Genetic Gains of Full-Sib Families from Disconnected Diallels in Loblolly Pine

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Abstract

Breeding values for the 2nd-cycle of the loblolly pine (*Pinus taeda* L.) breeding program were analyzed with the NCSU-Industry Tree Improvement Cooperative database to estimate genetic gains and compare different strategies for full-sib deployment. In the disconnected half-diallel mating design used for loblolly pine, six parents within each diallel were crossed to generate 15 full-sib families for general combining ability (GCA) and specific combining ability (SCA) estimates. Parents among disconnected diallels were never crossed, and the SCA and full-sib family breeding values cannot be estimated directly. Using the GCA and SCA estimates from 60 diallels in the Atlantic Coastal region of loblolly pine, genetic gains were estimated in this study for full-sib families within the disconnected diallels and then compared with the potential gains that would be expected if we select parents for full-sib families based on GCA values for all parents within a geographic region. As the dominance variance was found to be much less than the additive variance, the SCA contribution to the full-sib genetic gain was relatively small. Higher full-sib genetic gains were obtained by crossing the best GCA parents from different diallels within a geographic region than selecting only those within diallels. The difference increased with increasing number of selected full-sibs. Results from different selection scenarios, with various selection intensities and relatedness managements, suggest that selection based on GCA from all parents within a geographic region would result in a higher genetic gain for full-sib families in loblolly pine. The deployment of full-sib families are very important for achieving higher genetic gains in a loblolly pine breeding program. But they were not due to the SCA contribution, but rather due to high GCA of best parents in creating these full-sib crosses. The strategies for family and clonal deployment are very attractive based on the data from this study.

Key words: Pinus taeda L., full-sib crosses, volume gain, deployment, general combining ability, special combining ability.

Introduction

The North Carolina State University-Industry Tree Improvement Cooperative (NCSU-ICTIP) has been involved in genetic improvement of loblolly pine (*Pinus taeda* L.) for 48 years in the southeastern United States (LI *et al.,* 1996; MCKEAND *et al.,* 1997). Through the first 2 cycles of the breeding program, substantial genetic gains have been achieved from open-pollinated seed orchards (LI *et al.,* 1999). The first-cycle of the loblolly pine breeding program started in the late 1950's, and seed orchards started to produce genetically improved seeds in 1969 and have provided sufficient seed needs for annual planting since the early 1980's. The second-cycle seed orchards were established with selections from the first-generation progeny

tests in the late 1970's, and started to produce seeds in the late 1980's. Open-pollinated trees from first-generation seed orchards have produced 7–12% more volume per acre at harvest than trees grown from wild seed (TALBERT, 1982), while on average over all regions, second-cycle seed orchards have produced additional 7% to 18% volume gains over the 1st-generation gains (LI *et al.,* 1999). For such a large-scale tree improvement program, even small genetic gains can result in large economic gains (WEIR, 1973).

While the open-pollinated seeds, utilized mainly additive genetic variance, have had substantial impact on forest productivity from the two cycles of breeding, the low efficiency of wind-pollinated seed orchards has limited the genetic gain possible from the loblolly pine breeding program. The low efficiency and loss of potential gains are mainly due to high levels of pollen contaminations in the open-pollinated seed orchards, in addition to low selection intensity in typical seed orchards and inability to utilize the non-additive genetic variance. Thus, the deployment of full-sib families through controlled pollination may have great potential to maximize genetic gains by eliminating pollen contamination, increasing the selection intensity of the production population, and capturing the non-additive genetic variance.

The mating design of the 2nd-cycle loblolly pine breeding by NCSU-ICTIP was disconnected half-diallels with 6 parents and 15 crosses per diallel, *i.e.* each parent is represented by 5 full-sib crosses (Figure 1). This design was chosen to limit the number of crosses per parent, but still yield information on general combining ability (GCA) for all parents in the breeding population. Disconnected diallels were used to maximize the number of unrelated families for selection in the breeding population (TALBERT, 1979). This design has shown the efficiency for breeding and testing because parents can be grouped into diallels based on their reproductive maturity, crosses can be made in a short period of time, and progeny tests can be established quickly and at manageable size (TALBERT, 1979).

While this design has generated useful GCA values for all parents, many parents among disconnected diallels were never crossed. Thus the SCA estimates were only made for full-sibs within each diallel, and no direct SCA estimates for other possible full-sibs among diallels. Although the non-additive genetic component for SCA was often found to be less important than the additive genetic variance for growth traits of loblolly pine (BALOCCHI *et al.,* 1993; MCKEAND and BRIDGWATER, 1986; FOSTER, 1986), dominance variance estimated from disconnected diallels accounted for 20% to 40% of the total genetic variance (LI *et al.,* 1996; XIANG *et al.,* 2003a). Based on the genetic variance component estimates, XIANG *et al.* (2003b) demonstrated that additional and significant genetic gain can be achieved by partially capturing the non-additive genetic component through mass production of the best full-sib families, or all of the non-additive component through either clonal deployment or through vegetative propagation of the best individual trees in the best full-sib family. For example, full-sib selection based on total genetic component had the greatest genetic gain, followed by mid-parent full-sib selection (additive variance) and half-sib family selection; full-sib selection produced 40%

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genetic gain over selection on half-sib families (XIANG *et al.*, 2003b).

Based on the GCA and SCA estimates from the NCSU-ICTIP database, genetic gains could be directly estimated for full-sib families within the disconnected diallels and then compared with the potential gains that would be expected if we select parents for full-sib families based on GCA values for all parents across diallels within a breeding program. Unlike the predicted genetic gain based on the parameters (XIANG *et al.*, 2003b), these estimates are similar to realized gains at age 6 because they were based on breeding values from the BLUP analysis and unimproved check lot adjustment (XIANG and LI, 2001). Thus, SCA can be readily utilized in the production population for capturing genetic gains, with the limitation that SCA estimates were only available within diallels.

This study focused on several key questions. What is the relative advantage for the deployment strategy using only the best full-sib families available within disconnected diallels? How much additional gain, if any, might be achieved if full-sib families could be generated within the whole region based on GCA, with or without SCA adjustments? These are important considerations for maximizing genetic gains when making controlled crosses and full-sib deployment in loblolly pine. This study evaluated strategies for deploying full-sib families for highest gain in the loblolly pine breeding program. We compared genetic gains obtained from tested full-sib families with the potential gain obtainable from full-sib families based on good GCA estimates within the region.

Figure 1. – Illustration of the disconnected diallel mating design used by the Tree Improvement Program. Sixty disconnected diallels were evaluated in this study with 6 parents and 15 full-sib families in each diallel.

Material and Methods

Material

A disconnected half-diallel mating design was used to generate progenies for the 2nd-cycle loblolly pine breeding program (*Figure 1*, LI *et al.*, 1996). Each disconnected half-diallel consisted of 6 parents and a total of 15 full-sib crosses. For testing, two disconnected diallels with 30 full-sib crosses were planted on 4 test sites with 6 blocks and 6-tree row plots in each block. A total of 111 loblolly pine progeny tests with 338 parents in 60 disconnected diallels were evaluated for the Coastal region of loblolly pine in this study. All progeny tests were measured at age 6 for height and diameter at breast height, and then the volume was calculated. The best linear unbiased predictions (BLUP) of GCA, SCA and variance components were estimated using the mixed linear model and analytical method (XIANG and LI, 2001). Briefly, mixed model equations were used to predict GCA for all parents, and SCA for full-sib crosses, for 6-year height and volume, resulting in best linear unbiased predictors

Table 1. – Estimates of variance components (% of total phenotypic variance), heritability, and the type B genetic correlation among test sites for 6-year volume of loblolly pine in the Atlantic Coastal region. The parameters are from the NCSU-ICTIP database and they are based on all 2nd cycle tests within the region.

Parameter	Atlantic Costal Region
Number of tested parents	338
Population average volume, dm^3 per tree	36.2
Phenotypic coefficient of variation for volume (%)	19.0
Variance components in percent of total	
GCA	3.9
SCA	1.4
GCA×Test	0.9
SCA×Test	0.6
Plot error	5.1
Within plot	88.0
Total	100.0
Individual-tree heritability	0.14
Full-sib narrow-sense heritability	0.71
Full-sib broad-sense heritability	0.85
Type B genetic correlation	0.77
Relative importance of SCA (%)	15

(BLUP). Genetic gains were estimated and expressed in percentage gain compared to local commercial unimproved check lots (XIANG *et al.*, 2003b). Since the same check lot was used for all disconnected diallels within a region, a fair comparison can be made among disconnected diallels within the Coastal region. Genetic parameters for the Costal breeding region of loblolly pine are summarized in *Table 1*. The parameters are from the NCSU-ICTIP database and they are based on all 2nd cycle tests within the region (Technical report 2002). The parents used in the 2nd cycle are mainly selected from the 1st generation tests, but a few trees were also selected from plantations (LI *et al.*, 1999).

Genetic gain

The response to selection (ΔG) based on genetic parameters, estimated within the Coastal region, was calculated as:

$$\Delta G = i h_x^2 CV_P \qquad [1]$$

where i is the selection intensity, h_x^2 is the narrow-sense or broad-sense full-sib heritability, respectively, and CV_P is the phenotypic coefficient of variation.

The narrow-sense full-sib family mean heritability was calculated as (XIANG *et al.*, 2003b):

$$h_{FS}^2 = \frac{2\sigma_g^2}{2\sigma_g^2 + \sigma_s^2 + \frac{2\sigma_{gt}^2}{t} + \frac{\sigma_{st}^2}{t} + \frac{\sigma_p^2}{bt} + \frac{\sigma_e^2}{bnt}} \qquad [2]$$

and the broad-sib full-sib mean heritability:

$$H_{FS}^2 = \frac{2\sigma_g^2 + \sigma_s^2}{2\sigma_g^2 + \sigma_s^2 + \frac{2\sigma_{gt}^2}{t} + \frac{\sigma_{st}^2}{t} + \frac{\sigma_p^2}{bt} + \frac{\sigma_e^2}{bnt}} \qquad [3]$$

where σ_g^2 is the GCA variance, σ_s^2 is the SCA variance, σ_{gt}^2 is the GCA by test interaction variance, σ_{st}^2 is the SCA by test interaction variance, σ_p^2 is the plot variance, σ_e^2 is the within plot variance, t is the number of tests, b is the number of blocks per test, and n is the number of trees per plot. In our calculations we assumed 90% survival.

Using the appropriate gain formula for estimated gains, gain was predicted, based on genetic parameters, for: (1) selecting X full-sib families from the approx. 1000 tested in diallels, (2) selecting X crosses based on mid-parent selection (i.e. additive

value) from all possible combinations of 338 parents, or (3) selecting X full-sib families (i.e. total genetic value) using all possible combinations of the 338 parents. The gains are in scenarios (1) and (3) based on the broad-sense full-sib mean heritability, and in (2) on narrow-sense full-sib family mean heritability.

Selection scenarios

Based on the BLUP estimates of GCA and SCA of 6-year volume from the NCSU-ICTIP database, the genetic values of any full-sib crosses (B) were calculated based on GCA estimates only:

$$B_{ij} = GCA_i + GCA_j \qquad [4]$$

or based on both GCA and SCA estimates:

$$B_{ij} = GCA_i + GCA_j + SCA_{ij} \qquad [5]$$

where GCA_i and GCA_j are the general combining abilities for the first and second parent, respectively, and SCA_{ij} is the special combining ability between parent i and j. Crosses between related parents were omitted in the calculations.

The relative importance of SCA was calculated from the variance components as:

$$\text{Relative importance of SCA}\,(\%) = \frac{SCA \text{ variance}}{2(GCA \text{ variance}) + SCA \text{ variance}} \times 100$$

(BAKER, 1978).

Different selection scenarios for deployment were evaluated for comparing genetic gains on various selection intensities, 1 to 25 full-sib families. The following selection scenarios were compared:

1. Selection of tested full-sib families based on total predicted genetic value, *i.e.* GCA and SCA of crosses made within diallels.

2. Selection of full-sibs based on mid-parent values across disconnected diallels within the whole geographic region. Gain calculated from all possible combinations of crosses based on parental GCA only.

3. The same selection scenario as above (2), but restricted to allow the same parent only in 1, 2, 3, 4 or 5 crosses, respectively. Limiting the number of crosses per parent increases the number of required parents; thus reducing the selection intensity.
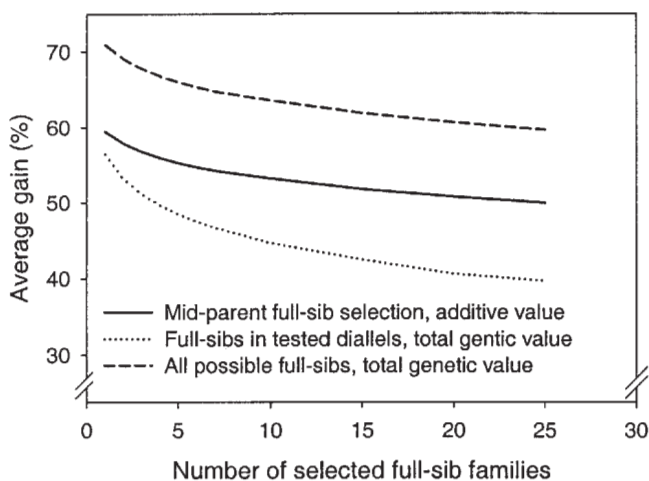
4. Linear deployment where parents ranking 1-5 were allowed in 4 crosses, parents ranking 6-10 in 3 crosses, parents ranking 11-15 in 2 crosses and parents ranking 16-20 only in one cross.

Selection scenario 4 is a simplified version of the linear deployment strategy described by LINDGREN (1974), *i.e.* using parents in proportion linearly related to their breeding value.

Results

Genetic parameters

Selection of the best 10 families based on genetic parameter estimates gave a gain of 53% for selection based on mid-parent value, and a gain of 45% for the 10 best full-sib families of 1000 crosses (*Figure 2*). The potential gain increased to 63%, *i.e.* by 10%, when selecting among all possible full-sib families compared with selection based on mid-parent value only. The gain was compared to the local commercial check lots. The SCA variance was 36% of the GCA variance in the Atlantic Coastal region (*Table 1*). The average heritability for the trials within the region was 0.14, and type B genetic correlation was 0.77.

Full-sibs made vs full-sibs of good GCA parents

Gain in volume growth from selection based on high GCA parents (middle-parent values) among disconnected diallels within the whole region produced significantly higher genetic gains than selection based on tested full-sib families made within diallels (total genetic value) (*Figure 3*). Selection of the 10 best field-tested full-sib families within diallels resulted in a gain of 45%, compared to 54% gain, when the best GCA parents across disconnected diallels within the whole region were mated. All gains were expressed in comparison with local commercial check lots. The mean of the tested population was for volume 4% higher than the local commercial check lot.

The difference in gain was small at high selection intensity but increased as more full-sib families were selected. When selecting 5, 10, or 25 full-sib families, respectively, the difference in gain from selection based on high-ranking GCA parents, compared to full-sib families selected within disconnected diallels, was 8%, 9%, and 11%, respectively (*Figure 3*).

Selection of 25 crosses among all possible crosses in the population based on mid-parent value corresponded to a selection intensity of approximately 0.05%. The gain from *Figure 3* was

Figure 2. – Predicted gains calculated from genetic parameters. Comparison of (1) selection of full-sib families based on total genetic value from full-sib families tested in diallels, (2) selection of full-sib families based on mid-parent value using all possible combinations of the parents, and (3) selection based on all possible full-sib families. Gains in volume (%) are presented in comparison to local commercial seed lots.
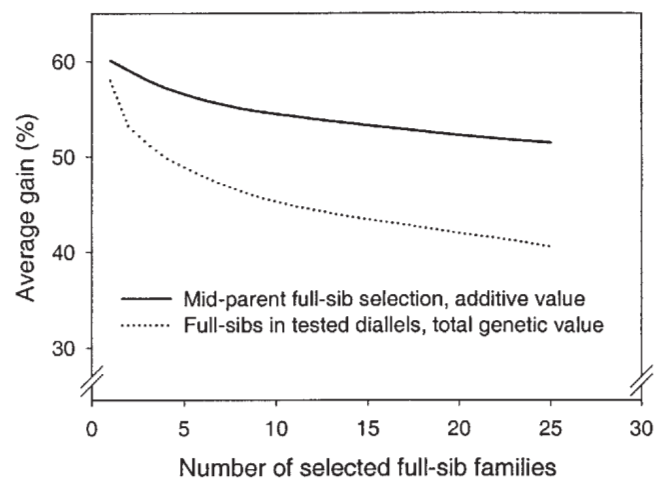

Figure 3. – Comparison of selection of tested full-sib families within diallels based on total genetic value, and selection based on full-sibs of parental GCA across diallels within the Atlantic Coastal region. Gains in volume (%) are presented in comparison to local commercial seed lots.

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51% whereas the corresponding gain based on genetic parameters was 53% (*Figure 2*), compared to the local commercial check lot. The results in *Figure 2* based on genetic parameters were very similar to the values in *Figure 3* based on tests.

SCA contribution

From the ranking of families with tested full-sibs it was obvious that those crosses with high GCA values also often had small positive SCA effects. The total gain, based on ranking for GCA was therefore nearly the same as ranking for total value, *i.e.* GCA+SCA. This was probably due to the low relative importance of the SCA (15%) variance component in this study (*Table 1*). When SCA was included, the gain increase was 1%, and 2%, respectively, compared to the gain calculated only from GCA when 10, or 25, full-sib families were selected, respectively.

Selection scenarios

The potential gains from different selection scenarios for the Atlantic Coastal region, based on selection of good GCA parents (*Table 2*), showed that restricting the number of full-sib crosses per parent to 1, 2, 3, 4, and 5 crosses resulted in decreased gain as the number of full-sib crosses per parent decreased. In other words, the gain with 5, 10 and 25 selected full-sib crosses was 47%, 40%, and 31% when the same parent was restricted to only one full-sib cross, while the corresponding gain increased to 56%, 53%, and 47%, respectively, when the same parent was allowed in 5 full-sib crosses.

Table 2. – Gain in volume (%) for different selection scenarios, restricted selection (one parent involved in 1–5 crosses) and linear deployment, in Atlantic Coastal region of loblolly pine. Gains were estimated for different selection intensities and expressed as the % superiority over to the local commercial seed lot.

No. of selected full-sib families	Selection based on good GCA parents, within whole region					
	Restricted selection					Linear deployment [1]
	1	2	3	4	5	
1	60	60	60	60	60	60
2	55	59	59	59	59	59
3	51	57	58	58	58	58
4	48	54	57	57	57	57
5	47	52	55	56	56	56
10	40	47	50	52	53	53
15	36	43	47	49	51	49
20	34	40	44	47	48	46
25	31	38	42	45	47	44

[1] Linear deployment where parents ranking 1–5 is allowed in 4 crosses, parents ranking 6–10 in 3 crosses, parents ranking 11–15 in 2 crosses and parents ranking 16–20 only in one cross.

The gain from disconnected diallels with 5, 10 and 25 selected full-sib crosses was 49%, 45%, and 40%, respectively (*Figure 3*). Restricting the number of full-sib crosses per parent from two to one reduced the gain more than restricting the number of full-sib crosses per parent from five to four. Compared with the scenario of only using crosses within disconnected diallels, there is still room for restricting the number of crosses per parent and also get a higher gain than selecting only within the disconnected diallals. The gain with linear deployment (*Table 2*) from selecting 5, 10, and 25 full-sib crosses, respectively, resulted in a gain of 56%, 53%, and 44%, respectively. By using the best parents in more full-sib crosses, high genetic gain was achieved, while at the same time the genetic diversity in the production population was higher.

Discussion

The purpose of this study is to evaluate strategies for deploying full-sib families for highest gain in a loblolly pine breeding program. The observed gain from tested full-sib families was compared with the potential gain obtainable from full-sib families based on good GCA estimates within the region. The parameter estimates based on the NCSU-ICTIP database showed that GCA effects were significantly more important than SCA effects in loblolly pine, at least for growth traits. XIANG *et al.* (2003b) found similar results, *i.e.,* that additive genetic variance from the second generation progeny tests was more important than dominance variance, using a subset of data from three geographic regions for loblolly pine. The relative importance of dominance over additive variance changed slightly over time but was always within 20% to 40% of the total genetic variance (XIANG *et al.,* 2003a; XIANG *et al.,* 2003b). In our study, which included all diallels under study within the Coastal region, dominance variance was relatively small compared to additive variance, *i.e.* 36% (*Table 1*). Therefore, selection based on realized gains of full-sib families within disconnected diallels only gave a small increase in gain compared to selection based on parents that had high GCA values within the same diallels. Gain based on GCA from all parents within a geographic region resulted in a higher gain than selection limited to tested full-sib families. One reason for the low increase in gain may be a consequence of a limited number of available full-sib crosses when selection is done only within diallels. The difference in gain increased with increasing number of selected crosses (*Figure 3*). When selecting between 5 and 25 full-sib families the potential gain could increase as much as 8% to 11%.

The SCA could be utilized directly for deployment by using SCA estimates available within diallels. Based on parameter estimates and similar to our results, XIANG *et al.* (2003b) found selection of best full-sib families, thus capturing SCA, to improve the gain by approximately 20% over selection of mid-parent values. However, the selection intensity is lower if we select only within diallels. Thus, the SCA effect cannot compensate for the gain that can be obtained from a higher selection intensity made possible by crosses based on mid-parent value.

Selection based on full-sib crosses on GCA-value only, without any restriction on number of crosses per parent, resulted in the same high-ranking parent being included in many crosses. With 10 crosses one parent was represented in 8 crosses, and with 20 crosses one parent was represented in 13 crosses. On the other hand, restricted selection may be a way to reduce risks to some extent and increase the genetic diversity in the production population. For example, if for some reason one parent should be susceptible to attacks by pests in a plantation, restricted selection may provide a better buffer by including more parents in the production population. The modified linear deployment (LINDGREN, 1974), where the best genetic material is used more intensively, may be a way to keep a high gain by using the best parents more intensively, but also to some extent use more parents and thereby increase the genetic diversity. In our calculations we only used crosses between unrelated parents to reduce the risk that can be associated with inbreeding. In this study the relatedness was very low and very few crosses were excluded because of that, but it is possible that relatedness may be a larger factor in future generations.

Given the moderate levels of SCA and the limited number of crosses that can be tested, maximum gains should be attainable by selecting for parental GCA in a breeding program for loblolly pine. Greater genetic gains should result from large-

scale production of the best general combiners, rather than selection and multiplication of best full-sib families. CARSON (1986) concluded based on a study of *Pinus radiata* in New Zealand that production of improved seed through crossing among the best general combiners is both an efficient and an effective strategy for optimizing gains from control-pollinated seed orchards.

SCA can be captured through mass controlled pollination or vegetative propagation techniques such as rooted cuttings or somatic embryogenesis. Full-sib families may be produced on a large scale, and this may also increase the motivation to look for non-additive effects. XIANG *et al.* (2003b) showed that additional and significant gain can be achieved by keeping all of the non-additive component through vegetative propagation of the best individual trees in the best full-sib families. Sometimes, it may be safer to use a tested full-sib family for deployment than an untested one. This should be considered together with the potential gains that can be obtained by using the best GCA parents. There are different errors associated with the presented gain predictions, but given the large difference among the comparisons, this may not be as important. Also from the empirical data (data not shown), the SCA is often estimated with larger error than GCA. The average of GCA of two parents should be a very conservative estimate of the full-sib performance.

To further exploit SCA in a production population, additional crossing among parents and planting their full-sib progenies in field trials is needed. This would require more resources and much more additional gain to justify the added expense. Results from radiata pine in New Zealand (CARSON, 1986) imply that resources expended on mass testing of crosses will yield marginal, if any, gains over the option of selecting on parental GCA.

In conclusion, results from different selection scenarios, using various selection intensities and relatedness managements in the NSCU tree breeding population, suggest that selection for full-sib families in loblolly pine based on GCA from all parents within a geographic region would result in a higher genetic gain. The relatively small importance of SCA in this population of loblolly pine, compared to GCA, gives little merit to exploitation of SCA. The specific crosses are very important for achieving higher genetic gains in a loblolly pine breeding program. But they were not due to the SCA contribution as expected, and rather the highest GCA of parents are most important in creating the full-sib crosses. So the strate-gies for clonal deployment are still very attractive based on the data from this study.

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