INHERITANCE OF BRANCHING AND CROWN TRAITS AND THEIR RELATIONSHIP TO GROWTH RATE IN LOBLOLLY PINE

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Abstract:-- Sweep, branching and crown traits were measured in ten-year-old loblolly pine *(Pinus taeda* L.) progeny tests for the purpose of studying inheritance patterns, for comparing them with growth characteristics and to study their genetic interrelationships. Branching and crown traits were analyzed as branches per whorl, branches between whorls, whorls per unit of height, branch diameter, live crown width, branch angle, branch diameter per unit volume, volume per unit of live crown width, and branches per unit of height. Of these traits, only branch angle, live crown width and volume per unit crown width were moderately heritable (greater than 0.10).

Genetic correlations with volume were generally favorable such that selection for volume should result in flatter branches, fewer branches per unit of height, greater stem volume per unit of crown width and lower branch diameter per unit of volume. Genetic correlations between North Carolina and Mississippi for branching and crown traits exhibited values less than 0.5 for all traits except branch angle, which had a correlation of 0.7.

Branch angle is the only trait which showed a consistent decline (perhaps a random effect) over two generations of selection, i.e., branch angle for improved material was steeper than for unimproved. While live crown width and branch diameter increased for improved material, this increase was more than offset by gains in stem volume such that volume per unit of live crown width increased and branch diameter per unit of volume decreased.

Key Words: *Pinus taeda,* tree improvement, branching, straightness, crown.

INTRODUCTION

In general, U.S. loblolly pine (Pinus taeda L.) improvement programs have not chosen to improve branching and crown characteristics through targeted selection programs. Most often, during selection for volume in tree improvement cooperative programs, some phenotypic selection for crown form has been practiced but with minor weighting. Realized gain from this phenotypic selection for crown form has not previously been estimated.

Improvement in branching and crown characteristics is of interest to decrease knot size and frequency resulting in enhanced value for solid wood products. Knotiness produces increased grain distortion, pitch deposition and compression wood and reduces wood strength and

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usually decreases appearance value (von Wedel et al. 1967). To undertake an improvement program for branching and crown characteristics, one must ascertain the genetic architecture of the traits and the measurement cost. From these factors, calculations can be made of the cost associated with a given amount of genetic alteration of the characteristic. Projecting benefits from the genetic alteration through to solid wood products would allow consideration of investment in genetic change in branching and crown characteristics. This study was designed to provide the background data necessary to determine the genetic architecture and measurement time of several branching characteristics.

MATERIALS AND METHODS

The four progeny tests measured in this study were in Kemper County, Mississippi (2), and in Jones and Beaufort Counties in North Carolina. The Mississippi tests were planted in 1986 at 2.1m by 3.4m spacing and the North Carolina tests were planted in 1985 at 2.4m by 3.0m spacing. The family material in the tests is open-pollinated coastal North Carolina families from Comfort, N.C. and Lyons, GA seed orchards. The design at each test is randomized complete blocks with eight replications and five trees per family per replication. The five trees were planted at random in the replications, i.e., noncontiguous plots.

Traits measured in the winter of 1995-1996 included height, diameter at breast height, sweep, branch angle, width of live crown, number of whorls, number of nodal branches, number of internodal branches and diameter of branches. Height in meters and DBH was measured in centimeters. Sweep was measured as the maximum deviation (in two centimeter classes) from a 2.4m straight-edge anywhere in the first four meters of height. For charting of sweep means it was assumed that the mean of each category is the midpoint of that category, i.e., the mean of the 0-2 cm category is 1 cm etc.. Branch angle (tallied in six fifteen degree classes with zero being the closest to horizontal) was measured at the first major whorl above three meters at the point where the branch met the stem. For charting of branch angle means it was assumed that the midpoint of the category represents the mean of that category, i.e. the mean of the first category is 7.5 degrees and the mean of second is 22.5 degrees, etc.. Width of live crown in meters was measured down the row and perpendicular to the row. A whorl was defined as at least three major branches located at the same height on the tree. Nodal branches were counted as total number of branches present at whorls. Internodal branches were counted as the total number of branches between whorls. Branch diameter was measured (in centimeters) on the three largest branches beginning at three meters and ending at four meters in height. Whorls, nodal branches and internodal branches were measured beginning at three meters and ending at seven meters in height.

These measured variables were used to create thirteen analysis variables. The analysis variables were branch angle, branches between whorls, branches per unit of height, branches per whorl, whorls per unit of height, diameter at breast height, mean branch diameter per unit of volume, height, mean crown width, mean branch diameter, volume, sweep and volume per unit of live crown width. The analysis model was

$$y_{ijkl} = \mu + T_i + B_{ij} + gca_k + t_i{*}gca_k + b_{ij}{*}gca_k + e_{ijkl}$$

where: μ is an overall mean,

T_i is the fixed effect location,

B_{ij} is the fixed effect block within location,

gca_k is the random effect general combining ability ~ $N(0,\sigma^2_{gca})$,

$t_i{*}gca_k$ is the random effect of the interaction between location and gca ~ $N(0,\sigma^2_{tg})$,

$b_{ij}{*}gca_k$ is the random effect of the interaction between block within location and gca ~ $N(0,\sigma^2_{bg})$ and

e_{ijkl} is the random error associated with the l^{th} observation of the k^{th} gca in the j^{th} block of the i^{th} location ~ $N(0,\sigma^2_e)$.

The analysis produced restricted maximum likelihood estimates of the variance components (Giesbrecht 1983) and best linear unbiased predictions of the gca's (White and Hodge 1989). Individual tree heritabilities were estimated as $3\sigma^2_{gca}/(\sigma^2_{gca}+\sigma^2_{tg}+\sigma^2_{bg}+\sigma^2_e)$, assuming that the genetic correlation among open-pollinated siblings is between that of half-sibs and full-sibs (Squillace 1974) and breeding values were estimated as 1.5 times gca. Pearson produce moment correlations among the predicted breeding values were used as estimates of genetic correlations. For genetic correlations estimated by Pearson product moment correlation, there may be some shrinking of the correlation for sets of breeding values known with little precision as in low heritability traits with few observations.

RESULTS AND DISCUSSION

Genotype-Environment (State) Interaction:

Genetic correlations between regions were generally less than 0.50 except for branch angle which had a reasonably high genetic correlation between regions of 0.69 (Table 1). These low correlations suggest genotype-environment interactions of sufficient magnitude that could impact tree improvement strategies. Consequently, heritability and genetic correlations are discussed on a regional basis and no analyses were done across regions.

Heritability:

The tendency is for heritabilities to be slightly lower in Mississippi than in North Carolina. Heritabilities for branching and crown traits were disappointing as a whole (Table 2). Of the crown traits, only branch angle and mean crown width are as heritable as the growth traits. Branches per whorl, branches between whorls and branch diameter as a function of stem volume had very weak heritability (<0.05) at both locations. Volume per unit of crown width had heritability estimates slightly lower than those for growth traits. Frampton and Huber (1995) found branches/m of height, whorls/m and branch angle to exhibit higher full-sib family and clonal mean heritabilities than those for growth rate in four-year-old rooted cutting trials in North Carolina. Their results may differ from these because their heritabilities are influenced by specific combining ability and/or an effect due to rooted cuttings versus seedlings in our study. McCrady and Jokela (1996) concluded that, among five families chosen for extremes in growth potential, there were significant

Table 1. Breeding value correlations for Mississippi and North Carolina, above and below diagonal respectively, and between regions, on the diagonal'.

	Branch Angle	Intern. Br./Whrl	Branch./ m Ht.	Branch./ Whorl	Whorls/ m Ht.	DBH	Br.Diam/ Volume	Height	Crown Width	Branch Diameter	Sweep	Volume/ Tree	Volume/ CrownW
Branch Angle	0.69	.	0.05	0.25	-.25	-.26	0.26	-.26	-.39	0.11	-.17	-.27	-.08
Intern.Bran./Whorl	0.03		.	.	.	.	.	.	.	.	.	.	.
Bran./m of Height	0.01	-.25	0.46	0.28	0.83	-.20	0.26	-.56	-.51	-.28	-.10	-.30	-.02
Branches/Whorl	-.12	-.13	0.06	0.44	0.03	-.02	-.02	0.12	-.26	-.08	-.11	0.02	0.22
Whorls/m of Ht.	-.12	-.55	0.87	-.19	0.36	0.16	-.21	-.15	-.19	-.31	-.11	0.09	0.28
DBH	-.21	-.00	-.42	-.00	0.05	0.43	-.80	0.46	0.71	0.39	0.52	0.97	0.82
Branch Diam./Vol.	0.21	0.06	0.06	0.09	-.21	-.78	0.42	-.73	-.55	0.05	-.28	-.84	-.78
Height	-.26	0.07	-.54	-.09	0.09	0.79	-.84	0.46	0.49	-.03	0.02	0.63	0.50
Crown Width	-.33	0.07	-.47	0.02	-.12	0.74	-.40	0.62	0.49	0.51	0.49	0.73	0.24
Branch Diam.	0.22	0.26	-.27	0.12	-.33	0.39	0.00	0.10	0.47	0.22	0.31	0.36	0.09
Sweep	0.12	-.04	-.08	0.10	-.09	0.25	0.02	0.22	0.48	0.12	0.46	0.45	0.33
Volume/Tree	-.24	0.00	-.46	-.02	0.06	0.98	-.77	0.86	0.75	0.31	0.29	0.45	0.83
Vol./m of Crown	-.07	-.04	-.30	-.06	0.18	0.83	-.83	0.77	0.28	0.08	0.00	0.84	0.28

Branch Angle is branch angle in 15° units from 0, near horizontal, to 5, near vertical.
Intern.Bran./Whorl is number of internodal branches divided by number of whorls.
Bran./m Height is number of nodal plus internodal branches divided by four meters.
Bran./Whorl is the average number of branches per whorl.
Whorls/m of Ht is the number of whorls divided by four meters.
DBH is diameter at breast height in centimeters.
Branch Diam./Vol. is branch diameter in centimeters divided by stem volume in cubic feet.
Height is height in meters.
Crown Width is average live crown width, down the row and across the row, in meters.
Branch Diam. is the average diameter of the three largest branches in centimeters.
Sweep is sweep as deviation from an 2.4 m straight-edge in two centimeters classes.
Volume/Tree is stem volume in cubic m.
Vol./m of Crown is stem volume in cubic feet divided by average live crown width.

'Values on and above the diagonal are significant at a = 0.10 if the absolute value is greater than 0.30.
Values below the diagonal are significant at a = 0.10 if the absolute value is greater than 0.28.

Table 2. Individual tree heritability for growth, sweep and branching characteristics in four 10 to 11-year-old progeny tests in North Carolina and Mississippi.

	North Carolina	Mississippi
Volume	.20	13
DBH	.21	.14
Height	.17	.08
Sweep	.25	.12
Branch Angle	.18	14
Crown Width	.17	.15
Volume per m Crown Width	.14	10
Branch Diameter	.08	.02
Branch Diameter per Cubic m Volume	04	04
Number of Whorls per m Height	08	.06
Branches per Whorl	03	04
Internodal Branches per Whorl	02	00
Branches per m Height	.09	04

differences among families for height growth but none for most branching characteristics after four years in the field. Other conifer species have shown the tendency for high heritability of branch angle but low to moderate heritability for branch diameter and frequency (Adams and Morgenstern 1991; King et al. 1992)

Genetic Correlations Among Traits:

There are several significant trait-trait, breeding value correlations within regions (Table 1). Branches *per* m of height *has several significant correlations with growth components, being* negatively correlated with height, mean crown width and volume in both Miss/Ala and North Carolina. Branches per meter is strongly correlated with whorls per m and not correlated with branches per whorl, suggesting that branchiness is primarily a function of variation in whorls per meter. The significant negative genetic correlation of branches per unit of height and mean crown width may suggest that foliage may be displayed either by increasing the number of branches or by increasing the branch length.

Branch angle is moderately, negatively correlated with crown width and growth for both regions such that flatter branch angles tend to be associated with wider crowns and bigger trees. Whorls per unit height is significantly and negatively associated with mean branch diameter in both regions while being uncorrelated with growth rate. Branches per unit height in both regions is positively associated with whorls per unit of height while being negatively associated with growth traits and mean crown width.

Mean crown width and mean branch diameter are associated with growth rate in both regions such that larger trees tend to have wider crowns and larger branches. Sweep has positive and moderate correlations with volume and mean crown width in both regions. This association implies that genetically superior volume growers tend to have slightly greater sweep.

The genetic correlations of crown and branching characteristics with volume indicate that selection for volume will result in fewer branches per unit of height, larger mean crown width and larger mean branch diameter. The relationships of volume with mean crown width and mean branch diameter are mitigated when considering the results for volume per unit of crown width and mean branch diameter per unit of volume. The results for volume per unit of crown width and mean branch diameter per unit of volume suggest that, while larger crown width and mean branch diameter are associated with larger stem volume, selection for volume will, on average, produce more stem volume per unit of crown width and smaller branch diameter per unit of volume. Trousdell et al. (1963) found similar results for loblolly.

Internode length is genetically independent of volume so that selection for internode length could proceed while maintaining volume gains. Increased internode length would provide more clear wood between nodes for shop grade lumber. This gain in internode length would be difficult without increasing branch diameter and gains may be slow due to little variation.

Branch angle and internode length are the two branching and crown characteristics that are not genetically correlated with volume. Since these characteristics are uncorrelated with volume, selection for volume allows these traits to fluctuate at random; thus the need to consider selection for these traits. Other branching and crown characteristics are genetically associated with volume so that favorable responses should result from volume selection.

Genetic Variation:

Besides heritability and intercorrelation among traits, it is also important to know how much exploitable variation there is in a breeding population in order to know how the trait will respond to selection and to determine how much gain can be made in seed orchards. Plots of some different generation and orchard production types are plotted in Figure 1 in order to illustrate the degree of variation for six traits of interest. In the interest of brevity not all traits are plotted and only results from the North Carolina trial are shown but the general results in the Mississippi trials was the same. The best and worst full-sibs are averages of the breeding values of the two best parents and the two worst parents, respectively. Differences between these two bars on the graphs indicate the degree of variability still left among potential crosses in the 2nd generation group of parents. They also illustrate the potential for improvement if one is able to make controlled crosses on a commercial scale.

The trends were similar to those for heritability of the same traits, i.e., traits with low heritability have little exploitable variation. There was surprisingly little variation in branches per whorl, whorls per meter of height, branch diameter and (though it is not graphed) branches per meter of height. There is still considerable variation and potential gain to be made in volume, sweep and branch angle. Sweep has the greatest relative variation left in the population in spite of significant gains after two generations of selection. Branching characters as a function of tree size still have considerable variation. The only traits where the worst possible full-sib cross was not worse than the unimproved check was volume,where the worst full-sib was equal to the unimproved check, and volume per meter of crown width where the worst possible cross was better than the unimproved check.

Figure 1. Genetic variation for various genotypes in coastal North Carolina, 10 to 11-year-old tests. **Unimp** = unimproved check, **1st-Gen Rog** = mix of families from a rogued 1st generation seed orchard, **2nd-Gen Unrog** = mix of families from an unrogued 2nd generation seed orchard, **Worst and Best Full-sib** = Average breeding values of the worst two parents and best two parents in the 2nd generation, respectively, or what could be achieved with controlled mass pollination in an orchard.

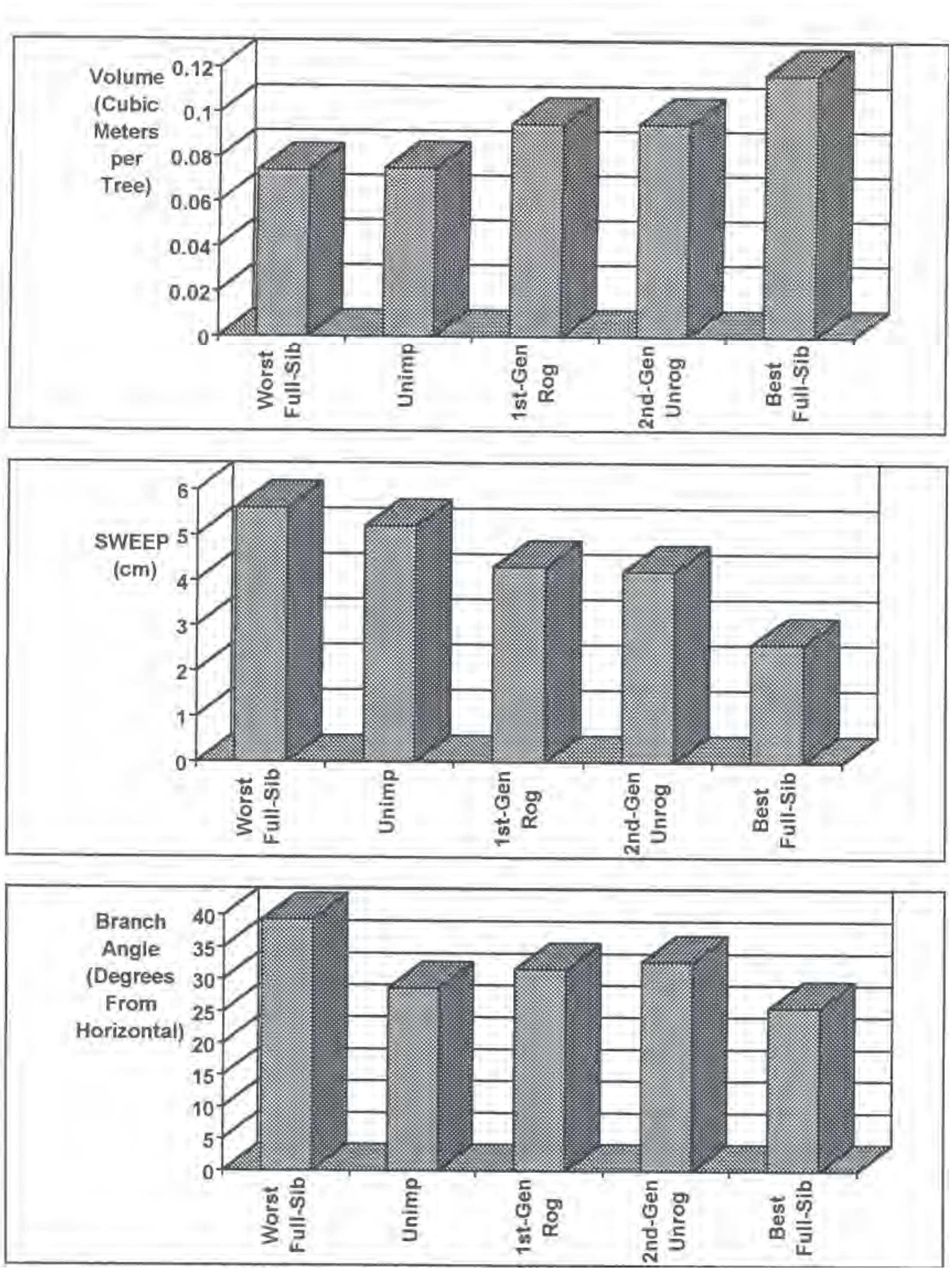
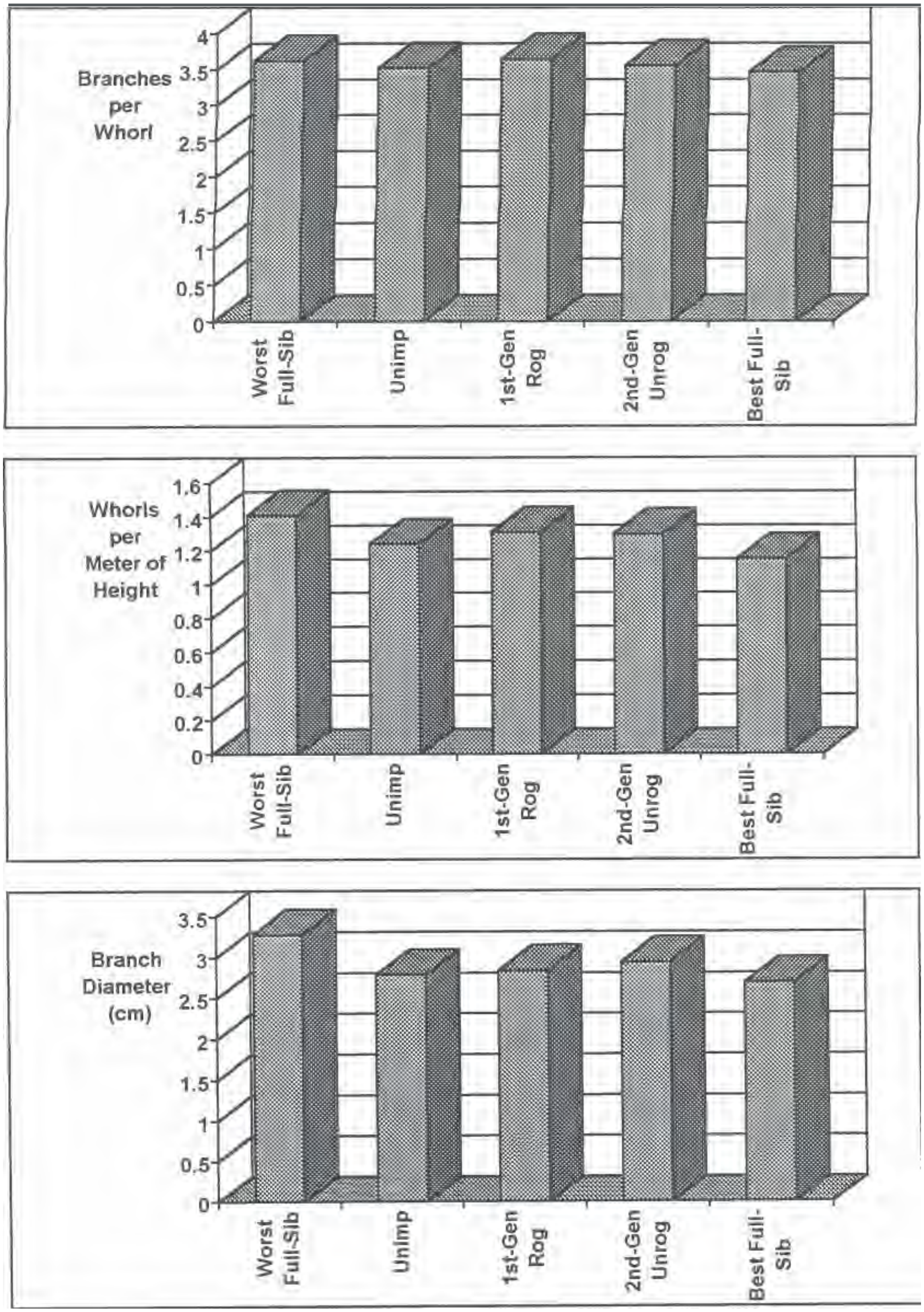


Figure 1. (cont.)



Seed Source Differences:

In the Mississippi trials first generation orchard checks of both local and coastal North Carolina provenances were included (Table 3). In general, the branching and sweep traits of the N.C. coastal source were more favorable than those of the central Mississippi source. Campbell, et al. (1995) reached the same conclusion about these two sources

Table 3. Differences between first generation, orchard mix check lots for N.C. coast and central Mississippi seed sources at age 10 in two tests in Kemper county Mississippi.

	Mississippi Source	N.C. Source
Branch Angle (degrees from horizontal)	34	27
Branches per Meter of Height	5.5	5.8
Whorls/Meter	1.2	1.8
Branch Diameter cm/Cubic m of Volume	.92	.75
Volume Cubic Meters/Meter of Crown Width	.94	1.02
Sweep (cm)	5.1	4.4
Volume Cubic Meters per Tree	.092	.098

Measurement Time:

Measurement time for the total of branching and crown traits was twice that of typical progeny test measurement which includes height, DBH, rust, condition code and sweep.

CONCLUSIONS

1. Heritabilities for several important branching traits such as branchiness, whorl frequency and branch diameter were significantly lower than those for stem height, diameter and volume. These branching characteristics also exhibited little genetic variability to exploit for genetic gain. Branch angle and crown width had heritabilities similar to those for height and volume and there is considerable genetic variation in branch angle that could be exploited if so desired. Sweep had moderate heritability and variability for further improvement in spite of the fact that improvements in through two generations of selection have been impressive.
2. Branch number, branch diameter and branch angle as measured in this study took twice as long to measure as the usual height, diameter, fusiform rust, condition code and sweep.
3. Branch angle was weakly but negatively correlated with growth rate (bigger trees tending to have flatter branch angle). In spite of the correlation, the second generation check had steeper branch angle than the first generation check which had steeper branch angle than the unimproved check, perhaps due to a random effect.
4. Bigger families tended to have wider crowns, and larger branch diameter in absolute terms but, when adjustments were made for size, they tended to have smaller branches and narrower crowns for their size and fewer branches per meter of height than smaller families. Therefore, selection for growth rate should result in improved branching characteristics.
5. In the Mississippi trials (there was no Mississippi material in the N.C. trials) the North Carolina coastal seed source had generally better quality characteristics with flatter branch

angle, less sweep, smaller branches for their size, slightly more volume per crown width but slightly more branches per meter of height than the local seed source.

The results of this study indicate that, barring significant economic impact for branching and crown traits, selection for volume is sufficient for these genetically correlated traits. The economic impact of the traits not genetically correlated with volume (internode length and branch angle) should be evaluated. Sweep should continue to receive weight in selection processes because of a modest but positive correlation with volume. The weights should be chosen according to the relative economic importance of growth rate and straightness.

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