SESSION I

GENETIC GAINS AND ADVANCED GENERATION BREEDING

MODERATOR: B. J. ZOBEL

COMPARISON OF SOME ALTERNATIVE SECOND-GENERATION BREEDING PLANS FOR SLASH PINE

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Abstract.--In the breeding program at Olustee, Florida, a disconnected half-diallel mating scheme, with 6 parents per diallel, was chosen in preference to other mating schemes for establishing a second-generation base population. Genetic gains under this scheme are expected to be appreciably greater than schemes involving fewer crosses and will also provide reliable combining ability data for the original parents. In selecting offspring for clonal orchards, relatives will be permitted to a limited extent. Allowing the use of relatives to a moderate degree permits greater emphasis on family versus within family selection and the resulting gain exceeds losses expected from the mild inbreeding. Although a clonal orchard will give greater genetic gain than a seedling seed orchard, the gains will come sooner from the latter. Hence, conversion of a portion of the base population into a seedling seed orchard will also be considered.

Additional keywords: Breeding methods, inbreeding effects, *Pinus elliottii*

Many forest tree improvement workers are now making second-generation breeding plans. At Olustee, we have studied various approaches proposed by several authors (Libby, 1969 and 1972; Burdon and Shelbourne, 1971; and van Buijtenen, 1972) and made estimates of genetic gains for some of them. This paper gives the results of these analyses and outlines our tentative plans. Hopefully, the results and discussion will be helpful to others making plans for future breeding.

BACKGROUND

Several years ago, we launched a program designed to breed a "multi-purpose strains" of slash pine, to combine high oleoresin yield with other desirable traits (Squillace 1965). This effort should not be confused with the earlier work at Olustee, which successfully resulted in a high gum yield strain but in which emphasis was almost entirely on high gum yield. In the more recent program, we selected over 100 trees having the desired qualities, through cooperation of federal, state, and private forestry organizations. Most of these selections have been progeny tested under our short-term testing scheme, (Squillace and Gansel 1968) and scions from the best of the selections will be used in establishing clonal orchards.

Thus, in the "multi-purpose strain" program, we have completed one generation of breeding. Our next objective is to establish a new base population, which will form the basis for second-generation orchards and further breeding. We plan to use approximately 100 selections in establishing the

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base population rather than only the clones being selected for first-generation seed orchards, in order to provide a broad base. The desirability of keeping base populations separate from seed orchards has been pointed out by Franklin (1973). The major question now is, "What breeding scheme should we use in developing the new base population?"

Without very much contemplation, we decided to use individual tree matings rather than polymix matings. The main reason for this choice is that by making individual tree crosses and keeping family identity, we will have control on future inbreeding.

The selection of a mating design for the 100 P_1 selections required more study. A minimum effort would be to breed each tree once. This "single-pair" mating scheme, proposed by Libby (1972), would require only 50 full-sib families, all of which would be unrelated. Alternatively, we could produce more matings on each tree. One practical method is the disconnected half-diallel (d.h.d.). Under this method, the parent trees are divided into a number of groups and then trees are crossed within each group in a half-diallel manner, excluding selfs and reciprocals. For example, we could divide the parent into 20 groups of 5 each, and there would then be a total of

$[Np(p-1)/2] =$ 200 full-sib families (N = number of groups, P = number of

parents per group). We shall call this a "5-parent d.h.d.". Note that a "single-pair" mating scheme can be called a "2-parent d.h.d.". Note also that for d.h.d.'s containing more than 2 parents per group, there will be half-sib relationships as well as full-sib relationships in the progeny. For convenience, all the progeny of one parent will be called a "half-sib family" although it actually consists of two or more full-sib families.

Disconnected half-diallels with say 5 or 6 parents per group would, of course, have the advantage of providing reliable combining abilities for each parent. In our case, this would be of some importance as it provides a basis for roguing of first-generation orchards. The major question is, however, would producing relatively large numbers of families provide greater genetic gains in second-generation orchards?

In order to get an answer to this question, a theoretical analysis of genetic gains possible for d.h.d.'s of varying group sizes was made. At the same time, it was considered desirable to determine the optimum selection scheme for development of second-generation clonal orchards. Finally, some attention was given to the desirability of converting a portion of the base population into a seedling seed orchard.

ESTIMATION OF GENETIC GAINS FROM DISCONNECTED HALF-DIALLEL SCHEMES

In computing the expected gains, the base population was held constant at 7500 trees. Thus, in a 2-parent d.h.d., we would produce and plant 150 offspring from each of 50 full-sib families. In a 3-parent d.h.d., we would plant 75 offspring from each of 100 full-sib families, etc.

It was further assumed that, under each scheme, 25 offspring would be selected for use in clonal orchards. Thus, the proportion of offspring to be selected in each case would be 25/7500 = 1/300. Narrow-sense heritability on an individual tree basis was assumed to be .25, a reasonable value for growth rate. However, computations for heritabilities of .50 and .75 were also made, mainly to reveal trends for changing heritability.

The selection schemes were designated 1 through 5, which are the number of offspring selected per full-sib family. In each case, the number of half-sib or full-sib families had to varied accordingly, so that the number of trees selected in each case totaled 25. For example, in the 2-parent d.h.d. under scheme 1, we select the best tree in each of the best 25 full-sib families; in scheme 2, we select the best 2 trees in each of the best 12-1/2 families, etc.; finally, in scheme 5, we select the best 5 offspring in each of the best 5 families.

For d.h.d.'s involving more than 2 parents, we had the alternative of varying the numbers of half-sib families to be selected as well as full-sib families within them. But preliminary analyses suggested that gains would be greatest by placing the greatest intensity of selection on full-sib families. Hence, the number of half-sib families and individuals to be selected were varied and the number of full-sib families were held constant at 1 per half-sib family.

Since in some cases, we would be choosing relatives, allowances were made for inbreeding. On the basis of Gansel's (1971) report, it was estimated that inbreeding losses, due to using relatives in seed orchards, might be approximately .4 standard deviations per .1 of F (the inbreeding coefficient). For stem volume, this is roughly equivalent to a loss of about 12 percent of the mean per .1 of F.

Computations of gross genetic gains were made using separate formulae for family and for within-family selection given by Falconer (1960, p. 235). Admittedly, combined selection (which gives proper weights to the individual's value and its family mean) would result in greater gains. But if combined selection was used, we could not properly deduct for inbreeding losses, since we would not know the numbers of relatives that would be chosen. Details of computations are exemplified in Appendix Table 1 and results are presented in Figure 1. Estimated gains are given in terms of phenotypic standard deviations (σ_p) of individuals, and this was assumed to be constant over all base populations. (As near as could be determined with a hypothetical model, increasing the number of families does not change the overall phenotypic standard deviation. An opportunity to check on this with actual data from diallel mating schemes was also available and no appreciable change could be found in σ_p, in going from 2-parent to 4-parent d.h.d.'s). If one knows the standard deviation and mean (and hence, the coefficient of variation) for a particular situation, the gains can be converted into a more understandable measure. For example, if the coefficient of variation in volume growth is 30 percent, a gain of .8 σ_p would be equivalent to about 24 percent of the mean.

Note that estimated gains increase in going from a 2-parent d.h.d. to a 6-parent d.h.d., rapidly at first and then more slowly (figure 1). For example, if one selects a single offspring per full-sib family, the expected gain is about .63 σ for a 2-parent d.h.d. and about .85 σ_p for a 6-parent d.h.d., which converts roughly to 19 versus 25 percent of the mean, assuming a coefficient of variation of 30 percent. Genetic gains for an 8-parent d.h.d., not shown in Figure 1, would be only slightly higher than those for the 6-parent d.h.d.

Apparently, the differences between mating schemes are due to differences in the allocation of the overall proportion of trees selected (1/300) to family and within-family selection and to the fact that, for low heritability, family selection is much more effective than within-family selection. For example, under a 2-parent d.h.d. with 1 selection per full-sib family, we select the best 25 of 50 families and the best 1 of 150 individuals within families. In a 5-parent scheme, on the other hand, we select relatively more intensively for families (1/8 for families and 1/37.5 for individuals within families).

Note also in Figure 1 that gains increase in going from selecting 1 offspring per full-sib family to 2 or 3 offspring per full-sib family and then decrease thereafter. Gross gains actually increase continuously in going from 1 to 5 trees selected per family. This is due, again, to increasing intensity of family versus within-family selection. The net gains, however, show a curvilinear effect, with an optimum, because of increasing inbreeding losses. Thus, selecting relatives up to a certain point (2 or 3 trees per full-sib family) results in greater net genetic gains than entire avoidance of relatives.

With high heritabilities, (.50 and .75) the results were similar to those for a heritability of .25, but the relative advantage of producing more families and of selecting more than one offspring per family decreases as heritability increases.

Under actual conditions, it may be preferable to make selections using a combined (family + within-family) index (Falconer, 1960, p. 236). If this procedure is used without restriction relatives will likely be chosen. In order to check further on the effect of selecting relatives, two kinds of selection were compared using data from 3 progeny tests at Olustee: 1) unrestricted combined selection and 2) combined selection restricted to avoid relatives. As expected, unrestricted combined selection resulted in highly varying numbers of selections per family (table 1). But the inbreeding coefficient in each case was rather small and the estimated losses were likewise small. The net genetic gains from unrestricted combined selection exceeded the gain from restricted combined selection in all three tests. In test G-62, unrestricted combined selection resulted in 9 selections from one family. In practice, one should avoid that many selections from one family, holding it to a maximum of say 5. This may reduce gains slightly, but it would perhaps be safer--a highly superior family may fail at a later date.

Figure 1.--Expected net genetic gains (after allowance for inbreeding losses) from establishing base populations by disconnected half-diallel (d.h.d.) mating schemes and selecting trees by several methods for use in clonal. orchards.

Conditions:

Breed 100 P_I selections by one of five schemes
Plant 7500 offspring
Select 25 offspring for clonal orchard by one of
five schemes (horizontal axis—see text)
$h^2 = .25$

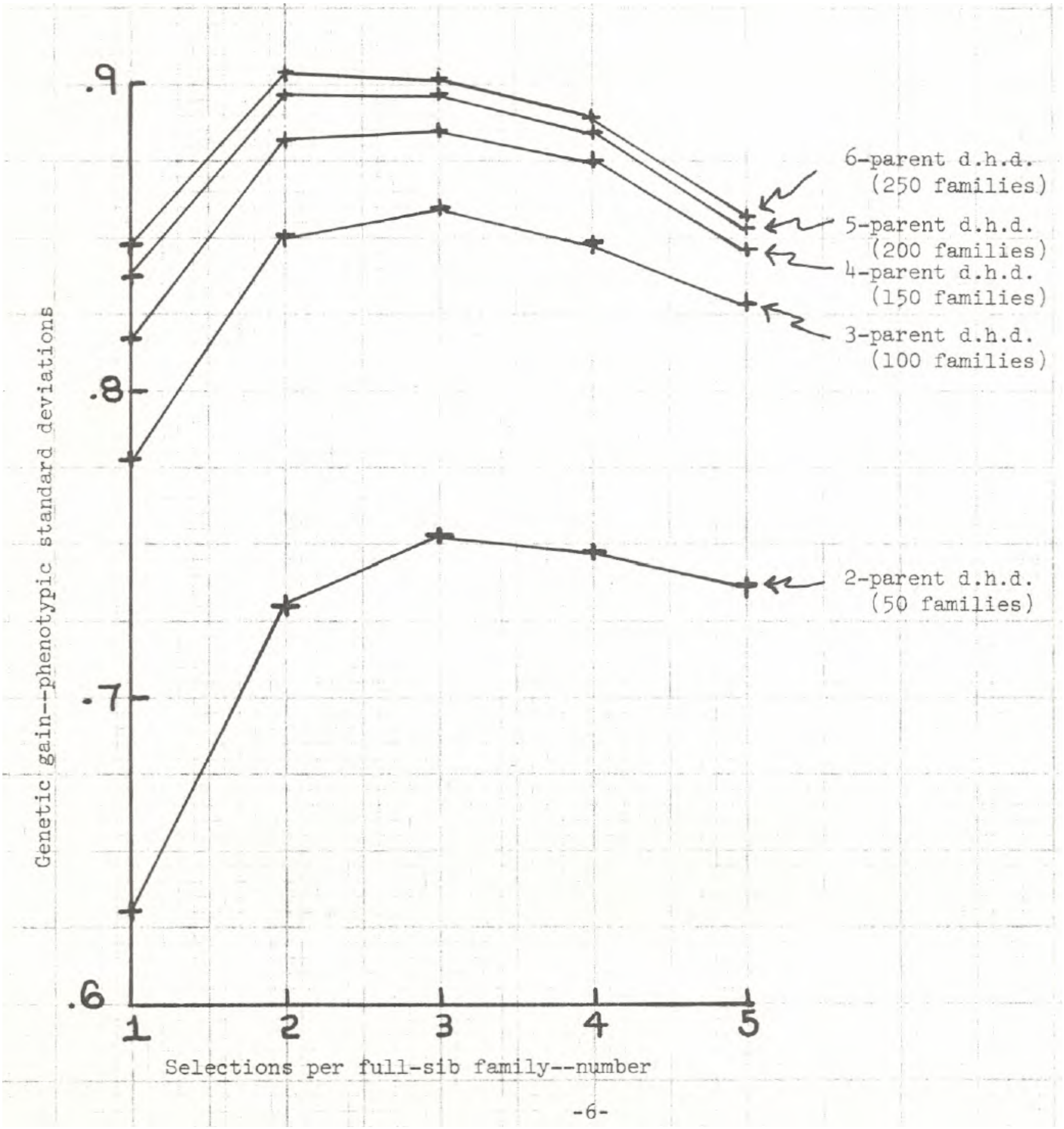

Table 1.--Estimated genetic gains in height growth from unrestricted combined selection versus combined selection restricted to avoid relatives, in three slash pine progeny tests.

	Test G-48A	Test G-62	Test G-49
TEST DATA			
Age of trees . . . . years	10	3	10
Total families . . . . number	31	30	50
Total trees. . . . . number	930	600	500
Average index value.	129.7	30.0	73.3
UNRESTRICTED COMBINED SELECTION			
Average index value for 25 selected trees	141.7[1]	34.2[2]	84.0[3]
Gross genetic gain . . . . percent	9.2	14.0	14.6
Estimated inbreeding coefficient for progeny of selected trees[4]	.008	.025	.011
Estimated loss from inbreeding . . percent	- .4	-1.5	-0.7
Net genetic gain . . . . percent	8.8	12.5	13.9
COMBINED SELECTION RESTRICTED TO AVOID RELATIVES			
Average index value for 25 selected trees	139.3	32.5	82.0
Genetic gain . . . . percent	7.4	8.3	12.0

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[1] Selections occurred in 14 families. The number of selections in them were 5, 3, 3, 2, 2, 2, 1, 1, 1, 1, 1, 1, 1, and 1, respectively.

[2] Selections occurred in 8 families. The number of selections in them were 9, 6, 5, 1, 1, 1, 1, and 1, respectively.

[3] Selections occurred in 10 families. The number of selections in them were 6, 5, 3, 2, 2, 2, 2, 1, and 1, respectively.

[4] Excluding selfing and assuming random mating among trees.

SEEDLING SEED ORCHARDS

Although we tentatively plan to use the clonal orchard approach, a cursory analysis was made to see what gains could be obtained by a seedling seed orchard approach. Here it was assumed that 1) the base population would be established from a 5-tree d.h.d.; 2) a 10-acre portion of it would be converted into a seedling seed orchard; and 3) that the trees for it would be planted at random in individual tree plots, at a spacing of 30 sq. ft. per tree. Thus, there would be about 1450 trees per acre. We would make a light early thinning (say at 5 years) and then a final one at 10 years, leaving 50 trees per acre. Thus, the proportion of trees selected is 50/1450 = .034. The selection intensity here is considerably less than that used in the clonal orchard approach and hence, the genetic gains cannot possibly be as great as in the latter. Allowance was made for the relative inefficiency of the early thinning. Heritability was again assumed to be .25.

The estimated gain from the seedling seed orchard approach could not be accurate because it was not possible to determine the numbers of relatives that would occur and hence, the inbreeding losses allowed were little more than guesses. But the genetic gain turned out to be .60 σ_p , which is appreciably less than expected gains from the clonal orchard in the 5-parent d.h.d., as expected.

However, there are other points to consider. When the base population is 10 years old, and is converted into a seedling seed orchard, it would perhaps start producing appreciable amounts of seed in a couple of years. On the other hand, if instead, we begin a clonal orchard at this time, a lapse of about 10 years would occur before seed production. Thus, genetic gains from the seedling seed orchard would come sooner than those from a clonal orchard. Also, the cost of establishing the former may be less. An economic analysis would be required to make a good comparison. At Olustee, we are considering converting a portion of the base population into a seedling seed orchard, on an experimental basis.

SUMMARY AND CONCLUSIONS

In our tree breeding program at Olustee, we are planning to establish a new base population from 100 genetically superior P_1 selections to be used for further selection and breeding. Analyses, based largely on theory, were conducted to help decide on a breeding approach and on schemes for developing second-generation orchards. Expected genetic gains were computed for disconnected half-diallel mating schemes, with from 2 to 8 parents per diallel, and for 5 selection schemes.

Estimated genetic gains increased appreciably with increasing number of parents per diallel up to about 4. We have tentatively decided to use a 6-parent scheme. But we expect to end up with the approximate equivalent of a 5-parent scheme because some matings will likely be difficult to make and we do not consider it necessary to make all of them. A 5- or 6-parent disconnected diallel will also provide reliable data on the combining ability of each parent. The analyses also suggested that in choosing offspring for a clonal orchard, the breeder will achieve appreciably greater genetic gains if he includes relatives to a modest degree (such as about 2 to 3 full-sibs per selected family) than if relatives are avoided entirely. This was true for conditions specified in the study, ($h^2 = .25$ and 25 clones per orchard) and would likely be true generally when heritability is low and when at least 25 clones per orchard are used. We have decided to use combined (family + within-family) selection, restricted to the extent of permitting not more than about 5 full-sibs per family.

Conversion of the base population into a seedling seed orchard was also considered as an alternative to establishing clonal orchards. Genetic gains are expected to be somewhat less than the clonal orchard approach. But improved seed will be obtained sooner and the costs may be less for the seedling seed orchard. This approach should be examined further.

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Appendix Table 1.--Estimated net genetic gains for a 5-parent disconnected half-diallel under 5 selection schemes.1/

Selection scheme			Inbreeding			Half-sib selection			Full-sib selection			Within full-sib family selection			Net gain
h	f	w	$\bar{r}_o$	$\bar{F}$	Loss	P_h	I_h	R_h	P_f	I_f	R_f	P_w	I_w	R_w	
No.	No.	No.			σ_p			σ_p			σ_p			σ_p	σ_p
25.00	1	1	.00	.00	.00	.50	.80	.22	.25	1.27	.34	.03	2.13	.28	.84
12.50	1	2	.02	.01	-.04	.25	1.27	.34	.25	1.27	.34	.05	1.93	.25	.89
8.33	1	3	.04	.02	-.08	.17	1.50	.40	.25	1.27	.34	.08	1.78	.24	.90
6.25	1	4	.06	.03	-.12	.12	1.65	.44	.25	1.27	.34	.11	1.66	.22	.88
5.00	1	5	.08	.04	-.17	.10	1.76	.47	.25	1.27	.34	.13	1.56	.21	.85

1/ Conditions

100 P_1 selections, divided into 20 groups of 5 each.
Selections mated to produce 200 full-sib families, each containing an average of 37-1/2 offspring.
Plant 7500 offspring (base population).
Select 25 offspring for use in developing a second-generation clonal orchard.

Computations for selection scheme 2 (second row of table).

1) Inbreeding loss $= 4\bar{F}\sigma_p = 4(.01)\sigma_p = .04\sigma_p$

$\bar{F}$ = average inbreeding coefficient of second-generation orchard, excluding selfing and assuming random mating among clones

$$= \frac{\bar{r}_o}{2} = \frac{.02}{2} = .01$$

$\bar{r}_o$ = average coefficient of relationship among offspring selected

$$= \frac{w(f + 1) - 2}{4(h\ f\ w - 1)} = \frac{2(1 + 1) - 2}{4[(12.5)(1)(2)]} = .02$$

h = number of half-sib families selected = 12.5
f = number of full-sib families selected within half-sib families = 1
w = number of individuals selected per full-sib family = 2

2) R_h = genetic gain from half-sib selection

$$= I_h \sigma_p h^2 \cdot \frac{1 + (n_h - 1) r_{e_h}}{\sqrt{n_h \{1 + (n_h - 1) t_h\}}} \text{, (Falconer, 1960, p. 235)}$$

$$= 1.27\ \sigma_p (.25) \cdot \frac{1 + (150 - 1)(.306)}{\sqrt{150\{1 + (150 - 1)(.077)\}}} = .34\sigma_p$$

I_h = 1.27 = selection differential in standard measure, corresponding to P_h.

P_h = proportion of half-sib families selected = .25 (Note. There will be 100 half-sib families, each containing 4 full-sib families, utilizing each full-sib family twice. Hence, although an average of only 12.5 half-sib families will be selected, P_h is considered to be 25/100 rather than 12.5/100 in order to avoid selection of the same full-sib family twice. This makes the overall proportion selected 1/300, as required (25/100 for half-sib selection, 1/4 for full-sib selection, and 2/37.5 for individual selection)).

σ_p = phenotypic standard deviation of individuals.

h^2 = heritability of individuals = .25

n_h = number of individuals per half-sib family = 150.

r_{e_h} = effective coefficient of relationship between members of half-sib families (Lush, 1945, p. 325).

$$= \frac{\bar{r}_{w_h} - \bar{r}_{b_h}}{1 - \bar{r}_{b_h}} = \frac{.3122 - .0082}{1 - .0082} = .306$$

$\bar{r}_{w_h}$ = average coefficient of relationship within half-sib families.

$$= \frac{n_h(f_h + 1) - 2}{4(f_h n_h - 1)} = \frac{150(4 + 1) - 2}{4[(4)(150) - 1]} = .3122$$

f_h = number of full-sib families per half-sib family = 4

$\bar{r}_{b_h}$ = average coefficient of relationship between half-sib families

$$= \frac{3p - 2}{4(N - 1)(p - 1)} = \frac{3(5) - 2}{4(100 - 1)(5 - 1)} = .0082$$

N = total number of parents = 100
p = number of parents per half-diallel group = 5
t_h = phenotypic correlation between trees in half-sib families

$= h^2 r_{e_h} = .25(.306) = .077$

3) R_f = genetic gain from full-sib selection

$$= I_f \sigma_p h^2 \cdot \frac{1 + (n_f - 1) r_{e_f}}{\sqrt{n_f\{1 + (n_f - 1) t_f\}}}$$, (Falconer, 1960, p. 235)

$$= 1.27\ \sigma_p (.25) \cdot \frac{1 + (37.5 - 1)(.333)}{\sqrt{37.5\{1 + (37.5 - 1)(.083)\}}} = .34\sigma_p$$

I_f = 1.27 = selection differential in standard measure corresponding to P_f
P_f = proportion of full-sib families selected = .25
n_f = number of individuals per full-sib family = 37.5
r_{e_f} = effective coefficient of relationship between members of full-sib families

$$= \frac{r_{w_f} - r_{b_f}}{1 - r_{b_f}} = \frac{.50 - .25}{1 - .25} = .333$$

r_{w_f} = coefficient of relationship within full-sib families = .50
r_{b_f} = coefficient of relationship between half-sib families = .25
t_f = phenotypic correlation between trees in full-sib families

$= h^2 r_{e_f} = .25(.333) = .083$

4) R_w = genetic gain from selection of individuals in full-sib families

$$= I_w \sigma_p h^2 \cdot (1 - r_{w_f}) \sqrt{\frac{n_f - 1}{n_f(1 - t_w)}}$$, (Falconer, 1960, p. 235)

$$= 1.93\sigma_p(1.25)(1 - .50)\ \sqrt{\frac{37.5 - 1}{37.5(1 - .125)}} = 25\sigma_p$$

I_w = 1.93 = selection differential in standard measure, corresponding to P_w

P_w = proportion of individuals selected within full-sib families = .05

t_w = phenotypic correlation between trees in full-sib families = $h^2 r_{wf} = .25(.50) = .125$

Net gain = Inbreeding loss + $R_h + R_f + R_w = (-.04 + .34 + .34 + .25)\sigma_p = .89\sigma_p$.