PHENOTYPIC VARIATION AND RELATIONSHIPS OF SEVERAL VARIABLES IN SHORTLEAF PINE IN OKLAHOMA

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CHAPTER I

INTRODUCTION

The forest industry complex in Oklahoma is in a constant state of growth to meet present and future demands for wood products. The addition of several new mills, including one of the world's largest paper mills, calls for increased wood production per acre. This demand will be met only by tree improvement programs and more intense management practices. At present most of Oklahoma's five million acres of commercial forests are growing shortleaf pine (*Pinus echinata* Mill.) in pure or mixed stands.

A tree improvement program was initiated in the fall of 1966 by Oklahoma State University's Forestry Department for the production of improved shortleaf and loblolly pine seed. At the time of conception it was assumed that Oklahoma contained more than one population of shortleaf pine because of geographic difference. Therefore, two seed orchards were established, one for areas higher than 1000 feet above sea level, or north of the Ouachita mountains, and another for areas less than 1000 feet above sea level. This study was begun during the same period to aid in determining if this division of the seed orchards was necessary.

Increased wood production depends upon many variables. Several, of the more important of these are:

1. Specific gravity
2. Summerwood percentage
3. Rings per inch
4. Tracheid length

The pattern of variation and relationships between these variables are of great importance to a tree improvement program (1) (2).

Specific gravity is of major importance to both lumber and pulp production. An increase in specific gravity yields lumber with greater strength properties (3) and wood dry weight can be increased as much as 50 pounds per cord with an increase of 0.01 in specific gravity (4). Summerwood percentage has been found to be strongly associated with specific gravity by many researchers (5) (6) (7). Rings per inch (a measure of radial growth) is of major importance in increasing wood production per acre. Tracheid length and wall thickness have been used by the paper industry to aid in determining quality, strength, and type of paper produced. Summerwood produces tracheids which are thicker walled, thus, influencing strength properties of both paper and lumber. Studies of the variables mentioned above for other species in other areas have shown considerable variation both among-stands and between-trees within a stand (8) (9) (10).

Basic to the success of any tree improvement program is an understanding of the natural variation in the species of interest and the factors which influence that variation in the important traits. To aid in determining this information, this study was initiated with the following objectives:

1. To determine the phenotypic patterns of geographic

variation, and attempt to explain the causes of such variation.

2. To determine if the phenotypic variance is of the kind and magnitude to imply the presence of usable genetic variance.

3. To determine the relationships among specific gravity, summerwood percentage, rings per inch, and tracheid length.

CHAPTER II

METHODS AND MATERIALS

Population Sampled and Stratification of Stands

The geographic area studied includes most of southeastern Oklahoma on which shortleaf pine grows commercially (Figure 1). Over this area elevation ranges from 350 feet above sea level in the southeast to 2400 feet above sea level in the Ouachita mountains. The soil types range from coastal-plain in the southeast to Ouachita highland soils to the west and north. Annual rainfall for this area varies from 55 inches in the southeast to 38 inches in the west. Because of the wide range of environmental variables and past cutting practices, site indices for shortleaf pine range from 26 feet to 75 feet.

Stands were established at the intersection of every fifteen minutes of longitude and latitude if shortleaf pine were present (Figure 1). Fifty stands were established with each stand containing at least 40 acres of timber. In areas with extreme topographic variation, two stands were established at lower and higher elevations. Because of loss of sample material, Stands 2 and 50 were not used in the analyses.

Selection of Trees

Ten dominant and codominant trees were selected from each stand, provided they were not open-grown. The likelihood of similar parentage

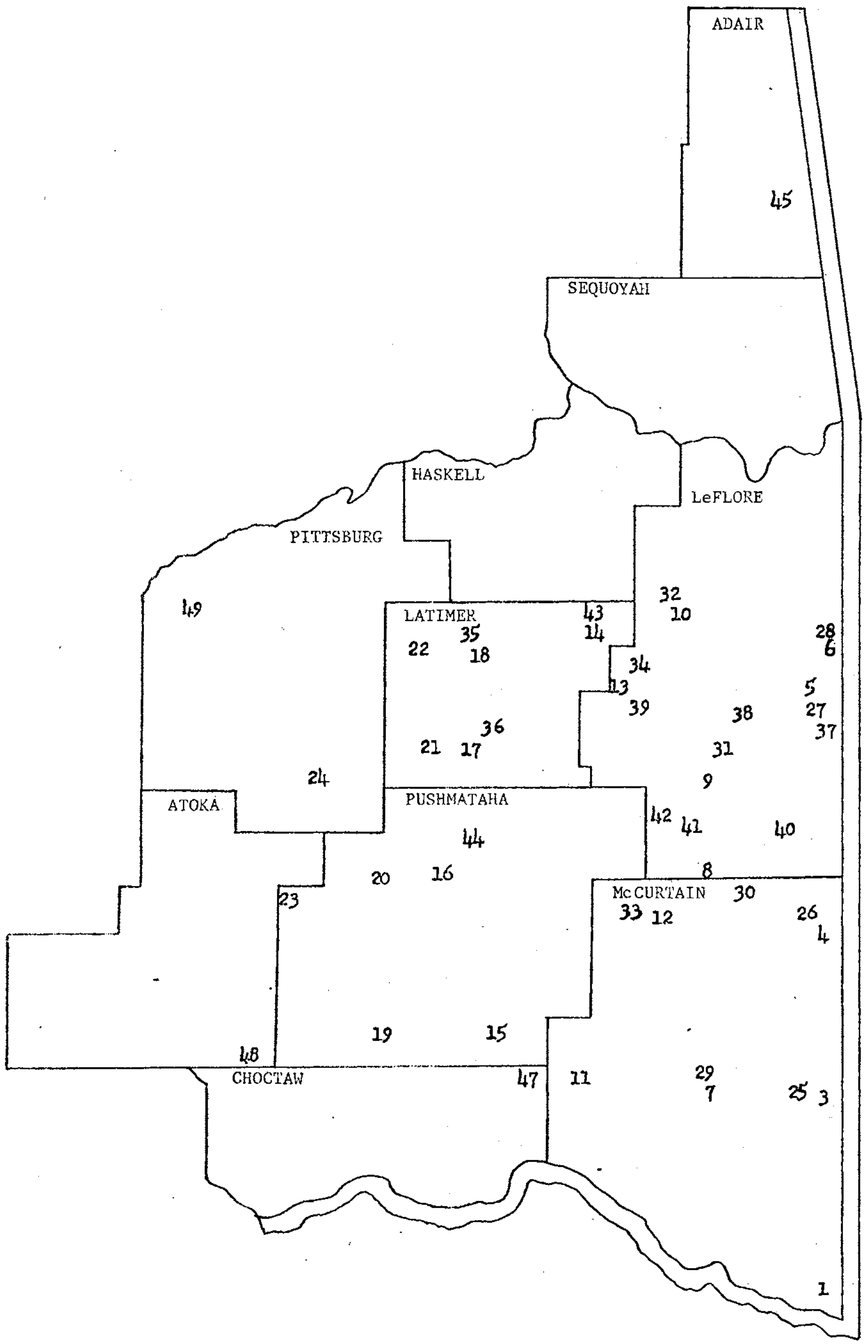

Figure 1. Approximate Location of the Study Stands by Counties in Southeastern Oklahoma (Stand 46, Located in Ottawa County is not Illustrated).

of selected trees was minimized by selecting sample trees a minimum of 200 feet apart.

Collection and Preparation of Wood Samples

A 12mm increment borer was used to core each sample tree, with one core taken completely through the tree at diameter breast high; i.e., four and one-half feet above the ground. Sample cores were labeled and placed in cold storage at thirty-five degrees Fahrenheit until analysis could be performed.

Cores were prepared for analyses by removing bark and dividing the core at the pith. Each core half was then separated into two segments as follows:

1. Segment 1 - growth rings 0-10, i.e., juvenile wood.
2. Segment 2 - growth rings 11-20, i.e., mature wood.

Stand, Tree, and Environmental Variables

Data collected at each sample tree included the following:

1. Total height to nearest tenth of a foot.
2. Diameter breast high to nearest tenth inch.
3. Basal area per acre based on a ten-factor prism.
4. Site index using age and height of ten dominant and codominant trees.
5. Elevation to nearest 20 feet.
6. Age of tree from ring count of core.

For each stand, average annual rainfall was obtained from the nearest weather recording station. Table I contains the tabulation of longitude, latitude, average elevation, and average annual rainfall data, for the 48 stands.

Wood Quality Variables

Extracted and unextracted specific gravity was determined by the maximum moisture technique as described by Smith (11). Each ten-year segment was extracted, using the modified ASTM (12) procedure as outlined by Goggans (13) which removes all of the alcohol-benzene and water soluble extractives. Extractive content and its relationship to the other variables in this study was reported in a paper by Posey et al. (14).

Summerwood percentage was determined for each segment using a modified bisecting scope fitted with a vernier caliper. Width of springwood and summerwood to the nearest thousandth inch was measured.

Tracheid length was determined from the summerwood of the mature wood segment containing rings 11-20. Slivers of summerwood from each of the 11th, 15th, and 20th rings of each mature wood segment were placed in labeled vials and macerated. The maceration procedure used was that described by Buxton (15). Two slides were prepared for each side of each core for a total of four slides per tree. The first 25 whole tracheids were measured on each slide. A "Bioscope" was used to project tracheids onto a graduated "bull's eye" scale for measurement (16).

TABLE I

SUMMARY OF LONGITUDE, LATITUDE, ELEVATION AND RAINFALL BY STANDS

Stand	Longitude	Latitude	Average Elevation	Annual Rainfall
1	94° 30'	33° 45'	403 ft.	46 in.
3	94° 30'	34° 15'	854 ft.	51 in.
4	94° 30'	34° 30'	874 ft.	51 in.
5	94° 30'	34° 45'	816 ft.	45 in.
6	94° 30'	35° 00'	599 ft.	45 in.
7	94° 45'	34° 15'	910 ft.	50 in.
8	94° 45'	34° 30'	899 ft.	52 in.
9	94° 45'	34° 45'	987 ft.	49 in.
10	94° 45'	35° 00'	757 ft.	44 in.
11	95° 00'	34° 15'	801 ft.	47 in.
12	95° 00'	34° 30'	1001 ft.	52 in.
13	95° 00'	34° 45'	820 ft.	46 in.
14	95° 00'	34° 00'	596 ft.	45 in.
15	95° 15'	34° 15'	840 ft.	49 in.
16	95° 15'	34° 30'	774 ft.	48 in.
17	95° 15'	34° 45'	808 ft.	46 in.
18	95° 15'	35° 00'	747 ft.	45 in.
19	95° 30'	34° 15'	576 ft.	48 in.
20	95° 30'	34° 30'	729 ft.	48 in.
21	95° 30'	34° 45'	940 ft.	44 in.
22	95° 30'	35° 00'	756 ft.	44 in.
23	95° 45'	34° 30'	861 ft.	47 in.
24	95° 45'	34° 34'	719 ft.	44 in.
25	94° 30'	34° 15'	1257 ft.	51 in.
26	94° 30'	34° 30'	1850 ft.	51 in.
27	94° 30'	34° 45'	1489 ft.	45 in.
28	94° 30'	35° 00'	1372 ft.	45 in.
29	94° 45'	34° 15'	1266 ft.	50 in.
30	94° 45'	34° 30'	1737 ft.	52 in.
31	94° 45'	34° 45'	1545 ft.	47 in.
32	94° 45'	34° 00'	1217 ft.	44 in.
33	95° 00'	34° 30'	1511 ft.	52 in.
34	95° 00'	34° 45'	1368 ft.	46 in.
35	95° 15'	35° 00'	1409 ft.	45 in.
36	95° 15'	34° 45'	1326 ft.	46 in.
37	94° 30'	34° 45'	2100 ft.	46 in.
38	94° 45'	34° 45'	2359 ft.	46 in.

TABLE I, Continued

Stand	Longitude	Latitude	Average Elevation	Annual Rainfall
39	95° 00'	34° 45'	2267 ft.	46 in.
40	94° 30'	34° 30'	2298 ft.	49 in.
41	94° 45'	34° 30'	2080 ft.	50 in.
42	95° 00'	34° 30'	2037 ft.	50 in.
43	95° 00'	34° 00'	1314 ft.	45 in.
44	95° 15'	34° 30'	1497 ft.	48 in.
45	94° 45'	36° 00'	1000 ft.	41 in.
46	94° 45'	36° 00'	850 ft.	41 in.
47	95° 15'	34° 00'	499 ft.	48 in.
48	96° 00'	34° 15'	699 ft.	44 in.
49	96° 00'	35° 00'	817 ft.	42 in.

Radial Growth

Radial growth (measured in rings per inch) was obtained for each segment by dividing the number of rings, usually ten, by the total length of the segment. Rings per inch has been considered to be an "illegitimate reversal of variables" Zobel et al. (9). However, in this study only wood of the same physiological age was compared, and since the stands were reasonably even-aged, the use of rings per inch should be a suitable measure of radial growth.

Statistical Analysis

The basic model used was the hierarchal or nested classification. Since the degree of nesting varied for different variables, it was necessary to use two forms of the analysis of variance and covariance. The hierarchal analysis of variance described by Snedecor (17) was used to test the significance of variations for all wood quality and growth variables.

Each segment was subjected to an analysis of the form in Table II. The two corresponding segment values for each side of each core were then averaged to give two samples per tree containing rings 0-20. This analysis also took the form found in Table II. The averaging procedure involved weighting the values obtained for each segment before finding a pooled average. The method used was to calculate weighting factors for each segment of each core by the following procedure:

$$\text{Weight Factor 1} = \frac{\text{Ln. of Segment (0-10)}}{\text{Ln. of Segment (0-10)} + \text{Ln. of Segment (11-20)}}$$

$$\text{Weight Factor 2} = \frac{\text{Ln. of Segment (11-20)}}{\text{Ln. of Segment (0-10)} + \text{Ln. of Segment (11-20)}}$$

These weighting factors were then multiplied by the corresponding variable values and the pooled average found. This procedure was necessary because of the large differences in volume of the segments involved. A simple average would have given equal weight to the two samples and produced erroneous values for a core containing rings 0-20. The calculation of a pooled average was necessary for specific gravity, summerwood percentage, and rings per inch. Summerwood percentage was first transformed using the arcsine $\sqrt{\text{Summerwood Percentage}}$ described by Snedecor (17).

It was not necessary to use a weighting procedure for tracheid lengths as they were obtained for only the segment containing rings 11-20.

Variation patterns of tree and environmental variables were studied with an analysis of the form in Table III. Longitude and latitude were transformed from degrees and minutes to degrees and tenths of degrees before analysis. Elevations for the 10 selected trees per stand were averaged to obtain the stand elevation.

Two types of correlations were calculated for this study. First, all possible simple correlations were computed using equation 1.

$$r_s = \frac{MCP_{x,y}}{\sqrt{MS_x}\ \sqrt{MS_y}} \qquad (1)$$

TABLE II

FORM OF ANALYSIS OF VARIANCE AS USED FOR GROWTH AND WOOD QUALITY VARIABLES

Source of Variation	Degrees of Freedom	Expected Mean Squares
Among Stands	s-1	$\sigma_e^2 + c\sigma_t^2 + tc\sigma_s^2$
Between Trees	s(t-1)	$\sigma_e^2 + c\sigma_t^2$
Error	st(c-1)	σ_e^2

s = Number of stands sampled (48).

t = Number of trees per stand sampled (10).

c = Number of cores per tree per stand sampled (2).

σ_s^2= Variance among-stands.

σ_s^2= Variance between-trees within a stand.

σ_e^2= Variance due to error.

TABLE III

FORM OF ANALYSIS OF VARIANCE AS USED FOR TREE AND ENVIRONMENTAL VARIABLES

Source of Variation	Degrees of Freedom	Expected Mean Squares
Among Stands	s-1	$\sigma_e^2 + t\sigma_s^2$
Error	s(t-1)	σ_e^2

s = Number of stands sampled (48).

t = Number of trees per stand sampled (10).

σ_s^2 = Variance among-stands.

σ_e^2 = Variance between-trees within a stand plus error.

Where:

r_s = Simple correlation coefficient.

$MCP_{x,y}$ = Mean cross products between variables x and y.

MS_x = Mean square of variable x.

MS_y = Mean square of variable y.

Simple correlation coefficients at both the among-stand and between-tree levels were possible for all wood quality and growth variables, but only the among-stand level was considered for tree and environmental variables.

For the second type, all possible variance component correlations were calculated, using equation 2 for the same variables and levels mentioned above.

$$r_g = \frac{\sigma_{x,y}}{\sqrt{\sigma_x^2} \quad \sqrt{\sigma_y^2}} \tag{2}$$

Where:

r_g = Variance component correlation coefficient.

$\sigma_{x,y}$ = Component of covariance between variables x and y.

σ_x^2 = Variance component for variable x.

σ_y^2 = Variance component for variable y.

For a simple correlation coefficient a level of significance can be established. However, because the distribution of the variance component correlation is unknown this type of test is not possible for this coefficient. This fact does not prevent the calculation of the variance of these coefficients by the method described by Becker (18) using a modified version of his equation. The modified equation used to calculate the variance of the component correlation for the stand level can be observed in Figure 2. The variance of the tree-level

$$\mathrm{VAR}(r_g) = r_g^2 \left[\frac{\frac{MS_{sx}MS_{sy} + MCP_s^2}{f_s + 2} + \frac{MS_{tx}MS_{ty} + MCP_t^2}{ft + 2}}{Ks^2\ COV_s} + \frac{\frac{2MS_{sx}^2}{fs + 2} + \frac{2MS_{tx}^2}{ft + 2}}{4Ks^2\ (\sigma_{sx}^2)^2} + \frac{\frac{2MS_{sy}^2}{fs + 2} + \frac{2MS_{ty}^2}{ft + 2}}{4Ks^2\ (\sigma_{sy}^2)^2} \right.$$

$$\left. - \frac{\frac{2MS_{sx}\ MCP_s}{fs + 2} + \frac{2MS_{tx}\ MCP_t}{ft + 2}}{Ks^2\ \sigma_{sx}^2\ COV_s} - \frac{\frac{2MS_{sy}\ MCP_s}{fs + 2} + \frac{2MS_{ty}\ MCP_t}{ft + 2}}{Ks^2\ \sigma_{sy}^2\ COV_s} + \frac{\frac{2MCP_s^2}{fs + 2} + \frac{2MCP_t^2}{ft + 2}}{2Ks^2\ \sigma_{sx}^2\ \sigma_{sy}^2} \right]$$

r_g = Stand Component Correlation.

fs = Degrees of freedom at stand level.

ft = Degrees of freedom at tree level.

Ks = Coefficient for stand component of variance.

MS_{sx} = Mean square at stand level for trait "x".

MS_{sy} = Mean square at stand level for trait "y".

MS_{tx} = Mean square at tree level for trait "x".

MS_{ty} = Mean square at tree level for trait "y".

MCP_s = Mean cross products at stand level for traits "x" and "y".

MCP_t = Mean cross products at tree level for traits "x" and "y".

σ_{sx}^2 = Stand component of variance for trait "x".

σ_{sy}^2 = Stand component of variance for trait "y".

COV_s = Stand component of covariance.

Figure 2. Modified Equation Used to Calculate The Variance of the Stand Component Correlation.

component correlation is found in a like manner. The standard deviation is calculated by simply finding the square root of the variance and is used to determine the reliability of the coefficient.

CHAPTER III

RESULTS AND DISCUSSION

An analysis of variance was calculated with three sources of variation for each variable by segment.

The first source was the variation among-stands; significance at this level indicates geographic differences exist among the 48 stands tested. The second was the variation between-trees within a stand; significance at this level is important to a selection program, because it can be an indication that genetic variance is present. The third source of variation, which is used to perform the F tests, includes the within-tree and error variance and was cumulatively called error.

Specific Gravity

Specific gravity of wood is probably the most investigated wood property in the history of forestry. The two major reasons for this interest in specific gravity are:

1. The importance to dry weight yield.
2. The ease with which it can be determined.

Basically, specific gravity is measured either from unextracted or extracted wood. Recently, several researchers have pointed out the hazards of using unextracted wood to point out trends and relationships between traits, Zobel et al. (9) and Goggans (20). The present study analyzed both unextracted and extracted wood. Posey et al. (14) used this data to report on extractive content of shortleaf pine in Oklahoma. Thus, extractive content will not be explored in this thesis.

Table IV presents simple correlations for growth and wood quality variables with several geographic variables and is used to point out the geographic trends if present. A significant trend for unextracted specific gravity to increase with increasing elevation is observed ($r = .30$) but disappears after extraction ($r = .10$). Specific gravity of shortleaf pine in Oklahoma shows a significant trend ($\alpha = .05$) to increase from west to east ($r = -.30$) and a slight tendency to increase from south to north ($r = .13$). These trends become stronger after extraction ($r = -.32$ and $r = .18$, respectively). Zobel et al. (9) working with loblolly pine (Pinus taeda L.) in eight southeastern states found specific gravity to have a tendency to increase from north to south and from west to east.

The magnitude of the among-stand and between-tree variation for the five study variables is presented in Table V. For both among-stands and between-trees, the variation in specific gravity is extensive. Many investigators working with forest tree species have reported extensive natural variation in specific gravity (8) (9) (10) (15). The magnitude of the between-tree variation is encouraging from a tree breeder's viewpoint for it is this variation that enables the geneticist to practice selection.

The presence of extractives in wood causes the estimates for specific gravity of unextracted wood to be inflated (Table V). After extraction, estimates of specific gravity not only have been reduced, but changes have occurred with the ranking of the stand means. For example, Stand 17 was ranked nineteenth before extraction and fifth

TABLE IV

SIMPLE CORRELATION COEFFICIENTS FOR GROWTH AND WOOD QUALITY VARIABLES WITH GEOGRAPHIC VARIABLES BY STANDS FOR RINGS 0-20

	Longitude	Latitude	Rainfall	Elevation
Unextracted Specific Gravity	-.30*	.13	-.03	.30*
Extracted Specific Gravity	-.32*	.18	.04	.10
Summerwood Percentage	-.17	.09	-.12	.22
Rings Per Inch	-.07	.10	-.17	.16
Tracheid Length	.15	-.25	.09	-.09

*Significant at $\alpha = .05$.

TABLE V

MEANS, MAXIMUM AND MINIMUM VALUES FOR GROWTH AND WOOD QUALITY VARIABLES ON THE BASIS OF STAND MEANS AND TREE MEANS FOR RINGS 0-20

Variables	Population Mean	Stand Min.	Means Max.	Tree Min.	Means Max.
Specific Gravity					
Unextracted	.50	.44	.60	.27	.80
Extracted	.44	.39	.49	.25	.55
Summerwood (%)	32.82	26.47	39.61	20.40	47.30
Tracheid Length (mm)	3.17	2.87	3.49	2.30	4.00
Radial Growth					
Rings Per Inch	10.20	5.92	18.41	4.50	32.80

after extraction. However, the two stands which ranked first and last before extraction remained ranked the same after extraction. Posey et al (22), working with a shortleaf pine seed source study in Oklahoma containing two plantations, found changes in ranked means for one and no change in the other after extraction.

Table VI contains the analysis of variance for unextracted specific gravity for rings 0-10, 11-20, and 0-20. It is seen that the mean squares for both the among-stand and between-tree levels are significant (α = .01). For juvenile wood (rings 0-10) the stand component does not contain as great a proportion of total variance as the mature wood segment (rings 11-20). Variation between-trees for juvenile wood is large (56.18%) as compared to the mature wood segment (27.86%). For the combined analysis (rings 0-20) the proportion of total variance due to variation between-trees is also large (50.18%).

Extracted specific gravity (Table VII) follows exactly the same pattern as unextracted specific gravity with all mean squares for among-stand and between-tree levels significant (α = .01).

The presence of geographic variation for specific gravity in significant amounts, supports the decision by Oklahoma State University's Forestry Department to create two shortleaf pine seed orchards. Forest tree improvement depends upon individual tree selection, or mass selection, and for selection to be effective, additive genetic variance must be present. For this study, no measure of genetic variance is possible but the magnitude of the between-tree variance appears to be of sufficient size to indicate the presence of genetic variance.

TABLE VI

ANALYSIS OF VARIANCE FOR UNEXTRACTED SPECIFIC GRAVITY FOR SEGMENTS CONTAINING RINGS 0-10, 11-20, AND 0-20 (COMBINED)

Source of Variation	d.f.	M.S.	F Calculated	Variance Component	Variance Component (%)
			Rings 0-10		
Among Stands	47	.028686	7.93**	.000804	7.97
Between Trees	362	.01496	4.13**	.00567	56.18
Error	410	.003619		.003619	35.85
			Rings 11-20		
Among Stands	47	.018512	4.76**	.000651	10.34
Between Trees	362	.007397	1.90**	.001753	27.86
Error	410	.00389		.00389	61.80
			Rings 0-20		
Among Stands	47	.01821	7.86**	.000588	10.08
Between Trees	362	.008171	3.53**	.002926	50.18
Error	410	.002318		.002318	39.74

**Significant at α = .01.
*Significant at α = .05.

TABLE VII

ANALYSIS OF VARIANCE FOR EXTRACTED SPECIFIC GRAVITY FOR SEGMENTS CONTAINING RINGS 0-10, 11-20, and 0-20 (COMBINED)

Source of Variation	d.f.	M.S.	F Calculated	Variance Component	Variance Component (%)
			Rings 0-10		
Among Stands	47	.007492	4.45**	.000221	7.55
Between Trees	362	.003723	2.21**	.00102	34.90
Error	410	.001682		.001682	57.55
			Rings 11-20		
Among Stands	47	.009928	3.43**	.000289	6.81
Between Trees	362	.005002	1.73**	.001055	24.90
Error	410	.002892		.002892	68.29
			Rings 0-20		
Among Stands	47	.006561	4.91**	.000193	7.73
Between Trees	362	.00327	2.45**	.000967	38.77
Error	410	.001335		.001335	53.51

**Significant at α = .01.
*Significant at α = .05.

Summerwood Percentage

The literature contains few reports concerning the geographic variation of summerwood percentage. Larson (5) working with slash pine (*Pinus elliottii* Engelm.) reported that summerwood percentage increased from north to south and from east to west within the species range. Between-tree variation was also observed, but could not be completely explained by environmental factors; thus, inheritance is expected to be important to summerwood percentage.

Geographic trends for summerwood (Table IV) showed a tendency for summerwood percentage to decrease with increasing rainfall ($r = -.12$), and to increase from west to east ($r = -.17$). Summerwood has a tendency to increase with increasing elevation ($r = .22$), but neither this correlation or the others proved significant.

The means and ranges for summerwood percentage based on stand and tree means for rings 0-20 are reported in Table V. The range on a stand mean basis is noticeably large (26.47 to 39.61), but is considerably larger between-trees (20.40 to 47.30).

The analysis of variance for summerwood percentage (Table VIII) was calculated after the arcsine transformation described by Snedecor (17) was performed. This change is necessary when dealing with percentage data to insure the normality of the data. In Table VIII all mean squares are significant ($\alpha = .01$) except for the between-tree mean square for the juvenile wood segment. Since summerwood is rarely present in measurable amounts in juvenile wood, this result is not surprising (9).

TABLE VIII

ANALYSIS OF VARIANCE FOR THE ARCSINE $\sqrt{\text{SUMMERWOOD PERCENTAGE}}$ FOR SEGMENTS CONTAINING RINGS 0-10, 11-20 and 0-20 (COMBINED)

Source of Variation	d.f.	M.S.	F Calculated	Variance Component	Variance Component (%)
			<u>Rings 0-10</u>		
Among Stands	47	126.192976	3.20**	4.918178	10.46
Between Trees	362	43.927336	1.14	2.686872	5.83
Error	410	38.553592		38.553592	83.70
			<u>Rings 11-20</u>		
Among Stands	47	190.249345	8.63**	8.961994	23.21
Between Trees	362	37.26388	1.69**	7.608357	19.70
Error	410	22.047165		22.047165	57.09
			<u>Rings 0-20</u>		
Among Stands	47	135.111763	6.95**	6.3055	21.19
Between Trees	362	27.4739	1.41**	4.022898	13.52
Error	410	19.428103		19.428103	65-29

**Significant at α = .01.
*Significant at α = .05.

In all cases, the among-stand component is larger than the between-tree component. The presence of the greater proportion of total variance attributable to the among-stand component is due in part to the range of environmental variables found in this study. Therefore, the possibility of racial variation cannot be excluded.

The between-tree variance component for the mature wood segment (rings 11-20) has a significant percentage of total variance (19.7%). This is evidence that summerwood is, in part, genetically controlled and indicates that progress through selection for summerwood percentage can be made.

Rings Per Inch

Geographic trends for rings per inch are not as pronounced as would be expected. The tendency exists for slower growing trees to be found at the higher elevations (r = .16), and in areas with low annual rainfall (r = 0.17); however, these correlations are not significant.

Radial growth expressed as rings per inch proved to be extremely variable both among-stands and between-trees. As shown in Table V, radial growth has a mean of 10.2 rings per inch with a range of 5.9 to 18.4 rings per inch on a stand mean basis. On a tree-to-tree basis the variability in growth rate proved to be much greater, with some trees having a radial growth rate of 32.8 rings per inch, and others having only 4.5 rings per inch. Since growth rate is dependent upon many environmental variables, it is not surprising, that extensive variation is observed for radial growth of shortleaf pine in Oklahoma, with its wide range of environmental conditions.

All means squares for rings per inch are significant at α = .01 (Table IX). The proportion of variance due to stands and between-tree sources remained reasonably constant for all three segments. The between-tree component of variance contained over 50% of the total variance for all three segments. Since radial growth has been reported to have a low heritability (23), most of this large between-tree variance is probably due to environmental variables associated with growth. Stand density, site index, and soil characteristics vary greatly from tree-to-tree within a stand are likely to be the principle variables causing this large between-tree variation.

Tracheid Length

Tracheid length has been reported by many investigators to vary significantly between-trees within a stand (9) (24). Highly significant differences among geographic sources of loblolly pine have been reported by Zobel et al (9) and Echols (25). Zobel et al. (9) also found a tendency for tracheid length of loblolly pine to increase from north to south. This same tendency was observed for shortleaf pine in Oklahoma, but the correlation coefficient is not significant, (r = .25, Table IV).

A great amount of variation among-stands and between-trees is observed with ranges of 2.87mm to 3.49mm and 2.30mm to 4.00mm respectively (Table V). Table X presents the analysis of variance for tracheid length; it is noted that a great amount of variation occurs within a tree (87.03). This source of variation also contains any experimental error associated with measurement. However, both the among-stand and between-tree mean squares proved significant, (α = .01 and α =.05 respectively). The between-tree component was almost twice as large

TABLE IX

ANALYSIS OF VARIANCE FOR RINGS PER INCH FOR SEGMENTS CONTAINING RINGS 0-10, 11-20, and 0-20 (COMBINED)

Source of Variation	d.f.	M.S.	F Calculated	Variance Component	Variance Component (%)
			Rings 0-10		
Among Stands	47	101.656395	17.77**	4.390449	21.29
Between Trees	362	26.709353	4.65**	10.479658	50.82
Error	410	5.750037		5.750037	27.89
			Rings 11-20		
Among Stands	47	240.33647	22.85**	10.899371	25.17
Between Trees	362	54.279065	5.16**	21.879484	50.53
Error	410	10.520098		10.520098	24.30
			Rings 0-20		
Among Stands	47	150.841105	38.31**	7.101886	29.75
Between Trees	362	29.608562	7.52**	12.835336	53.76
Error	410	3.937890		3.937890	16.49

**Significant at α = .01.
*Significant at α = .05.

TABLE X

ANALYSIS OF VARIANCE FOR THE AVERAGE TRACHEID LENGTH OF SUMMERWOOD RINGS 11, 15, and 20

Source of Variation	d.f.	M.S.	F Calculated	Variance Component	Variance Component (%)
Among Stands	47	.305924	2.13**	.007953	4.83
Between Trees	362	.17017	1.19*	.013414	8.14
Error	410	.143341		.143341	87.03

**Significant at α = .01.
*Significant at α = .05.

as the among-stand component (8.14% vs. 4.83%). The possibility that tracheid length is in part genetically controlled is suggested by the relationship between the sizes of these two components. In support of this possibility, Dadswell et al. (27), working with slash pine, found the heritability of tracheid length to be high (0.73).

Correlations

The use of simple correlations with phenotypic studies is widespread (8) (9) (10). However, to the author's knowledge this study is the first to calculate variance component correlations for this type of study. Although these correlations are not true genetic correlations, a high correlation with a small standard deviation would imply that a possible genetic relationship exists. A genetic correlation is calculated in the same manner, as the variance component correlations for this study. However, the components used to calculate the genetic correlation contains only genetic variance, while those for this study contain both genetic and environmental variances.

The following discussion concerns the variance component correlations for the mature wood segment. This segment is used because mature wood (not confounded with juvenile wood) is the better estimate for whole tree wood, and makes possible comparisons between trees of different ages (26). All other component correlations and simple correlations are tabulated in the Appendix for comparison by the reader. The variance component correlations for rings 0-10 and 0-20 are found in Tables XIII through XVI and the simple correlation coefficients are found in Tables XVII through XXII.

Relationships between Growth and Wood Quality Variables

The correlation coefficients for mature wood are found in Table XI, with the standard deviations given in parentheses immediately under each coefficient. The coefficients based on the among-stand component are above the diagonal line and those based on the between-tree component are below the line.

The relationship between unextracted specific gravity and tracheid length at both the stand and tree levels proved weak (r = .344 $\pm$ .267 and r = .131 $\pm$ .228 respectively). For extracted specific gravity and tracheid length the coefficients are larger, but standard deviations remained large (r = .480 $\pm$ .285) for stand and (r = .236 $\pm$ .252) for tree levels. Thus, the tendency exists for tracheid length to increase with increasing specific gravity. The opposite trend was found in loblolly pine by Zobel et al. (9). Because increasing specific gravity and tracheid length are both important to tree improvement, a problem could occur with selection for high specific gravity, if a resulting decrease in tracheid length occurred. However, this does not appear to be a problem for shortleaf pine in Oklahoma.

At the stand level, a strong relationship exists between rings per inch and unextracted specific gravity (r = .768 $\pm$ .123). After extraction, this relationship is not as strong (r = .460 $\pm$ .198) but appears reliable. It seems that a tendency exists on a racial basis for faster-growing stands in Oklahoma to produce wood with lower specific gravity. This relationship appears to imply that selection in fast-growing stands would result in trees with lower specific gravity. However, the consensus of researchers in forestry is that radial growth has little

TABLE XI

COMPONENT CORRELATION COEFFICIENTS AND STANDARD DEVIATIONS (IN PARENTHESIS) FOR GROWTH AND WOOD QUALITY VARIABLES FOR RINGS 11-20 BASED ON THE AMONG-STAND (ABOVE LINE) AND BETWEEN-TREE (BELOW LINE) COMPONENTS

	Unextracted Specific Gravity	Extracted Specific Gravity	Summerwood Percentage	Rings Per Inch	Tracheid Length
Unextracted Specific Gravity		.899 (.056)	.507 (.159)	.768 (.123)	.344 (.267)
Extracted Specific Gravity	.865 (.034)		.521 (.173)	.460 (.198)	.480 (.285)
Summerwood Percentage	.662 (.115)	.821 (.118)		.313 (.166)	.458 (.224)
Rings Per Inch	.464 (.085)	.376 (.094)	.347 (.097)		-.134 (.244)
Tracheid Length	.131 (.228)	.236 (.252)	-.283 (.254)	.140 (.160)	

to do with specific gravity per se (20). This study compared mature wood of the same age (rings from pith); however, the stands varied in ages from 21 to 87 years old. Thus, wood compared was the same age from pith but was grown under many different environmental conditions, which may have influenced the relationship between rings per inch and specific gravity.

On a between-tree basis, the correlations between unextracted and extracted specific gravity with rings per inch are r = .464 $\pm$ .085 and r = .376 $\pm$ .094, respectively. These correlations are not large but their standard deviations imply that they are reliable; therefore, a tendency exists for faster-growing trees to have lower specific gravity. However, even if this relationship should prove in part due to heredity, the large variation found between-trees will allow the selection of fast-growing trees with no reduction in specific gravity. Zobel et al. (9) working with loblolly pine reported a tendency for faster-growing trees to have lower specific gravity but found no indication that a fast-growing stand on a good site produced wood of lower specific gravity.

Summerwood percentage is observed to be related to specific gravity on a stand basis and extraction did not affect the coefficient in a significant manner (for unextracted r = .507 $\pm$ .159 and for extracted specific gravity r = .521 $\pm$ .173). On a between-tree basis the coefficients are of a greater magnitude and after extraction the coefficient becomes considerably larger, (r = .662 $\pm$ .115 before and r = .821 $\pm$ .118 after). The direct relationship between specific gravity and summerwood percentage has been consistently reported in the literature (5) (6) (7). The meaning of this relationship to tree improvement is that selection in stands with high specific gravity for trees with high specific gravity will also yield wood with a high summerwood content, if this relationship is genetic in nature.

The relationship between rings per inch and summerwood percentage does not appear to be strong for both the stand and tree levels ($r = .313 \pm .166$ and $r = .347 \pm .097$, respectively). Thus, a tendency for faster growing trees to produce wood of low summerwood content exists. As with specific gravity and rings per inch, much of this relationship can probably be accounted for by environmental variables rather than heredity.

A tendency exists for stands producing wood of high summerwood content to produce longer tracheids ($r = .458 \pm .224$). The reverse is true on a between-tree basis ($r = -.283 \pm .254$), but the standard deviation is of a size to raise questions as to the reliability of this coefficient. The relationship between tracheid length and rings per inch at both the stand and tree levels have standard deviations of a size to render interpretation impossible.

As was expected, the correlation between unextracted and extracted specific gravity is high (for the stand level $r = .899 \pm .056$ and for the tree level $r = .865 \pm .034$). Even though this correlation is strong, for the best interpretation of the data, extracted specific gravity is preferred because extractive content can mask the true relationships (20).

Relationships Between Growth and Wood Quality Variables with Tree and Environmental Variables

Table XII presents the correlation coefficients for the among-stand level only. Before extraction, specific gravity showed a strong relationship to age of tree ($r = .667 \pm .137$), which after extraction was reduced ($r = .315 \pm .209$). This is a result of older trees containing more extractives, which inflates specific gravity of unextracted wood. The relationship between specific gravity and elevation is present though not strong ($r = .329 \pm .190$). Therefore, a tendency exists for stands at the higher elevations to produce wood with higher specific gravity. The same tendency is noticed for percentage of summerwood with elevation ($r = .387 \pm .138$). Rings per inch also showed a slight tendency to increase with increasing elevation, that is, slower growing stands are found at higher elevations. Tracheid length did not show meaningful relationships with the other variables included in this study.

TABLE XII

COMPONENT CORRELATION COEFFICIENTS AND STANDARD DEVIATIONS (IN PARENTHESIS) FOR GROWTH AND WOOD QUALITY VARIABLES WITH TREE AND ENVIRONMENTAL VARIABLES FOR RINGS 11-20 BASED ON THE AMONG-STAND COMPONENTS

	Age	Height	Diameter Breast Height	Site Index	Basal Area	Elevation
Unextracted Specific Gravity	.667 (.137)	.178 (.189)	.330 (.201)	-.248 (.184)	-.296 (.197)	.444 (.158)
Extracted Specific Gravity	.315 (.209)	.293 (.201)	.149 (.238)	.112 (.211)	-.050 (.229)	.329 (.190)
Summerwood Percentage	.179 (.171)	-.028 (.169)	.089 (.188)	-.140 (.164)	-.191 (.176)	.387 (.138)
Rings Per Inch	.933 (.044)	.046 (.171)	.446 (.165)	-.556 (.121)	-.439 (.156)	.265 (.152)
Tracheid Length	-.161 (.235)	.276 (.216)	-.013 (.257)	.296 (.214)	.368 (.226)	-.138 (.212)

CHAPTER IV

SUMMARY AND CONCLUSIONS

This study was designed to determine the phenotypic patterns of variation and the relationships among specific gravity, summerwood percentage, rings per inch, and tracheid length in shortleaf pine in southeast Oklahoma. Patterns of variation were studied with the aid of analyses of variance and relationships with correlation coefficients calculated with variance components.

Phenotypic variation for three age classes of wood was evaluated: juvenile wood (rings 0-10), mature wood (rings 11-20), and the combined segment (rings 0-20). The mature wood segment was used to discuss the relationships among traits and among traits and environmental variables.

Geographic variation was responsible for a significant proportion of the total variance for specific gravity, summerwood percentage, rings per inch, and tracheid length, for rings 0-10, 11-20, and 0-20. Evidence of racial variation in shortleaf pine for specific gravity was present with a tendency to increase from south to north and from west to east. A weak tendency for tracheid length to increase from north to south was observed. Summerwood was observed to increase from west to east. Only the trend for specific gravity to increase from west to east was significant ($\alpha = .05$). The possibility of inter-specific hybridization occurring between shortleaf and loblolly pine, exists at the eastern and southern edges of the study area and could have affected these relationships. Specific gravity, summerwood percentage, and rings per inch all showed a tendency to increase with increasing elevation. Summerwood percentage and rings per inch both show a tendency to increase with decreasing annual rainfall, but specific gravity and tracheid length showed no relationship to rainfall. The presence of these trends and the significance of the among-stand variance seems to support the decision by Oklahoma State University's Forestry Department to establish two shortleaf pine seed orchards on the basis of geographic location.

Between tree variation was significant for all four variables. The magnitude of the between-tree variance suggests that genetic variance of a magnitude to justify a selection program may be present for specific gravity, summerwood percentage, tracheid length, and rings per inch. However, further study to determine the magnitude of genetic variance and the heritability of these traits is needed to plan a program of breeding and selection.

The use of specific gravity of extracted wood is preferred to specific gravity of unextracted wood. For estimates of phenotypic variation in specific gravity the differences between unextracted and extracted specific gravity were not significant; however, several relationships were changed.

Extracted specific gravity had a tendency to increase as tracheid length increased at both the stand the tree levels. The reliability of these correlations was questionable due to their standard deviations; however, it is encouraging that selection for specific gravity may not result in a decrease in tracheid length.

The tendency exists for faster-growing trees to produce wood of lower specific gravity and summerwood content, but much of this relationship is explainable with environmental variables at the stand level. This relationship at the tree level would be discouraging were it not for the large between-tree variation resulting in many fast-growing trees with high specific gravity and summerwood content.

Trees with a high percentage of summerwood had a strong tendency to produce wood with high specific gravity and a slight tendency to produce wood with longer tracheids. Tracheid length and rings per inch were not related.

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APPENDIX

TABLE XIII

COMPONENT CORRELATION COEFFICIENTS AND STANDARD DEVIATIONS (IN PARENTHESIS) FOR GROWTH AND WOOD QUALITY VARIABLES FOR RINGS 0-10 BASED ON THE AMONG-STAND (ABOVE LINE) AND BETWEEN-TREE (BELOW LINE) COMPONENTS

	Unextracted Specific Gravity	Extracted Specific Gravity	Summerwood Percentage	Rings Per Inch	Tracheid Length
Unextracted Specific Gravity		.798 (.173)	.201 (.249)	.925 (.136)	-.124 (.317)
Extracted Specific Gravity	.636 (.041)		.459 (.207)	.662 (.168)	.019 (.313)
Summerwood Percentage	.284 (.197)	.665 (.272)		.342 (.188)	.008 (.260)
Rings Per Inch	.312 (.066)	.448 (.080)	.500 (.252)		-.188 (.249)
Tracheid Length	.198 (.170)	.265 (.216)	.013 (.485)	.061 (.161)	

TABLE XIV

COMPONENT CORRELATION COEFFICIENTS AND STANDARD DEVIATIONS (IN PARENTHESIS) FOR GROWTH AND WOOD QUALITY VARIABLES WITH TREE AND ENVIRONMENTAL VARIABLES FOR RINGS 0-10 BASED ON THE AMONG-STAND COMPONENTS

	Age	Height	Diameter Breast Height	Site Index	Basal Area	Elevation
Unextracted Specific Gravity	1.036 .117	.173 (.213)	.490 (.208)	-.502 (.186)	-.225 (.230)	.340 (.193)
Extracted Specific Gravity	.611 (.169)	.311 (.198)	.180 (.235)	-.100 (.209)	-.200 (.224)	.073 (.201)
Summerwood Percentage	.230 (.190)	-.169 (.183)	-.104 (.208)	-.283 (.175)	-.350 (.183)	.148 (.179)
Rings Per Inch	.929 (.056)	.096 (.175)	.474 (.166)	-.504 (.135)	-.482 (.156)	.042 (.166)
Tracheid Length	-.161 (.235)	.276 (.216)	-.013 (.257)	.296 (.214)	.368 (.226)	-.138 (.212)

TABLE XV

COMPONENT CORRELATION COEFFICIENTS AND STANDARD DEVIATIONS (IN PARENTHESIS) FOR GROWTH AND WOOD QUALITY VARIABLES FOR RINGS 0-20 BASED ON THE AMONG-STAND (ABOVE LINE) AND BETWEEN-TREE (BELOW LINE) COMPONENTS

	Unextracted Specific Gravity	Extracted Specific Gravity	Summerwood Percentage	Rings Per Inch	Tracheid Length
Unextracted Specific Gravity		.791 (.111)	.359 (.193)	.956 (.096)	.121 (.290)
Extracted Specific Gravity	.717 (.040)		.456 (.183)	.558 (.178)	.320 (.294)
Summerwood Percentage	.292 (.116)	.650 (.115)		.293 (.166)	.295 (.234)
Rings Per Inch	.352 (0.63)	.380 (.072)	.285 (.115)		-.157 (.239)
Tracheid Length	.237 (.181)	.254 (.207)	-.150 (.304)	.119 (.151)	

TABLE XVI

COMPONENT CORRELATION COEFFICIENTS AND STANDARD DEVIATIONS (IN PARENTHESIS) FOR GROWTH AND WOOD QUALITY VARIABLES WITH TREE AND ENVIRONMENTAL VARIABLES FOR RINGS 0-20 BASED ON THE AMONG-STAND COMPONENTS

	Age	Height	Diameter Breast Height	Site Index	Basal Area	Elevation
Unextracted Specific Gravity	.981 (.092)	.203 (.196)	.445 (.197)	-.423 (.178)	-.277 (.115)	.405 (.171)
Extracted Specific Gravity	.494 (.187)	.384 (.190)	.160 (.236)	.072 (.210)	-.120 (.227)	.137 (.199)
Summerwood Percentage	.178 (.173)	-.066 (.169)	-.003 (.190)	-.164 (.164)	-.234 (.173)	.245 (.151)
Rings Per Inch	.943 (.039)	.066 (.168)	.462 (.159)	-.543 (.120)	-.462 (.150)	.181 (.155)
Tracheid Length	-.161 (.235)	.276 (.216)	-.031 (.257)	.296 (.214)	.368 (.226)	-.138 (.212)

TABLE XVII

SIMPLE CORRELATION COEFFICIENTS FOR RINGS 0-10 BETWEEN GROWTH AND WOOD QUALITY VARIABLES BASED ON THE AMONG-STAND (ABOVE LINE) AND BETWEEN-TREE (BELOW LINE) LEVELS

	Unextracted Specific Gravity	Extracted Specific Gravity	Summerwood Percentage	Rings Per Inch	Tracheid Length
Unextracted Specific Gravity		.720**	.179	.628**	-.016
Extracted Specific Gravity	.644**		.394**	.489**	.047
Summerwood Percentage	.157**	.316**		.277	.020
Rings Per Inch	.211**	.238**	.131*		-.097
Tracheid Length	.076	.073	.036	.026	

**Significant at $\alpha = .01$.
*Significant at $\alpha = .05$.

TABLE XVIII

SIMPLE CORRELATION COEFFICIENTS FOR RINGS 0-10 FOR GROWTH AND WOOD QUALITY VARIABLES WITH TREE AND ENVIRONMENTAL VARIABLES BASED ON THE AMONG-STAND LEVEL

	Age	Height	Diameter Breast Height	Site Index	Basal Area	Elevation
Unextracted Specific Gravity	.710**	.164	.356*	-.339*	-.122	.233
Extracted Specific Gravity	.451**	.251	.138	-.073	-.121	.051
Summerwood Percentage	.141	-.137	-.118	-.208	-.255	.119
Rings Per Inch	.794**	.095	.357*	-.454**	-.369*	.035
Tracheid Length	-.091	.208	.031	.200	.235	-.095

**Significant at α = .01.
*Significant at α = .05.

TABLE XIX

SIMPLE CORRELATION COEFFICIENTS FOR RINGS 11-20 BETWEEN GROWTH AND WOOD QUALITY VARIABLES BASED ON THE AMONG-STAND (ABOVE LINE) AND BETWEEN-TREE (BELOW LINE) LEVELS

	Unextracted Specific Gravity	Extracted Specific Gravity	Summerwood Percentage	Rings Per Inch	Tracheid Length
Unextracted Specific Gravity		.878**	.459**	.599**	.193
Extracted Specific Gravity	.864**		.470**	.344*	.246
Summerwood Percentage	.380**	.450**		.279	.245
Rings Per Inch	.252**	.176**	.152**		-.060
Tracheid Length	.034	.040	-.087	.052	

**Significant at α = .01.
*Significant at α = .05.

TABLE XX

SIMPLE CORRELATION COEFFICIENTS FOR RINGS 11-20 FOR GROWTH AND WOOD QUALITY VARIABLES WITH TREE AND ENVIRONMENTAL VARIABLES BASED ON THE AMONG-STAND LEVEL

	Age	Height	Diameter Breast Height	Site Index	Basal Area	Elevation
Unextracted Specific Gravity	.529**	.171	.263	-.196	-.208	.343*
Extracted Specific Gravity	.240	.242	.115	.079	0.023	.231
Summerwood Percentage	.158	.002	.050	-.108	-.128	.347*
Rings Per Inch	.836**	.057	.345*	-.520**	-.350*	.233
Tracheid Length	-.091	.208	.031	.200	.235	-.095

**Significant at α = .01.
*Significant at α = .05.

TABLE XXI

SIMPLE CORRELATION COEFFICIENTS FOR RINGS 0-20 BETWEEN GROWTH AND WOOD QUALITY VARIABLES BASED ON THE AMONG-STAND (ABOVE LINE) AND BETWEEN-TREE (BELOW LINE) LEVELS

	Unextracted Specific Gravity	Extracted Specific Gravity	Summerwood Percentage	Rings Per Inch	Tracheid Length
Unextracted Specific Gravity		.759**	.311*	.709**	.098
Extracted Specific Gravity	.727**		.429**	.423**	.183
Summerwood Percentage	.244**	.441**		.250	.165
Rings Per Inch	.243**	.220**	.078		-.078
Tracheid Length	.076	.061	-.030	.048	

**Significant at α = .01.
*Significant at α = .05.

TABLE XXII

SIMPLE CORRELATION COEFFICIENTS FOR RINGS 0-20 FOR GROWTH AND WOOD QUALITY VARIABLES WITH TREE AND ENVIRONMENTAL VARIABLES BASED ON THE AMONG-STAND LEVEL

	Age	Height	Diameter Breast Height	Site Index	Basal Area	Elevation
Unextracted Specific Gravity	.726**	.195	.345*	-.309*	-.176	.299*
Extracted Specific Gravity	.365*	.307*	.127	.052	-.068	.096
Summerwood Percentage	.129	-.046	-.037	-.125	-.174	.218
Rings Per Inch	.853**	.075	.364*	-.515**	-.373**	.162
Tracheid Length	-.091	.208	.031	.200	.235	-.095

**Significant at $\alpha = .01$.
*Significant at $\alpha = .05$.

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