COMMON FAMILIES ACROSS TEST SERIES – HOW MANY DO WE NEED?

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ABSTRACT

In order to compare families that are planted on different sites, many forest tree breeding programs include common families in their different series of trials. Computer simulation was used to examine how many common families were needed in each series of progeny trials in order to reliably compare families across series. Average gain and its associated variation stabilized after the addition of four to six common families.

Key words: progeny testing, common seed lots, connectedness

INTRODUCTION

Many forest tree breeding programs do not proceed in discrete generations. Typically an organization begins field testing families once a sufficient and appropriate number of full-sib families (crosses) have been created. Later, when more crosses have been completed, another series of tests will be established. In this way, gain per unit time is maximized; time is not lost in waiting for every desirable cross to be completed (BORRALHO & DUTKOWSKI 1998).

Members of the Northwest Tree Improvement Cooperative (NWTIC) are in the midst of establishing second-cycle progeny tests of Douglas-fir (*Pseudotsuga menziesii*), and most breeding cooperatives are establishing two series of trials separated by two or three years. Several thousand second-generation full-sib crosses are being tested (NWTIC 2001, JOHNSON 1998). This is different from the first cycle of testing where, typically, open-pollinated seed from selected ortets were planted together in one large progeny test series over multiple sites (all families tested on all sites) (SILEN & WHEAT 1979).

Because second-generation test series will likely be planted on different sites in different years, breeding programs will not be able to simply compare unadjusted family means across series to properly rank families. Breeding programs recognize this limitation and typically do not compare unadjusted family means from different series without some type of adjustment for site variation, because trees in a field series that are planted on faster growing sites will be larger than trees from a series planted on slower growing sites. Unbiased within-series comparisons are possible without site adjustments, but among-series comparisons are biased because site effects are confounded with the genetic effects of a single series. Although progeny test series are planted on multiple sites, the among-site variation typically overwhelms family variation because the among-site variation is an order of magnitude larger than among-family variation in most forest tree breeding programs. For example, the ratio of among-site variation to among-half-sib family variation ($¼\sigma^2_a$) in three first-generation NWTIC Douglas-fir programs was 1:12, 1:15 and 1:38. STONECYPHER *et al.* (1996) examined 65 Douglas-fir half-diallels planted on 2 to 4 sites and found that, on average, the ratio of the GCA variance component ($¼\sigma^2_a$) to the site variance component was 1:29.

One can account for site differences across series by (1) examining family-means adjusted for site/series averages (i.e. as deviations from site/series means), (2) using common check control lots or common families to estimate site effects and then make appropriate adjustments (deviations from common families and/or check lots), or (3) by having common or related families in each series so that a best linear unbiased prediction (BLUP)

Table 1. Common families and check lots used to tie together different field series for a number of breeding programs.

Program	Families	Bulked check lots
Texas Gulf Coop[1]		Double replicated bulked check lot of 10
Loblolly pine		families
NCSU Industry Coop[2]		
Loblolly pine	7 polycross	3 bulked check lots
Florida Coop[3]		
Slash pine	25 polycross	
Loblolly pine	11 OP	
SkogForest, Sweden[4]	2 to 3 full-sib	1 to 6 bulk seed lots
British Columbia MOF		
Hemlock[5]	6 full-sib	
Douglas-fir[6]	6 OP	
Pines[7]	5 OP	5 operational controls
New Zealand[8]		
Radiata pine		3 or 4 common checklots
Eucalyptus	10	
Finland[9]		1 to 8 (mean of 3.5)
CAMCORE[10]		3 bulked provenance collections
Scotland[11]		
Spruce		3 bulked seedlots (2 provenance, 1 seed orchard)

[1] Tom Byram, pers. comm.
[2] Bailian Li, pers. comm.
[3] Dudley Huber pers. comm.
[4] Bengt Andersson, pers. comm.
[5] John King, pers. comm.
[6] Michael Stoehr, pers. comm.
[7] Michael Carlson, pers. comm.
[8] Satish Kumar, pers. comm.
[9] Matti Haapanen, pers. comm.
[10] Gary Hodge, pers. comm.
[11] Steve Lee, pers. comm.

analysis can make appropriate adjustments for the fixed effects of the different sites. None of these methods are perfect, however, because there is some amount of variation associated with the series, check lots, and/or family means used to tie the different series together. Series means have less variation than common control seed lots or common families because of the large number of trees used in calculating the mean, but the genetic value of the series (average of the families) is confounded with the site effect.

Common families and check lots are used in many forest tree breeding programs (Table 1) and can be used to estimate site effects when there are a sufficient number of trees from each of these seed sources planted at each site. Use of common families may be preferable to bulked seed lots because families are less variable than bulked seed lots for a given number of plots (less genetic variation). As the number of common families/seed lots between progeny test series increases, we would expect that the family comparisons across series will be improved. While "more is probably better", there is reason to limit the number of common families because each extra cross in a NWTIC second generation program will cost around US $ 1,000–1,500 in 2003 dollars (JAYAWICKRAMA, unpublished data). BRISSETTE (1984) suggested that a minimum of 2

control seed lots (plots) be used in each replication and that 4 to 6 would be excellent in most cases, but did not provide a statistical basis for his recommendation.

Animal breeders typically use BLUP to adjust for herd differences (analogous to series differences) in their calculations of breeding values. As early as the 1970s and 1980s, animal breeders have utilized artificial insemination (AI) to establish linker sires in order to establish breeding values across herds (eg. FOULLEY & CLERGET-DARPOUX 1978, FOULLEY & SAPA 1982, PARNELL *et al.* 1986). BLUP analyses are then used to derive breeding values that can be used to compare sires from different herds. Studies have examined the number of common AI sires needed to obtain accurate connections and suggest that the AI progeny should be between 1/16 to 1/3 of the population (eg. FOULLEY & CLERGET-DARPOUX 1978, HUDSON *et al.* 1980, HANOCQ *et al.* 1996). Most of the research examined the effect of connectedness on the variance-covariance structure and its resulting effect on measures such as the prediction error variance, loss of precision, and generalized coefficient of determination (see KENNEDY & TRUS 1993 and LALOË *et al.* 1996 for details).

Forest tree breeding programs also utilize BLUP techniques to establish breeding values, and lessons learned in animal breeding can be used to improve our efficiency. A direct transfer of animal breeding recommendations to forest trees should not be made; for two reasons. The environmental component of the herd effect relative to the additive genetic variance is much smaller than the environmental component of sites relative to the additive genetic variance in forest trees; therefore more related families may be needed across series (herds) than that recommended in animal breeding. However, in forestry we replicate families over multiple sites to reduce the overall effect of the site variation. The other difference is that in forestry we have the opportunity to replicate full-sib families (and even clones) in different series of trials; an option not available to animal breeders.

The objective of this study was to answer the question: 'How many common families are needed to bridge two different series of progeny tests in order to achieve a reliable comparison among families in different test series?" Instead of examining estimates of variance as done in most animal breeding studies, this study examined estimates of gain through computer simulation. By using computer simulation we can simulate some of the complexities of breeding programs and better understand the outcomes. In order to simplify the programming, I chose to model the situation where common families are used to directly estimate the site effects, and these are used to adjust family means. If a certain number of common families are sufficient for these simple methods, then they may be sufficient for more efficient methods such as BLUP.

METHODS

The computer simulations examined gains from family selection in a second-cycle breeding program. First-generation data was generated so that second-generation families could be assigned to field series based on their parent's estimated breeding values. The simulations initially generated a first-generation open-pollinated population that represented 900 open-pollinated families. Family-mean heritability for the first generation was set to 0.70. The best 300 parents based on family-means were used as the second-cycle breeding parents. These 300 parents were used to generate a second-generation full-sib breeding population where they were assigned to a series of disconnected 2×2 factorials resulting in 300 full-sib families. Gains from selecting the top 30 families out of the population (best 10 %) were determined by examining the additive genetic values of the 30 families. The families from the 2×2 factorial crossing were grouped into field series three different ways in order to investigate situations when there is minimal genetic differences betweens series (random allocation), a steady progression of gain over time, and the case of comparing an elite-population tested in one field series with a main-population tested in another field series. The baseline scenario assumed that each series would be planted on four test sites and that 20 trees per family would be planted in single-tree plots at each site.

The "random" scenario emulates the situation where there are no expected genetic differences among series. Parents were randomly assigned to the 2×2 disconnected factorials and the resulting 300 full-sib families were randomly allocated to six series, where each series contained 50 different full-sib families and was "planted" on a unique set of four sites. In addition to the 50 families, a different number of common families from the first series were included in every other field planting series (as was done in the following scenarios). The "steady gain" represents the scenario where there could be non-discrete generations and the genetic values of families slowly improve over time as selections from more advanced cycles accumulate in the breeding program. Parents were randomly

assigned to 2×2 factorials, and the resulting families were grouped by mid-parent breeding values, which were obtained from the first-generation breeding values. The bottom ranked 50 families were placed in the first series, the next best 50 families in the second series, and so forth. The elite scenario simulated a breeding program that may have developed an elite population in addition to their main program. The top 48 parents, based on the 1st-generation family means, were randomly assigned to twelve 2×2 factorials and the resulting 48 full-sib families assigned to one field series of plantings. The remaining 252 parents were randomly assigned to factorials and the resulting full-sib families placed in a second field series.

The baseline genetic variance components used in the simulations conformed 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 represented 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) at age 7 and 12. The among-site variance was set to four times the additive variance (16 times the GCA variance). The variance components for the baseline scenario were:

Site variation (σ^2_s) = 76

Additive genetic variation (σ^2_a) = 19

Additive-by-location variation ($\sigma^2_{a\text{-}by\text{-}e}$) = 6

Dominance variation (σ^2_d) = 6.75

Dominance-by-location variation ($\sigma^2_{d\text{-}by\text{-}e}$) = 2.25

Environmental variation (σ^2_e) = 66.

The model assumed the use of single-tree plots and the absence of replication-by-family variation (usually none found in cooperative progeny tests).

Parental GCA values were used to generate the GCA values of each cross such that $GCA_{cross} = (GCA_{male\ parent} + GCA_{female\ parent})/2$. In order to generate a family mean for each cross within a series, variation was generated using the SAS rannor function (SAS 1999) to simulate the variation according to the following equation:

$$\sigma^2_{full\text{-}sibs} = \sigma^2_{site}/s + \tfrac{1}{2}\sigma^2_a + \tfrac{1}{4}\sigma^2_d + (\tfrac{1}{2}\sigma^2_{a\text{-}by\text{-}e} + \tfrac{1}{4}\sigma^2_{d\text{-}by\text{-}e})/s + ((\tfrac{1}{2}\sigma^2_a + \tfrac{3}{4}\sigma^2_d + \tfrac{1}{2}\sigma^2_{a\text{-}by\text{-}e} + \tfrac{3}{4}\sigma^2_{d\text{-}by\text{-}e} + \sigma^2_e)/ns)$$

where:

s is the number of sites = 4,

n is the number of trees per family per site = 20,

$\tfrac{1}{4}\sigma^2_{site}$ was generated with the SAS rannor function such that all families within a series received the same value, but the variation among series was $\tfrac{1}{4}\sigma^2_{site}$. This represents the variation associated with each series being on four different sites,

$\tfrac{1}{2}\sigma^2_a$ was generated as a function of constructing the cross GCA values,

$\tfrac{1}{4}\sigma^2_d$ was generated with the SAS rannor function such that each full-sib cross received a unique value. Full-sib crosses used across series had the same SCA effect.

The remaining variation was generated with the SAS rannor function such that each full-sib cross-series combination received a unique value.

The final full-sib cross mean also included an estimate of the overall population mean (μ). The coefficient of additive genetic variation (σ_a/μ) was set to 0.08; this is an average value the author has found for a number of NWTIC trials. This results in an estimate of μ = 54.5.

Three methods were used to adjust family means (full-sib crosses) across series.

- No adjustment, simply use the family means

  Family value = family mean
- Adjust each family mean for the series mean:

  Family value = (family mean - series mean) / series mean
- Adjust each family mean for the mean of the common families, for differing numbers of common families:

  Family value = (family mean – mean of common families) / mean of common families

The top 30 families out of 300 were selected based upon the different adjustment methods and the mean of their "real" GCA values was calculated. The percentage of the maximum possible gain was calculated by comparing the GCA value of the 30 selected families with the 30 families with the largest actual GCA values.

The specific steps are shown in Figure 1, and were as follows:

1 Generate 900 half-sib family genetic values with a variance of $\tfrac{1}{4}\sigma^2_a$, and environmental deviations such that the heritability of half-sib family means = 0.70.

2 Select the best 300 parents based on family

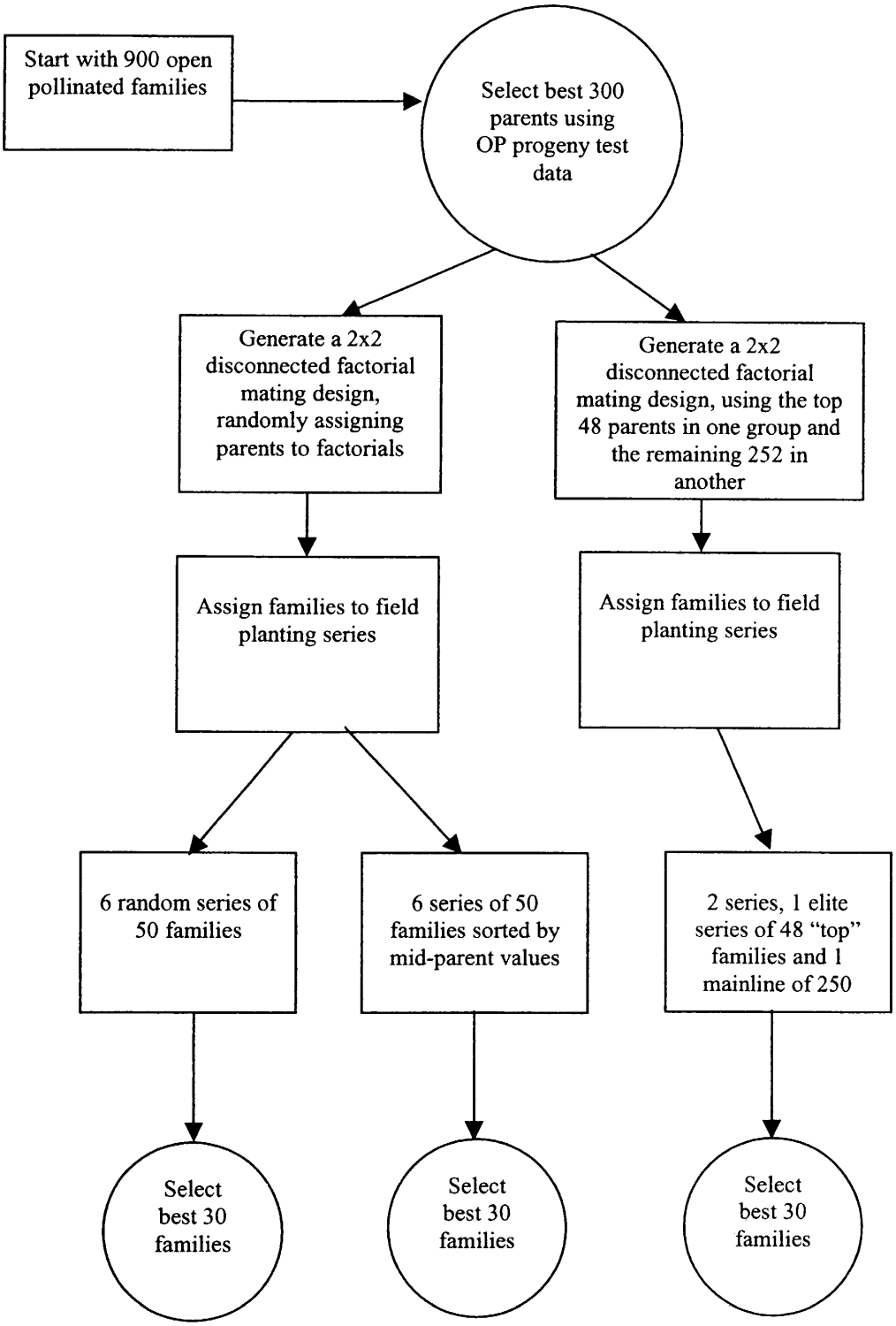

Figure 1. Diagram of breeding and testing steps simulated.

means.

3 Divide the 300 parents into 75 sets of 4 parents.

4 Generate a series of disconnected 2×2 factorials,

5 Sort the crosses based on their parent's 1st-generation family means,

6 Place the crosses into 2 or 6 series,

7 Choose common families from the first series,

8 Generate full-sib family means that represent

testing each cross on four sites in each series,

9 Calculate means of common families in each series,

10 Use adjusted family values to select the top 30 families (best 10 %).

These steps were repeated 300 times for each set of initial conditions. Means and measures of distribution for the gain estimates were calculated.

Sensitivity to changes in heritability and number of sites was also investigated. The scenario that examined 6-series with differing GCA was modified to see if the results changed when examining a trait with a lower or higher heritability, or when fewer sites are planted. The variation in heritability was accomplished by reducing the additive genetic variation (σ_a^2) by one-half to 9.5 (within-site $h^2 = 0.17$) and doubling it to 38 (within-site $h^2 = 0.37$); all other variance components were kept as before for each of these scenarios. This also increased or decreased the relative amount of genotype-by-environment interaction, since this value was not changed. The number of sites for the 6-differing series scenario was reduced to 2 by changing s from 4 to 2 in equation 1.

Some programs that have test series of different ages, or extremely different sizes, standardize their data by dividing by the standard deviation of family means rather than dividing by the series mean and calculating a percentage. For the 6-differing-series scenario, the standardization was altered to:

Family value = (family mean – mean of common families)/(STD family means),

where (STD family means) is the standard deviation of the family

Table 2. Percent of possible gain when using differing numbers of common families for 300 simulations. Reported are means, standard deviations, and coefficients of variation and minimums. Simulations were for three ways of constructing field-testing series (see text).

No. of common families	6 random series of 50, equal GCA				6 series of 50, differing GCA				48 elite/252 main			
	Mean	Std. dev.	CV	Min	Mean	Std. dev.	CV	Min	Mean	Std. dev.	CV	Min
0*	58.4	14.6	25.0	15.6	54.0	24.8	45.9	–16.7	77.0	20.2	26.2	28.1
1	77.4	7.7	9.9	50.6	74.7	12.7	17.0	17.2	83.8	11.6	13.9	34.6
2	80.7	5.5	6.8	65.9	79.8	8.2	10.3	42.5	86.0	9.2	10.7	47.2
3	82.1	5.0	6.1	69.5	81.8	6.4	7.8	55.2	86.6	7.8	9.0	51.1
4	82.8	4.9	6.0	67.5	82.2	6.3	7.6	49.6	87.2	6.8	7.8	54.8
5	82.9	4.9	5.9	65.0	82.5	5.7	6.9	51.5	87.5	6.2	7.0	60.1
6	83.3	4.9	5.9	69.7	82.9	5.7	6.9	52.0	87.7	5.9	6.7	63.9
7	83.2	4.9	5.9	66.6	83.0	5.6	6.7	61.5	88.1	5.4	6.1	64.5
8	83.4	4.9	5.8	71.5	83.3	5.3	6.3	65.3	88.0	5.5	6.3	63.9
9	83.6	4.8	5.7	67.3	83.5	5.1	6.2	69.1	88.1	5.2	5.9	64.5
10	83.6	4.6	5.5	68.2	83.4	5.1	6.1	67.6	88.2	5.1	5.7	64.5
15	84.1	4.5	5.3	71.9	83.8	4.9	5.8	66.4	88.3	4.8	5.5	64.5
20	84.4	4.5	5.4	69.9	83.9	4.9	5.8	65.5	88.5	4.7	5.3	63.9
25	84.6	4.2	5.0	70.1	84.0	4.8	5.7	66.0	88.5	4.6	5.2	63.9
30	84.5	4.3	5.1	69.9	84.1	4.7	5.6	67.6	88.6	4.5	5.1	64.5
Series**	84.3	4.1	4.8	70.6	63.3	7.3	11.6	41.6	56.0	8.2	14.6	32.4

* Family means with no adjustment
** Family means adjusted with series mean

Table 3. Average genetic values for the different field series, calculated over 300 simulations.

	Family allocation method		
	6 random series	6 different series	Elite and main
Series 1	3.99	2.26	3.28
Series 2	3.94	2.91	7.33
Series 3	3.93	3.44	
Series 4	3.97	4.01	
Series 5	3.97	4.75	
Series 6	3.96	6.21	

means for each series calculated over all 4 test sites. The common families were discarded from the calculation of the standard deviation in all series except for the series from which they originated (the first).

RESULTS

As expected, standardizing the data was necessary to compare families across series. Using unadjusted family means resulted in the lowest gains for the scenarios with 6 series of field plantings, and was associated with the largest amount of variation in all scenarios (Table 2). Four of the 300 simulation runs for the 6 series with differing genetic values resulted in negative gain when unadjusted family means were used.

Standardizing with series means was an adequate method of adjusting the data when the series were randomly selected because there were small differences between the genetic values of the series (Table 3). However, when the series means differed, the use of the series means to standardize the data resulted in considerably less gain than using a single common family to standardize. In the cases where elite and mainline populations were planted in different field series, standardizing with series means was the worst option because the superiority of the elite families was ignored. The variation (standard deviation or coefficient of variation) associated with using the series means was similar to using 2 or 3 common families to standardize the data (Table 2) for series of differing values.

Increasing the number of common families used to standardize the data had little effect on the average gain or the associated variation after using 3 or 4 common families (Table 2). Even the use of one common family gave fairly reliable results, the average gain for a single common family yielded, on

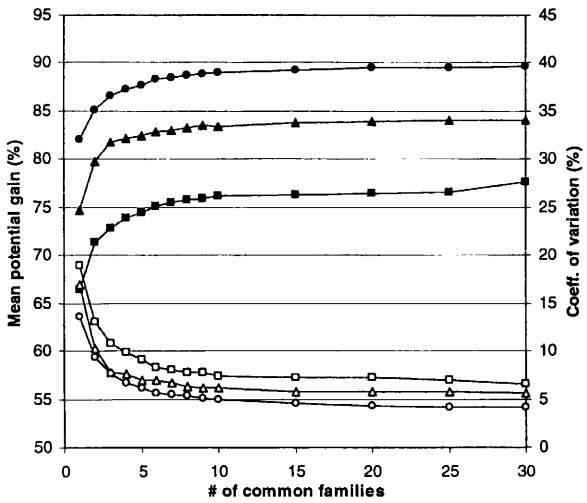

Figure 2. Mean percent of possible gain (filled markers) and coefficients of variation (open markers) when using differing numbers of common families for 300 simulations. Simulations were for within-site heritabilities of 0.17 (squares), 0.25 (triangles) and 0.37 (circles). All scenarios had 300 families divided into 6 different field series of differing genetic values.

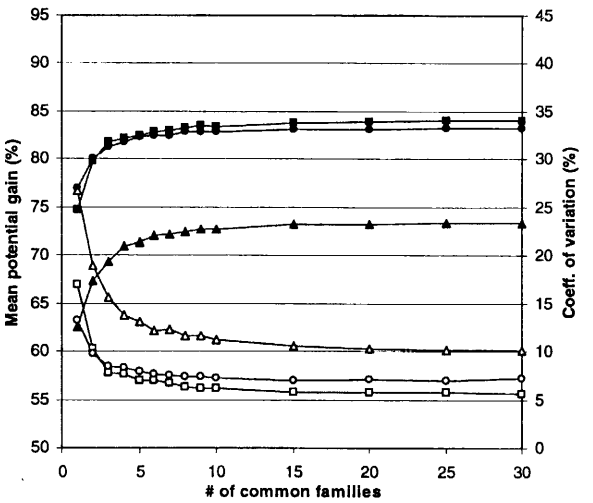

Figure 3. The mean percent of possible gain (filled markers) and coefficient of variation (open markers) when using differing numbers of common families for 300 simulations. Simulations were for having four (squares) or two field planting sites (triangles) per series and where families were standardized with the standard deviation of family means rather than with the series average (circles). All scenarios had 300 families divided into 6 different field series of differing genetic values.

average, over 92% of the same estimates when using 30 common families. However, the coefficient of variation associated with the use of a single family

was significantly greater than the coefficient of variation associated with using 3 to 4 common families (Table 2). Therefore, the impact of using a small number of common families (3 or less) will not be so much on the average expected gain, but on the probability of achieving a minimum level of gain.

As expected, decreasing the heritability of a trait resulted in lower gains and more variability in the achievable gains (Figure 2). The variation associated with the gain estimates did not level off until 5 or 6 common families were used to standardize the data. Gains were reduced, but not by one-half, because the family-mean heritability was still relatively large due to test design (4 sites with 20 trees per family). Increasing the heritability increased gains and decreased the variation associated with the gains (Figure 2). Variation in achievable gain leveled off after 3 common families.

Decreasing the number of test sites to 2 decreased gain and increased the variability, but did not change the overall trends (Figure 3). The decrease in gain and increase in variability was a function of reducing the family-mean heritability.

Changing the standardization procedure from dividing by the series' mean to the series' standard deviation of family means had little effect on the outcome (Figure 3). Gains and measures of variation both stabilized around 4 or 5 common families for both methods of standardizing. This was expected given the constraints of the modeling; both the variation of family means and the coefficient of variation were modeled the same in each series.

DISCUSSION

These simulations suggest that for a typical trait such as growth, three to six common families would be sufficient to ensure that comparisons across test series would consistently give acceptable levels of gain. Heritabilities for growth traits in the more-recent NWTIC trials tend to be close to the 0.25 value used in the baseline scenario modeled here (JOHNSON *et al.* 1997, JOHNSON 2002). Other species have similar heritiabilities for growth traits (CORNELIUS 1994). Heritability of form traits tend to be in the same range as those for growth (CORNELIUS 1994, TEMEL & ADAMS 2000), and wood density typically has higher heritabilites that those for growth (*e.g.*, CORNELIUS 1994). Foliage health traits have been shown to have smaller heritabilities than growth for Douglas-fir (JOHNSON 2002).

Many breeding programs use open-pollinated families, check lots from seed orchards, or field collections in their trials rather than control-pollinated families, as were modeled here (Table 1, see also JAYA-WICKRAMA & CARSON 2000, STONECYPHER *et al.* 1996, WHITE *et al.* 1999). These OP families and check lots theoretically have more variation associated with them than for a single full-sib family. For example the within-family variation associated with a full-sib family at a single site is all the within-plot environmental variation and the genetic variation not associated with the among-family and the among-site components:

Variation within a full-sib family =

$$\sigma^2_w = \tfrac{1}{2}\sigma^2_a + \tfrac{3}{4}\sigma^2_d + \tfrac{1}{2}\sigma^2_{a\text{-}by\text{-}e} + \tfrac{3}{4}\sigma^2_{d\text{-}by\text{-}e} + \sigma^2_e$$

For our simulated data this would be:

$9.5 + 3 + 5.0625 + 1.6875 + 66 = 85.25.$

The variation within a half-sib family would be:

$$\sigma^2_w = \tfrac{3}{4}\sigma^2_a + \sigma^2_d + \tfrac{3}{4}\sigma^2_{a\text{-}by\text{-}e} + \sigma^2_{d\text{-}by\text{-}e} + \sigma^2_e = 93.25$$

The variation within a population of a random sample of unlimited parents would be all the variation except the among-site component:

$$\sigma^2_w = \sigma^2_a + \sigma^2_d + \sigma^2_{a\text{-}by\text{-}e} + \sigma^2_{d\text{-}by\text{-}e} + \sigma^2_e = 100$$

The standard error (square root of (σ^2_w/n)) associated with a mean with 20 individuals would be 2.06 for a full-sib family, 2.16 for a half-sib family, and 2.24 for a population, suggesting that a population mean of a bulked check lot would be only 10 % more variable than a full-sib family mean. To compensate for using the more-variable check lots, one could either increase the total number of common check lots or increase the number of individuals of a check lot. Theoretically the standard error associated with 23 trees of a bulked seed lot (2.04) is as good as the stand error associated with 20 trees of a full-sib family. However, the concern with a check lot of bulked seed is not so much that there is increased theoretical variation in its mean, but whether random samples are chosen each time it is used. Cones are typically collected by tree, and without thorough mixing one cannot be assured of a random sample. It would be inappropriate to use a seed orchard mix if one year's seed came predominantly from one or two families and in the following year a different set of families was heavily sampled.

Check lots used as controls can also serve other objectives, such as providing estimates of realized gain (BRISSETTE 1984). When using check lots for such comparisons, it has been recommended that the number of plots be increased. In summarizing a discussion following BRIDGWATER *et al.* (1983), MCKEAND (1983) noted that the number of control plots should equal the number of plots making up the treatment mean to be evaluated. By doubling the number of individuals of such check lots, the variation of its mean should be in line with that of a full-sib family. As long as a check lot is over represented in each trial and present in all series, it could substitute for one of the common full-sib families used to compare test series.

Families used as checks should also be stable across sites, i.e. exhibit very little genotype-by-environment interaction (BRISSETTE 1984). Many programs do not have information that will allow them to make such choices, and in such cases use of multiple families can reduce the impact of genotype-by-environment interaction. For example, MCKEAND *et al.* (2003) demonstrated that a group of 6 families gave a much more stable prediction of fusiform rust resistance than any single family alone.

It would appear that four common families can provide a stable comparison across series. This number could be increased to 5 or 6 if a breeder was dealing with a low-heritability trait or if there is indication of severe genotype-by-environment interaction. Common families can also be tested with standard check lots, and these results then also be used to compare progeny-tested families against standard check lots indirectly in later tests, without having the standard check lots in the tests.

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