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Evaluating the Impact of Management Strategies on Genetic Gain and Diversity in Closed Breeding Populations

by

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Abstract

In this report, the use of a second-generation software tool for the simulation and analysis of tree breeding population management strategies on modern personal computers is demonstrated.

The purpose of the program, called POPSIM, is to provide breeders with a generalized decision-support tool to critically examine multi-generation breeding plans. The program runs on any Intel-compatible 386 or better personal computer and a user's guide is available (Mullin and Park, 1995a).

Résumé

Le présent rapport montre qu'il est possible d'utiliser un outil logiciel de seconde génération pour la simulation et l'analyse des stratégies d'amélioration génétique des arbres à l'aide d'ordinateurs personnels modernes.

Le programme POPSIM a pour but de fournir aux généticiens forestiers un outil général d'aide à la décision leur permettant d'examiner d'un oeil critique les plans d'amélioration génétique pour plusieurs générations. Le programme peut être exécuté par n'importe quel ordinateur personnel muni d'un microprocesseur 386 ou plus puissant compatible avec celui d'Intel, et il existe un guide de l'usager (Mullin et Park, 1995a).

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Table 1. Population and selection parameters for simulated breeding strategies

Parameter	Base strategy	Varied settings
Population		
No. of trees in breeding population	400	
No. (size) of sublines	20(2)	1(400), 20(20), 100(4)
Mean value of trait in base population	100	
Standardized rate of inbreeding depression	0	
Additive genetic variance	30	20, 30, 50
Dominance genetic variance	0	
Epistatic genetic variance	0	
Environmental variance	170	180, 170, 150
Narrow-sense heritability	0.15	0.10, 0.15, 0.25
Selection		
Assortment of trees in sublines	non-assorted	non-assorted, positive assortment
Initial assignment to sublines	random	random, uniform
Polycross test family size (offspring per parent)	Nil	Nil, 20 (50)
No. of full-sib crosses in progeny test	600	200, 400, 600, 800
Progeny test family size (offspring per cross)	100	300, 100, 75
Total no. of tested progeny	60 000	
Breeding population selection method	combined index	2-stage, combined index, phenotypic
Max. no. of selections per full-sib family	2	unlimited, 2
Max. no. of progeny per parent	unlimited	unlimited, 3
Other restrictions on relatedness	Nil	
Seed orchard selection method	combined index	
No. of parents selected for orchard	20	20, 100
Max. no. selections per full-sib family	unlimited	
Other restrictions on relatedness	Nil	

cal by descent and describes the proportion of homozygotic loci in excess of that found in an infinitely large, random-mating population. The effective population size reported here is based on the concept of coancestry, which is defined as the probability that genes sampled from parents will be identical by descent and is equivalent to the coefficient of inbreeding that would occur *after* mating. The effective population size can then be defined as the number of individuals that would give rise to the calculated average coefficient of inbreeding in the *next* generation if bred in the manner of an idealized population. Lindgren has suggested calling this parameter "status effective number," refer-

ring to the status of a population at a particular moment (Dr. Dag Lindgren, Swedish University of Agricultural Sciences, Umeå, *pers. comm.*).

Comparison strategies were defined by modifying one management factor at a time, to demonstrate the simple effect of each on gain and diversity (Table 1). As much as possible, the level of effort was kept constant; for example, for scenarios that required polycross testing, the numbers of crosses tested for selection of the next generation was reduced by a corresponding amount. In each case, the simulation was continued through five generations of breeding and the interpre-

Table 2. The effect of population subdivision on genetic gain and diversity (seed orchard has 100 trees)

Population Parameter	Strategy and generation														
	1 subline of 400 trees					20 sublines of 20 trees					100 sublines of 4 trees				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Breeding Population															
Gain %	6.7	11.5	15.1	17.8	19.9	6.4	11.0	14.5	17.5	20.1	5.3	9.2	12.8	16.1	19.3
Additive variance	19.0	12.7	8.9	6.5	5.0	20.3	15.9	13.8	13.2	13.1	25.0	26.9	29.3	31.7	34.7
Average inbreeding	.000	.001	.003	.005	.007	.000	.026	.061	.097	.129	.000	.142	.254	.331	.416
Effective number	159.3	93.3	64.8	49.4	40.2	324.2	200.1	147.6	119.2	100.2	205.1	147.9	197.4	163.5	143.4
Seed Orchard (100 untested selections)															
Gain %	9.4	13.7	16.8	19.2	21.1	8.6	12.7	15.9	18.6	21.0	6.2	10.0	13.4	16.6	19.8
Additive variance	17.7	11.9	8.1	6.1	4.6	19.0	15.1	13.9	13.4	12.6	25.6	26.8	28.6	31.9	35.8
Average inbreeding	.000	.001	.002	.005	.007	.000	.023	.058	.092	.122	.000	.138	.252	.329	.414
Effective number	51.6	40.6	33.8	28.9	25.7	56.6	50.8	44.6	40.3	51.7	100.0	67.9	79.9	73.3	68.4

tation based on the average result for 25 runs. Comparisons are presented for the breeding population itself, as well as the seed orchard that would produce progeny for operational planting.

Results and Discussion

Effect of Population Subdivisions

Breeding populations may be subdivided into "subline" groups, with full-sib mating for generation advancement, *i.e.*, to produce progeny for selection of the next-generation breeding population, restricted to crosses among parents within sublines. As the accumulation of inbreeding is restricted to within sublines, crosses among orchard parents selected from different sublines will always be totally outcrossed.

In the base strategy, the population was subdivided into 20 sublines of 20 trees. This was compared with strategies that employed no subdivision, *i.e.*, one subline of 400 trees, and another with 100 small sublines of four trees (Table 2).

Genetic gain was maximized in the early generations without subdivision, but this superiority was much reduced after five generations. The smaller difference in gain in later generations is likely due to the rapid erosion of genetic variance and decrease in effective number. On the other hand, the strategy with very small four-tree sublines produced a little less gain, but experienced an increase in genetic variance. Although very successful at maintaining diversity, the accumulation of inbreeding within the sublines was very rapid.

Comparing the strategies at the orchard level is complicated by the fact that different numbers of parents must be selected from the different-sized sublines. We have specified a rather large number of orchard parents, 100 trees, to ensure that at least one parent is selected from each subline. Only in the case of the four-tree sublines will all of the orchard progeny be outcrossed, but managing orchard parents with this extreme level of inbreeding might be very difficult. The strategy with 20-tree sublines appeared to be a good

Table 3. The effect of selection method on genetic gain and diversity

Population Effect	Strategy and generation														
	2-stage selection					Cmbd.index selection					Phenotypic selection				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Breeding Population															
Gain %	6.4	10.9	14.5	17.5	20.2	6.4	11.0	14.5	17.5	20.1	5.2	9.4	13.1	16.5	19.5
Additive variance	20.5	16.2	14.1	13.2	13.0	20.3	15.9	13.8	13.2	13.1	25.5	23.3	22.1	21.4	20.9
Average inbreeding	.000	.026	.064	.100	.134	.000	.026	.061	.097	.129	.000	.025	.054	.080	.108
Effective number	318.1	195.4	144.2	115.8	97.4	324.2	200.1	147.6	119.2	100.2	387.4	250.3	185.5	149.3	126.6
Seed orchard (20 untested selections)															
Gain %	9.7	13.4	16.6	19.1	22.0	9.7	13.4	16.4	19.1	21.5	9.6	13.4	16.9	20.0	22.9
Additive variance	20.3	15.7	13.7	13.0	14.5	20.3	17.3	13.6	13.7	13.6	20.3	16.5	19.5	20.3	20.3
Average inbreeding	.000	.018	.058	.092	.126	.000	.020	.055	.088	.119	.000	.025	.053	.079	.104
Effective number	20.0	19.7	18.9	18.3	17.8	20.0	19.6	19.0	18.4	17.9	20.0	19.5	19.0	18.5	18.2

compromise, yielding good gain throughout the five generations and maintaining strong effective size and additive variance, while inbreeding was held to tolerable levels.

Selection Method

Selection in the base strategy was based on combined index selection. An index was constructed that weighted family and individual performance by their respective heritabilities, thus leading to very efficient selection. Phenotypic selection is less complicated, basing selection solely on individual performance, but is expected to be less effective. In two-stage selection, a fixed number of individuals (in this case two) are selected from each of the best families, thereby giving some weight to family performance, but excluding exceptional individuals in poorer families.

In the simulations (Table 3), two-stage selection yielded gain and diversity results that were very little different from those of combined-index selection. Not surprisingly, gain in the breeding population from simple phenotypic selection was less effective in the first few generations, but these differences became smaller after each cycle of breeding. At the same time, phenotypic selection maintained higher effective population size and genetic variance. Most importantly, seed orchard selections from this breeding population had as much or more gain, while retaining higher levels of variance and lower levels of inbreeding.

Assortative Mating

In the base strategy, the pairing of parents in the mating design was done at random. As an alternative, the breeding value of parents can first be evaluated by means of a short-term polycross, followed by "assortative mating," in hope of increasing the likelihood of mating the best parents with each other. If polycross information is available, initial assignment of the trees to sublines can be done "uniformly," so that the best trees are equally distributed. Information from the polycross can also be used to assemble a "tested" seed orchard or to rogue an existing orchard.

Table 4. The effect of assortative mating on genetic gain and diversity

Population Effect	Non-assort. mating random assignment					Positive assortment random assignment					Positive assortment uniform assignment				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Breeding Population															
Gain %	6.4	11.0	14.5	17.5	20.1	5.5	9.9	13.8	17.2	20.3	6.1	10.8	14.9	18.3	21.3
Additive variance	20.3	15.9	13.8	13.2	13.1	21.9	19.2	17.5	16.9	16.7	23.1	19.9	17.8	16.5	15.8
Average inbreeding	.000	.026	.061	.097	.129	.000	.025	.056	.092	.123	.000	.028	.066	.099	.131
Effective number	324.2	200.1	147.6	119.2	100.2	377.1	219.8	157.7	125.1	104.8	331.2	205.0	149.3	119.4	100.8
Seed orchard (20 untested selections)															
Gain %	9.7	13.4	16.4	19.1	21.5	9.6	13.8	17.0	19.8	22.9	11.3	15.2	18.2	21.2	23.9
Additive variance	20.3	17.3	13.8	13.7	13.6	20.9	17.0	18.5	15.3	15.1	21.3	20.7	17.3	15.6	14.1
Average inbreeding	.000	.020	.055	.088	.119	.000	.027	.054	.091	.119	.000	.031	.068	.099	.124
Effective number	20.0	19.6	19.0	18.4	17.9	20.0	19.5	19.0	18.3	17.9	20.0	19.4	18.7	18.2	17.8
Seed orchard (20 polycross-tested selections)															
Gain %						11.9	15.3	18.3	21.5	24.4	13.3	16.8	19.8	22.7	25.3
Additive variance						14.6	14.4	14.0	13.3	14.0	15.0	14.5	15.7	14.5	13.1
Average inbreeding						.000	.037	.070	.110	.136	.000	.048	.087	.115	.147
Effective number						20.0	19.3	18.7	18.0	17.6	20.0	19.1	18.4	17.9	17.5

While this may yield better progeny for advance-generation selection and more efficient selection of seed orchard parents, testing resources must be committed to the polycross test that might otherwise be available for advance-generation progeny tests and the extra testing step will lengthen the breeding cycle.

Positive assortment only yielded small increases in genetic gain, although meaningful improvements were made to orchard gains as a result of the polycross assessment (Table 4). The assortative mating schemes maintained slightly higher levels of additive variance, particularly in the breeding population, but effective population size was essentially the same as the non-assortative scheme. The similarity in outcome among the three scenarios is probably a reflection of the trade-off between increasing gain from polycross-tested parents and the level of testing effort directed at advance-generation selection.

Number of Crosses and Family Size

While the base strategy specified that progeny testing for advance-generation selection would evaluate 60 000 trees, this number could be generated from different numbers of crosses and family size. Producing fewer crosses is attractive and increases the likelihood that the mating design can be completed in a reasonable time, but large family sizes may also prove difficult to achieve with limited numbers of seeds from controlled crossing.

Higher genetic gain was achieved by strategies that tested smaller numbers of trees from a larger number of crosses, but the differences in gains at the orchard .

Table 5. The effect of numbers of crosses and family size (n) on genetic gain and diversity

Population Effect	200 crosses, $n=300$					600 crosses, $n=100$					800 crosses, $n=75$				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Breeding Population															
Gain %	3.0	5.9	8.8	11.5	14.3	6.4	11.0	14.5	17.5	20.1	6.7	11.3	15.0	18.2	21.0
Additive variance	29.3	28.2	28.1	28.5	28.6	20.3	15.9	13.8	13.2	13.1	19.4	15.8	14.2	14.0	13.8
Average inbreeding	.000	.013	.027	.040	.511	.000	.026	.061	.097	.129	.000	.029	.073	.112	.148
Effective number	533.3	394.9	314.3	261.6	224.5	324.2	200.1	147.6	119.2	100.2	295.3	181.3	132.5	106.7	90.5
Seed Orchard (20 untested selections)															
Gain %	9.1	12.0	14.4	17.0	19.6	9.7	13.4	16.4	19.1	21.5	9.5	13.5	16.9	19.5	22.6
Additive variance	20.3	22.6	21.1	20.5	21.1	20.3	17.3	13.6	13.7	13.6	21.3	14.8	13.5	14.4	13.2
Average inbreeding	.000	.085	.015	.029	.044	.000	.020	.055	.088	.119	.000	.026	.069	.107	.143
Effective number	20.0	19.8	19.7	19.4	19.2	20.0	19.6	19.0	18.4	17.9	20.0	19.5	18.7	18.1	17.5

level were modest (Table 5). On the other hand, there were substantial differences among the strategies with respect to maintenance of additive variance and accumulation of inbreeding. The comparison suggests that larger family sizes combined with a smaller number of crosses would be a preferred approach to advance-generation progeny testing.

The Impact of Heritability

While the heritability of the selected trait may be beyond the control of the breeder, it would be wise to test the sensitivity of any breeding plan to differences in heritability. For the base strategy, the heritability was set at 0.15. Comparison strategies were developed that retained the same level of total phenotypic variance, but modified the levels of genetic and environmental variance to produce heritabilities of 0.1 and 0.25.

As one would expect, more genetic gain was achieved at the higher heritability (Table 6). Of greater interest, the rate at which additive variance declined and the accumulation of inbreeding, in both the breeding population and seed orchards, was only slightly greater at higher heritabilities. There was also very little difference in the observed reduction in effective population size.

Restrictions on Relatedness

There are many approaches that can be used to restrict the selection and mating of related individuals, and thereby regulate the accumulation of inbreeding and loss of genetic variance. In the base strategy, we simply applied a selection limit of two individuals from each cross, and pairings within the sublines were done at random. For the first comparison strategy, we relaxed the restrictions completely, allowing any number of selections to be made from each cross. For the second comparison, we restricted the number of progeny that could be contributed by a given parent to three, but applied no other limits to how many were selected from any given cross.

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Table 6. The effect of heritability (h^2) on genetic gain and diversity

	Strategy and generation														
Population	h^2=0.1					h^2=0.15					h^2=0.25				
Parameter	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Breeding Population															
Gain %	4.7	8.2	10.9	13.3	15.5	6.4	11.0	14.5	17.5	20.1	9.5	16.0	21.0	25.1	28.8
Additive variance	14.3	11.7	10.6	10.2	10.0	20.3	15.9	13.8	13.2	13.1	31.7	24.1	20.5	19.5	19.5
Average inbreeding	.000	.025	.058	.095	.126	.000	.026	.061	.097	.129	.000	.028	.066	.101	.135
Effective number	324.6	202.6	149.7	120.7	101.7	324.2	200.1	147.6	119.2	100.2	322.1	196.5	144.7	116.4	98.2
Seed Orchard (20 untested selections)															
Gain %	7.1	10.2	12.6	14.6	16.6	9.7	13.4	16.4	19.1	21.5	14.0	19.3	23.7	27.2	30.9
Additive variance	14.1	12.2	11.1	10.5	9.1	20.3	17.3	13.6	13.7	13.6	30.0	21.5	19.2	20.4	20.6
Average inbreeding	.000	.020	.050	.086	.118	.000	.020	.055	.088	.118	.000	.028	.060	.095	.128
Effective number	20.0	19.6	19.1	18.4	17.9	20.0	19.6	19.0	18.4	17.9	20.0	19.5	18.9	18.3	17.7

Table 7. The effect of restricting relatedness on genetic gain and diversity

	Strategy and generation														
Population	No restrictions					Up to 2 selections per cross					Up to 3 selections per parent				
Parameter	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Breeding Population															
Gain %	8.5	13.8	17.9	21.2	24.2	6.4	11.0	14.5	17.5	20.1	5.0	9.1	12.8	16.2	19.3
Additive variance	19.2	17.3	17.0	17.5	18.6	20.3	15.9	13.8	13.2	13.1	24.9	22.0	20.8	19.8	19.1
Average inbreeding	.000	.117	.229	.315	.393	.000	.026	.061	.097	.129	.000	.008	.033	.058	.083
Effective number	99.9	69.8	53.3	44.5	38.9	324.2	200.1	147.6	119.2	100.2	410.6	270.5	199.9	159.9	133.9
Seed Orchard (20 untested selections)															
Gain %	9.7	14.8	18.3	21.6	24.7	9.7	13.4	16.4	19.1	21.5	9.7	13.1	16.4	19.3	22.4
Additive variance	20.3	20.0	16.6	18.2	18.6	20.3	17.3	13.6	13.7	13.6	20.3	18.0	16.9	17.9	18.2
Average inbreeding	.000	.116	.229	.314	.395	.000	.020	.055	.088	.119	.000	.011	.037	.060	.081
Effective number	20.0	17.9	16.3	15.2	14.3	20.0	19.6	19.0	18.4	17.9	20.0	19.8	19.3	18.9	18.5

Genetic gain at the breeding population level was dramatically higher in the early generations, becoming less pronounced in later cycles (Table 7). The differences in gain were much smaller at the seed orchard level. Nevertheless, when relatedness was unrestricted, the accumulation of inbreeding and the decline in effective population size was very rapid.

Surprisingly, the greatest loss of genetic variance was observed in the base strategy where selections were limited to two per cross. Restricting parental contributions achieved good genetic gain, while maintaining the highest level of genetic variance, lowest accumulation of inbreeding, and largest effective population size.

Summary

Alternative breeding strategies can be simulated with stochastic computer models to evaluate the impact on genetic gain and diversity. This study demonstrated the flexibility and utility of the POPSIM program to evaluate options for managing populations in tree improvement programs.

Even a moderate amount of subdivision in the breeding population was shown to be very effective in maintaining genetic diversity. Aggressive selection methods such as combined index achieved slightly more gain at the orchard level in the first few generations, but this advantage over simple phentotypic selection was soon lost due to rapid erosion of genetic variance and effective population size of the main breeding population. The advantages of assortative mating are somewhat offset by the testing effort that must be redirected to a polycross test. The preferred approach to progeny testing for generation advancement would be to use larger family sizes, rather than testing a greater number of families. Loss of genetic diversity is only slightly greater at higher heritabilities. Restrictions on selection and mating of relatives can have a major impact on the genetic gain and diversity, with limits on parental contributions showing the greatest promise.

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