PARENT VS. OFFSPRING SELECTION: A CASE STUDY

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Abstract.--A comparison was made between genetic gains and program benefits to be expected from parent selection after progeny testing, and offspring selection of the best trees in the best families, given the constraints of the N. C. State Industry Tree Improvement Cooperative disconnected half diallel mating scheme. At moderate heritability levels ($h^2 = 0.15$), offspring selection yielded higher expected genetic gains. However orchards established with juvenile scion material from genetic tests may not reach commercial production levels as rapidly as orchards established with scion material from older parent trees. Economic analysis shows that a delay of only one year in reaching full production levels can make offspring selection less profitable than parent selection, i.e., the cost of delay exceeds the increased return of higher genetic gains.

INTRODUCTION

Parent selection is a selection strategy where individuals are selected on the basis of the performance of their progenies. The best individuals (the parents of the best progeny families) form the commercial production population. Offspring selection is a strategy where the selected individuals are the best members of the progeny families. The main advantage of offspring selection is that it offers breeders the opportunity to do within family selection at high selection intensities. This generally allows the achievement of higher expected genetic gains, and thus is quite attractive to breeders. The primary objective of breeding programs, however, is not to achieve maximum genetic gains, rather it is to generate maximum dollar value or economic return. In making a decision about which selection strategy to use, it is important to consider factors other than those which maximize genetic gain. A case study of the situation involving the N. C. State Industry Tree Improvement Cooperative illustrates this point.

At this time, the N. C. State Cooperative plans to use offspring selection to select its third generation population of loblolly pine (Pinus taeda L.) (Anon., 1983). There has been some concern, however, that seed orchards established after offspring selection may not develop strobili as quickly as orchards established after parent selection. This possibility arises because the two selection strategies will yield scion material of quite different ages and in different states of sexual maturity. Loblolly pine grown in the field does not begin to flower consistently until it is 10 to 15 years-old (Dorman and Zobel, 1973). Since the N. C. State Cooperative plans on making selections in its genetic tests at age eight (McKeand and Weir, 1983), scion material from offspring selection will be sexually immature. Scion material from parent selection would be sexually mature, and the two

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types of orchards could conceivably show different patterns of strobili production over time. The objective of this case study is to compare genetic gains expected from parent and offspring selection, and to examine the effect of production delays on expected program benefits.

ESTIMATION OF GENETIC GAINS

The following assumptions were made in calculating genetic gains:

a. The seed orchard will be composed of 24 unrelated individuals.

b. The foundation population consists of 480 unrelated individuals.

c. The foundation population will be mated using six parent disconnected half-diallels formed at random with respect to general combining ability.

d. Non additive genetic variance equals additive genetic variance.

e. Field trials of the diallels will be conducted according to the N. C. State Cooperative Genetic Testing Manual (Talbert et al., 1981).

The specific calculations for genetic gains for both parent and offspring selection are presented in the Appendix. Calculations for genetic gains from offspring selection were made using separate formulae for family and within family selection, following a technique outlined by Squillace (1973). Estimates of genetic gains obtained from this technique are conservative, as combined selection would give greater genetic gains (Falconer, 1981). However, in calculating genetic gains from combined selection a priori, one cannot account for the requirement to maintain unrelatedness.

Expected genetic gains (Table 1) are presented in terms of phenotypic standard deviations of individuals (σ_p), and this was assumed to be equal for both parent and offspring populations.

Results of Genetic Gain Calculations

As expected, at most heritabilities offspring selection yielded higher expected genetic gains than parent selection. At very low heritabilities (individual, narrow sense, parent selection was more efficient, although a change occurred between $h = 0.10$ and $h^2 = 0.15$. One should note that this was primarily due to the effect of within family selection. As heritability increased from 0.05 to 0.50, gains from half-sib, full-sib, and parent selection increased approximately three-fold. Over the same range, gains from within family selection increased ten-fold.

If the decision between the two selection strategies were simply a question of maximizing genetic gains, one need only determine the heritability of the trait of interest to make the correct decision. As the program objective is to maximize economic return, however, other factors must be considered.

Table 1.--Expected genetic gains[a] from offspring and parent selection.

				Selection	
h^2	Half sib	Full sib	Within Family	Offspring[b]	Parent
.05	.2197	.0935	.0707	.3839	.4379
.10	.3167	.1377	.1442	.5986	.6354
.15	.3903	.1711	.2209	.7823	.7581
.20	.4522	.1991	.3009	.9522	.9107
.25	.5065	.2236	.3847	1.1148	1.0209
.30	.5556	.2456	.4727	1.2739	1.1204
.40	.6426	.2847	.6632	1.5905	1.2967
.50	.7192	.3191	.8773	1.9156	1.4517

[a] Values expressed in units of phenotypic standard deviation of individuals.

[b] Gain from offspring selection equals the sum of gains from half-sib, full-sib, and within family selection.

SEED ORCHARD DEVELOPMENT

Grafted seed orchards (using sexually mature scion material) have generally reached commercial production levels 10 to 15 years after orchard establishment (Anon., 1979), and a rule of thumb developed in the N. C. State Cooperative is that 8 to 12 years usually elapse before meaningful production occurs (Talbert et al., 1983). Good choice of seed orchard sites, along with intensive irrigation and fertilization can promote the development of young seed orchards (Jett, 1983). The possibility that seed orchards established with sexually mature material may come into production sooner than orchards established with juvenile material forces one to consider the economic costs of a delay in production. To do this, one must know when the returns from the increased genetic gains will be available, i.e. when the improved trees will be harvested.

TIME LINES

The following assumptions were used in developing time lines scheduling the harvest of improved trees:

a. Two years to establish orchard after selection.
b. Breeding and testing for the subsequent generation begins immediately and will be completed in 14 years. A new orchard will then be established.
c. Two years after first commercial cone harvest until actual planting of the improved seedlings.
d. 25 years rotation.
e. Seed orchards go from zero to full strobili production in a single year.

Assumption e. is unrealistic and was made only to simplify analysis. Using these assumptions, one can generate a timeline for an orchard established after parent selection, assuming eight years to reach full production (P8):

Event	Year
Year to finish orchard establishment	2
Year to first commercial production	10
Year to first planting	12
Earliest that next generation orchard could be established	16
Time when next generation orchard would produce	24
Last year planting	25
First year next generation material planted	26
Years of harvest	37 to 50

A similar time line can be developed for offspring orchards. Comparisons were made between the P_8 situation above and offspring orchards taking 9, 10, and 11 years to reach full production (0_9, 0_{10}, and 0_{11}, respectively).

One should note that in the P_8 situation, harvests are made from year 37 to year 50. For all offspring orchard situations, the next generation orchard is assumed to take eight years to develop. This would be the case if offspring selection was utilized, and then followed by parent selection for the next cycle of improvement. Thus for the 0_9 situation, the years of harvest are years 38 to 50, and it is the harvests over these years that are compared to the P_8 situation.

DISCOUNTING PROCEDURES

In order to compare the economic values of the two selection schemes, one needs to convert the genetic gains calculated earlier into dollar values. The information needed is the mean of trait p, the standard deviation of trait p, and the relationship of trait p to dollar value. At the time that the selections would be made, this information would be in hand. For the sake of comparison in this general analysis, however, one can make the assumption that trait p is linearly related to dollar value. This is a reasonable assumption for volume growth with a product objective of pulpwood. It then becomes possible to make relative comparisons between the two selection schemes, simply treating genetic gain as if it were dollar value. Another assumption is that the amount of land planted and harvested is equal each year and from year to year. For example, the organization may be planting and harvesting 10,000 acres every year. The organization would then receive an annual annuity over the years of harvest outlined above.

One can calculate the present value of a terminating annual annuity with the formula:

$$V_{0(n)} = a \frac{(1+i)^n - 1}{i\ (1+i)^n} \quad \text{(Lundgren, 1971)}$$

where: a = value of annuity
i = interest rate
n = year the annuity terminates

The present value of an annual annuity to be received between the year n and year x is:

$$V_{0(n \text{ to } x)} = V_{0(x)} - V_{0(n-1)}$$

including heritability, interest rate, economic value function, and generation interval. The effects of heritability and interest rate have already been discussed. Economic value function can also be important. In this study, an assumption was made that the trait of interest is linearly related to dollar value. In fact, the economic value function could be some type of stepwise function where an increase of the trait beyond a certain point yields a very large increase in dollar value. If the trait has this sort of relationship to dollar value, the discounted genetic gain estimates for offspring selection may be low relative to parent selection. The more the population mean is increased, the greater the probability the population will reach the next step in dollar value.

Generation interval is also important. In this study, it was assumed that six years would be necessary to complete the matings, and eight years to complete the field testing, for a generation interval of 14 years. If selections were made at **six** years instead of eight, the generation interval would be 12 years. Under this circumstance, the relative cost of missing the first year of production is greater than with a 14 year generation interval. Therefore, if a breeder expected orchards established with offspring scion material to be slower in reaching full production than orchards of parent scion material, a 12 year generation would tend to push him even more in the direction of parent selection.

For this specific case study, the primary question becomes "Will there be a difference in the development of seed orchards established with sexually mature and immature scion material?" Although there is very little in the literature on this subject, I suspect that there would be little differnce. Consider that if selection occurs at eight years, it takes two years to establish the orchard, and a minimum of **six** to eight years are necessary for the trees to have enough vegetative growth to support full production levels, offspring scion material would be 16 to 18 years-old, and would probably be sexually mature. More concrete evidence is presented by Talbert et al. (1982). In a study of four seed orchards, although sexually immature grafts tended to produce more pollen catkins and less female strobili than mature grafts, the differences were not statistically significant.

Other Time Factors

A difference in the rate of seed orchard development is not the only way that a time difference could have an impact on the decision between parent and offspring selection. Another source of difference might be the time required for orchard establishment. It may take more time to establish offspring seed orchards from single eight year-old trees than parent orchards from numerous ramets kept in a greenhouse or clone bank.

Breeders should also consider that it is generally possible to identify the best families in field tests earlier than it is possible to identify the best individuals in those families. In the case of the N. C. State Cooperative, it is likely that one could be nearly as effective in parent selection at age four or **six** as at age eight. To identify the best individuals in offspring selection, however, is very difficult at younger ages. One could then argue that a breeder is imposing a two year delay on his program in order to gain the additional benefit of within family selection. The results of this study would suggest that this is not worthwhile.

One can then discount the genetic gains presented in Table 1 by multiplying by the appropriate value for v_0 (n to x)• This allows a comparison of the two selection schemes taking the delay in reaching full production into account.

Discounted Genetic Gains

Genetic gains were discounted at interest rates of 6% and 9% (Tables 2, 3). Discounted genetic gains were calculated at h^2 = 0.15. Solely on the basis of genetic gains, offspring selection was more efficient at all heritabilities in Tables 2 and 3. But comparing the P_8 and 0_9 situations at 6% interest, the cost of a one year delay in reaching full production levels was enough to make parent selection more valuable than offspring selection at heritabilities up to 0.25. Not unless h^2 was as high as 0.30, did the increased genetic gains from offspring selection offset the cost of missing the first year of production.

Longer delays had higher costs. Comparing the P_8 and the 0_{10} situations in Table 2, a two year delay at 6% interest, only at a heritability of 0.50 was offspring selection more valuable than parent selection. For a three year delay, P_8 and 0_{11}, parent selection was always more valuable.

The effect of higher interest rates was to place a higher premium on reaching production earlier. At 9% interest with a one year delay, offspring selection became more valuable than parent selection at h^2 = 0.40, as opposed to a h^2 = 0.30 with 6% interest.

Table 2.--Discounted genetic gains at an interest rate of 0.06.

h2	P8	09	010	Oil
.15	.8649	.8019	.7165	.6349
.20	1.0390	.9761	.8721	.7739
.25	1.1647	1.1428	1.0210	.9061
.30	1.2783	1.3059	1.1668	1.0354
.40	1.4794	1.6304	1.4567	1.2928
.50	1.6562	1.9637	1.7545	1.5570

Table 3.--Discounted genetic gains at an interest rate of 0.09.

h2	P8	0_9	O10	Oi 1
.15	.2340	.2119	.1848	.1598
.20	.2811	.2580	.2249	.1945
.25	.3152	.3020	.2633	.2278
.30	.3459	.3451	.3009	.2603
.40	.4003	.4309	.3757	.3249
.50	.4481	.5189	.4525	.3914

DISCUSSION

The most striking result of this study was that only a one year delay had a significant impact on the choice between parent and offspring selection. In making this decision, tree breeders must consider a number of factors

CONCLUSIONS

In making a decision between parent and offspring selection, tree breeders should consider when genetic gains will be available, in addition to the size of those genetic gains. Even a delay of as little as one year can change which selection scheme yields the highest overall benefit to the program.

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Appendix.--Genetic Gain Calculations.

A. Conditions

480 P_1 selections, divided into 80 groups of 6 each.
Selections mated to prduce 5 full-sib families within each half-sib family.

Field test design involves (4 locations) (6 reps/loc.) (6 trees/family/rep) yielding 144 trees/cross.
o_f = 144 = number of full-sib family members
n_h = 720 = number of half-sib family members

B. Offspring Selection Scheme

1. All half-sib and full-sib families are ranked.
2. The highest ranking half-sib family is identified (Family A).
3. The best of the five full-sib families involving Family A is identified (Family AxB).
4. The best individual tree in the full-sib family AxB is identified to be grafted into the seed orchard.
5. Half-sib families and full-sib families involving A or B are eliminated from the list of candidate families.
6. Return to Step 2.

C. Genetic Gain From Parent Selection

$$R_p = i\sigma_p h^2 \sqrt{\frac{n}{4 + (n-1)h^2}} = 2.063\ \sigma_p h^2 \sqrt{\frac{720}{4 + (720-1)h^2}}$$

where:

R_p = expected response from progeny testing (parent selection)

i = selection intensity expressed in standard measure

σ_p = phenotypic standard deviation of individuals

h^2 = individual tree heritability

n = number of progeny = 720

Selection of parents of the top 24 half-sib families = 24/480 yielding i = 2.063.

D. Genetic gain from offspring selection - adapted from Squillace (1973).

$$R_O = R_{HS} + R_{FS} + R_{WF}$$

where:

R_O = expected response from offspring selection
R_{HS} = expected response from half-sib family selection
R_{FS} = expected response from full-sib family selection
R_{WF} = expected response from within family selection

1. Half-sib selection

$$R_{HS} = i\sigma_p h^2 \frac{1 + (n_h - 1)r_{eh}}{\sqrt{n_h\,[1 + (n_h - 1)\hat{t}_h]}} = 2.013\ \sigma_p h^2 \frac{1 + (720-1)(.2987)}{\sqrt{720[1 + (720-1)(.3495h^2)]}}$$

where:

variables as before
n_h = number in half-sib family
r_{eh} = effective coefficient of relationship between members of half-sib families (Lush, 1943)

$$r_{eh} = \frac{r_{wh} - r_{bh}}{1 - r_{bh}} = \frac{.2999 - .0017}{1 - .0017} = .2987$$

r_{wh} = average coefficient of relationship within half-sib families

$$= \frac{n_h(f_h + 1) - 2}{4(f_h n_h - 1)} = \frac{720\ (5 + 1) - 2}{4[(720)(5) - 1]} = .2999$$

f_h = number of full-sib families per half-sib family
r_{bh} = average coefficient of relationship between half-sib families

$$= \frac{3p - 2}{4(N-1)(p-1)} \quad \frac{(3)(6) - 2}{4(480-1)(6-1)} = .0017$$

where:

N = total number of parents = 480
p = number of parents per diallel group = 6

$\hat{t}_h$ = phenotypic correlation between trees in half-sib families = .3495 h^2

If all genetic variance was additive, t could be calculated for a half-sib family by multiplying the h^2 by the average coefficient of relationship: $t = h^2 r$. In this case, however, non-additive variance equals additive variance, and may contribute to phenotypic correlation as the half-sib families are not truly half-sibs, but have full-sibs in them. Full-sib families have a covariance of $1/2V_a + 1/4V_d$. If all non-additive variance is dominance, one can calculate t for full-sibs as $t_f = (1/2V_a + 1/4V_a)h^2$. Thus $t_f = 0.75\ h^2$. One can then determine $\hat{t}_h$ for half-sib families by weighting t_h and t_f by the probability of selecting two half-sibs and two full-sibs, respectively, when randomly choosing two members of a half-sib family.

$$\hat{t}_h = Pr(FS) + t_f + PR(HS)t_h$$
$$\hat{t}_h = 143/719\ (.75h^2) + [(719-143)/719](.25h^2) = .3495h^2$$

Selection Intensity: We are selecting 24 half-sib families, but our selection scheme eliminates two half-sib families each time through the cycle. We may not be able to actually select the top 24 half-sib families. It is possible to determine, however, the probability that a diallel contains zero of the top 27 half-sib families:

$$\text{Pr(diallel has zero of top 27)} = C^{(480-27)}_{6} \; / \; C^{480}_{6}$$

$$= (453 \times 452 \times 451 \times 450 \times 449 \times 448)/(480 \times 479 \times 478 \times 477 \times 476 \times 475)$$
$$= 0.7052$$

0.7052 x 80 diallels = 56 diallels that contain none of the top 27 families; therefore 24 different diallels contain the top 27. We can then be confident of selecting the top 27 half-sib families from 480 yielding i = 2.013.

2. Full-sib selection

$$R_{FS} = i\sigma_p h^2 \frac{1 + (n_f-1)r_{ef}}{\sqrt{n_h\,[1 + (n_h-1)t_f]}} = 1.163\sigma_p h^2 \frac{1 + (144-1).333}{\sqrt{144[1 + (144-1)(.75h^2)]}}$$

where:

variables as before

r_{ef} = effective coefficient of relationship between members of full-sib families

$$= \frac{r_{wf} - r_{bf}}{1-r_{bf}} = \frac{0.5 - 0.25}{1 - 0.25} = 0.333$$

r_{wf} = coefficient of relationship within full-sib families = 0.5

r_{bf} = coefficient of relationship between full-sib families = 0.25

t_f = phenotypic correlation between members of full-sib families = $0.75h^2$

Selection intensity is 1 of 5 yielding i = 1.163.

3. Within family selection

$$R_{WF} = i\sigma_p h^2\,(1-0.5)\sqrt{\frac{n_f - 1}{n_f\,(1-t_f)}} = 2.784\,\sigma_p h^2(0.5)\sqrt{\frac{144-1}{144(1 - .75h^2)}}$$

where:

variables as before

Selection intensity is 1 of 144 yielding i = 2.784.