APA: A USEFUL TOOL FOR ANALYSES OF PROGENY TESTS

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Abstract.--Area Potentially Available (APA), an index of a tree's growing space, is a useful tool for adjusting family differences in basal area growth caused by differences in local density. APA also has utility in assessing family responses to changes in local density and to interfamily competition. Two loblolly pine progeny tests are analyzed to illustrate procedures, and the results have implications for testing and deployment of genetically improved varieties.

Additional keywords: *Pinus taeda*, stand density, interfamily competition.

All forest tree progeny tests are variable density studies. Each tree eventually has its own unique amount of growing space, or local density, as a result of (1) mortality of adjacent trees, (2) differential growth of the subject tree and adjacent trees, and/or (3) designed differences in spacing for stand density tests. Variable densities can lead to both problems and opportunities in the analyses of these progeny tests for family differences, once competition begins among adjacent trees.

Area Potentially Available (APA) is an index of local density for individual trees and has been described by Smith (1987) at this conference. Daniels et al. (1986) have shown that it is an excellent predictor of future growth of individual trees in closed stands. The present paper illustrates the application of APA in analyses of progeny tests to (1) adjust for differences in local density and (2) evaluate genetic differences in response to competition. Data from two loblolly pine (*Pinus taeda* L.) studies will be used to provide results for discussion.

MATERIALS AND METHODS

The APA Method

The APA index is the area of an irregular polygon constructed around a subject tree (Nance et al. 1983). The polygon is formed by intersecting lines (influence lines) that are located between and perpendicular to the lines connecting the subject tree with each of its competitors. The distance (LP) from the subject tree to the competitor's line of influence may be unweighted (half the distance between the two trees) or weighted by

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the relative sizes of the two trees. In this paper the squared d.b.h. of each tree is used to weight the LP.

Progeny Tests

Data are used from two loblolly pine studies planted at the same site in northeast Mississippi (Oktibbeha County, 33°18'N latitude, 88°47'W longitude). Open-pollinated families from eight clones in the Weyerhaeuser Company seed orchard near Aliceville, Alabama, are represented in both studies. Origins of these clones are Lamar, Pickens, and Greene Counties in west central Alabama.

The first study, hereafter called the "Nelder's Study", has the families planted along spokes of a Nelder's Wheel design (Namkoong 1965). There are five spokes per family in a 42-spoke wheel (including two border spokes) that represents a replication, and there are ten replications. The five-spoke family plot is arranged in the spoke order -- A4-B1-A5-B2-B3-B4-Cl-B5-C2 -- (where A, B, and C are different families). Spoke 3 of each family represents a "pure" single-family deployment, whereas the other four spokes are in "mixed" family deployments. There are five measurement positions and an interior and exterior border on each spoke, with the measurement positions having local densities of 1210 (6 x 6 feet), 938 (6.8 x 6.8 feet), 727 (7.7 x 7.7 feet), 563 (8.8 x 8.8 feet), and 436 (10 x 10 feet) trees per acre. Measurements of d.b.h. have been taken annually from age five to age ten.

The second study, hereafter called the "Design Study", contains three progeny tests having common families but different plot designs. The "Block Plots Test" has 40 trees per family planted in a 4 x 10-tree block plot in each replication. The "Row Plots Test" has 40 trees per family planted in four 10-tree row plots assigned randomly to 32 row positions in each replication. The "Non-Contiguous Plots Test" has 40 trees per family assigned randomly to 320 single-tree positions in each replication. All trees are planted at 8 feet x 8 feet (681 trees/acre) , and there are six replications. Measurements of d.b.h. have been taken at ages 5, 7, 9, and 11 years after planting.

PROCEDURES AND RESULTS

A recommended stepwise procedure is given below for using APA in progeny test analyses to adjust for differences in local density and to evaluate genetic differences in response to competition. It should only be used after crown closure, when available growing space becomes limiting. Accomplishment of each step with SAS computer software (SAS Institute 1985) is described and illustrated with results for the two loblolly pine studies.

Step 1--Determine if differences in local density exist in the study and affect growth. A new computer program to calculate polygons and APA's may be obtained from W. L. Nance. The output file from the program contains the APA value and coordinates for the polygon of each tree. The coordinates can be used by SAS GRAPH to print a polygon map of the study for visual verification of results (Figure 1). The APA values can be merged with a SAS data

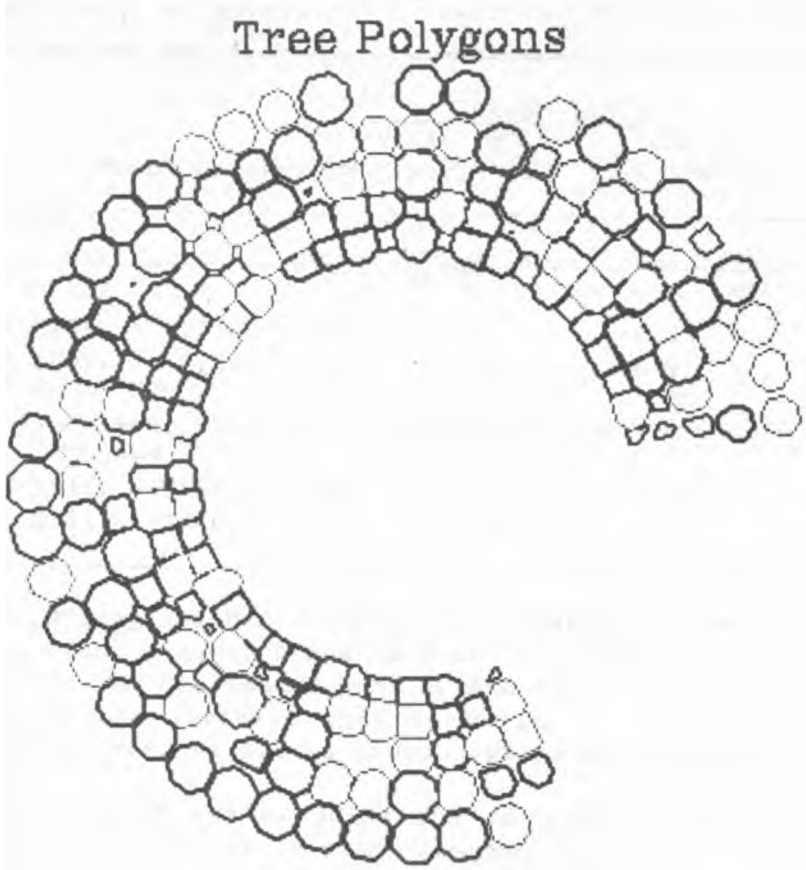

Figure 1. Polygon map of one replication of the Nelder's Study at age eight. Border trees are not shown in this illustration.

file containing basal area growth (BAG) for each tree, and the SAS procedure PROC REG can then be used to calculate the regression equation for BAG per tree from time "A" to time "B" as a function of the APA of the tree at time "A". Significance of regression and size of the coefficient of determination (RZ) will indicate whether or not local density differences are affecting growth. Local density differences existed in the loblolly studies after crown closure and explained from one-third to two-thirds of the variation in BAG, as indicated by the sizes of R^2 (Table 1).

Step 2--Determine if families are growing at different local densities. Family means and an analysis of variance for individual tree APA's can be obtained by the SAS procedures PROC MEANS and PROC GUI on the merged data file. If the "Family" source of variation for APA is significant, then families are growing under different local densities. Analyses of family differences for BAG in the following years will be biased by the effects of these differences in local density.

The Nelder's Study and the Non-Contiguous Plots Test had significant family differences in APA (Table 2). In both of these tests family 530 is growing under a significantly higher APA (lower local density) than family 509. Subsequent BAG should be greater for 530 than for 509 as a result of

Table 1. Regression equations for Basal Area Growth (BAG) per tree as a function of APA per tree in the Design Study and Nelder's Study.

BAG Interval start (Yr.)	BAG Interval end (Yr.)	Study Means BAG (in^2/tree)	Study Means APA at start (ft^2/tree)	Regression Equation	Adjusted R^2
Design Study					
7	9	11.9	48.3	BAG = 2.1913 + .2043 APA	.39
9	11	9.8	61.2	BAG = 1.2141 + .1403 APA	.29
Nelder's Study					
7	9	11.2	44.3	BAG = 1.6327 + .2122 APA	.62
8	10	10.6	50.9	BAG = 2.0541 + .1670 APA	.52

more space and resources being available to 530 for growth, but the results will not indicate how the two families would compare under equivalent competitional stress (same APA). That comparison may be very relevant for forest crops of the future, where high survival and homogeneity in tree sizes from intensive crop culture could result in less variability in APA's.

Table 2. Family mean APA's at age eight in the Nelder's Study and at age nine in the three progeny tests of the Design Study, with significance levels for F tests of family variation.

	Family Mean APA (ft^2/tree)			
		Design Study		
Family	Nelder's Study	Non-Contiguous Plot	Row Plot	Block Plot
505	51.2	61.3	61.2	59.1
507	51.3	62.4	59.2	58.8
509	47.7	57.4	58.2	63.2
519	51.0	59.0	59.8	58.2
526	50.4	59.9	60.8	57.8
528	51.3	61.6	59.3	59.7
530	52.6	63.5	61.5	60.8
532	51.1	61.6	58.0	61.5
Test Mean	50.8	60.9	59.8	59.8
Family F-test (PR F)	2.48 (0.025)	2.40 (0.041)	1.02 (0.436)	1.47 (0.210)

Step 3--Determine if families respond differently to changes in local density. The appropriate adjustment procedure for comparing families at the same local density will depend on whether or not families respond differently to changing APA. The SAS procedure PROC GLM can be used to test for homogeneity of slopes of the individual family regressions for BAG as a function of APA. The model contains two independent variables, APA and APA*FAMILY. A significant F-test of the Type I mean square for APA*FAMILY (coming after APA in the model) indicates that the slopes are not homogeneous. Should this happen, the separate family regression lines can be plotted to see if the lines cross and where the greatest family differences occur.

The APA*FAMILY interaction was significant in all of the loblolly tests. A plot of regression lines for the Non-Contiguous Plot Test revealed that families 509 and 530 were major contributors to this interaction (Figure 2). This is a G x E interaction that (1) creates problems for the

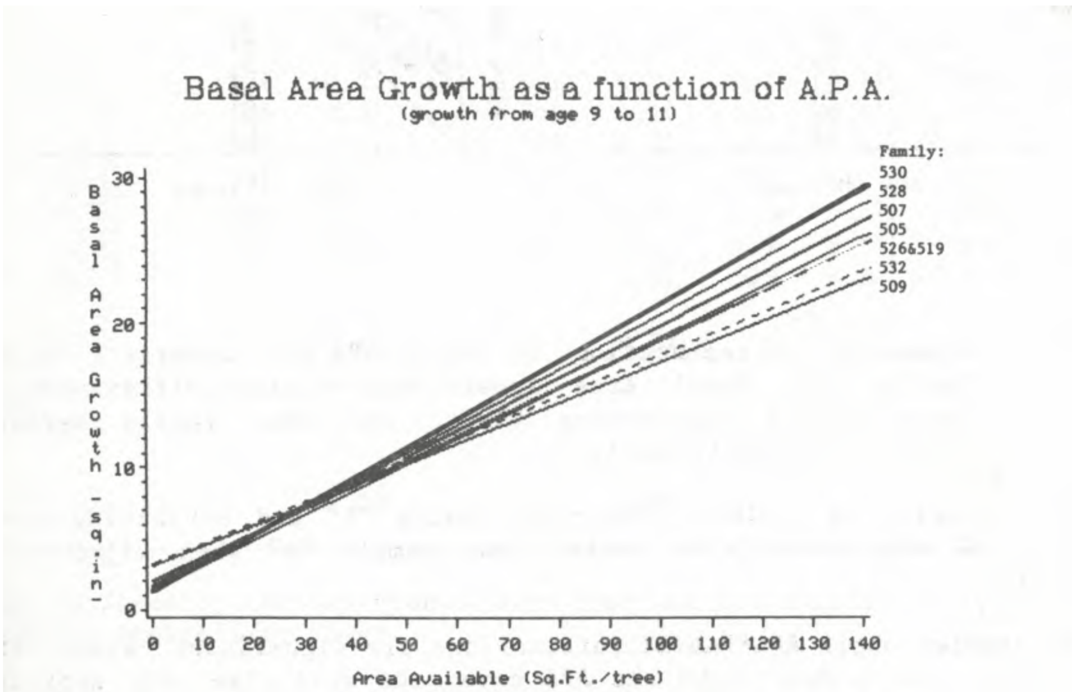

Figure 2. Separate family regression lines for Basal Area Growth per tree as a function of APA per tree in the Non-Contiguous Plot Test.

adjustment of families to comparable local densities (discussed below) and (2) raises questions about the need to conduct progeny tests over a range of densities (discussed later).

Step 4--Adjust for differences among families in local density. The reasons for adjusting individual-tree BAG values for differences in APA include (1) more accurate assessment of family differences for growth under competition and (2) reduction in error to provide greater precision in detecting family differences. The method of adjustment will depend, however, on whether or not the APA*FAMILY interaction is significant. In those studies where no APA*FAMILY interaction exists (no slope differences), APA can be used as the covariate in a covariance analysis by PROC GLM to compare families adjusted to the study mean APA (left side of Figure 3). Family "a"

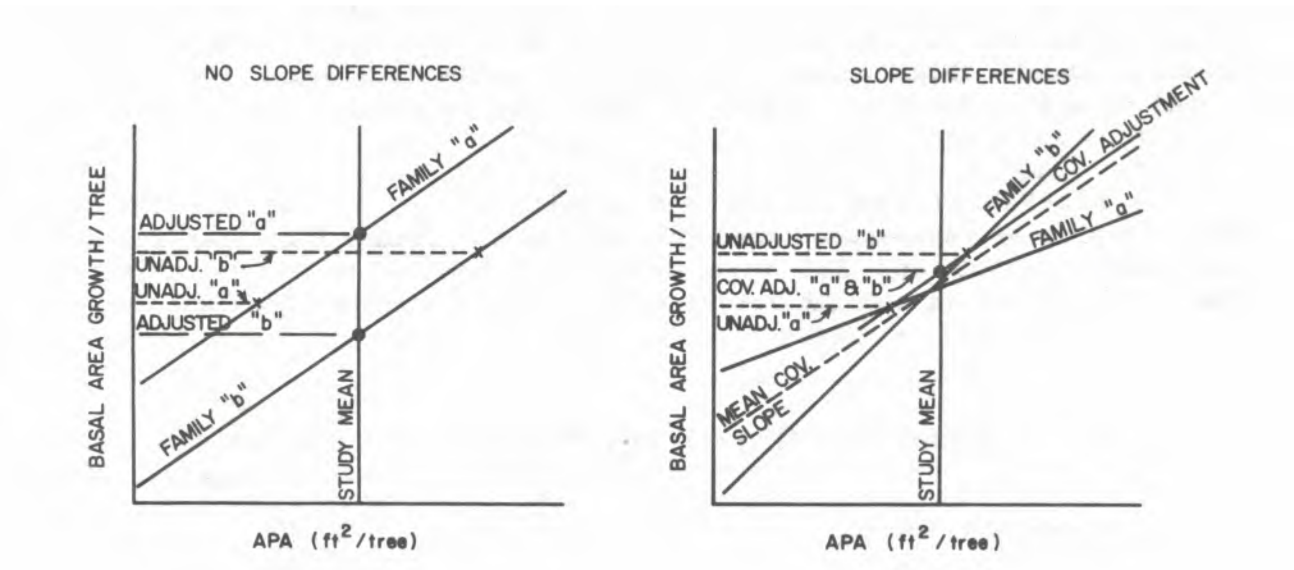

Figure 3. Schematic representation of using APA as a covariate to adjust family mean Basal Area Growth when no slope differences exist among family regressions (left) and when family regressions differ in slope (right).

that was growing at a lower APA than family "b" and exhibiting a lower measured BAG may actually be better than family "b" when adjusted to a common APA.

In studies where APA*FAMILY interactions are significant (slope differences exist), adjustment with the APA covariate will give only approximate tests of family differences near the study mean APA (right side of Figure 3). The covariance adjustment in that example results in no difference between families "a" and "b" at the study mean, but "a" is actually slightly poorer than "b" at that mean APA and much different at APA's distant from the mean. The use of APA and APA*FAMILY as multiple covariates, which is the same as using APA (FAMILY) as a single covariate, will adjust for both APA effects and family effects. Since we wish to study family effects, not remove them, this multiple covariance procedure is not appropriate. The authors recommend that when APA*FAMILY interactions exist, a target APA should be chosen and families compared for that target. This can be done by breaking the data file into separate APA classes, with a class centered on the target APA. PROC GLM can then be used to conduct an analysis of variance on the unbalanced data set for the trees in the target APA class.

Results from PROC GLM with Tukey's test of ranked family means for the Non-Contiguous Plot Test illustrate how simple covariance adjustment for APA reduced the error and family mean differences in BAG (Table 3). This is an

Table 3. Ranked family means for Basal Area Growth in the Non-Contiguous Plot Test before and after adjustments for differences in local density (APA).

Basal Area Growth (square inches per tree) from Age 9 to Age 11[a/]									
Not Adjusted for APA at Age 9		Adj. by APA Cov. to 60.9 ft^2 (1 slope)		File Separated into APA Classes					
				APA=15-45ft^2		APA=45-75ft^2		APA=75-105ft^2	
Family	Mean	Family	Mean	Family	Mean	Family	Mean	Family	Mean
530	10.8	530	10.4	519	6.7	530	10.4	528	14.7
528	10.3	528	10.2	528	6.3	507	9.9	530	13.8
507	10.0	526	9.8	509	6.1	526	9.8	507	13.2
526	9.7	507	9.7	530	5.8	532	9.8	509	13.1
505	9.5	519	9.6	526	5.7	528	9.7	519	12.4
532	9.5	505	9.5	532	5.5	505	9.6	532	12.3
519	9.4	532	9.4	507	5.4	519	9.5	505	12.3
509	8.7	509	9.2	505	5.0	509	8.8	526	11.9
MSE =	21.91		15.84		9.02		13.77		12.94
Tukey's Min. Sign. Diff. =	1.60		1.36		2.83		1.54		3.13

[a/] Means followed by the same continuous line are not significantly different at the 0.05 probability level.

approximate adjustment, since slopes for the individual family regressions were different. In fact, the only significant rank correlations (Steel and Torrie 1960) among the family means in the five columns of Table 3 are for (1) the unadjusted means versus the covariate-adjusted means and (2) the unadjusted means versus the means in the restricted APA class for 45-75 square feet. When APA*FAMILY interactions are significant, family superiority at one stand density level should not be extrapolated to other densities.

Step 5--Determine if families respond differently to the genetic composition of their neighboring competitors. The purpose of this step is to determine if family mean BAG is influenced not only by the amount of available growing space, but also by the genetic composition of the trees surrounding that growing space. An affirmative answer would imply that intergenotypic competition exists among trees in these field studies, supporting results detected in seedling studies by Adams (1980) and Tuskan (1984).

Nance et al. (1983) have already described a procedure for using APA, APA*FAMILY of the subject tree, and the "relative influence" of each competitor family in a multiple regression model to predict subsequent BAG of the subject tree. The data were from the same Nelder's Study used here, but for BAG from age 7 to age 8. APA*FAMILY interactions (differences in subject family competitive abilities) contributed significantly to the predictive ability of the model, but relative influences of competitor families (intergenotypic interactions) were not significant.

Another approach for studying effects of intergenotypic competitive interactions is to compare family ranks in mixed-family deployments and in single-family "pure" blocks. Mixed-family deployments experience inter-family competition, while single-family blocks experience only intrafamily competition. If ranks differ in the two deployments, indicating the presence of interfamily competitive interactions, then plots of BAG over APA for the families can be used to help explain the interactions.

The Nelder's Study data were divided into (1) a "pure family" file containing only trees from spokes surrounded on both sides by spokes of the same family and (2) a "mixed family" file containing all other trees. The Block Plot Test provides a "pure-family" arrangement, the Non-Contiguous Plot Test provides a true "mixed-family" situation, and trees in the Row Plot Test experience a partial "mixed-family" and a partial "pure-family" situation. Family rank correlations for BAG (unadjusted for APA) were not significant between "mixed" and "pure" deployments within either the Design Study or the Nelder's Study, although the partial "mixed + pure" of the Row Plots correlated with both "mixed" and "pure" in the Design Study. However, significant correlations were obtained between the two studies for comparable deployments ("pure" versus "pure" and "mixed" versus "mixed"), indicating the repeatability of the interfamily competitive interactions.

Families 509 and 530 contribute greatly to the lack of a significant rank correlation between "mixed" and "pure" family deployments, with 509 being better in "pure" than in "mixed" situations of the Design Study and 530 being the opposite (Figure 4). The same relationship is found in the Nelder's Study. APA provides the mechanism for evaluating this relationship. The response of family 509 to changing local density is quite different in the "mixed family" competition of the Non-Contiguous Plot Test than in the "pure family" competition of the Block Plot Test, whereas family 530's response is quite similar in both situations (Figure 5). The key, however, is the response of 509 versus 530 in the mixed situation. When family 530 is planted in mixture with other families (such as 509), it grows faster than the other families under conditions of low competition (large APA) and captures growing space from the surrounding trees. In this sense family 530 is typical of the "competition ideotype" described for crops (Donald 1968). However, when 530 is grown in "pure" blocks it must compete with its aggressive siblings. Its mean APA per tree drops, and it performs no better across a wide range of APA's than family 509 competing with itself.

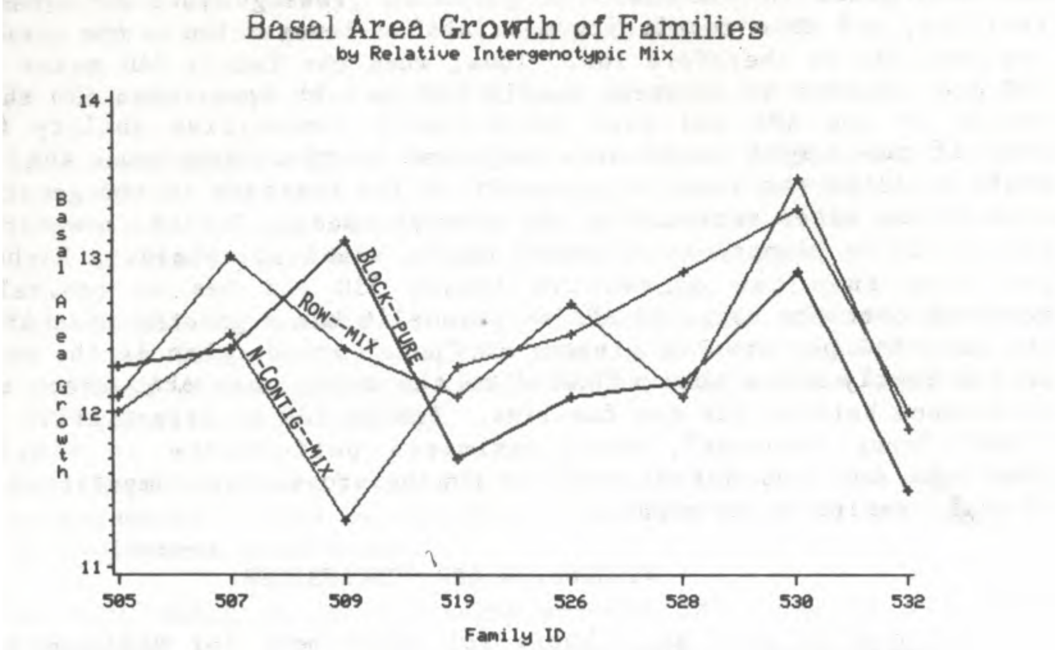

Figure 4. Family means for each of three progeny test designs having different family deployments in the Design Study.

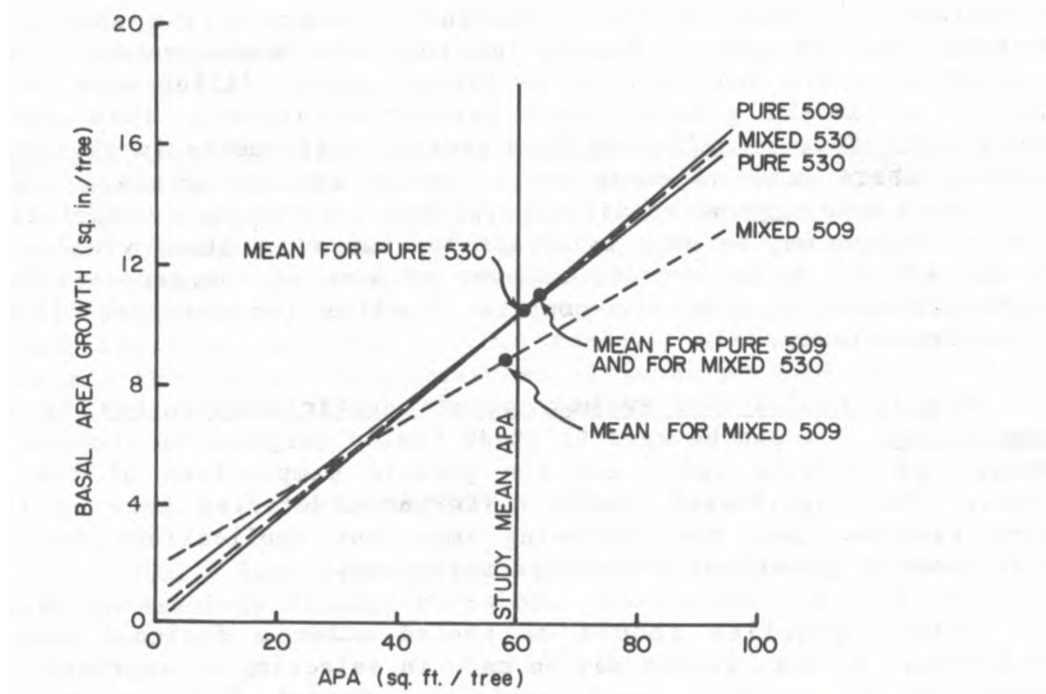

Figure 5. Family regression lines of Basal Area Growth from age 9 to 11 as a function of APA at age 9 for families 509 and 530 in the Non-Contiguous Plot Test (mixed) and in the Block Plot Test (pure).

Conversely, family 509 suffers from the competition of families like 530 when grown in mixture. It gives up growing space to trees from such families, and as a result its mean APA is lowered below the study mean APA. Its mean BAG is therefore low. Thus, when the family BAG means for 509 and 530 are compared in mixture, family 509 is much lower than 530 as a combined result of low APA and poor inter-family competitive ability (Figure 5). Even if the family means were adjusted to the study mean APA, family 509 would still be the loser as a result of its reaction to the genetic composition of the trees surrounding the growing space. Notice, however, that when family 509 is planted in a "pure" family stand it retains a higher mean APA per tree than the aggressive family 530 and has an equivalent growth response over the range of APA's. Since it has a greater mean APA than 530, its mean BAG per tree is greater in "pure" stands than is the mean for 530. If the family means were adjusted to the study mean APA, there would be no difference between the two families. Family 509 is illustrative of Donald's (1968) "crop ideotype", which maximizes performance in single variety plantings and does not do well in the heterogeneous competitive situations of mixed varieties or blends.

DISCUSSION AND CONCLUSIONS

<u>APA can be used as a basis for adjustment for differences in local density.</u> The method is not perfect. It should not be used as a simple covariate if family-by-APA interactions exist. Instead, the authors recommend subdividing the data into APA classes and examining family differences in growth within each class. Another complaint about the technique will be the fact that its calculation is dependent in part on the genetically-controlled trait "d.b.h.". Some of the genetic difference between families may be removed by the adjustment process. We are most interested here, however, in defining genetic differences in ability to utilize a limited growing space (growth efficiency when resources are limiting). This is different from genetic differences in ability to capture growing space from adjacent trees (prior aggressiveness). Both growth efficiency and aggressiveness contribute to a family's competitive ability, but the former may be more important for improving stand yields. Therefore, we are willing to accept the removal of some of the genetically-controlled aggressiveness in order to compare families for genetic differences in growth efficiency.

<u>APA is useful for evaluation of genetic differences in response to competition.</u> It can be used to study family response to changes in both the amount of growing space and the genetic composition of the surrounding trees. The significant family differences detected here in the loblolly pine examples have the following important implications for testing and deployment of genetically improved varieties.

First, families should be tested under a designed range of local densities. If not, errors may be made in selecting appropriate families for deployment at specific target densities. Second, families should be tested under a variety of competitive situations involving both pure block and family mixture plot designs. Otherwise, mistakes may be made in the family rankings for growth and in the families selected.

Some unanswered questions remain.

(1) Are there some families that perform best over a wide range of densities? Obviously, these would be the most desirable, because they would allow greater flexibility in deployment.

(2) If not, what type of family response is most desirable?

  (a) Are families that rank best in BAG at high densities (low APA's) the most shade tolerant, least nutrient demanding, etc.? If so, should they be selected to allow maximization of stand yield by packing more trees per acre?

  (b) Should one select for maximum growth per tree at low densities (high APA's), as this might allow the quickest achievement of merchantable size? Will such families require heavy and frequent thinning?

(3) Are there families that perform best in both mixed and pure family arrangements? Here again, these families would be most flexible in deployment strategies.

(4) If not, which is more desirable--crop ideotypes or competition ideotypes?

  (a) Crop ideotypes are those families that perform best in pure family blocks at high densities. Are they the more desirable type for total fiber yield?

  (b) Competition ideotypes are families that perform best in mixtures and/or low densities. Will they be best for rapid production of large-sized products?

<u>APA is easy to use and can be applied to data already collected.</u> Recent improvements in the APA computer program make it easily adaptable to any data set containing d.b.h. measurements and tree-position coordinates (usually row and column). It can be calculated for each living tree, which is desirable in progeny tests where analyses are based on individual-tree observations. Furthermore, it requires no special designs, so that it can be used immediately on existing progeny tests. Although refinements in calculations and the use of other measures of local density can and should be tested, APA is a useful tool for analyses of forest tree progeny tests today.

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