Parental GCA testing: How many crosses per parent?

G.R. Johnson

Abstract: The impact of increasing the number of crosses per parent (k) on the efficiency of roguing seed orchards (backwards selection, i.e., reselection of parents) was examined by using Monte Carlo simulation. Efficiencies were examined in light of advanced-generation Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) tree improvement programs where information is available from previous generations, seed orchards have reduced genetic variation as a result of selection, and dominance variation is small compared with additive variation. Both the efficiency of reselection and its associated variance leveled off after two or three crosses per parent. The information from previous generations did not significantly increase reselection efficiency.

Résumé : À l'aide de simulations Monte Carlo, l'auteur a étudié les effets d'une augmentation du nombre de croisements par parent (k) sur l'efficacité des éclaircies dans les vergers à graines (sélection à rebours, c.-à-d. sélection répétée des parents). L'étude s'est inscrite dans le cadre des programmes avancés d'amélioration génétique chez le sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) et où l'information est disponible à partir des cycles antérieurs d'amélioration. Ces programmes sont caractérisés par des vergers à graines démontrant une diversité génétique réduite suite à la sélection, et également une prépondérance de la variation génétique additive comparativement à la variation de dominance. Les résultats démontrent que l'efficacité de la sélection à rebours ainsi que sa variance se stabilisent après deux ou trois croisements par parent. L'information découlant des cycles précédents d'amélioration n'a pas augmenté de façon significative l'efficacité de la sélection à rebours.

[Traduit par la Rédaction]

Introduction

Tree breeding programs must supply both trees and information for various purposes; including providing a selection base for the next generation, providing breeding value estimates for the selection base and the parents, and providing estimates of genetic variation parameters (Burdon and Shelbourne 1971). Most second-generation programs have reasonable estimates of genetic variation parameters, such as heritabilities and genetic correlations, and the primary goal is most often to optimize gain in subsequent generations by providing an optimum selection population. The goal of providing parental breeding values for roguing seed orchards is usually secondary and is more important in long-rotation species than in short-rotation species. For long-rotation species, seed orchards are longer lived, and the rogued orchard population represents a larger proportion of the orchard life. For short-rotation species, the next-generation orchard can sometimes provide seed soon after the current-generation orchard is rogued.

Reselection of parents has been addressed in the literature to varying degrees (van Buijtenen 1976; Lindgren 1977; Pepper and Namkoong 1978; Burdon and van Buijtenen 1990). Lindgren (1977) and Burdon and van Buijtenen (1990) demonstrated that in many situations, using parents in as few as one or two crosses yields approximately 70% (one cross) to over 85% (two crosses) of the gain achieved by using each parent in eight crosses. Burdon and van Buijtenen (1990) further examined the impact of types of crossing designs and the

number of crosses per parent and found most mating designs give similar reselection efficiencies, except that small, disconnected factorial sets tend to be less efficient.

The average gain estimates of Burdon and van Buijtenen (1990) are helpful in determining an efficient crossing design for parental GCA testing, but the uncertainties of achieving these gains must also be understood. For example, Magnussen and Yanchuk (1993) demonstrated that optimum selection age could be later than what simple age–age correlation averages would infer when risk (probability of achieving a certain level of gain) was factored into the decision model. Likewise, one needs to understand the probability of achieving a level of gain through roguing when choosing mating designs.

The gains and efficiencies presented in the literature are from a first-generation and 1.5-generation point of view. They used only information from crosses among the parents and assumed that the genetic variation represented in the parents was not truncated. Advanced-generation orchards, however, represent a truncated population and therefore reduced genetic variation. Moreover, additional information from the previous generation is available for use in a selection index. These two factors work in different directions; less genetic variation implies that ranking the parents will be more difficult, yet the additional information used originally to select the parents could increase the ability to rank parents in subsequent generations.

The objectives of this paper were to examine the stochastic variation associated about the mean expected gain from roguing seed orchards when differing numbers of crosses per parent are used and to examine the added usefulness of information from the previous generation. These questions are examined in light of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) breeding within the framework of the Northwest Tree Improvement Cooperative. The Cooperative is in the process of

developing second-generation breeding strategies for the various local forest tree breeding cooperatives in the Pacific Northwest.

Methods

Monte Carlo simulations were used to examine correlations between estimated breeding values and actual genetic values of clones in a second-generation seed orchard and to examine gains from orchard roguing. The procedures generally followed those of King and Johnson (1993) in that family means and individual phenotypes are generated from predetermined variance components. The process used SAS software (SAS Institute Inc. 1990) to generate independent normal distributions for genotypic values and environmental deviations. Phenotypes of individuals and family means were constructed by summing the genotypic values and environmental deviations (phenotype = genotype + environment). The process allows one to estimate breeding values using phenotypes and then correlate the estimated breeding values with the true genotypes.

The base model assumed that 24 clones are selected from a first-generation program for seed orchard establishment. Twelve clones are randomly assigned to each of two sets. Crossing is limited to within a set and the mating design is a balanced partial diallel. Based on the results of the partial-diallel progeny test, the worst 12 clones are rogued from the orchard without respect to breeding group.

The baseline genetic variance components conform to the general pattern of genetic variation found in Douglas-fir breeding programs in the Pacific Northwest for growth and form. The simple genetic model assumed additive (GCA) and dominance (SCA) variation, but no interaction (epistatic) components of genetic variation. They represent narrow-sense heritabilities of 0.25 on a single site and 0.19 across sites. Dominance variance was set to 35% of the additive variance, which is in line with Douglas-fir growth trait estimates of Yanchuk (1996). The variance components for the baseline scenario were set to the following: additive genetic variation (σ_a^2) = 19, additive-by-location variation (σ_{a-by-e}^2) = 6, dominance variation (σ_d^2) = 6.75, dominance-by-location variation (σ_{d-by-e}^2) = 2.25, and environmental variation (σ_e^2) = 66.

The model assumed the use of single-tree plots and the absence of replication-by-family variation (none usually found in cooperative progeny tests). Because both the location and replication effects can be removed from individual estimates and they do not affect family mean rankings, they were ignored in the model.

The simulations first generated a first-generation open-pollinated population that represented 300 open-pollinated families, each having 80 individuals. Family-mean heritability for the first generation was set to 0.70 to represent first-generation trials where field test layout and design were not as refined as present. The best individuals (phenotype adjusted for location and replication) from the best 24 families were used as the second-generation seed orchard parents, and their actual GCA values were used to generate the family means that were later used to estimate their breeding values. The specific steps were as follows.

(1) Generate 300 half-sib family genetic values with a variance of $0.25\sigma_a^2$ and environmental deviations such that the heritability of half-sib family means = 0.70.
(2) Generate 80 individuals per half-sib family with the variation of $0.75\sigma_a^2 + \sigma_d^2 + 0.75\sigma_{a-by-e}^2 + \sigma_{d-by-e}^2 + \sigma_e^2$.
(3) Select the best individual from each of best 24 half-sib families.
(4) Randomly divide the 24 progeny selections (seed orchard parents) into two sets of 12 parents.
(5) Generate a series of crosses (partial diallels) that represents a parent being involved in one to six crosses (k). A parent involved in only one cross represents single-pair mating and results in generating six families for a 12-parent set.

(6) Generate full-sib family means that represent testing at each of five sites.
(7a) Calculate estimated parental breeding values using the best linear prediction (BLP) solution for the full-sib family means that represents one to six crosses per parent. The BLP solution was obtained by solving the equation for the index weights (b) as $b = P^{-1}G$ where P is the variance–covariance matrix of full-sib family means (an $n \times n$ matrix for n full-sib families) and G is the covariance matrix of the full-sib family means with the parental breeding values (an $n \times 12$ matrix, since there are 12 parents per breeding group).
(7b) Calculate estimated parental breeding values using the BLP solution, using the full-sib family means, first-generation half-sib family means, and parental phenotypic values.
(8) Correlate the estimated breeding values from step 7 with the actual genetic values for all 24 parents (without adjusting for differences in breeding group means).
(9) Rogue half the clones from the seed orchard, regardless of breeding group, using the estimated breeding values and examine the increase in gain.

These steps were repeated 200 times and used to generate means and standard deviations of the 200 correlations and gain estimates.

The increase in the seed orchard's genetic value from roguing was examined using the mean genetic values of the rogued and unrogued orchards. Because the first generation started with a genetic value of 0, the formula is

% increase in orchard gain =
   [(rogued orchard mean/unrogued orchard mean) – 1] × 100

The breeding model was developed to simulate operational second-generation breeding strategies for the Northwest Tree Improvement Cooperative's Douglas-fir breeding programs. In these programs, second-generation progeny tests are being designed to investigate genotype-by-environmental interactions as a secondary objective. To examine this interaction, it was decided that at least five progeny test sites will be established in any testing zone. Therefore, the baseline model assumed that the 24 parents would be tested with 2400 progeny over five progeny test locations. Variations of the baseline program were also examined. These included the following: alter the number of progeny to 4800, 1200, and 600; start with 150 full-sib (single-pair cross) families instead of 300 half-sib families (heritability of family means set to 0.75); set the dominance (SCA) genetic variance equal to the additive genetic variance; use three breeding groups of eight parental selections; model a fixed family size (20 progeny per site) and allow the number of progeny to increase; and for the fixed family size model, increase breeding group size to 24 and the number of sets to 4, thus increasing the selection population to 96.

Results and discussion

The added efficiency of making more crosses per parent dropped markedly after only two crosses (Table 1) and is in line with Burdon and van Buijtenen's (1990) gain estimates and the correlations of Lindgren (1977). The trend was the same whether only second-generation data (progeny) were used to estimate of the breeding values or, in addtion to the second-generation information, the first-generation information was also used to estimate breeding values. The percent increase in orchard gain from roguing closely followed the correlation of estimated breeding value with actual genetic value (r). This is expected because the correlation is the square root of the index heritability (h^2) and the formula for gain is

[1] $Gain = ih^2\sigma_p = ih\sigma_a = ir\sigma_a$

where i is the selection intensity, σ_p^2 is the phenotypic variation, and σ_a^2 is the additive genetic variation.

Table 1. Correlations between estimated breeding values and actual genetic values, and percent increase in initial seed orchard gain from roguing half the clones based on estimated breeding values.

Variable	Crosses per parent					
	1	2	3	4	5	6
r using only second-generation data						
Mean	0.655	0.849	0.905	0.917	0.924	0.926
SD	0.1292	0.0674	0.0509	0.0475	0.0456	0.0461
CV	0.179	0.079	0.056	0.052	0.049	0.050
Min.	0.276	0.573	0.716	0.735	0.741	0.727
1%	0.366	0.660	0.739	0.758	0.775	0.780
5%	0.418	0.722	0.809	0.833	0.833	0.831
10%	0.482	0.751	0.839	0.852	0.868	0.868
r using first- and second-generation data*						
Mean	0.666	0.848	0.899	0.925	0.935	0.942
SD	0.1214	0.0649	0.0523	0.0447	0.0425	0.0412
CV	0.182	0.076	0.058	0.048	0.045	0.044
Min.	0.277	0.596	0.634	0.731	0.758	0.780
1%	0.398	0.636	0.746	0.787	0.798	0.817
5%	0.457	0.731	0.798	0.841	0.852	0.858
10%	0.493	0.772	0.833	0.864	0.877	0.887
% increase in orchard gain from orchard roguing using only second-generation data						
Mean	28.2	35.7	37.9	38.3	38.4	38.6
SD	8.69	8.65	8.68	8.50	8.75	8.59
CV	0.31	0.24	0.23	0.22	0.23	0.22
Min.	6.7	8.7	13.3	14.5	8.9	17.2
1%	12.7	19.2	22.2	22.9	22.1	22.4
5%	15.0	22.8	24.3	24.2	25.9	24.8
10%	17.7	25.7	27.3	28.1	27.4	28.3
% increase in orchard gain from orchard roguing using first- and second-generation data						
Mean	28.6	35.4	37.5	38.8	39.0	39.1
SD	9.43	9.04	8.68	8.45	8.60	8.47
CV	0.33	0.26	0.23	0.22	0.22	0.22
Min.	3.9	11.7	8.7	13.8	12.9	12.5
1%	9.6	17.2	21.8	22.9	23.0	23.4
5%	14.3	22.3	24.2	26.1	26.1	26.1
10%	17.5	23.4	26.6	28.5	28.6	28.8

Note: Means, standard deviations, coefficients of variation, minimums, and the 1, 5, and 10 percentile values are reported.

*Second-generation data are the diallel progeny test of the parents; first-generation data are the half-sib family values from the first-generation progeny tests from where the parents were selected and the parental phenotype in those tests.

The standard deviation (and variance) and coefficient of variation calculated from the 200 estimates quickly stabilized after three crosses per parent for the correlation coefficients and after two crosses for the percent increase in orchard gain (Table 1). The trends for the percentiles were similar to the trends for the means.

While the percent increase in orchard gain and correlations generally followed the same trend, there were differences. The coefficients of variation for the gains were considerably larger than those for the correlations. This resulted in the percentiles being a smaller proportion of the means for the gains compared with the correlations (Table 1). For example, the 10 percentile correlations were 74, 88, 92, 93, 94, and 94% of the means for one to six crosses per parent (*k*). For the percent increase in orchard gains the 10 percentile values were 63, 72, 72, 73, 71, and 73% of the means for *k* = 1–6.
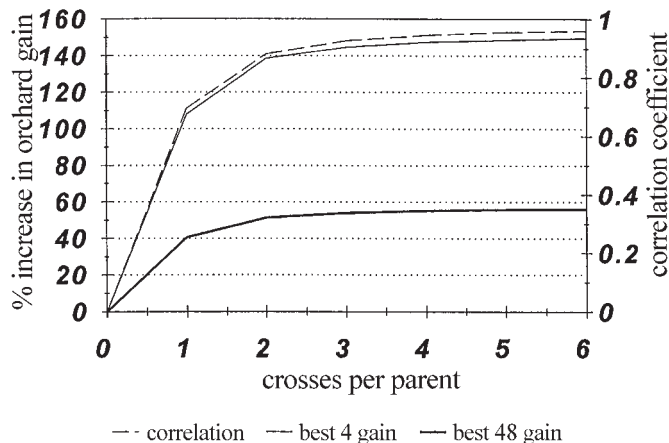
The percent increase in orchard gain averaged 28.2% for one cross per parent and up to 38.6% for six crosses per parent, when half the orchard clones were rogued (Table 1). Thus, if the unrogued orchard had a 10% gain, the rogued orchard would have from 12.8 to 13.9% gain. In this exercise the unrogued orchard averaged a gain of 6.9 units. The average percent increase in orchard gain for two crosses per parent was 35.7%, but fell below 18% in 10% of the simulations and in the worst case was less than 10%. Although gain from four or more crosses averaged 39%, gain was less than 29% in 10% of the simulations and less that 25% in 5% of the simulations (Table 1).

Examination of the stochastic variation associated with the correlations and gain estimates would not change the decision-making procedure to a large degree because the percentile values all stabilized in a manner similar to the means.

Agronomic crops can achieve one or more generations a year, and as a result, realized gain can be examined over multiple

Fig. 1. Percent increase in orchard gain for selecting the best four or 48 parents from an orchard (population) of 96, and correlation between estimated and actual breeding values for differing numbers of crosses per parent.

Fig. 2. Correlation coefficients between predicted parental breeding values and actual genetic values for four levels of testing (number of progeny) and differing numbers of crosses per parent.


generations. Unfortunately, forest tree breeders require considerably more time to complete a generation and the fate of a breeding program can rest on the results of one generation. Thus, it important that we account for the variation in gain estimates because if we fail to meet expectations in a single generation, the fate of the breeding program may be in jeopardy. Managers must be aware of the variation associated with gain estimates and should probably use estimates less than the averages for financial forecasting. The greater variation in percent increase in orchard gain compared with the correlations suggests that theoretical variation estimates may underestimate the actual variation associated with realized gain.

A simpler fixed family size model was used to examine whether these trends held true for higher selection intensities. When the selection base (orchard population) was increased to 96 parents, the percent increase in orchard gain from reselecting the best four or 48 showed the same trends, although gains were higher for the higher selection intensity (Fig. 1). As before, gains from both selection intensities followed the same trend as the correlation between the estimated and actual breeding value (Fig. 1).

The use of the first-generation information to increase selection efficiency was of little value because the correlation coefficient and percent increase in orchard gain increased scarcely at all for all values of k (Table 1).

One reason that the first generation data added little information was because it did not have a strong correlation with the parental breeding values. The correlation between the first-generation index ($0.59 \times$ half-sib family mean + $0.16 \times$ phenotype) and the actual breeding values for the total first-generation population averaged 0.56 and ranged from 0.53 to 0.59. The seed orchard population, however, was a truncated population with less genetic variation (75% of the original), and the correlation between the index and the breeding value for the 24 orchard selections averaged 0.31 and ranged from –0.17 to 0.66. While the truncated genetic variation affected forward selection efficiency in the first generation for the subset of orchard parents, it had little effect on the backwards selection efficiency. This is in line with the observations of Lindgren (1977) and Burdon and van Buijtenen
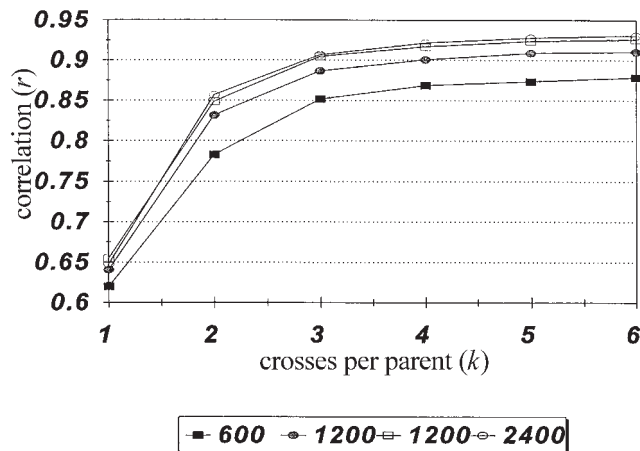
(1990) where they found that moderate changes in heritability had minimal effects on backwards selection efficiency.

Using first-generation information from full-sib families in addition to the second-generation data (progeny) increased the correlations and percent increase in orchard gain slightly for single-pair matings ($k = 1$). The correlation for single-pair mating rose from 0.645 to 0.685 (Table 2), and percent increase in orchard gain increased from 27.9 to 29.7%. The first-generation full-sib information did not increase selection efficiencies when k was greater than 1. The minor increase in the single-pair matings was because indices generated from full-sib families tend to be superior to those generated from half-sib families. More of the genetic variation (and therefore, index score) is associated with the family mean for full-sibs than for half-sibs. Family means are more stable than individual phenotypes, hence the greater stability of the full-sib indices. The correlation between the first-generation full-sib index ($0.64 \times$ full-sib family mean + $0.12 \times$ phenotype) and breeding value for the seed orchard parents increased to 0.42 and ranged from –0.07 to 0.77.

Changing the number of progeny tested had little effect on the rate at which efficiency plateaued, but did affect the level at which it plateaued (Table 2; Fig. 2). Doubling the number of progeny never doubled the efficiency of selection. After 2400 progeny, very little increase in efficieny was noted. It should be noted that three crosses per parent with a given number of progeny was always superior to two crosses per parent with twice the number of progeny.

Reducing the breeding group size to eight parents and using three sets did not reduce the efficiency of reselection (Table 2). At five and six crosses per parent, the correlations between estimated breeding values and actual genetic values increased relative to the baseline scenario. These increases are probably due to being able to accurately estimate most of the full-sib values in a diallel. Sampling does not play a significant role when moderately sized diallels are complete. For each parent in the diallel, both its effect and the effect of the other parents that it is crossed with can be well estimated. For example, in a complete six-parent half diallel with no selfs, the five full-sib families in which a parent is represented represent one-half its breeding value and one-half the average of the other five

Table 2. Correlations of estimated breeding values with actual genetic values for modifications of the baseline model. Standard deviations are in parentheses.

Modification	Crosses per parent					
	1	2	3	4	5	6
Baseline (2400 progeny)	0.655 (0.1292)	0.849 (0.0674)	0.905 (0.0509)	0.917 (0.0475)	0.924 (0.0456)	0.926 (0.0461)
4800 total progeny	0.648 (0.1194)	0.857 (0.0615)	0.907 (0.0499)	0.922 (0.0458)	0.928 (0.0460)	0.931 (0.0471)
1200 total progeny	0.641 (0.1229)	0.832 (0.0691)	0.887 (0.0578)	0.901 (0.0535)	0.909 (0.0509)	0.911 (0.0500)
600 total progeny	0.620 (0.1194)	0.783 (0.0807)	0.852 (0.0581)	0.869 (0.0588)	0.874 (0.0563)	0.879 (0.0549)
$\sigma_d^2 = \sigma_a^2$	0.620 (0.1256)	0.805 (0.0795)	0.870 (0.0578)	0.893 (0.0504)	0.907 (0.0477)	0.914 (0.0479)
Start with 150 full-sib families	0.645 (0.1100)	0.842 (0.0739)	0.896 (0.0543)	0.912 (0.0534)	0.919 (0.0506)	0.924 (0.0512)
Start with 150 full-sib families and use first- and second-generation data	0.685 (0.1021)	0.843 (0.0641)	0.898 (0.0512)	0.923 (0.0448)	0.935 (0.0429)	0.942 (0.0425)
Three eight-parent breeding groups	0.613 (0.1139)	0.845 (0.0609)	0.888 (0.0548)	0.906 (0.0526)	0.974 (0.0109)	0.982 (0.0072)
Fixed family size	0.634 (0.1137)	0.858 (0.0601)	0.908 (0.0542)	0.924 (0.0509)	0.932 (0.0496)	0.937 (0.0486)

Note: Unless otherwise indicated, values are for using second-generation information only.

parents. The average of the other five parents is estimated with reasonable precision by the remaining 10 families. The actual solution is easily obtained using a BLP solution. For moderate-sized diallels the effect of sampling is probably unimportant if dominance variation is not extreme.

Increasing the dominance variation to equal the additive variation decreased the overall efficiency of GCA testing and slightly decreased the rate at which the correlations plateaued (Table 2). Still, the correlation coefficients plateaued after three crosses per parent. The standard deviations of the correlations were higher than the baseline and plateaued later. With only two crosses per parent, there was a noticeable decrease in reselection efficiency compared with the baseline scenario (0.805 versus 0.849, Table 2), but the difference decreased with each successive cross per parent. Three crosses per parent resulted in only a minor decrease in efficiency with the increased dominance variation; therefore, it seems to take a considerable amount of dominance variation to require more than three crosses per parent to effectively estimate the breeding value of parents. Although at first, this may seem incorrect, one must remember that the variance of full-sib family means for a trial with s sites and n replicates of single-tree plots at each site is

$$[2] \quad \sigma_{\text{full-sibs}}^2 = \frac{1}{2}\sigma_a^2 + \frac{1}{4}\sigma_d^2 + \left(\frac{1}{2}\sigma_{a-by-e}^2 + \frac{1}{4}\sigma_{d-by-e}^2\right)/s$$
$$+ \left[\left(\frac{1}{2}\sigma_a^2 + \frac{3}{4}\sigma_d^2 + \frac{1}{2}\sigma_{a-by-e}^2 + \frac{3}{4}\sigma_{d-by-e}^2 + \sigma_e^2\right)/ns\right]$$

The additive variation has almost twice the effect of dominance variation on the variance of full-sib families with large

n. Consider also that for the variance of "half-sib" family means composed of equal amounts of c full-sib families for a single site is

$$[3] \quad \sigma_{\text{half-sibs}}^2 = \left[\left(\frac{1}{2}(1/c)\right) + \left(\frac{1}{4}(c-1)/c\right)\right]\sigma_a^2 + \left(\frac{1}{4}(1/c)\right)\sigma_d^2$$
$$+ (\text{remaining variation}/n)$$

When $\sigma_d^2 = \sigma_a^2$ and three crosses are made per parent, the variance of the half-sib family for a single site is

$$[4] \quad \sigma_{\text{half-sibs}}^2 = \frac{1}{3}\sigma_a^2 + \frac{1}{12}\sigma_d^2 + \left[\left(\frac{2}{3}\sigma_a^2 + \frac{11}{12}\sigma_d^2 + \sigma_e^2\right)/n\right]$$

In this case the additive variance has almost four times more influence than the dominance variance for large n.

These results appear counterintuitive in light of the relatively large number of crosses per parent used in many breeding programs (e.g., six-parent half diallels) and the literature which reports significantly different efficiencies when one changes crossing designs or the number of crosses per parent (e.g., Kempthorne and Curnow 1961; Curnow 1963; Arya and Narain 1990). With regard to existing programs, one must remember that crossing designs are selected for more than the reselection of parents. The studies that show substantial differences in efficiency for crossing designs and number of crosses per parent examined the variances of the breeding value estimates, not necessarily the impact that they have on a testing program per se. Decreasing the variance of an estimate one half does not mean that selection efficiency would increase double. These Monte Carlo simulations, Lindgren's (1977) estimated correlations, and the Burdon and van Buijtenen (1990)

gain estimates all report that one cross per parent gives surprising accurate estimates ($r > 0.6$), even though both parents in a cross receive the same estimated breeding value. If one cross can yield better than 60% of the potential gain from the reselection of parents, it is impossible to even double the efficiency of reselection because $r = 1.0$ is the maximum.

Conclusions

The expected gains from backwards selection increase very little after two or three crosses per parent. The variation associated with gain estimates also plateaus quickly after two or three crosses per parent; therefore, the trends in stocastic variation would not alter decisions on the number of crosses with regard to backwards selection. However, the variation associated with breeding value estimates needs to be considered when projecting gain estimates, especially for single-pair matings which have the largest coefficients of variation. Even in the presence of substantial dominance variation ($\sigma_d^2 = \sigma_a^2$), three crosses per parent appears sufficient to provide reliable breeding value estimates for reselection of parents. Use of information from the previous generation did little to improve breeding value estimates.

Acknowledgements

References

Arya, A.S., and Narain, P. 1990. Asymptotically efficient partial diallel crosses. Theor. Appl. Genet. **79**: 849–852.

Burdon, R.D., and Shelbourne, C.J.A. 1971. Breeding populations for recurrent selection: conflicts and possible solutions. N.Z. J. For. Sci. **1**: 174–193.

Burdon, R.D., and van Buijtenen, J.P. 1990. Expected efficiencies of mating designs for reselection of parents. Can. J. For. Res. **20**: 1664–1671.

Curnow, R.N. 1963. Sampling the diallel cross. Biometrics, **19**: 287–306.

Kempthorne, O., and Curnow, R.N. 1961. The partial diallel crosses. Biometrics, **17**: 229–250.

King, J.N., and Johnson, G.R. 1993. Monte Carlo simulation models of breeding-population advancement. Silvae Genet. **42**: 68–78.

Lindgren, D. 1977. Genetic gain by progeny testing as a function of cost. *In* Third World consultation on Forest Tree Breeding, Canberra, Australia. FAO IUFRO Pap. 6.9. pp. 1223–1235.

Magnussen, S., and Yanchuk, A.D. 1993. Selection age and risk: finding the compromise. Silvae Genet. **42**: 25–40.

Pepper, W.D., and Namkoong, G. 1978. Comparing efficiency of balanced mating designs for progeny testing. Silvae Genet. **27**: 161–169.

SAS Institute Inc. 1990. SAS/STAT user's guide, version 6. 4th ed. SAS Institute Inc., Cary, N.C.

van Buijtenen, J.P. 1976. Mating designs. *In* Proceedings, IUFRO Joint Meeting on Advanced-Generation Breeding, 14–18 June 1976, Bordeaux, France. Institut national de la recherche agronomique, Laboratoire d'amélioration des coniféres, Bordeaux, France. pp. 11–27.

Yanchuk, A.D. 1996. General and specific combining ability for disconnected partial diallels of coastal Douglas-fir. Silvae Genet. **45**: 37–45.