54.3 | 0.82 | 0.45 | 12.51 | 58.1 | 0.87 |
| | | 0.70 | 16.21 | 59.9 | 0.85 | 0.62 | 17.07 | 63.1 | 0.87 |
| Single-tree plots | B | 0.48 | 13.80 | 65.9 | 1.01 | 0.50 | 15.06 | 69.9 | 1.01 |
| | | 0.66 | 19.43 | 71.8 | 1.04 | 0.69 | 20.24 | 74.8 | 1.00 |
| | N | 0.48 | 13.51 | 64.5 | 0.99 | 0.50 | 14.71 | 68.3 | 0.99 |
| | | 0.66 | 19.08 | 70.5 | 1.02 | 0.69 | 19.75 | 73.0 | 0.97 |

[a] Selection systems based on: B – deviations from block means, N – deviations from neighborhood means and P – deviations from plot means

ed in slightly higher gains than were attained with the smaller number of families. Thus, at the heritability values tested, the increased number of families with fewer trees per family, allowing higher among-family selection intensity, led to greater gains when the most efficient designs were used. The higher among-family selection intensity did not result in higher gains, however, when the less efficient designs were used. This result implies that if the more efficient designs are used, a greater number of families may be tested in the same space, resulting in increased genetic gain as well as increased economic efficiency.

The realized gain increased by approximately 1%–2% in the full-sib tests when the higher number of families was tested. Genetic gains were slightly lower at the Dierks plantation when the number of families was increased, in spite of increased selection accuracy. The within-family genetic variance was three times the size of the among-family component, and with smaller family size, the within-family selection intensity was reduced. The greater parity between among- and within-family selection intensities, resulting from the higher number of families, benefitted selection in the full-sib tests more than in the half-sib test.

The differences in realized gains between the design-selection system combinations decreased with increased heritability. The genetic gain increased by 3%–5% with the higher heritability, and the increase was generally greatest for the least efficient designs. At the Dierks and Hempwallace sites, the realized gains were consistently higher than expected gains, except when selection was based on deviations from plot means and plot size was five trees or less. The realized and expected gains were more similar at the Cloudy site. It was expected that the progeny test design-selection system combination would be most important on the most variable site. The Cloudy site appeared to be the most variable, but differences between ten-tree row plot, five-tree row plot and five-tree noncontiguous plot designs were the same or less than those for the other plantations with 30 trees per family. The higher heritability at the Cloudy plantation would partially account for this. Blocks of five- and ten-tree row plots on the Cloudy site were arranged so that the family plots extended up the slope, parallel to the gradient. As most of the variation in the site was due to the gradient, each family row plot sampled most of the variation within a particular block, allowing relatively accurate estimates of family genetic value. Thus, five- or ten-tree row plots may be very efficient on sites in which a strong, identifiable gradient is the main source of variation, if the plots parallel the gradient, at least for among-family selection.

Selection based on deviations from neighborhood means was expected to achieve higher selection accuracy relative to the other methods on the most variable site, as this selection method was an attempt to adjust for environmental effects on a smaller scale than block effects. Only 5 × 5-tree neighborhoods were tested in this study, however, and this is probably not the optimum size or shape for neighborhoods on a site with a strong gradient. A long, narrow neighborhood would be expected to be more useful in adjusting for environmental variation on a gradient.

## Conclusions

Differences in genetic gain for a given within-family selection method among field test designs which include ten or less trees in replicated family plots do not seem to be important when 50–60 trees per family are tested. With 30 trees per family, however, the single-tree, two-tree, and five-tree noncontiguous plot designs result in higher selection accuracies than the larger row plot designs. With lower numbers of trees per family, the advantages of these designs would be expected to be greater. The single-tree plot design consistently results in highest genetic gain under these conditions in spite of a 5%–15% level of mortality resulting in missing families in some blocks.

Selection based on either deviations from block or neighborhood means results in higher gain than selection based on deviations from plot means. The optimum neighborhood size for selection in the tested plantations may be larger than 25 trees, but it is probably smaller than block size with five-tree plots and 30 or more families. Selection based on deviations from block means was as good as selection based on deviations from 25-tree neighborhood means when blocks contained family plots of five trees or less.

Expected genetic gain estimated using the general linear model generally underestimates the realized gain when within-family selection is based on deviations from block or neighborhood means, especially when there is not a pronounced gradient in the test plantation.

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