Forty Years of Genetic Improvement of Shortleaf Pine in Missouri

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Abstract: Shortleaf pine (*Pinus echinata* Mill.) is the only native pine species in Missouri, and its restoration is a top priority in the state. Because of the great interest in the species, a genetic conservation and breeding program for the species was initiated in the1960s by the Mark Twain National Forest, in collaboration with the Missouri Department of Conservation and the Ouachita National Forest. In the 1960s, seed production areas were established by the Missouri Department of Conservation and Mark Twain National Forest. The Missouri Department of Conservation also established provenance tests during the same period. Early results indicated that provenance variation was small, but within provenance variation was large. In the late 1960s, the Mark Twain National Forest selected 66 superior trees from natural stands throughout Missouri. Fifty of the superior trees were grafted into a 1st –generation seed orchard on the Ouachita National Forest in Arkansas. Operational seed collections from the clonal seed orchard were made in 1981, 1983, 1986 and 2003. Currently, all planting and seeding needs in Missouri are met with genetically improved seed from this clonal seed orchard. Open pollinated progeny tests were established in the early 1980s to evaluate orchard parents. A controlled pollinated progeny test was established in 2002 to further evaluate parents in the seed orchard, and to develop a 2nd-generation seedling seed orchard. Progeny test results suggest that genetic variation exists within shortleaf pine, and genetic gain is predicted to be significant. Future challenges and opportunities are discussed.

Key words: Shortleaf pine, selection, testing, breeding, seed production

INTRODUCTION

Shortleaf (*Pinus echinata* Mill.) is one of the four major southern pines in the United States. It is the only native pine species in Missouri. The range of shortleaf pine has been reduced from an estimated 2.6 million ha to 162000 ha by 1976 in the Missouri Ozarks (Essex and Spencer 1976) due to extensive logging from 1880 to 1920, frequent wildfires and overgrazing (Cunningham and Hauser 1984). Today, sites formerly occupied by shortleaf pine have many hardwoods species, many of which are not as well adapted as shortleaf pine to the dry, nutrient-poor and eroded sites in the Ozark Highlands of Missouri and Arkansas. Currently, these less adapted hardwood species are experiencing problems with oak decline associated with red oak borers and *Armillaria* root rot. The role of shortleaf pine in maintaining an ecologically stable and productive ecosystem in Missouri is well recognized (Law et al. 2004).

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In Missouri, shortleaf pine is important for both wildlife habitat and timber products. The coopers (*Accipiter cooperi*) and the sharp-shinned hawks (*Accipiter striatus*) nest in shortleaf pine stands in Missouri (Kritz 1989). The red-cockaded woodpeckers (*Picoides borealis*) prefer mature or over-mature shortleaf pine forests and are endangered because of the overexploitation of mature shortleaf pine trees (Cunningham 1940). Shortleaf pine has excellent stem form yielding high-valued posts and poles. It has dense, strong and easy to work wood valued as sawn timber and pulpwood.

Due to its ecological and economic importance, restoration of shortleaf pine is a priority in Missouri. Consequently, with considerable collaboration over the years, shortleaf pine tree improvement programs were started in the early 1960s by the Mark Twain National Forest and in 1967 by the Missouri Department of Conservation (Stelzer 1981).

The objective of this paper is to give a historical account of the shortleaf pine tree improvement activities in Missouri, provide recent estimates of genetic parameters and genetic gain, and to discuss future options for the genetic improvement of shortleaf pine in Missouri.

BREEDING OBJECTIVES AND SELECTION CRITERIA

In the 1960s when the improvement program was started, shortleaf pine was grown primarily for timber production. Breeding objectives were thus related to the requirements of fast-growing trees to provide valuable timber and income. These breeding objectives were focused on an increase in profitability to the landowners and processors through shortening the rotation, increasing volume growth, and by increasing stem quality. A secondary, but important objective was to maintain a broad genetic base. This broad genetic base would serve to buffer against changes in climate, pests and diseases, products or markets. The major selection criteria for shortleaf pine improvement in Missouri were (Stelzer 1980):

- Superior height growth,
- Superior diameter growth,
- Good self-pruning ability,
- Straight bole,
- Small well formed crown
- Resistance to insects, and
- Resistance to diseases.

Today shortleaf pine forests are less important as a source of wood products and more important as a source of ecological services – e.g. biodiversity and mitigation of oak decline. Although selection criteria for ecological purposes may differ from those for timber production, many traits are common to both objectives. For example, one of the most important traits for selection for ecological purposes is broad adaptability. Because growth is a reflection of adaptive traits, such as tolerance to specific environments and tolerance of pests and diseases, selections made for timber production in the past will also be useful for restoring shortleaf pine for ecological purposes.

Family Composition Changes Over Time in a 17-Year-Old Mixed-Family Loblolly Pine Stand

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Abstract: The family composition of the dominant and co-dominant crown classes (D-C crown class) in a mixed-family deployment of loblolly pine (*Pinus taeda* L.) was studied. Eight open-pollinated families representing four ideotypes from North Carolina were planted in a random mixture at two sites. Various stand measurements were taken at ages 5, 9, 13, and 17. A dominance percentage was calculated by dividing the number of trees of a given family in the D-C crown class by the total number of trees planted of that family. Family dominance percentages were analyzed with ANOVA at ages 9, 13, and 17. Significant family differences were found at all three ages. Pure-family plots were also present in the same field trial. Since family selection is primarily based on pure-family plot performance, correlations between mixed family dominance percentages and pure-family stand traits were identified.

Keywords: Stand composition, mixture deployment, loblolly pine, selection

Species mixtures have been used to improve growth and quality in forest stands. Oak-sweetgum mixtures can be beneficial to overall stand growth and development (Blackburn et al., 1999), while pure oak stands can stagnate (Meadows and Goelz, 1999). The better growth and quality in a mixed species stand is often attributed to a minimization of intra-specific competition (competition between trees of the same species). In a mixed species stand, inter-specific competition is the dominant form of competition. Use of different species, with differing growth rates, attainable heights, and tolerance levels, minimizes direct competition along the same axis in the stand.

While different species are deployed to achieve this inter-specific form of competition, deployment which exploits the genetic differences in growth rate, attainable height, and shade-tolerance level of a single species could be used to achieve the same competitive effect as a mixed species stand. Such intra-specific tolerance differences have been demonstrated. Hasenauer et al. (1994) found tolerance differences, expressed through mortality associated with stand closure, both between species and within species. Dickmann (1985) classified genotypes into broad categories or ideotypes through identification of differences in tolerance. These ideotypes were defined by tree response to inter-genotypic competition. Three ideotypes (isolation, dominating, and crop) were defined. Classifications of isolation and dominating ideotypes produced maximum individual-tree stem growth at the expense of the stand, while crop ideotype trees maximize growth production of the entire stand.

Loblolly pines are selected from pure-family plots; however, stands are often composed of family mixtures when planted for production. Thus, genotypic response to genotypes of different

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competitive ability is often unknown. Tuskan (1984) found that families do perform differently when grown in family mixtures, inter-genotypic conditions, than in pure-family conditions. Considerations of family-by-family interactions and resulting family composition changes throughout stand development should be made when using mixed-family deployments.

The objectives of this project were to (1) examine stand volume differences that existed between mixed and pure family deployments at age 17, (2) determine if representation of families in the dominant and co-dominant crown classes in the mixed stand changed, and (3) examine the effectiveness of ideotypes, defined by growth and crown characteristics, as a method of classifying families.

METHODS

Plant Material and Experimental Design

Seedlings from eight open-pollinated families of loblolly pine in North Carolina (NC) and one open-pollinated "commercial check" from east-central Mississippi (MS) and west-central Alabama (AL) were provided by Weyerhaeuser Company. The eight families were selected based on 12-year-old progeny tests to represent ideotypes with (1) fast growth with small crown (families NC1 and NC8), (2) fast growth with large crown (families NC4 and NC7), (3) slow growth and small crown (families NC3 and NC6), and (4) slow growth with large crowns (families NC2 and NC5).

Seedlings were planted from April 22 to May 7, 1985 at two sites on the John Starr Memorial Forest (Mississippi State University School Forest) in Winston County, MS. The experimental design was a randomized complete block design with four blocks at each site. The two sites were an old field and a cutover and site-prepared area. Treatments were arranged in split-split plots, with each replication split into three spacings (1.5x1.5, 2.4x2.4, 3.0x3.0-meter). Each spacing was split into a mixed-family deployment and a set of pure-family deployments. The mixed-family deployment did not include the check. Around each pure-family subplot a single or double border row was planted. The interior trees of each pure family subplot covered an area of 0.015 hectares. Survival, dbh, total height, and crown class of all trees were measured at ages 5, 9, 13, and 17 years.

Analysis

Age 17 stand volumes were calculated for families in the mixed-family deployment and the pure-family deployment. Analysis of variance (ANOVA) was used to determine if (1) overall stand volume differences existed between the sum of the eight pure-family-subplots and the mixed-family-plot, and (2) individual families produced different volumes when deployed as a pure family than when deployed in a mixture of families. Duncan's New Multiple Range Test was used to detect differences between both deployments of a family.

Data from the mixed plots were used to determine if representation of families in the dominant and co-dominant crown classes (D-C crown class) changed with age. All trees classified in the dominant and co-dominant crown classes were summed by family at ages 9, 13, and 17. A "dominance percentage" (DP) was calculated by dividing the number of each family's D-C crown class trees by the total number of stems initially planted. The DP value was then used as the response variable in ANOVA at each age. The following fixed effects model was assumed:

$$y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \delta_k + (\alpha\delta)_{ik} + (\beta\delta)_{jk} + (\alpha\beta\delta)_{ijk} \begin{cases} i = 1,2,\ldots,8 \\ j = 1,2,3 \\ k = 1,2,\ldots,8 \end{cases}$$

where y was the DP value, α was the effect of the i^th replication, β was the effect of the j^th spacing, and δ was the effect of the k^th family. Variation due to site factors was non-significant and dropped from analysis to simplify the model. Family-rank correlations were determined between the mixed-family DP values and pure-family tree height, BA per acre, and survival. Spearman's test for independence based on ranks (Spearman 1904) was used to test these correlations.

RESULTS AND DISCUSSION

Volume Differences

The differences in age 17 stand volume between the pure family deployment (sum of the eight pure family subplots) and the mixed family deployment was not significant (p-value=0.28). The average volumes of the pure family and mixed family deployments were 277.9 cubic meters per hectare and 283.2 cubic meters per hectare respectively. At age 17, deployment of the families in a mixture did not produce a higher or lower overall cubic foot volume yield than the sum of the pure-family subplots. However, the individual family volumes did significantly differ between deployments (p-value≤0.0001).

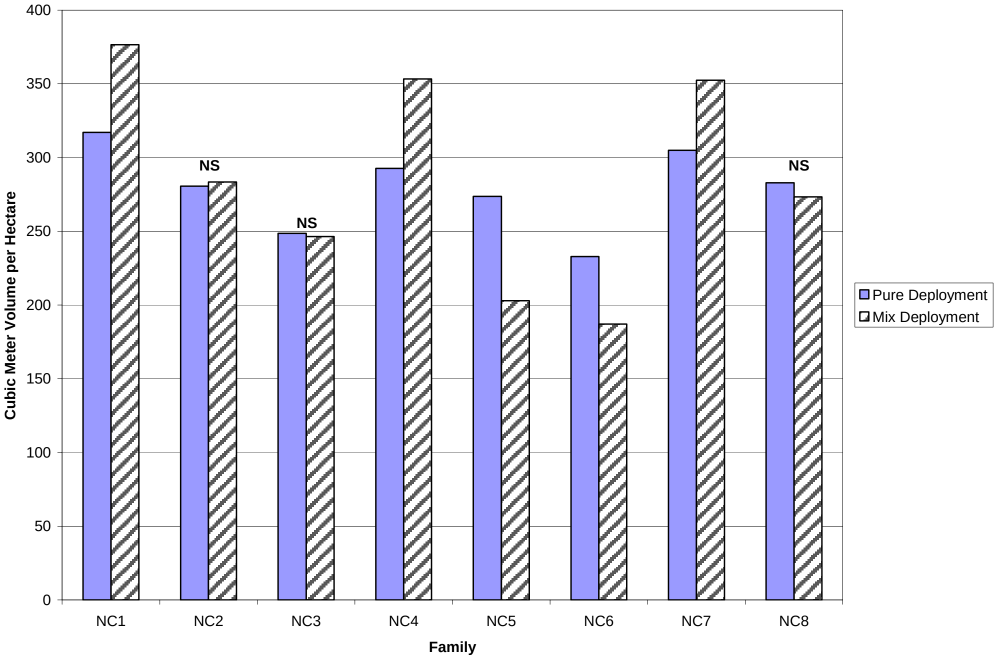

Figure 1. Deployment-by-family cubic foot volume differences. (NS=mixture and pure deployment volumes were not significantly different, α=0.05)

Families NC1, NC4, and NC7 all produced significantly greater volumes in a mixed family deployment than in pure-family deployment, while families NC5 and NC6 produced significantly less per acre volume in mixture than pure deployment (Figure 1). This explains why a total volume difference between the two deployments did not exist. As volume increased in the top three families in the mixed family deployment, relative to the pure family volumes, decreases occurred in family NC5 and NC6 that negated those gains. There were also three families (NC2, NC3, and NC8) that showed no significant difference in stand volume between the deployments.

Dominance Percentage Differences

Family composition change was investigated to determine the reason for the large significant increases or decreases in volume by five of the families when deployed as a mixture. Trees that are in the D-C crown class will, by definition, be larger in height than neighboring intermediate and suppressed trees and have less mortality; thus, families that have increased their representation in this D-C crown class will make gains in stand volume. Family DP values show that some differences in representation were occurring as early as age nine years (Figure 2). These DP values show that some families have more of the initial trees growing into the D-C crown class (e.g., NC1) and have a greater representation than other families such as NC5. The three families with the highest DP (NC1, NC4, and NC7) were the families that had significantly greater volume production in the mixed deployment than in the pure-family deployment. Similarly, the two families with the lowest DP (NC5 and NC6) were the families that had a significant decrease in volume production in the mixed-family deployment as compared to the pure-family deployment.

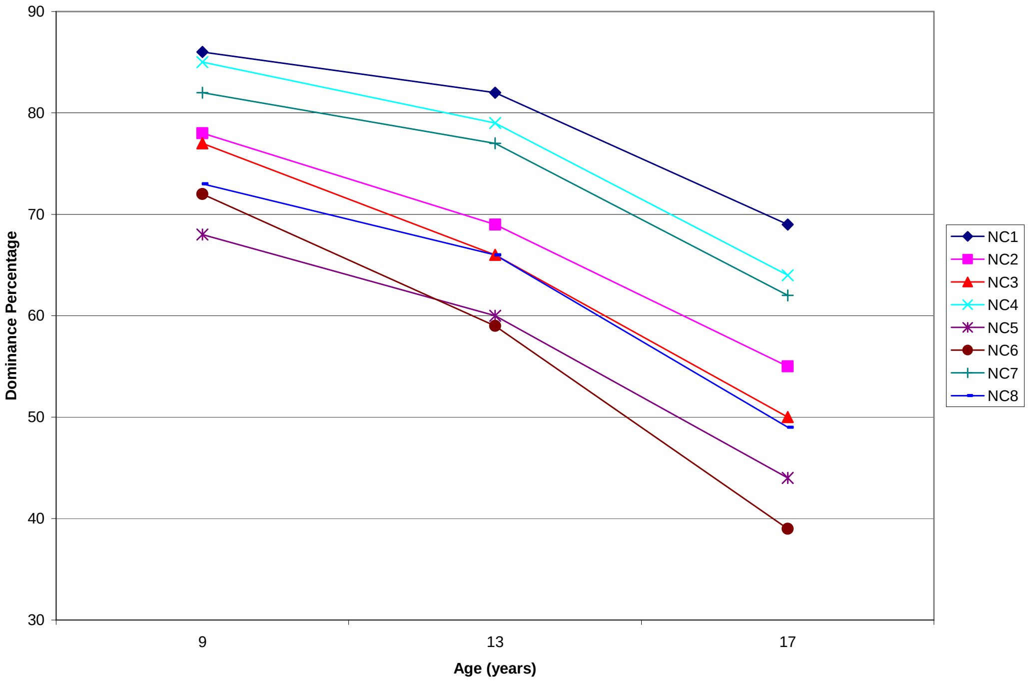

Figure 2. Change in dominance percentage (stems in the D-C crown classes relative to the amount of stems initially planted) for each family.

The three spacings also resulted in differences in the number of stems initially planted that grew into the D-C crown classes (Figure 3). As the stand aged the number of D-C crown class trees decreased. The 2.4x2.4-meter and 3.0x3.0-meter spacings initially had nearly identical DP values, but the 2.4x2.4-meter spacing began decreasing more rapidly than the 3.0x3.0-meter spacing after age nine and had a DP value that was 16 percent
less by age 17 . The 1.5x1.5-meter spacing had far fewer stems in the upper crown classes at each age than the two wider spacings. By age 17 the 1.5x1.5-meter spacing had a DP value 42 percent less than the 3.0x3.0-meter.

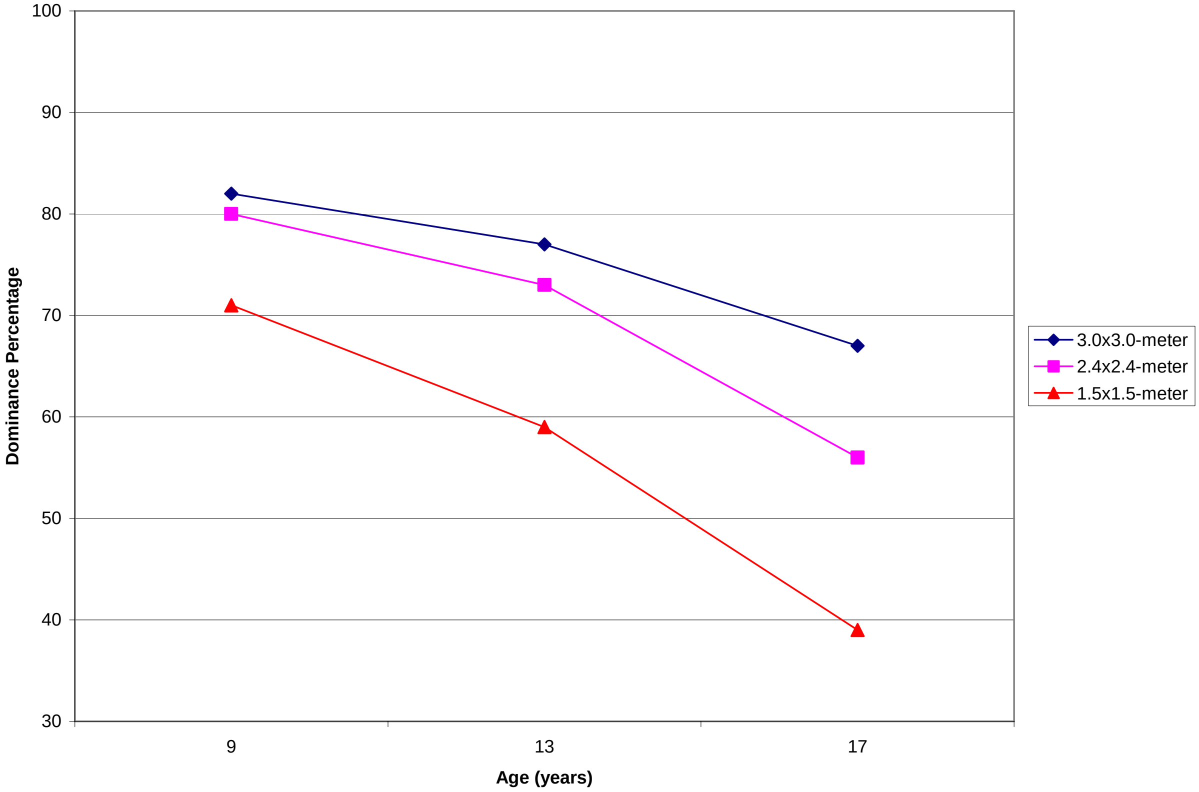

Figure 3. Change in the amount of stems in the D-C class relative to the amount of stems initially planted (DP) for each spacing.

ANOVA results showed that both spacing and family independently affected percentages of trees that were in the D-C crown class (Table 1). Significant differences were present at all ages. Interactions between spacing and family were nonexistent at all ages. Duncan's New Multiple Range Test was used to detect differences among families' and spacings' average DP value (Table 2 and 3 respectively).

Table 1. ANOVA results of crown dominance percentage across ages 9, 13, and 17

		Age 9		Age 13		Age17	
Source	Df	MS	F-value	MS	F-value	MS	F-value
Rep	7	0.009	1.38	0.013	1.88	0.025	2.67
Space	2	0.249	36.40*	0.537	71.24*	1.281	128.15*
Rep*Space	14	0.014	2.04	0.027	3.57	0.035	3.50
Fam	7	0.096	13.56*	0.183	26.15*	0.268	28.25*
Rep*Fam	49	0.007	1.04	0.007	0.93	0.009	0.95
Space*Fam	14	0.005	0.68	0.009	1.14	0.014	1.37
Error	98	0.007		0.008		0.009	

*-indicates F-value significant at the alpha=0.05

Table 2. Duncan's test of ranked family DP means

Year 9			Year 13			Year17		
Family	Mean	Grouping[a]	Family	Mean	Grouping[a]	Family	Mean	Grouping[a]
NC1	85.97	A	NC1	82.49	A	NC1	69.33	A
NC4	84.82	A	NC4	78.59	A	NC4	63.98	AB
NC7	82.08	AB	NC7	76.87	A	NC7	62.47	B
NC2	77.98	BC	NC2	68.77	B	NC2	55.16	C
NC3	76.63	CD	NC8	66.21	B	NC3	50.18	CD
NC8	73.41	CDE	NC3	66.09	B	NC8	49.17	CD
NC6	71.84	DE	NC5	60.22	C	NC5	43.88	DE
NC5	68.29	E	NC6	58.60	C	NC6	38.67	E

[a]Means followed by the same letter and case are not significantly different at the 0.05 probability level

Table 3. Duncan's test of ranked spacing DP means

	Year 9		Year 13		Year17	
Spacing (meters)	Mean	Grouping[a]	Mean	Grouping[a]	Mean	Grouping[a]
3.0x3.0	0.82	A	0.77	A	0.67	A
2.4x2.4	0.80	A	0.73	B	0.56	B
1.5x1.5	0.71	B	0.59	C	0.39	C

[a]Means followed by the same letter and case are not significantly different at the 0.05 probability level

Significant family differences in DP were already present at age nine (Table 2), indicating that separation of families occurred before crown closure. As the stand aged, the original separations generally increased between families. The top three families began to exert their dominance over the stand at age nine, and by age 17 had significantly higher representation in the D-C crown class (nearly twice as much as the lowest family NC6). These three families were all members of the fast-growth ideotype, which suggests that a fast-growth/slow-growth ideotype classification may be an adequate method for describing competitive ability. The one exception to the growth-ideotype trend was NC8, which ranked sixth in mean DP. The crown-size classification showed no relationship with DP. This was unexpected since the "large crown" ideotype might be expected to take more growing space from adjacent "small crown" ideotypes and increase their own representation in the D-C crown class.

The 1.5x1.5-meter spacing had a significantly lower DP value by age nine than the other two spacings (Table 3). Not until age 13 did the 2.4x2.4-meter spacing become significantly less in DP than the 3.0x3.0-meter spacing. As the stand aged, the percentage of trees that were in the D-C crown class decreased. No rank changes were present, but the spread of percentages did increase as the stand aged. This can be attributed to the increased competition following crown closure, which caused differences in dominance to increase.

Variation in DP values among both families and spacings increased as the stand grew older. This can be attributed to increased competition during stand development, causing some families to amplify their representation in the D-C crown class while other families have their representation reduced. The same phenomenon could also be expected by increasing competition using tighter spacings. The 1.5x1.5-meter spacing had a much lower DP value than the other spacings at all ages which would, by amplifying competition in the stand, allow the detection of family differences to occur at earlier ages. Since spacings and families did not interact to affect DP, use of tight spacings could be implemented in progeny tests to cause family DP separation and detection at earlier ages. This would allow families to be selected early in progeny tests for their ability to get into the D-C crown class in a mixed deployment.

Correlations

Positive family-rank correlations were found between pure-family-plot heights and mixed-family-plot DP (Table 4). Correlations with height were strong at all ages, reaching their maximum strength at age 13. These positive correlations indicate that families with taller average heights will exert dominance over shorter families in a mixed deployment.

Basal area per acre was significantly correlated with DP at ages nine and above, and the correlation peaked in value at age 13. The correlations were positive and indicate that families which produce more basal area in pure-family plots will have more representation in the D-C crown class in mixed stands. However, these correlations were the weakest of all the pure-family-plot traits, so that basal area's use for selection purposes will be relatively poor compared to early selection for height or survival.

Survival was significantly correlated with increasing DP. This correlation increased in strength as the stand grew older, peaking at age 17. This trait had the strongest correlations of all the traits studied. Yet, for selection purposes at age nine or 13, correlations were comparable in strength to the height correlations. This correlation must be used with caution. It may give a misleading characterization of a family's true ability to dominate in the stand. Families with poor survival early in life, which could be attributed to poor genotypic hardiness or merely random mortality, will initially have fewer trees able to grow into the D-C crown class. This gives an early advantage to families with higher juvenile survival that is not attributable to competition.

Table 4. Correlations between pure-family-plot traits and mixed-family-plot DP at age 17.

Trait	Age	Spacing (meters)			Average for each Trait and Age	Average for each Age
		1.5x1.5	2.4x2.4	3.0x3.0		
		Correlation Coefficient				
Height	5	+0.24*	+0.31**	+0.30**	+0.28	Age 5=+0.29
Height	9	+0.59**	+0.49*	+0.48**	+0.52	Age 9=+0.44
Height	13	+0.68**	+0.63**	+0.48**	+0.60	Age 13=+0.56
Height	17	+0.62**	+0.60**	+0.48**	+0.57	Age 17=+0.56
Basal Area	5	+0.14	-0.02	+0.10	+0.07	
Basal Area	9	+0.25*	+0.25*	+0.24*	+0.25	
Basal Area	13	+0.34**	+0.52**	+0.30**	+0.39	
Basal Area	17	+0.21*	+0.44**	+0.28**	+0.31	
Survival	5	+0.33**	+0.25**	+0.55**	+0.38	
Survival	9	+0.45**	+0.50**	+0.68**	+0.54	
Survival	13	+0.75**	+0.57**	+0.79**	+0.70	
Survival	17	+0.86**	+0.66**	+0.85**	+0.79	
Average for each Spacing		+0.40	+0.39	+0.46		

*- trait significantly correlated at 0.10
**-trait significantly correlated at 0.05

Families with greater early height growth achieved dominance by the time of crown closure (around age nine) in a mixed-family-stand and established greater representation in the D-C crown class during subsequent years. In a mixed-family deployment, once these families achieved a lead in height they continued that lead through age 17. Doing so allowed these families to exert dominance by receiving needed light while at the same time denying that resource to others. These fast-growth ideotype families (NC1, NC4, and NC7) resembled Dickmann's (1985) dominating type in this sense. However, they could also fit into his crop type, because these families had the greatest pure-family-plot yields (Table 1). These families will be defined as an "efficiency" ideotype. Families NC2, NC3, and NC8 fit into a "stable" ideotype classification by maintaining a relatively stable percentage of stems in the D-C crown class throughout stand development. These families did not exert dominance, yet they exhibited little loss of stems in the D-C crown class by having neighboring families that were competitors. One type apparent in this study that was not defined by Dickmann is a "submissive" ideotype. Families NC5 and NC6 decreased in representation in the D-C crown class. These two families had the smallest average height at age nine of any family in the study (10.2 feet and 10.4 feet respectively). Once they began to fall behind in height early in stand development, these two submissive families continued to decline in representation in the D-C crown class and would eventually be excluded from the stand.

SUMMARY AND CONCLUSIONS

Differences did not exist in overall cubic foot volume between the mixed-family-plot and the pure-family-plot. However, volume differences did exist between pure-deployments and mixed-deployments for individual families. Three families had large volume increases from pure-plot yield to mixed-plot yield, while two families decreased in volume. A third group of families showed no significant change in volume between deployments.

The percentage of trees planted that reached the dominant and co-dominant crown classes differed by family in mixed-family plantings at ages nine, 13, and 17 years. All of these families were equally represented in the mixture at time of planting (12.5 percent for each of the eight families). The family differences increased with increasing age, and three families had significantly higher DP values by age 17 than the other families. The mixed stand will thereby become less diverse with increasing age. These were the same three families that had increased volume production in the mixed-deployment. Family ranks were constant from age nine to age 17.

Classification of families into ideotypes for fast and slow early height growth was effective for 75 percent of the families in identifying subsequent dominance performance in mixed stands. Ideotype classification for small or large crown types before crown closure was not effective. Selection of families that will dominate in mixed stand can be achieved at an early age in pure-family-plots. Selection based on pure-family height and survival at early ages showed promise. All traits tested increased their correlation with DP as the stand aged.

Many studies have favored height as a selection tool for genetically improved families (McKeand 1988, Foster 1986, and Gwaze et al. 1997). By selecting for height, selection is also being made for families that exert dominance in mixed-family deployment. In light of mixed-species hardwood studies, use of families that all express this increase of dominance with age may not be advantageous for stand level volume production or quality. Based on the hardwood practice of mixing species of different competitive levels, mixtures of dominant families (e.g., NC1, NC4, and NC7) in conjunction with stable families (e.g., NC2, NC3, and NC8) may be optimal.

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