INTER-GENOTYPIC COMPETITION IN FOREST TREES AND ITS IMPACT ON REALIZED GAIN FROM FAMILY SELECTION

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Abstract.--The impact of inter-genotypic competition on realized gains from tree improvement programs remains largely unknown. Empirical results for individual tree traits demonstrate generally non-significant family x plot type (e.g., block, row, and non-contiguous) interactions and moderately strong, positive, family rank correlations between pairs of plot types. Therefore, results to date seem to indicate that average family performance is stable across a range of levels of inter-family competition. Inter-family competition either increased or decreased family variance, hence the estimate of additive genetic variance. Estimated genetic parameters, including genetic gain, for the same population tested in both block plots and row or non-contiguous plots bear little resemblance. Therefore, data from row plot or non-contiguous plot tests should not be used to estimate genetic parameters, including realized genetic gain.

Testable hypotheses are developed which integrate current experimental results to provide a framework for future research regarding the influence of inter-genotypic competition on realized gain from selection.

Keywords: additive genetic variance, growth and yield

INTRODUCTION

Competition is a dominating factor in the development of forest stands. This fact has been known for well over a hundred years and has provided the basis for many of the silvicultural techniques used by foresters. Inter-tree competition acts to shape the individual tree (Harper 1977), to induce mortality (Harper 1977; Drew and Flewelling 1979) and to influence the shape of population distributions (Mohler et al. 1978). As forest geneticists explore the effects of selection and breeding on trait improvement, the confounding effects of inter-genotypic competition become important (Ford 1976; Cannell 1984).

The focus of this paper will be on the importance of inter-genotypic competition to the efficiency of selection of superior families and the subsequent realized gain. Competition in this sense is defined as the stress which is placed on a plant by the phenotype and spatial arrangement of the surrounding plants (Hinson and Hanson 1961). Research results regarding inter-genotypic competition in forest trees up to 1980 were reviewed by Adams (1980).

Competition cart result in changes in the population mean or in phenotypic or genetic variance (Hamblin and Rosielle 1978). In their study with rice (*Oryza sativa* L.) and barley (*Hordeum sativum* L.), Hamblin and Rosielle (1978) found relatively small changes (largest effect was an 11.5% increase) in the means due to competition between varieties; however, the additive and dominance genetic

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variances were strongly affected. The competitive variance was: 1) up to twice the size of the additive genetic variance and of the same or opposite sign and 2) up to half the size of the dominance genetic variance and of opposite sign. Therefore, genetic variance can be either inflated or suppressed by competitive variance. Hamblin and Rosielle concluded that estimates of genetic parameters obtained in mixtures may have little relevance for pure cultures. Sakai (1955), in his work with several agronomic species, demonstrated that competitive pressure increases as the density of the plants becomes larger (e.g., closer spacing). For simplicity, the research results in forestry pertaining to the effects of plant density on genetic parameters will not be reviewed in this paper.

Genetic test design (e.g., pure block plots, row plots or non-contiguous plots) and deployment strategy of improved seed remain in a state of flux for forest trees. In general, organizations are using small plots (e.g., 1 to 5 trees) in either rows or in non-contiguous fashion (Figure 1) for progeny testing; yet improved seed is being deployed in reforestation as both large (50 acres or more) half-sib family blocks and bulk mixtures of families in varying proportions. Forest geneticists are increasingly concerned about the disparity between the testing and selection environment and the deployment environment (e.g., Cannell 1979, 1984; Gladstone et al. 1987). Traditionally, progeny test design and subsequent selection in forestry have emphasized individual tree traits (e.g., means for height, d.b.h., and volume); yet the production unit is volume per unit area. Little emphasis has been placed on rectifying the inconsistency between selection unit and production unit. The current paper will summarize research results to date, draw some conclusions regarding the effects on inter-genotypic competition on realized gain from selection for both individual tree traits and per unit area traits, and formulate testable hypotheses to guide future research.

INDIVIDUAL TREE TRAITS

Estimation of genetic value and genetic variances is a statistical as well as a genetic problem. The statistical issues center around sampling theory to estimate environmental effects precisely and separate these effects and their interactions from genetic effects. Environmental effects can be divided into 3 broad classes: location differences, patchiness or gradients within a location, and microenvironmental effects among trees within small areas. Progeny test design has been optimized to sample each of these levels of environmental variation for the efficient estimation of family means and family ranking (e.g., Lambeth et al. 1983; Cotterill and James 1984).

Impact on family means

Detection of family mean differences appears to be optimized by using 10 to 20 individuals per family at each test location (Cotterill and James 1984) with plot sizes of 1 to 5 trees (e.g., Johnstone and Samuel 1974; Cotterill and James 1984) in which the trees are arranged in a non-contiguous plot fashion (e.g., Lambeth et al. 1983; Cotterill and James 1984). There is a clear tradeoff between plot size and number of families versus replication size. Maximum available replication size subsequently depends upon the patchiness of the environment at each location, which is clearly a limiting factor. Enough locations must be sampled to detect significant macroenvironmental differences as well as potential family x location interactions.

Although the optimum design, as stated above, provides for efficient estimation of family means, no consideration is made of the influence from inter-family competition. The question of level of influence pivots on the issue of whether trees with more similar genotypes (sibs) will compete more, the same, or less than trees with less similar genotypes (unrelated trees) (Mather 1969). A continuum exists in the level of inter-family competition, which ranges from intense (single-tree plot or non-contiguous multi-tree plot) to no inter-family competition (pure family block plot with interior border rows)(Figure 1). The row plot represents an intermediate level of inter-family competition since an individual tree may compete with 1 sibling and individuals from 3 different families (row end position) or with 2 siblings and individuals from 2 different families (mid row position).

Researchers have used 2 basic approaches to establish the influence of various levels of inter-family competition on the determination of family means or ranks. The first approach involves planting the same families in various plot configurations and then comparing the means by analysis of variance or comparing the family ranks between plot configuration treatments by rank correlation. The second approach involves some type of statistical adjustment procedure to equalize the level of inter-family competition. Comparisons are made between: 1) results of an analyses of variance before and after data adjustment or 2) family ranks between adjusted and unadjusted treatments using rank correlation.

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                       Non-contiguous    Row
       Block plot           plot         plot

     *****+++++00000
     *****+++++00000        -o++-        -*+o-
     *****+++++00000        -*+o-        -*+o-
     *****+++++00000        -**o-        -*+o-
     *****+++++00000        -o*+-        -*+o-
                            -+*o-        -*+o-
                            -oo*-        -*+o-
                            -+*+-        -*+o-
                            -*o+-        -*+o-
                            -o+*-        -*+o-
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Figure 1. Layout of 1 replication each of 3 plot types: block, non-contiguous, and row. Each replication contains 3 families (represented by: *, +, and o) with 9 individuals per family. The block plot has a border row of the same family surrounding the 9 measurement trees while the replications of the non-contiguous and row plots contain a single border row (represented by: -) around the outside.

Using different plot configurations

Closely spaced seedling trials and regularly spaced field trials have been used to examine the effects of varying levels of inter-family competition on family means or ranks. Adams et al. (1973) and Tuskan and van Buijtenen (1986) utilized seedlings, less than 1-year-old, of loblolly pine (*Pinus taeda* L.) in competition studies. The studies were similar in approach in designating a subject tree, of a certain family, which was surrounded by either 5 (Tuskan and van Buijtenen 1986) or 6 (Adams et al. 1973) seedlings from the same family (pure combination) or differing numbers of seedlings from another family (binary combination). Adams et al. (1973) tested 4 full-sib families using a diallel arrangement (totaling 12 pure or binary combinations) while Tuskan and van Buijtenen (1986) tested 5 open-pollinated families using a diallel arrangement (totaling 20 pure or binary combinations). In both studies, the families responded differently to competition. The family means depended on the proportion of the surrounding seedlings which were from the competing family (dose level) and the specific binary combinations (e.g., some families interacted while others were neutral in combination). The authors in both studies noted growth performance of family combinations which were overcompensatory (treatment performance exceeds the weighted mean of the 2 pure family performances), complementary (the treatment performance is balanced-what one family loses the other one gains), undercompensatory (treatment performance is significantly less than the weighted mean of the 2 pure family performances), or neutral (families coexist with little effect on each other).

At least four studies have been reported in the literature which compared the field growth of the same families in various plot configurations. Unfortunately, the results have been somewhat conflicting in that the generally positive relationship between family means or ranks is consistent, yet the closeness of the relationship varies.

In their loblolly pine study, Williams et al. (1983) found no significant interaction between family and plot type for height or individual tree volume at 4 years. Their study included pure family block plots and a mixed plot of 4 seedlings, planted in non-contiguous fashion, from each of the families. The trees in the study were only 4 years old and planted at a 9.8 ft (3 m) square spacing; however they had grown rapidly, and the consistency of treatment performance at age 8 (Gladstone et al. 1987) supports the implication of at least moderate competition effects at age 4.

Rockwood (1983) reported on 3 studies with slash pine (*Pinus elliottii* var. *elliottii* Engelm.) which compared the same families in block plots with plots in which the measurement tree was surrounded by 8 trees from the other families (like a non-contiguous plot). Each of the 3 studies contained both plot types at the same location. There was no significant difference in family height or diameter at breast height (d.b.h.) between the plot types after 4 (2 studies) or 5 (1 study) years in the field, which agrees in principle with Williams et al. (1983). As with the study by Williams et al. (1983), these trials were somewhat young to be assessing competition effects; however the trees averaged about 3 ft of annual growth and had probably started to compete for resources.

In his report of a group of 10-20 year old loblolly pine studies, Morrow (1983) compared growth differences for 3 sets of families planted in both block plots and row plots in progeny tests. A single plot type was represented at each of several locations. For 2 sets of families, each of the plot types was represented by 2 locations while the third set of families had 2 locations of the row plot type and only 1 location of the block plot type. Some locations within a set of families varied in age. No significant plot type x family interaction occurred with any of the 3 sets of families for height, d.b.h., or individual tree volume. Spearman rank correlations for family rankings between block and row plot tyres were positive in all cases (Table 1) and were significant for each family set and trait for which family differences were significant in the analysis of variance. The analyses of variance for family differences for height and d.b.h. for the third family set were non-significant; similarly, the associated rank correlations were non-significant. Therefore, the results of the analysis of variance in this study compare favorably with those of Williams et al. (1983) and Rockwood (1983); however, the rank correlations reveal that some rank change, although not statistically significant, was occurring.

Table 1. Spearman rank correlations between family mean rankings for: 1) block plots and row plots (Morrow 1983), and 2) block plots, row plots, and non-contiguous plots (Hart 1986) for height, d.b.h., and individual tree volume for loblolly pine progeny tests.

	Rank correlations		
Plot comparison	Height	D.b.h.	Volume
1. Morrow 1983			
analysis 2 - block vs. row	0.83**	0.72**	0.87**
analysis 3 - block vs. row	0.63*	0.65*	0.66*
analysis 4 - block vs. row	0.12NS	0.24NS	0.74*
2. Hart 1986			
Block versus row	0.55NS	0.02NS	0.07NS
Block versus non-contiguous	0.62NS	0.36NS	0.31NS
Row versus non-contiguous	0.76*	0.52NS	0.52NS

NS not significant at p=0.05; * significant at p=0.05; significant at p=0.01

Hart (1986) analyzed differences in family mean performance for an 11-year-old loblolly pine trial which included the same 8 fanilies in 3 plot types: block, row, and non-contiguous. Family rank correlations between pairs of plot types were used to examine family differences resulting from an interaction with level of inter-family competition. All family rank correlations between pairs of plot types were positive .lthough only the rank correlation for height between the row plot and the non-contiguous plot was statistically significant (Table 1). For height, d.b.h., and individual tree volume, the rank correlations between the row plot and the non-contiguous plot types were consistently the largest (range of 0.523 to 0.761); and the correlations between the block plot and the row plot types were consistently the lowest (range of 0.023 to 0.547). Among the 3 traits, height produced the highest correlations. One family was reutral, and 2 families exhibited positive yield responses to increased levels of inter-family competition. The rank correlations given by Hart (1986) were generally lower and less statistically significant than Morrow's (1983). One contributing factor was that Hart's trial only included 8 families which was lower than any of Morrow's trials.

Using adjustment procedures

A variety of data adjustment procedures have been used in an attempt to equalize the effects of inter-family competition on family mean growth and family ranking. Five studies are reviewed in this paper: 1 used the average of the surrounding plots, 1 used differences in subject tree and competitor heights, while 3 used some measure of available growing space for data adjustment.

In their radiata pine (Pinus radiata D.Don) study, Correll and Anderson (1983) used the mean of the 2 adjacent row plots to adjust each family row plot for local environmental effects within the progeny test. Although the adjustment resulted in improvement of the analysis of variance results, there was little change in the ranking of the families.

Angle of height difference between a subject tree and its neighbors formed the basis for a competition adjustment model used by Magnussen (1989) on a closely-spaced, single-tree plot trial of jack pine (Pinus banksiana Lamb.) for ages 1-5. Height, through age 5, displayed little effect from inter-family competition; however family-mean basal area and volume were strongly influenced and required significant adjustment. Comparing unadjusted and adjusted data, the difference between the fastest and slowest growing families declined by 1/3 for basal area and 1/2 for volume. Despite the reduction in the ranges of family means for basal area and volume, the family-mean rank correlations between adjusted and unadjusted values were 0.998, 0.792, and 0.818 at age 5 for height, basal area, and volume, respectively. These results concur with those of Correll and Anderson (1983) in showing only slight changes in family rank following data adjustment.

The concept of effective growing space utilized by each tree was used by Pinker (1982) to adjust individual tree volume for differential competition in an 11-year-old eastern white pine (Pinus strobus L.) and a 14-year-old Virginia pine (Pinus virginiana Mill.) progeny tests. Both tests utilized row plots. The area of effective growing space assumes the shape of a polygon and was estimated in this study as a function of the volume of the subject tree and the volume of each competitor tree and distances between the subject tree and each competitor. Spearman rank correlations between adjusted and unadjusted family means were highly significant and reached 0.759 and 0.631 for white pine and Virginia pine, respectively. Therefore, this adjustment procedure had little effect on the ranking of the families within each species, agreeing in results with Correll and Anderson (1983) and Magnussen (1989).

In their loblolly pine study, Nance et al. (1983) employed the same concept as Pinker (1982), with a slightly different formula, to calculate the area potentially available (APA) to each subject tree. Diameter at breast height and the distance apart of the subject tree and its competitors were used to calculate the APA as an irregularly shaped polygon. Furthermore, the polygon was subdivided into components due to competitors, from either the same family as the subject tree or different families. The data set employed in the analysis arose from a Nelder's design study with row plots of 8 families. Height, d.b.h., and live crown length were measured at ages 7 and 8 years. Multiple regression models were developed which included basal area growth (BAG) in the seventh year as the dependent variable and a variety of components (e.g., tree measurements and APA) as the independent variables. APA was the single best predictor of BAG. In addition, the average APA of the family of the subject tree (APA_1) added significantly to basal area of the subject tree, height of the subject tree, crown length as a ratio of total height of the subject tree, and APA of the subject tree as predictors of BAG. Neither the general relative influence (at the family level) of the competitors or the specific relative influence between the competitors and subject tree added significantly to the model predicting BAG.

These results indicated that families differed in their use of available growing space for basal area growth; yet after considering APA, the family effect of the competitor was unimportant. Two of the 8 families expressed significantly different APA_i : 1 family was more and 1 family was less efficient than average in using the available growing space.

In further analysis, Hart (1986) used the procedures developed by Nance et al. (1983) to examine his loblolly data from the 3 plot type study discussed previously in this paper. He calculated the APA for each tree using age 9 data. Judging by average APA, the block plots exhibited the highest amount of inter-tree competition (79.6 ft^2) with row plots being intermediate (80.7 ft^2) and non-contiguous plots displaying the least (81.1 ft^2). Although there was little actual difference in average APA among the plot types, the range of average family APA within the non-contiguous plot type was about 3 times that for the block plot type. Therefore, the more intense inter-family competition inherent in the non-contiguous plot type resulted in much more variable APA among families. Families differed significantly in their basal area growth (age 9 to 11)(BAG) per unit of APA in the non-contiguous plot type but not in either the block plot or row plot types. However, both row plot and non-contiguous plot types displayed significant volume growth differences per unit APA among families while no family differences were apparent in the block plot type. Therefore, even though the APA was slightly less for the block plot type, the level of competition among the families was more uniform for the block plot type; and competition-induced family differences in volume or basal area growth per unit APA were not apparent in the block plot type. There was not a strong relationship between either volume growth per unit APA or BAG per unit APA and volume production as a percentage of anticipated production; so the most efficient users of APA were not always the highest volume producers.

Summary

Family means or ranking for individual tree traits, especially for height, appeared to be more or less unaffected by varying levels of inter-family competition. Although the relationships between family means or ranks between different plot types or unadjusted versus adjusted data were not perfect, they were correlated strongly enough to indicate little negative impact on realized gains from family selection (e.g., breeding value was estimated with reasonable precision). This result was due, at least in part, to a large number of data points contributing to the mean. Randomization procedures assured that the individuals within a family sampled the entire range of competitive interactions. As the number of replications increases, the assumption is more closely met that the effects of interactions among families is at random, hence unbiased estimates of family means are obtained.

The significance of family differences varied by plot type; however, this finding may be due to changes in real differences among treatment means or the size of the error variance. Therefore, the family means may vary slightly among plot types; yet changes in the error variance, by plot type, may alter the significance levels. The effects of changes in inter-family competition on variances are discussed in the next section.

Impact on family and block x family variances

One possible objective of progeny testing is the estimation of genetic and environmental variances. Much research has been devoted to constructing designs which provide accurate estimates of these variances (e.g., Namkoong 1979).

Researchers have recognized for some time that inter-genotypic competition may, and probably does, bias estimates of genetic variances (e.g., Sakai 1955; Sakai and Mukaide 1967). Theoretically, the variance among half-sib families (σ_{HS}^2) estimates 1/4 of the additive genetic variance; while the variance among full-sib families estimates 1/2 of the additive genetic variance, 1/4 of the dominance genetic variance, and differing amounts of epistatic components of genetic variance (Becker 1984). These models of gene action do not acknowledge the presence of changes in family variance due to competition and would apply only to family block plots. With other plot types which encourage the interaction among families, a variance term (σ_{comp}^2) must be included in the model to account for either added or subtracted variance due to inter-family competition.

Using different plot configurations

Three published studies have documented the effect of different plot configurations on family and block x family variances. When the same families are included in 2 or more plot types within the same replication, an estimate of σ_{comp}^2 can be obtained by calculating the difference between the estimates of family variance (e.g., from block plot to row plot type).

Williams et al. (1983) found that the family variance for height was only 52% as large ($\sigma_{HS}^2 = 0.0115$; non-significant at $p=0.05$) for the block plot type as compared to the non-contiguous plot type ($\sigma_{HS}^2 = 0.0223$; significant at $p=0.01$). The added variance due to increased inter-family competition (σ_{comp}^2 ; Table 2) would result in inflated estimates of additive genetic variance. The inflation was 94% for height and 147% for volume. They analyzed plot mean data; therefore, the block x family variance served as the error variance and included 1/n of the sampling variance (within plot variance). The block x family variance for height was twice as large for the block plot type (0.04) as for the non-contiguous plot type (0.02). Hence increasing inter-family competition appeared to increase the family (e.g., genetic variance) variance while decreasing the block x family variance. Family-mean heritability for height increased from 0.43 to 0.76 from the block plot to the non-contiguous plot, respectively, while for individual-tree volume, it increased from 0.34 to 0.70 from the block plot to the non-contiguous plot, respectively.

In their study, Lambeth et al. (1983) provided family and block x family variance components for both the row and non-contiguous plot types. Generally, the row plot type provided family variance components that were 13% higher than the non-contiguous plot type. In 4 of the 8 trials, the family variance was larger for the row plot type; while in 3 of the 8 trials, the non-contiguous plot type resulted in a larger family variance. Competitional variance (σ_{comp}^2), as a ratio of family variance for the row plot type, averaged a reduction of -0.05 (Table 2); however, the effects among the individual tests ranged from 1.08 to -0.75. Hence the estimates of genetic variance could be affected tremendously by inter-family competition. The non-contiguous plot type resulted in block x family variance estimates which were essentially 0.0 while the row plot type estimates were even larger than the family variance components. In this study, the block x family variance did not include the sampling variance (within plot variance); that is, individual tree data were analyzed. Therefore, the family variance decreased slightly with increasing inter-family competition (as opposed to the findings of Williams et al. 1983); yet the block x family variance decreased markedly, as Williams et al. (1983) found.

Table 2. Inter-family competition variance (σ^2_{comp})[a] estimated from loblolly pine studies which included the same half-sib families in various plot types.

Study	Block to row		Block to non-contig.		Row to non-contig.	
	σ^2_{comp}	$\sigma^2_{comp}/\sigma^2_{HS}$	σ^2_{comp}	$\sigma^2_{comp}/\sigma^2_{HS}$	σ^2_{comp}	$\sigma^2_{comp}/\sigma^2_{HS}$
1. Williams et al. (1983)						
height			0.0108	0.94		
volume			2.46	1.47		
2. Lambeth et al. (1983)						
height						
Test-set						
1-1					-0.010	-0.22
2-1					-0.005	-0.07
3-1					0.011	0.14
4-1					0.013	1.08
5-1					-0.036	-0.75
6-1					0.003	0.25
7-1					-0.010	-0.59
8-1					-0.003	-0.20
average					-0.004	-0.05
3. Hart (1986)						
height	0.1412	---	0.2369	---	0.0957	---
d.b.h.	0.0039	1.26	0.0207	6.68	0.0168	5.42
volume	29.57	0.59	200.01	3.97	170.44	3.38

[a] Assumes that the family variance component derived from pure family block plot types expresses genetic variance that is free from inter-family competition variance; all other plot types confound family variance with inter-family competitional variance.

Hart's (1986) study provided an excellent comparison of variance component estimates among 3 plot types: block, row, and non-contiguous. The pattern was virtually the same for height, d.b.h., and individual tree volume. Family variance increased from block plot to non-contiguous plot with row plot being intermediate (Table 3). Family differences were not significant for the block plot type for any of the 3 traits or for the row plot type for either d.b.h. or volume while they were significant for the non-contiguous plot type for all 3 traits (Table 3). Competitional variance (σ^2_{comp}) always increased the estimate of genetic variance (Table 2). The inflation ranged from 59% to 668%. The block x family variance included sampling variance (within plot variance) in this study A pattern of decreasing variance from the block plot to the row plot and finally to the non-contiguous plot was expressed for the block x family variance (Table 3). Therefore, the pattern was clear in this study that family variance increased and block x family variance decreased with increasing inter-family competition. Family-mean heritabilities increased dramatically from the block plot to row plot to non-contiguous plot type, more than doubling from the block plot to the non-contiguous plot type (Table 3). This pattern of change for both variances and heritabilities mimics the results of Williams et al. (1983).

Table 3. Family and block x family variance components and family-mean heritability' for height, d.b.h., and volume derived from a loblolly pine progeny test which included block plot, row plot, and non-contiguous plot types (adapted from Hart 1986).

	Family variance			Block x family variance		
Trait	block	row	non-contig.	block	row	non-contig
Height	<0NS	0.1412*	0.2369**	1.9253	0.4968	0.4294
D.b.h.	0.0031NS	0.0070NS	0.0238**	0.0592	0.0498	0.0378
Volume	50.42NS	79.99NS	250.43**	722.21	551.58	483.30

	Family-mean heritability		
	block	row	non-contig.
Height	0.00	0.63	0.77
D.b.h.	0.24	0.46	0.79
Volume	0.29	0.47	0.76

NS not significant at p=0.05; significant at p=0.05; ** significant at p=0.01

[a] $$h_F{}^2 = \frac{\text{family variance}}{\text{family var.} \quad \frac{\text{(block x family var.)}}{\text{\# blocks}}}$$

Using adjustment procedures

The influence of inter-family competition on family variance has been examined by means of data adjustment procedures. Two authors, using either height difference adjustment or effective growing space adjustment, demonstrated clear differences in family variance (i.e., additive genetic variance estimates) between unadjusted and adjusted data.

In his jack pine study, Magnussen (1989) showed a small, non-significant difference in family variance ($\sigma_{HS}{}^2$) for height for ages 1-4 and a slightly larger, yet non-significant, difference at age 5. However, for basal area at ages 4 and 5, the family variance for unadjusted data was about 200% of the size of the adjusted data value. At age 5, family variance for unadjusted volume was 700% the size of the family variance for the adjusted data. Therefore, family variance and subsequent estimates of additive genetic variance may be inflated only slightly for unadjusted height in single tree plot experiments; however, inter-family competition, as evidenced by adjustment procedures, strongly inflates family variance for basal area or volume in such studies.

Pinker (1982) utilized an adjustment procedure to investigate the amount of bias, from inter-family competition, on family variance (σ_{HS}^2). He found that the family variance for adjusted individual-tree volume was only 22% and 9% the size of family variance for unadjusted volume for Virginia pine and white pine, respectively. The block x family variance was estimated as a separate parameter from the sampling variance or within-plot variance (i.e., individual tree data were analyzed). While family variance decreased from unadjusted to adjusted data (as with Magnussen 1989), the block x family variance increased from unadjusted to adjusted data. Therefore, the pattern of change, from removing the effects of inter-family competition by data adjustment, mimics the pattern that results from comparing the same families in row plots or non-contiguous plots with block plots (Table 3).

Summary

Among-family variances seem to be strongly impacted by varying levels of inter-family competition. This finding with forest trees parallels the findings of Hamblin and Rosielle (1978) who noted large changes (both positively and negatively) in genetic variances due to inter-genotypic competition in rice and barley. Genetic parameters (e.g.. additive, dominance, and epistatic effects. heritability, and genetic gain), which are determined from variance component estimates, are subsequently biased. Additionally, variance due to competitional effects (σ_{comp}^2) is trial specific (e.g., specific families and environmental effects) and therefore cannot be wholly transferred to operational plantations as part of genetic gain (although a remnant of inter-family competitional variance will remain). This is especially true since row plot trials are often used to project genetic gain in operational plantations with either large pure family blocks or seed orchard mixtures of families, including families not combined in the original progeny tests and families in different proportions.

To provide valid estimates of realized genetic gain, trials must be established with a plot type and family components that closely mimic the operational plantation procedure. If pure family blocks are planted operationally, then they should be used in the realized gain trial. If mixed plots (e.g., like non-contiguous plots) are used operationally (e.g., orchard bulk lot), then the trial should use that plot type. Since block plots avoid inter-family competition, then the same trial could serve as both a progeny test and a realized gain trial for an organization which operationally planted large family blocks. Families which are not selected, based on progeny test results, would be purged from the data set prior to re-analysis for a realized gain estimation.

STAND LEVEL TRAITS

Yield per unit area is the factor of major concern to forest managers. Although the mean height, d.b.h., and individual tree volume are positively related to yield per acre, other factors such as site index, age, stand density, and quadratic mean diameter are more closely related to yield per acre (Clutter et al. 1983). Of these stand level factors, site index (mean height of the dominant-codominant trees at a base age) appears to be most amenable to genetic manipulation.

Nance and Wells (1981) first fit site index curves to seed source data. They demonstrated the more reliable behavior of site index rather than mean height to detect seed source differences, especially when unusual events (i.e., insect damage) reduce stocking levels below normal. Additionally, Nance and Bey (1979) explored the use of a growth and yield model, driven by source-specific site index curves, to project per acre yield in simulated genetically improved stands. Finally, Knowe and Foster (1989) fit site index equations to individual loblolly pine families, growing in block plots, and then utilized the specific equations to simulate per acre yield with a stand simulator. The simulated per acre yields compared very closely to actual yields to age 15 (age of oldest data). Assuming a continuingly accurate prediction, the authors predicted yield to age 25 and then estimated genetic gain from selection of the top families. Through age 15, the predicted and realized genetic gains in per acre yield were very close. Therefore, prediction of realized genetic gain in per acre yield appears feasible when considering family blocks.

The ability to estimate per acre yields, hence genetic gain, in mixed family stands remains empirically untested. Nance (1983) simulated the per acre yields of family blocks and mixed family stands of loblolly pine and found that an additive model adequately estimated the yields of the mixed stands. He did, however, uncover several minor inter-family interactions as a result of competition.

In general, the impact of inter-family competition on stand level yield remains largely untested. Studies must be established which relate individual tree level data to stand level yield. Given the general insensitivity of height growth in stands of varying density (Smith 1962), site index for each family in a progeny test may enable accurate simulations of per acre yield at rotation length. In this case, progeny test design may need to be revised to better estimate site index.

CONCLUSIONS

Varying levels of inter-genotypic competition, as displayed in different plot types, appear to have a relatively small effect on family means or ranks; however, estimates of genetic and phenotypic variances and the resultant genetic parameters differ widely by plot type. Family selection for individual tree traits should be effective despite whether the tree breeder uses block plot, row plot, or non-contiguous plot types as long as the progeny test is well designed and implemented. However, selection for per acre yield may depend largely on accurate estimation of site index which may require larger plots or plots with different configurations (e.g., not row plots).

Conversely, genetic and phenotypic variances, family-mean heritabilities, and estimates of realized genetic gain are strongly affected by plot type. Block plots, which involve no inter-family competition, provide family variance estimates that are not confounded with inter-family competition. Not surprisingly the block plot type yields the lowest estimates of family variance and family-mean heritabilities. Accurate estimates of realized gain from family selection for individual tree traits can be derived from block plot progeny tests if the families will also be planted operationally in family blocks. However, if families will be planted operationally in mixtures, the same families must be mixed similarly in trials with appropriate checklots to estimate realized gain. Other progeny test results will provide unrealistic gain estimates. Another approach would utilize growth and yield models to simulate yields from mixed family stands.

TESTABLE HYPOTHESES

1. In pure blocks, families which have been shown to be efficient users of available growing space (e.g., higher volume per unit APA) produce more bole wood volume per acre than families which are inefficient users of available growing space.
2. Families which have been shown to use less than the average growing space and are efficient users of the available space produce more bole wood volume per acre in pure blocks than families which **use** more than the average growing space and are also relatively inefficient in its use.
3. Binary mixtures, in different ratios, of families are neutral or complementary when both families use less than the average growing space and are efficient users of their available growing space.
4. Binary mixtures, in different ratios, of families are overcompensatory when one family efficiently uses more than the average growing space and the other family efficiently **uses** less than the average growing space.
5. Binary mixtures, in different ratios, of families are undercompensatory when both families are inefficient in their use of growing space and also use more than the average growing space.
6 Families selected as superior in block plot, row plot and non-contiguous plot tests maintain their relative superiority when compared to a common checklot in: 1) large operational pure block trials and 2) a large operational mixture of the families.
7 There is a large, positive correlation between tree growth and average growing space needed and a large, negative correlation between tree growth and efficient use of available growing space.
8 Data adjustment procedures (e.g., Pinker 1982; Nance et al. 1983; Magnussen 1989) in row or non-contiguous plot trials result in the same ranking of families as in pure block trials.
9 Genetic correlations, before versus after the onset of competition, are larger for block plot trials than either row plot or non-contiguous plot trials.

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