MODELING ELITE POPULATIONS AND POSITIVE ASSORTATIVE MATING IN RECURRENT SELECTION PROGRAMS FOR GENERAL COMBINING ABILITY

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Abstract.-- An algorithm for allele modeling demonstrated the efficacy of adding an elite, highly selected population to the hierarchy of populations currently employed in tree breeding programs. Reselection in a large main-line breeding population (N=498) to establish an elite breeding population (n=48) gave an immediate increase in genetic gains that was not offset by inbreeding depression and declining additive genetic variance until after 10 generations of breeding and selection. Positive assortative mating within the elite population yielded a small additional increment of genetic gain. Positive assortative mating did not significantly increase the proportion of extreme genotypes that might be used in vegetative propagation programs in the presence of selection.

Keywords: elite populations, positive assortative mating, computer simulation, enrichment.

INTRODUCTION

Tree breeders continually seek ways to increase the genetic gains that are realized from current tree breeding programs. If vegetative propagation was practical, specific combining ability (sca) could be capitalized upon to increase genetic gains in addition to the general combining ability (gca) upon which most current programs are based. But methods to vegetatively propagate the southern pines economically are still being sought. Genetic gains could also be increased by employing breeding strategies that would advance sca in breeding populations. However, questions about the levels and persistence of sca effects over time (Byram and Lowe 1986), and the requirement for multiple breeding populations (McKeand et al. 1986), are the major reasons that breeding strategies have not been adopted that would advance both sca and gca.

Positive assortative mating (PAM), coupled with vegetative propagation, has been proposed as a method to increase genetic gains from traditional breeding programs (Foster 1986). In theory, more gain can be achieved with PAM by increasing the component of additive genetic variance available for selection (by generating gametic phase disequilibrium) and by producing good specific crosses at a higher frequency than by present methods, where good specific combinations only occur at random. Assortative mating is the mating of individuals with the same phenotype more often than would occur by chance.

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It is positive when the phenotypic value of both parents deviates from the population mean in the same direction (Gianola 1982). That is, PAM mates the first-ranked parent to the second-ranked, third-ranked to fourth-ranked, etc., until the next-to-last and the last ranked are mated.

In practice, breeders are likely to cull, not mate, the poorest individuals. Thus, PAM would be practiced on a selected subset of the breeding population. In such a scheme, genetic gains would arise not only from PAM, but also from reselection to form a smaller, elite population. Relatedness would be expected to increase more rapidly in smaller, elite populations than in the larger, main-line population from which they were drawn. Thus, inbreeding depression would eventually offset genetic gains and necessitate enriching the smaller population from the larger.

In this study, elite populations were considered as an additional level in the hierarchy of populations currently employed in tree improvement programs. PAM could practically be employed in elite populations to enhance gains from reselection.

Specifically, this study was undertaken to: (1) evaluate the use of elite populations in an hierarchical breeding strategy, (2) evaluate the use of PAM in elite populations, (3) estimate the impact of inbreeding depression within elite populations of two sizes, and (4) evaluate the effectiveness of enrichment from a larger main-line population.

METHODS

The computer simulation used FORTRAN 77 to model one quantitative trait with 50 loci. Every locus had partial dominance gene action with a degree of dominance of one-half, i.e. AA genotype=2.0, Aa genotype=1.5, and as genotype=0.0. Dominance variance was approximately one-seventh of the total genetic variation. There were two alleles per locus of equal frequency at time zero that were permitted to recombine freely, i.e., there was no linkage. Two elite population sizes, n=48 and n=12, were reselected from a large (N=498), main-line population. Heritabilities of 0.1, 0.2, and 0.3 were modeled. Only the results with the highest heritability (0.3) are reported here.

Increases in the inbreeding coefficient result when relatives are mated. In the presence of dominance variance, increased inbreeding results in inbreeding depression in cross-bred species. Phenotypic means of offspring populations were reduced to account for inbreeding depression. Based on the reduction in growth of *Pinus radiata* D. Don (Griffin et al. 1986) and *Pinus elliottii* Engelm. (Gansel 1971) with increasing inbreeding coefficients, a 5% reduction in growth was made for every 0.1 increase in F-value.

All genotypes were generated in the first generation in the main-line breeding population, which was modeled to approximate current tree improvement practices (Figure 1). It was assumed that it would take twice as long to complete a breeding cycle in the large, main-line population as in the small, elite population. Thus, the main-line and elite populations were modeled for

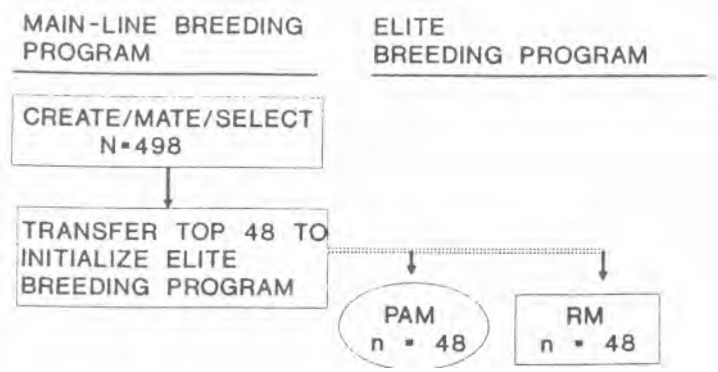

Figure 1. Initiation of genotypes in the hierarchy of breeding populations modeled.

11 and 21 generations, respectively. Results were based on averages of twenty replicate runs for each combination of factors modeled. Realized gains were the differences between the phenotypic means of successive progeny populations. The units of gain were arbitrary, i.e. an individual's phenotypic value was the sum of genotypic values over loci plus a randomly-assigned environmental deviate.

The best genotypes were copied from the main-line population after one breeding cycle was completed to create identical initial populations for two elite populations in generation one. One elite population was mated using positive assortative mating (the PAM population) while the second was randomly mated (the RM population, Figure 1). Thus, differences in cumulative gains, adjusted for inbreeding depression, between the RM and main-line populations were due to reselection and establishing a new level in the breeding population hierarchy, while differences between the PAM and RM elite populations were due to positive assortative mating.

All three population sizes were maintained over generations. Family plus within-family selection was employed with the restrictions that only one individual was selected from a full-sib family; and no half-sib parent was represented more than three times in the selected population. Random or positive assortative mating was done using six-parent disconnected half diallels.

RESULTS AND DISCUSSION

The incremental gain from reselection to establish elite populations is shown in Figure 2A. For the elite populations of size 48, gains for the RM population were 4% to 45% greater than for the main-line population for 12 generations, while the PAM population was 1% to 40% greater for 14 generations (Table 1). The increase in gain from positive assortative mating (PAM versus RM) varied between 0%-6% through 14 generations of mating. The percentage gains declined because the base for their calculation, cumulative adjusted gains in the main-line population, increased over time. The absolute value for incremental gains from reselection were maintained for 10 generations of mating and selection in the elite populations.

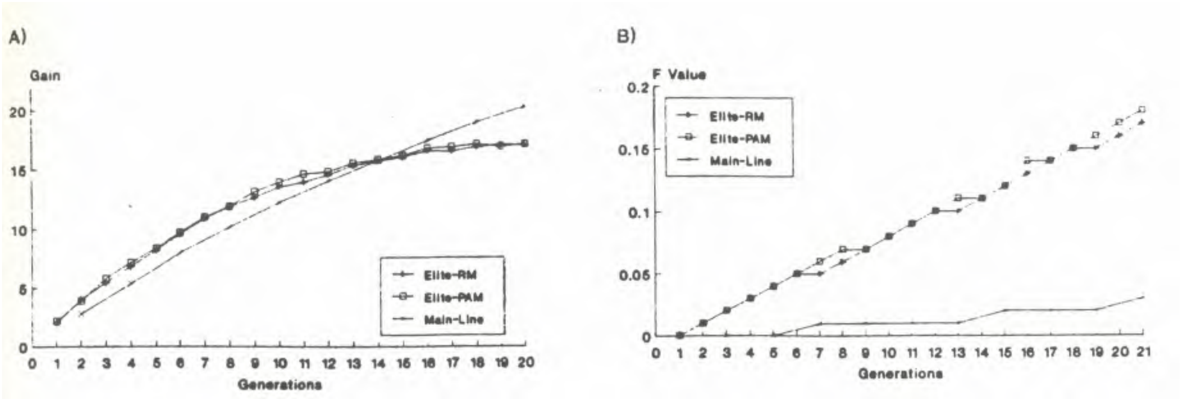

Figure 2. Adjusted cumulative $_{2}$gain (A) and inbreeding coefficient (B) for elite population size 48 and h =0.3.

Table 1. Percentage change in adjusted cumulative gain for elite populations over the main-line population.

Generation	Elite-PAM(%)	Elite-RM(%)
2	40	45
4	34	28
6	21	20
8	17	17
10	14	11
12	6	4
14	1	-.5
16	-4	- 5
18	-10	-11
20	-16	-16

Closed breeding in the elite population led to increased inbreeding. Inbreeding coefficients reached 0.16 to 0.18 by generation 21 for the n=48 populations (Figure 2B). The penalty for inbreeding depression and reductions in the additive genetic variance (Figure 3) began to offset gains in the elite population after generation 10. Additive genetic variance declined as the result of selection.

The small (n=12) breeding population reached an inbreeding coefficient of 0.15 in generation four (Figure 4B), in contrast to generation 19 for n=48 (Figure 2B). Adjusted cumulative gain fell below that for the main-line by the third generation for both PAM and PM populations (Figure 4A). Enrichment would thus have been required at generation two to maintain gains above those possible in the main-line population. Done on this schedule, enrichment would

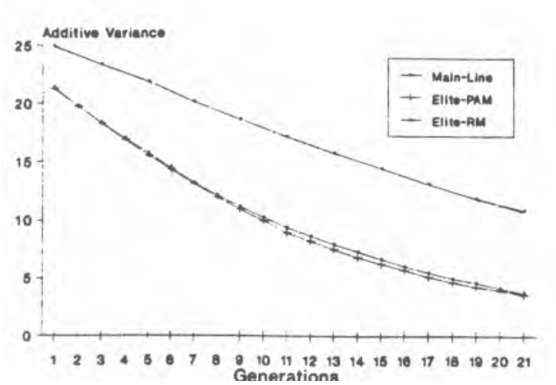

Figure 3. Additive genetc variance for the main-line population and elite populations of size 48, h =0.3.

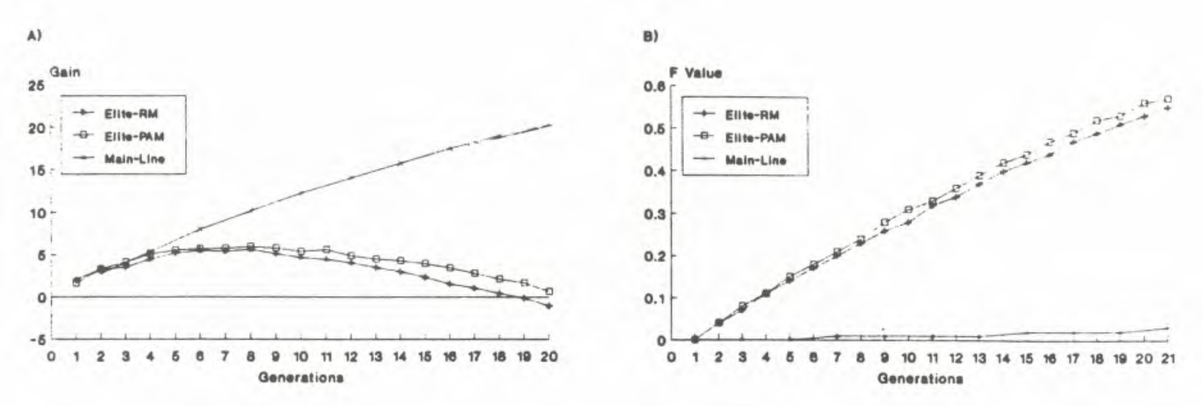

Figure 4. Adjusted cumulative ${}_2$gain (A) and inbreeding coefficient (B) for elite population size 12 and h =0.3.

simply be sampling another small population from the main-line population, and gains would again quickly decline again with closed-population breeding. Thus, periodic enrichment to offset increases in inbreeding and restore additive genetic variance was evaluated only for elite populations of size 48.

The enrichment methodology employed began in generation two. Each time a breeding cycle was completed in the main-line population, the top 24 individuals from the main-line population replaced the poorer half of the selected individuals in the elite populations. This enrichment strategy was chosen because at least 50 phenotypes in the main-line population exceeded the mean of the selected offspring in the elite population. No restrictions were placed on the pedigrees of the transferred phenotypes. It was assumed that the level of coancestry among individuals transferred from the main-line would be small in a large, randomly-mated population.

Enrichment reduced the F-value of the elite populations from their previous levels of 0.16 and 0.18 in generation 21 to 0.03; and additive genetic variance increased moderately in the elite populations with enrichment. However, cumulative genetic gains in the elite populations were not greater than for the elite populations without enrichment. This occurred because selection was imperfect at the low heritability used (0.3), and the replacement genotypes were no better, on average, than the genotypes they replaced in the elite populations.

Even though simulation of this strategy showed that elite populations of size 48 would best be handled as closed breeding populations, enrichment may still be a viable alternative. If replacement genotypes were more accurately estimated, perhaps by progeny testing, and less than 50% of the of the elite population were replaced, gains might be increased or at least maintained in elite populations.

The increase in the numbers of extreme individuals produced with PAM was small. The number of phenotypes greater than two standard deviations above the mean of the elite populations (n=48) varied from two to six per breeding cycle. This agreed with the findings of Breese (1956), who demonstrated that the increase in extreme genotypes was not large when the number of loci controlling a trait was large and heritability was not one. Also, the present model combined selection with PAM. Thus, the poorer phenotypes were discarded and the population variance decreased, resulting in fewer extreme phenotypes.

CONCLUSIONS

Establishing an elite, closed breeding population with 48 individuals selected from a large, main-line breeding population yielded more gain than the large main-line population until generation 14. Positive assortative mating in the elite population added a small, additional increment of gain, and slightly increased the numbers of extremely good individuals.

Inbreeding depression and reduced additive genetic variance in a smaller (n=12) elite population reduced gains from reselection below that for the main-line by generation three. With n=48, gains from reselection did not begin to decline relative to those in the main-line population until generation 10.

The one enrichment strategy modeled demonstrated that it may be necessary to progeny test genotypes before transfer to elite populations, and/or replace fewer than one-half of the selected individuals in the elite population.

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