# Inheritance of Branching and Crown Characteristics in Slash Pine

**RAY K. STRICKLAND and RAY E. GODDARD**[1/]

Although we seldom find a tree that is "ideal" for use in production of a given product, we try to keep the "ideal" in mind. It is usually a tree that is perfectly straight; has little taper throughout its length; grows at a rate at least 50 percent greater than its neighbors; and has a narrow, well-formed crown.

This study is concerned with the crown, the photosynthetic surface of the tree; specifically the slash pine tree. Slash pine crowns come in many shapes--long and narrow to short and broad--with short slim branches to long thick branches and with branch angles ranging from a ramicorm condition to 90 degrees. Occasionally the tree with a perfect crown is found, but one with a perfect crown, near perfect bole form, and outstanding growth rate is very rare. This latter type is in a class all its own, a jewel to the tree breeder.

Why is the "ideal" slash pine tree so rare? If the characteristics tree breeders seek in select trees had high natural selection values when in combination, our pine forests would be full of "ideal" trees. Branches which are short, small in diameter and have a flat angle are "ideal". These traits effect wood quality but are quantitative genetic traits with low to moderate heritability and our "ideal" is of doubtful survival value to the tree.

This study was made to learn correlations among branching and crown characteristics,

[1/] The authors are Research Associate and Associate Professor respectively at the School of Forestry, University of Florida, Gainesville, Florida.

their heritabilities, and their effects on total volume.

Materials and Methods:

The data used in this report was collected during the spring of 1964 on one of four parts of an intensive culture study [2]/. The part measured was irrigated and contained four subplots; one was cultivated and fertilized, another cultivated alone, another fertilized alone, and the fourth neither cultivated nor fertilized (control). Treatment effects were not considered, but they do show up as replicate differences and line times replicate interactions.

Seedling lots used in this study were outplanted during the spring of 1961 and had grown four years from seed when measured. Included in the study were twelve seedling lots, nine half-sib (open-pollinated) progeny lines and three bulk check sources. The basic plot consisted of four seedlings from each lot; a total of 16 seedlings per lot were included in the study. Of the 192 seedlings planted, 188 survived. A 10 X 10 foot spacing was used.

The following tree measurements were taken on all 188 trees in the study:

1. Diameter breast high (inches and tenths).

2. Total height (feet and tenths).

3. Crown width/total-height ration (crown width taken at 1/2 total height)

The following branching characteristics were measured on every branch of the first whorl of the third growing season (from seed) on all 188 trees:

1. Branch length (inches).

2. Branch diameter (inches and hundredths taken at a point 1" from bole intercept).

3. Branch angle (to nearest 5 degrees).

A total of 793 branches were measured in this study. Records were kept in such a manner as to be directly read by a keypunch operator. Analyses were calculated, for the most part, using an I.B.M. 709 computer.

Results:

Regression analyses, correlations and analyses of variance were completed on these data.

A multiple (stepwise) regression analysis was calculated to discern the contribution of a number of crown characteristics to tree volume growth. The variables included in this analysis, the order in which they entered the stepwise regression, their regression coefficients and standard error of coefficients are shown in Table 1.

Table 1. Variables included in the stepwise regression analysis.

| Variable | Characteristic | Coefficient | Std. Error of Coef. | Order Entering | Multiple Correlation Coef. |
|---|---|---|---|---|---|
| Y | Approx. Volume | | | | |
| X-1 | Cr. Width/height | -60.2435** | 7.2693 | 3 | 0.510 |
| X-2 | Branch diameter | 42.7538** | 7.3192 | 1 | 0.322 |
| X-3 | Branch angle | 0.5730** | 0.0518 | 2 | 0.450 |
| X-4 | Branch length | 0.6857** | 0.1378 | 4 | 0.532 |

** Coefficient significant at the 1 per cent level.

[2]/ Appreciation is extended to special problems student Robert W. Simons (currently at N.C. State College, Raleigh, N. C.) for assistance with the field data collection and to Dr. Frank G. Martin of the Statistics Department at the University of Florida, Gainesville, Florida for his assistance with the analyses.

The standard error of "volume" was reduced from 15.99 to 13.57 by the regression. Volume in this study is approximated by the formula, diameter breast high squared times tree height ($dbh^2h$). The constant 0.005454 and the taper factor for each tree were excluded from volume computations. The mean of "volume" was 31.17; therefore, the coefficient of variation was 51 percent based upon the standard deviation of "volume" and 44 percent after regression. The coefficient of determination ($R^2$) was 0.283 indicating that the independent variables explain 28.3 percent of the variation in approximated volume. All the regression coefficients were highly significant. The prediction equation from this analysis was:

$$Y = -17.730 - 60.244X_1 + 42.754X2 + 0.573X_3 + 0.686X4$$

The regression analysis was based on individual branch measurements. There was an average of 4.18 branches measured per tree on the 188 trees.

Six of the 10 simple correlation coefficients among the five variables used in the multiple regression were significant (Table 2).

Table 2. Simple correlation coefficients between the variables used in the stepwise regression.

| Variable | | Cr. Width / Total Ht. $X_1$ | Branch Diameter $X_2$ | Branch Angle $X_3$ | Branch Length $X_4$ |
|---|---|---|---|---|---|
| Volume | Y | -0.201* | +0.322** | +0.080 | +0.313** |
| Cr. width/height | $X_1$ | - - | +0.127 | -0.079 | +0.140 |
| Branch diameter | $X_2$ | | - - | -0.560** | +0.848** |
| Branch angle | $X_3$ | | | - - | -0.554** |
| Branch length | $X_4$ | | | | - - |

* Significant at the 5 per cent level.
** Significant at the 1 per cent level.

Branch angle was not directly correlated with "volume" but was the second variable entering in the stepwise regression. This is no doubt due to the fact that branch angle is moderately correlated negatively with both branch diameter and branch length which are themselves very closely correlated positively. Graphs of these relationships are shown in Figures 1 and 2. These correlations are in close agreement with the findings of Barber (1964).

Analyses of variance calculated for both approximated volumes and crown width/height ratios showed highly significant differences between lines plus check sources for approximated volume and significant differences between lines for the crown width/height ratio (Table 3). Intraclass correlations (even considering block X line interaction as a phenotypic component) were considerably higher than expected among half-sib progeny lines. Means for lines and check sources (Table 4) showed a particularly wide range of values for approximated volume and a considerable latitude of variation for the crown-height ratio. Also an element of common environment (not explained) contributed to the low variances within progeny lines.

Three branching characteristics (branch diameter, branch length, and branch angle) were analyzed to discern differences between lines and between trees within lines. The results of these analyses along with intraclass correlations and heritability estimates are shown in Table 5. Variation due to differences in individual branches was the residual error term. There were significant differences between lines for branch diameter and branch angle but no significant differences between lines for branch length. All three variables had highly significant differences between trees within lines when tested with the residual error term.

Discussion:

This study was designed to determine if our slash pine selection and breeding program is emphasizing characteristics of tree crown form that are readily attainable. Barber (1964)

Table 3. Analyses of variance and intraclass correlation for crown width/height ratios and approximated volumes.

| Source of Variation | Degrees of Freedom | Mean Squares | Variance Components | Intraclass Correlation |
|---|---|---|---|---|
| Crown width/height | | | | |
| Replicates | 3 | 0.0267 | | |
| Lines | 8 | 0.0128* | $0.730 \times 10^{-3}$ | 0.312 |
| Rep. X Lines | 24 | 0.0045** | $0.609 \times 10^{-3}$ | |
| Trees/Lines | 103 | 0.0010 | $0.100 \times 10^{-2}$ | |
| Volume ($d^2h$) | | | | |
| Replicates | 3 | 1695.6 | | |
| Lines | 11 | 1182.1** | 64.48 | 0.266 |
| Rep. X Lines | 33 | 305.8 | 6.00 | |
| Trees/Lines | 140 | 171.6 | 171.64 | |

Table 4. Mean values of progeny lines and check lots.

| Progeny line | Volume ($d^2$ Xh) | Crown width / height | Branch Dia. (ins.) | Branch Lgt. (ins.) | Branch Angle (deg.) | Diameter Breast high |
|---|---|---|---|---|---|---|
| 1 | 29.7 | 39.2 | 0.552 | 25.6 | 61.7 | 1.68 |
| 2 | 32.8 | 41.3 | 0.574 | 27.5 | 56.8 | 1.73 |
| 3 | 45.2 | 40.6 | 0.565 | 26.9 | 56.4 | 1.99 |
| 4 | 42.2 | 41.9 | 0.581 | 27.9 | 55.9 | 1.92 |
| 5 | 31.6 | 47.4 | 0.625 | 29.9 | 51.8 | 1.78 |
| 6 | 29.2 | 44.6 | 0.544 | 27.4 | 53.8 | 1.63 |
| 7 | 32.5 | 40.1 | 0.572 | 26.8 | 54.4 | 1.76 |
| 8 | 12.1 | 44.3 | 0.476 | 24.2 | 55.3 | 1.12 |
| 9 | 27.1 | 45.5 | 0.567 | 29.2 | 56.8 | 1.58 |
| 10 | 24.4 | 42.1 | 0.537 | 25.5 | 56.4 | 1.54 |
| 11 | 31.8 | 45.1 | 0.576 | 29.6 | 52.5 | 1.70 |
| 12 | 18.9 | 43.9 | 0.573 | 27.0 | 51.7 | 1.37 |
| $\bar{X}$ | 31.2 | 42.6 | 0.564 | 27.4 | 56.0 | 1.65 |

Check lots, other lots are half-sib progeny lines.

Table 5. Analyses of variance and variance components for branch diameter, branch length, and branch angle. (Based on individual branch measurements)

| Source of Variation | Degrees of freedom | Mean squares | Variance Components | Intraclass Correlation | Heritability estimate |
|---|---|---|---|---|---|
| Branch Diameter | | | | | |
| Replicates | 3 | 0.125 | | | |
| Lines | 11 | 0.066* | $0.590 \times 10^{-3}$ | 0.0367 | 17.9% |
| Trees/Lines | 139 | 0.024** | $0.281 \times 10^{-2}$ | | |
| Branches/Trees | 609 | 0.013 | $0.127 \times 10^{-1}$ | | |
| Branch Length | | | | | |
| Replicates | 3 | 287.0 | | | |
| Lines | 11 | 179.1 | 1.16 | 0.0262 | 12.8% |
| Trees/Lines | 139 | 76.9** | 10.60 | | |
| Branches/Trees | 609 | 32.4 | 32.38 | | |
| Branch Angle | | | | | |
| Replicates | 3 | 48.33 | | | |
| Lines | 8 | 490.25* | 11.44 | 0.0829 | 33.2% |
| Trees/Lines | 104 | 213.13** | 27.21 | | |
| Branches/Trees | 446 | 99.28 | 99.28 | | |

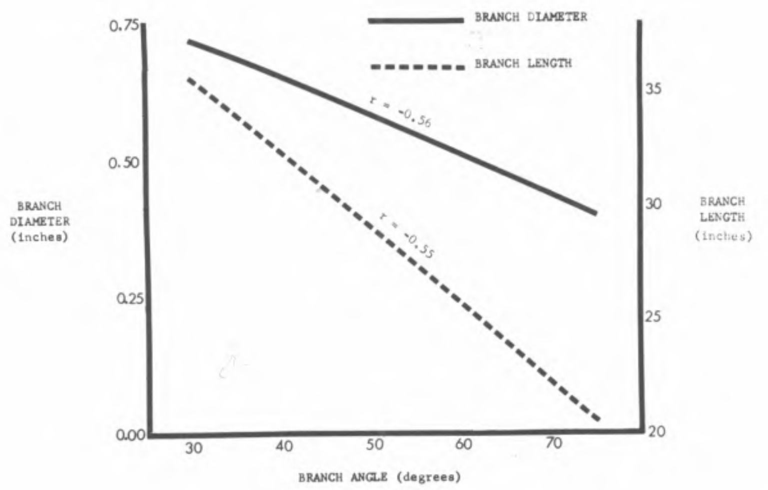


*Figure 1 -- The regression of branch diameter on branch angle ($Y = 0.9067 - 0.0062\ X$) and branch length on branch angle ($Y = 45.4400 - 0.3262\ X$).*

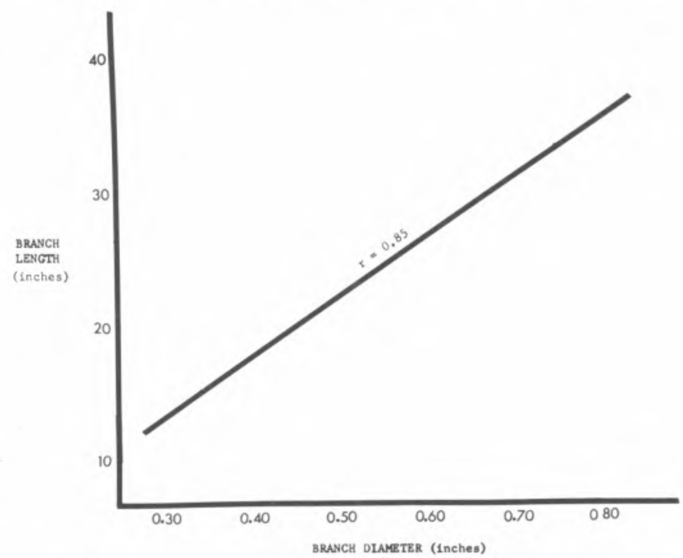


*Figure 2 -- The regression of branch length on branch diameter ($Y = 2.0927 + 44.8824\ X$).*

reported negative correlations between some of the branching characteristics that are considered desirable in the selection of plus phenotypes. He found correlation coefficients of r= +0.95 for branch diameter X branch length, r= -0.43 for branch diameter X branch angle and r = -0.48 for branch length X branch angle. Our correlations (r = +0.85, r = -0.56 and r = -0.55 respectively) were in close agreement with Barber's. Since we are attempting to select slash pine trees with branches that are short, flat angled and of small relative diameter our job, in this respect, is simplified. These traits are favorably correlated. However, large branches tend to go along with large volume. The correlation coefficients for these characteristics were; branch length X volume, r = +0.31 and branch diameter X volume, r = +0.32 (both highly significant). The coefficients of determination were only about 10 percent and rigorous selection for volume carried on simultaneously with selection for branching characteristics may prevent losses in volume. Occasional select slash pine trees are found that have large volumes and branches that are short, thin and flat angled when compared to the dominant population. These individuals rate high on our selection index and if they are also straight, they are quite rare and extremely valuable.

The multiple (stepwise) regression analysis indicates that all of the dependent variables; crown width/total height ratio, branch diameter, branch angle, and branch length either add to or detract from "volume". The ratio of crown width to tree height was the only variable significantly correlated negatively with "volume". It also has a negative regression coefficient in the stepwise regression. Trousdell et al. (1963) concluded that the ratio of crown width to tree height was generally higher for loblolly pine progeny groups with short trees than for the tall groups. The close relationship between tree height and volume coupled with the above observation is an explanation of the negative relationship found. Branch angle, which is not directly correlated with "volume", contributes significantly in the stepwise regression. The reason for this is the close correlations between the three branching characteristics. Two of these, branch length and branch diameter were significantly correlated positively with "volume" However, only about 28 percent of "volume" variation is explained by the inclusion of all four independent variables in a multiple regression analysis with this trait.

Analyses of variance for the "volumes" and crown width/tree height ratios showed significant differences between lines for these traits and also much higher intraclass correlation coefficients than expected. The variance components from these data cannot be used to estimate "volume" and crown width/height ratio heritabilities because of an unusually wide range of mean values and relatively small components of phenotypic variance when compared to the additive component. The unexplained uniformity within lines plus a wide range of variation between lines makes such an estimate invalid. Using the formula for estimating heritability of half-sib lines (H = 4 X additive genetic variance/total variance) would give values greater than one.

Trees used in this study were among the early slash pine selections and were selected primarily on the basis of volume growth. Since several persons selected the trees it is probable that volume was sacrificed for form in some instances and form was sacrificed for volume in other instances. This is still the general case since it is very difficult to find all of the desirable characteristics of growth and form in one slash pine tree. It is probable that the branching traits themselves represent a random sample from the dominant slash pine population. Heritability estimates for the three branching characteristics were made on this assumption. The estimated variance components were obtained following the procedures outlined by Henderson (1953).

The heritability estimates found in this study were: branch diameter 18 percent, branch length 13 percent, and branch angle 33 percent. Comparisons of these findings with the results of other investigations are shown in. Table 6.

Table 6. Comparison of heritability estimates on crown and branching characteristics of coniferous species by five investigators.

| Investigator | Species | Trait | Heritability Broad Sense | Heritability Narrow Sense |
|---|---|---|---|---|
| Barber (1964) | Pinus elliottii | Cr. width/ht. | | 0.16 & 0.19 |
| Toda (1958) | Cryptomeria | Crown diameter | 0.61 | |
| | | Branch angle | 0.72 | |
| Trousdell et al. (1963) | Pinus taeda | Cr. width/ht. | | 0.17 & 0.34 |
| Ganzel (1965) | Pinus elliottii | Branch diameter | 0.31 & 0.48 | |
| | | Cr. width/ht. | 0.40 & 0.47 | |
| This report | Pinus elliottii | Branch diameter | | 0.18 |
| | | Branch length | | 0.13 |
| | | Branch angle | | 0.33 |

The analyses of variance based upon the measurement of all the branches within the first major whorl of the third growing season showed that there is some consistency of measurements within trees. Branch diameter, branch length, and branch angle analyses showed highly significant differences between trees within lines for these traits. This was expected on the basis of half-sib lines and bulk check sources.

Repeatability of measurements on individual trees within lines can be calculated from these data. This was done and the repeatability results were: branch diameter, 18%; branch length, 25%; and branch angle, 22%. These estimates were obtained by dividing the variance component for trees within lines by the variance component for branches within trees. These repeatabilities indicate that there is considerable variation in the individual traits within a tree and that the measurement of a number of branches is required to obtain a reliabl mean for an individual tree.

## SUMMARY

Individual branches of the first major whorl of the third growing season (from seed) were measured on nine half-sib progeny lines and 3 bulk check sources. Measurements taken on the branches included branch diameter, branch length and branch angle; whole tree measurements included diameter breast high, total height and crown width at height/total height ratio. Multiple regression analysis showed that all three branching characteristics and the crown-width ratio contributed significantly to the prediction of approximated volume (dbh$^2$ X ht.). The four independent variables accounted for 28 percent of the variation in "volume" (r = 0.53). Correlations between the three branching characteristics showed negative relationships between branch angle and branch length (r = -0.55) and between branch angle and branch diameter (r = -0.56); branch diameter and branch length themselves were closely positively correlated (r = +0.85)(the greater the branch angle from the vertical, generally the shorter and thinner the branches). Branch length and branch diametei were both positively correlated with volume and have coefficients of determination of about 10 percent each. Breeding for decreased branch size may concurrently decrease volume unless

this selection pressure is coupled with rigorous selection for volume.

Heritability estimates for branch diameter, branch length and branch angle were 18, 13 and 33 percent respectively. Repeatability of measurements on individual trees for the above traits were 18, 25 and 22 percent respectively indicating that it is necessary to measure a number of branches for each trait in order to obtain reliable tree means.

## Literature Cited


Barber, J. C., 1964. Inherent variation among slash pine progenies at the Ida Cason Callaway Foundation. Southeast For. Expt. Sta., U.S. For. Serv. Res. Paper SE-10, 90 pp illus.

Gansel, C.R., 1965. Inheritance of stem and branch characteristics in slash pine and relation to gum yield. Eighth Sou. Conf. on For. Tree Improvement. Savannah, Georgia, June 16-17.

Henderson, C.R., 1953. Estimation of variance and covariance components. Biometrics 9:226-252.

Toda, R., 1958. Variation and heritability of some quantitative characters in Cryptomeria. Silvae Genetica 7:87-93.

Trousdell, K.B., K.W. Dorman and A.E. Squillace, 1963. Inheritance of branch length in young loblolly pine progeny. Southeast For. Expt. Sta., U.S. For. Serv. Res. Note SE-1, 2 pp.