# ESTIMATION OF GENETIC VARIATION IN SOME WOOD PROPERTIES OF SHORTLEAF PINE IN SOUTHEASTERN OKLAHOMA

By

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IN SOUTHEASTERN OKLAHOMA

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# CHAPTER I

## INTRODUCTION

Shortleaf pine (Pinus echinata Mill.) has the widest range of any of the southern pines (Figure 1). It currently comprises about 25 percent of the total standing cubic volume of southern pine forests, and is an important commercial species in many areas throughout the southeastern United States.

As with most commercial tree species, research is needed to improve the quantity and quality of shortleaf pine wood produced. Knowledge of variation in wood properties due to genetic influences will help tree breeders make informed decisions concerning improvements in wood quantity and quality.

There have been many published reports on both geographic variation in and heritability of wood characteristics of many commercial forest tree species. Loblolly (Pinus taeda L.) and slash (Pinus elliottii Engelm.) pine have been studied more than shortleaf pine because of their comparatively rapid initial growth rate. Some research on geographic variation in wood properties of shortleaf pine has been reported, but no work could be found on estimating the genetic variability available in wood properties of the species.

The shortleaf pine wood properties which were examined in this study are: unextracted specific gravity, extracted specific gravity, percent extractive content, number of rings per inch, percent

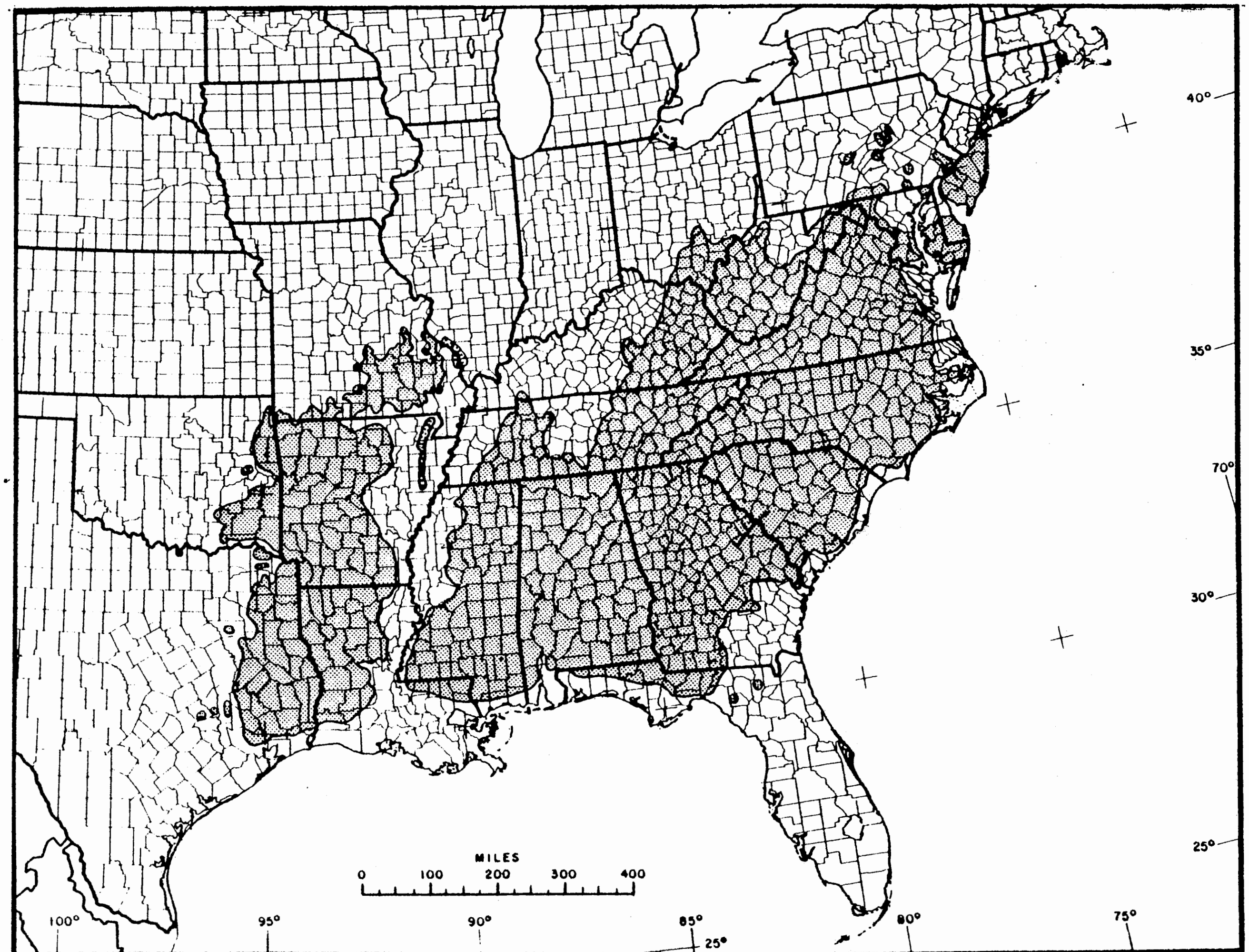


Figure 1. Natural Range of Shortleaf Pine (Pinus echinata Mill.)

summerwood, and tracheid length. Individually and jointly, these wood properties are of interest to industries which desire to produce quality wood products efficiently.

# CHAPTER II

# LITERATURE REVIEW

## Sampling Procedures for Measurements of Wood Properties

Cores with diameters ranging from 10 to 12 millimeters have been used for about two decades as an efficient, nondestructive method of obtaining wood samples from a tree. There have been several studies which have shown that increment cores are acceptable wood samples for the estimation of specific gravity and tracheid lengths (Boyce and Kaeiser, 1960; TAPPI Forest Biology Subcommittee No. 2, 1968; Gilmore et al., 1966; Spurr and Hsiung, 1954). Such cores are usually taken at breast height. High correlations between wood properties of cores taken at diameter breast height and wood properties of the merchantable portion of the stem have been reported (Goggans, 1962; Smith, 1966).

An important consideration to be made when using core samples is the number of core samples needed per tree to produce reliable estimates of wood properties. Goggans (1962) reported that two core samples from opposite sides of a tree would yield about the same information as a disk cut from a tree. However, many studies in the past have used only one radial core (Fielding and Brown, 1960; Wahlgren and Fassnacht, 1959). According to Zobel and Rhodes (1955), success in using only one radial core depends on the sampling of a large number of trees. In studies which use only a small number of trees, Goggans (1962) felt that two radial cores per tree were needed to obtain measurable between tree variation.

## Wood Properties and Their Measurement

### Specific Gravity

Wood specific gravity is probably the most widely studied wood property. Specific gravity is a principle factor in the segregation of poles, pilings, and structural-grade timber (Mitchell, 1958). Zobel et al. (1961) found that specific gravity was strongly correlated with pulp yield, and Namkoong et al. (1969) reported that specific gravity had a major affect on paper tear strength. The quantity and quality of wood products produced from a tree is dependent upon the specific gravity of the merchantable stem of the tree.

A specific gravity estimate is affected by many different factors within the wood sample. Some of these factors are: the presence or absence of juvenile wood, the amount of extractives, the percent summerwood, and the rate of diameter growth. The influence of these factors on specific gravity varies from tree to tree. If they are not accounted for, erroneous conclusions may be drawn about specific gravity estimates.

The presence of juvenile wood is a recognized concern in the estimation of whole tree specific gravity. Juvenile wood is produced near the pith (Paul, 1960), and is typified by low density and high longitudinal shrinkage relative to mature wood. Juvenile wood has a highly variable specific gravity which is lowest near the pith and increases outward (Larson, 1957; Paul, 1960; Spurr and Hsiung, 1954; Zobel and McElwee, 1958). Zobel et al. (1972) found that trees which produce juvenile wood of high specific gravity also produce mature wood of high specific gravity. The reason trees first produce juvenile wood and then change production to mature wood is not completely understood. Paul (1960) and Zobel and McElwee (1958) both found that trees grown in plantations produced juvenile wood several years longer than trees in natural stands. They suggested that competition for some vital factor triggers the trees' conversion from juvenile wood production to mature wood production. In most cases it was found that pines grown in plantations on good sites were producing mature wood around the age of eight (Larson, 1957; Zobel and McElwee, 1958). The trees required a transition period of one or two years to switch from production of juvenile wood to mature wood (Zobel and McElwee, 1958).

Wood extractives found in pines include resin acids, essential oils, fats, fatty acids, and unsaponifiable or inert matter (Tarras and Saucier, 1967). If extractives are present in a core sample they will alter the specific gravity measurements. For example, resins have a lower density than the wood, but they fill the lumans and intercellular cavities which would otherwise be empty (Spurr and Hsiung, 1954). The filled cavities will increase the specific gravity of the core sample.

It has been noted by several researchers that the rate of diameter growth influences the extractive content in pine (Ifju and Labesky, 1972; Tarras and Saucier, 1967). Ifju and Labesky (1972), showed that springwood contained more extractives on a per weight basis than summerwood. This fact supports findings by other researchers who reported that faster growing trees contain more extractives (Kurth, 1933; Tarras and Saucier, 1967). In shortleaf pine, Posey and Robinson (1969) found age to be one of the most important influences on extractive content. As the pine tree ages it builds up extractives. These extractives are stored primarily near the pith, and the amount of extractives present decreases outward. Stonecypher and Zobel (1966) determined that extractive content in five year old loblolly pine was extremely low. However, most researchers feel that conclusions based on unextracted specific gravity in pine may be risky (Goggans, 1962; McCullough, 1972; Posey and Robinson, 1969; Zobel et al. 1960). The effects of extractives on specific gravity can easily be nullified by removing the extractives from the wood samples.

It has been widely publicized that specific gravity and percent summerwood are strongly correlated (Dadswell and Wardrop, 1959; Gilmore et al. 1966; Goggans, 1962; Ifju and Labesky, 1972). The relationship is due to the fact that summerwood is more dense than springwood (Dadswell and Wardrop, 1959; Goggans, 1962; Mitchell, 1958). In a study by Squillace et al. (1962), specific gravity was found to be only weakly correlated with percent summerwood. They suggested the possibility that in relatively young trees large amounts of juvenile wood would tend to weaken the expected relationship between specific gravity and percent summerwood.

There have been several reports on the relationship between diameter growth and specific gravity in pines. These reports contain conflicting data on whether specific gravity is positively or negatively correlated with growth rate, but all reports show only weak correlations between the traits (Schafer, 1949; Squillace et al., 1962; Wheeler and Mitchell, 1949; Zobel et al., 1961). Later studies have shown that the environment, which greatly influences diameter growth, summerwood production, and specific gravity, may be the cause of the observed correlations between diameter growth and specific gravity (Jayne, 1958; Larson, 1957; McCullough, 1972; Paul, 1958).

Zobel and Rhodes (1955) observed that they could not account for all the variation in specific gravity with correlations of specific gravity with other wood properties and environmental factors. Many other studies confirmed the findings of Zobel and Rhodes. These studies reported large tree to tree variation in specific gravity (Dadswell et al., 1961; Echols, 1958; Goggans, 1962; Mitchell, 1958; Zobel and Rhodes, 1955). Zobel and McElwee (1958) felt that there was enough unexplained tree to tree variation in specific gravity to warrant additional investigation into the genetics of the trait.

Studies of specific gravity in pines have demonstrated the presence of enough genetic variation to allow acceptable gains in the trait through selection (Namkoong et al., 1969). When reviewing the literature it becomes apparent that not all genetic control over specific gravity is additive in nature.

Narrow sense heritability estimates of .37 and .49 calculated by using different procedures in loblolly pine (van Buijtenen, 1962), .56 for control pollinated and .12 for open pollinated families in slash pine (Squillace et al., 1962), and .2 in Monterey pine (*Pinus radiata* D. Don.) (Fielding and Brown, 1960), can be compared with broad sense heritabilities of .64, .84, .73, .54, and .74 by the same authors for the same species. Most studies which report both narrow sense and broad sense heritability estimates indicate that a considerable amount of the genetic variation present in specific gravity can be attributed to additive genetic variation.

Number of Rings Per Inch

The diameter growth of a tree may be measured as rings per inch. Rings per inch is a relatively easy method of measuring diameter growth rate when working with core samples. Zobel et al. (1959, p. 347) suggested that "rings per inch is an illegitimate reversal of variables," but then stated it was an acceptable method of measuring diameter growth in even aged stands.

The influence of diameter growth rate on wood properties in pine is of interest. This interest stems from the fact that diameter growth rate responds to silvicultural practices. Tracheid lengths seem to be weakly correlated to diameter growth rate. Most studies conclude that fast diameter growth rate will cause a slight increase in summerwood tracheid length (Spurr and Hyvarinen, 1954; Zobel et al., 1960; Zobel et al., 1972). Significant correlations of diameter growth rate with percent extractive content has also been reported. Several authors have demonstrated that faster growing trees contain a higher extractive content than slower growing trees (Paul, 1958; Tarras and Saucier, 1967). However, extractive content does not appear to greatly affect other wood properties.

Stonecypher et al. (1972) reported low narrow sense heritability estimates for radial growth in loblolly pine. The low heritability indicated that most of the variation in radial growth is due to the environment. It has been found that in general, environmental factors that increase radial growth increase tracheid lenth and extractive content, but decrease specific gravity and percent summerwood. However, the environmental factors that may significantly improve radial growth have only a minor effect on these other wood properties (Zobel et al., 1959).

Percent Summerwood

There are distinct anatomical differences between summerwood and springwood. Mark (1928, p. 48) defined summerwood as "all tracheids in which the common wall between two cell cavities multiplied by two is numerically equal to or greater than the width of the luman." Springwood contains tracheids with thin cell walls. The thicker cell walls of summerwood account for its greater density. The higher density of summerwood helps to explain the large number of reports which found high correlations between percent summerwood and specific gravity.

The amount of summerwood produced by a tree in a growing season seems to depend on four major factors. The first two are environmental; available moister and available nutrients. The other factors are the age of the tree producing the summerwood and the genetic influence of the genotype on summerwood production (Larson, 1957; Paul, 1958; Smith and Wilsie, 1962; Zahner and Oliver, 1962).

Larson (1957) presented strong evidence that moisture stress affects the production of auxins. Auxins in turn influence the rate and type of radial growth put on by a tree. He suggests that moisture stress is needed to initiate summerwood production in pines. Many studies have reported that heavy spring rains greatly increase the amount of springwood produced in a single growing season, and that dry springs with adequate rain in the mid summer results in increase in production of summerwood in a single growth season (Gilmore et al., 1966;

Jayne, 1958; Larson, 1957; Smith, 1956). Zahner and Oliver (1962) demonstrated that with the use of thinning and pruning they could delay moisture stress and reduce the annual amount of summerwood produced by a tree.

Paul and Marts (1954) found that when they fertilized longleaf pine with nitrogen, specific gravity was reduced. It was discovered that the amount of springwood and summerwood was increased, but the proportion of springwood produced was greater than normal. Zobel et al. (1961) supported these findings in a later study on loblolly pine. In addition, they reported that there was tree to tree variation in response to the nitrogen fertilizer.

Only a few heritability estimates have been reported for percent summerwood. Dadswell et al. (1961) estimated broad sense heritability in Monterey pine for percent summerwood as .47 in seedlings and .54 in clones for growth rings two through eight. Squillace et al. (1962) calculated both narrow and broad sense heritabilities for percent summerwood in slash pine. The narrow sense heritability estimates were .08 for open pollinated progeny and .26 for controlled pollinated progeny. The broad sense heritability estimate was much higher at .48, than were the narrow sense heritability estimates. Squillace's broad sense heritability estimate for slash pine was very similar to Dadswell's estimate for Monterey pine. These heritability estimates suggest that summerwood production is under a fair amount of genetic control, but a large portion of this genetic control may be nonadditive.

## Tracheid Length

Tracheid length is a wood property of special interest to paper manufacturers. The length of tracheids used in the manufacturing of paper has some influence on the strength and quality properties of the paper produced (Dadswell and Wardrop, 1959).

There have been a large number of studies reported on variation in tracheid length of pines. These studies can be divided into two main types: those that deal with variation within trees, and those that deal with variation among trees.

The first major work performed on tracheid length variation within a tree was by Sanio (1872). He developed some general conclusions on variation of tracheids within a tree which were later referred to as "Sanio's laws" by Bailey and Shepard (1915). The laws developed by Sanio (1872) are:

> 1. In the stem and branches the tracheids everywhere increase in size from within outward, throughout a number of annual rings, until they have attained a definite size, which then remains constant for the following annual rings.
>
> 2. The constant final size changes in the stem in such a manner that it constantly increases from below upward, reaches its maximum at a definite height, and then diminishes toward the summit.
>
> 3. The final size of the tracheids in the branches is less than those in the stem, but is dependent on the latter, inasmuch as those branches which arise from the stem at a level where the tracheids are larger themselves have larger tracheids than those which arise at a level where the constant size is less.
>
> 4. In the gnarled branches of the summit the constant size in the outer rings increases toward the apex, and then falls again, but here irregularities occur which may be absent in regularly grown branches.
>
> 5. In the root the width of the elements first increase, then falls, and next rises to a constant figure. An increase in length also takes place, but could not be exactly determined (p. 69).

There has since been considerable controversy about the validity of Sanio's laws. The statement which created the main controversy is the last part of the first law which concludes that tracheids eventually reach a maximum length which then remains constant for the following growth rings. Bailey and Shepard (1914) were the first to disagree with this statement. They found that tracheid lengths varied greatly from growth ring to growth ring in the mature wood. Several other studies reached the same conclusion as Bailey and Shepard (Gerry, 1916; Ifju and Labesky, 1972). However, there are some studies which supported the phrase in Sanio's first law (Goggans, 1962; Jackson and Greene, 1958; Zobel et al., 1959). Spurr and Hyvarinen (1954) feel that they may have cleared up the controversy with the results of their study. Their findings are that if a tree has relatively steady growth, the tracheid length will remain constant from growth ring to growth ring, and if the tree has sporadic growth, tracheid length will vary from growth ring to growth ring.

Ifju and Labesky (1972), working with loblolly pine, studied tracheid variation within trees further. They observed that tracheid length increases across the growth ring. The shortest tracheids were found in the early springwood growth and the length increased through to the last formed summerwood. This report of the gradual increase in tracheid length across the growth ring is new. However, it has been reported many times that there is a difference in the average springwood and summerwood tracheid length (Goggans, 1962; Jackson and Greene, 1958; McCullough, 1972). Summerwood tracheids are always longer.

Within tree variation in tracheid length can be reduced considerably when comparing trees by taking tracheid samples from the same height and same age growth ring of each tree. In studies comparing tracheid lengths among trees in a stand, significant variation was found (Dorman, 1976; McCullough, 1972; Zobel and Rhodes, 1955). Other studies involving large segments of a species' range showed geographic variation in tracheid length (Dorman, 1976; Echols, 1958). The variation among trees and the lack of evidence that environment has much affect on tracheid length seems to indicate that tracheid length is largely under genetic control (Dadswell et al., 1961; Goggans, 1962; Jackson and Greene, 1958). Goggans (1962) estimated narrow sense heritabilities for loblolly pine at two different locations for both summerwood and springwood tracheid lengths. These estimates were .97 and .85 for summerwood tracheid length and .54 and .77 for springwood tracheid length. Goggan's narrow sense heritability estimates supported a report by Mitchell (1958), who concluded that summerwood tracheid lengths are under more genetic influence than springwood tracheid lengths. In a study reported by Jackson and Greene (1958), evidence was found that the female parent may have more influence over tracheid length than the male parent in slash pine. For shortleaf pine, McCullough (1972) reported that there was significant among tree and among stand variation for tracheid length.

With the combination of high narrow sense heritability and a large amount of among tree variation, genetic improvement in tracheid length for pines seems practical. With information generated by this study shortleaf pine breeders will be able to obtain some idea of the possible improvements obtainable through breeding procedures for tracheid length and the other wood properties examined.

# CHAPTER III

# MATERIALS AND METHODS

## Introduction

Considerable care was taken to duplicate the field and laboratory procedures used by McCullough (1972). McCullough's procedures were duplicated in order to use his data as parent information for parent progeny regression heritability estimates.

## Field Collection

The trees used in this study are open pollinated progeny from the measurement trees used in a study of geographic variation in Oklahoma shortleaf pine reported by McCullough (1972). The parent trees are from natural stands in southeastern Oklahoma (Figure 2). The open pollinated progeny from these parents were planted at two locations in southeastern Oklahoma (Figure 2), and were sampled in their 14th growing season. The two locations are Broken Bow, which is in the coastal plain, and Stilwell, which is in the Quachita mountains. Heritability estimates and genetic correlations calculated from data on these trees will be applicable to the shortleaf pine population in southeastern Oklahoma.

The study material was outplanted in a randomized complete block design at each location. A location consists of six replicates, each of which contain 100 families in four tree row plots. Fifty-six unrelated

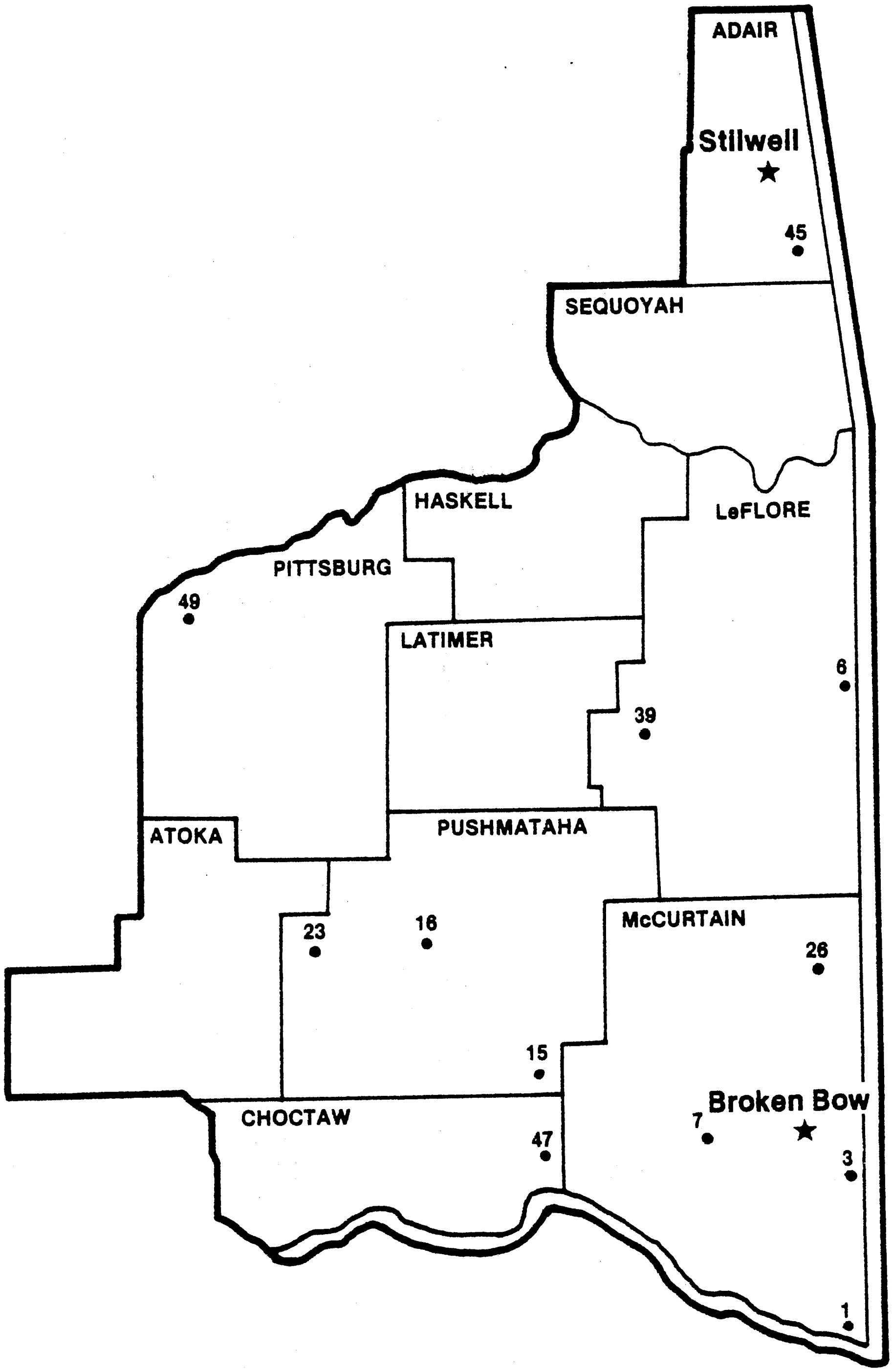


Figure 2. Locations of Parent Shortleaf Pine Stands and Progeny Test Sites

half-sib families were sampled at each location for this study. These fifty-six families were sampled because they had no missing plots. One core taken all the way through the diameter of the sample tree was obtained. The core was removed at diameter breast high with a 12 millimeter increment bore. Care was taken to avoid taking core samples which contained wood from limbs or knots. A soft lead pencil was used to label each core with its tree number. The core samples were placed in plastic tubes and the tubes were labeled with location and rep. numbers for the tree which the core sample represented. These tubes were stored in a freezer at zero degrees centigrade until processed in the laboratory.

## Laboratory Procedures

### Introduction

The core samples from each replication were randomly divided into two equally sized batches within a location. Each batch went through all laboratory procedures together. A total of 24 different batches were processed through the laboratory procedures.

Each core sample was divided into four core segments. The core was first divided at the pith, producing two radial core segments. Each radial core segment was divided to produce one core segment containing growth rings 1 to 10 and a second core segment containing growth rings 11 through 13. The core segments were then individually labeled in pencil with their tree number and segment letters. Segment letters were assigned by reconstructing the core sample, and assigning letters A, B, C, and D in alphabetical order to core segments across the core sample

(Figure 3). The method used to assign segment letters always gave the letters A and D to the core segments consisting of growth rings 11 through 13, and letters B and C to core segments consisting of growth rings 1 to 10.

Unextracted Specific Gravity

The maximum moisture method as described by Smith (1954) was used to measure specific gravity. The maximum moisture method requires the weight of a wood sample at maximum moisture and the weight of the same wood sample void of moisture. The two weights for the sample are then placed in a formula used to calculate specific gravity (Smith, 1954).

$$\text{specific gravity} = \frac{1}{\frac{x-y}{y} + \frac{1}{1.531}} \qquad (3.1)$$

x = sample weight at maximum moisture, in grams

y = sample weight, dried, in grams

The maximum moisture of the core segments was obtained by placing the core segments into an air tight container. A vacuum was applied for a period of one hour. Water was then added to the air tight container possessing the core segments. A shut-off valve prevented the loss of vacuum when the water was added. The core segments were then allowed to soak in the vacuum for 24 hours. After soaking, the vacuum was removed and core segments were weighed. The core segments were kept submerged in water until weighing. Surface moisture was removed from the core segments by rolling them across damp paper towels. All core segments were weighed individually to the nearest .001 of a gram.

The dry weight of the core segments was obtained by placing the

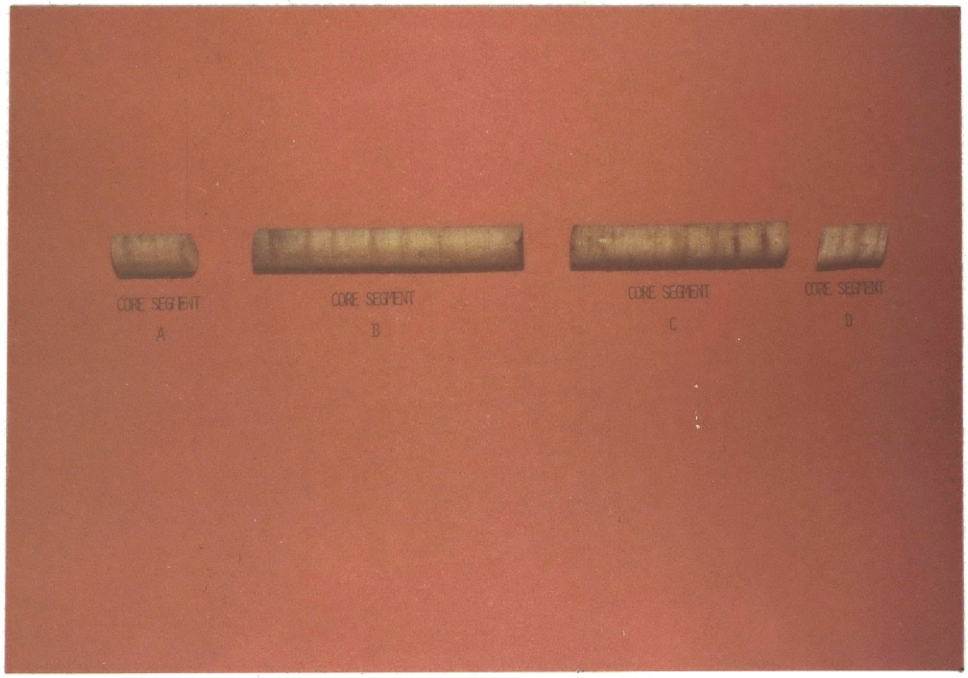


Figure 3. Division of a Core into Segments

core segments in a drying oven set at 107 degrees centigrade for 48 hours. The core segments were then removed from the drying oven and placed in desiccant jars. While in the dessicant jars, the cores were allowed to cool to room temperature. Each core segment was removed individually from the desiccant jar and weighed immediately to the nearest .001 of a gram.

The time intervals and the weighing precision used to obtain the maximum moisture and oven dry weights were derived by the use of a trial batch of cores. An extra batch of cores was gathered for this purpose while in the field. These cores were soaked for several different time intervals and weighed after each soaking. The same was done for the oven drying procedure. Duncan's new multiple range test (Steele and Torrie, 1960) was used to compare the different time interval means at a .05 significance level. In both tests no significant differences were discovered between the minimum and maximum time intervals. For maximum moisture, the minimum soaking interval was 24 hours. The maximum soaking interval was 96 hours. For oven dried weight, the minimum drying interval was 48 hours, and the maximum drying interval was 96 hours. While weighing the cores in the test batch it was discovered that moisture gain for oven dried weighings and moisture loss for maximum moisture weighings could be observed at .00001 gram on the Mettler scale. An actual rate of moisture gain or loss in a certain time interval was never calculated. However, it was felt that no additional accuracy would be gained by weighing the core segments at the .00001 gram level.

Extracted Specific Gravity

The extractives found in southern pines contain resin acids, essential oils, fats, fatty acids and unsaponifiable or inert material. These extractives can be removed from wood samples by the use of several different regeants and an extraction procedure. A modified ASTM (1954) procedure for extraction, as described by Goggans (1962), was used in this study. A modified soxhlet, described by Brown et al. (1977), was used to perform the extractions. The chemical regeants, soaking times, and soxhlet processing times are as follows:

1. Soak wood samples in a 2 part benzene and 1 part ethanol solution for 8 hours.
2. Process wood samples in the soxhlet with a 2 part benzene and 1 part ethanol solution for 16 hours.
3. Soak wood samples 8 hours in ethanol.
4. Process wood samples in the soxhlet with ethanol for 8 hours.
5. Remove ethanol from soxhlet and replace it with water, and process the wood samples in the soxhlet for 8 hours.
6. Boil wood samples in water for 4 hours or until all traces of benzene are removed.

At the completion of the extraction process, the extracted specific gravity was determined by the maximum moisture method. The maximum moisture method is the same method used to determine unextracted specific gravity and has been previously described.

Number of Rings

The length of each core segment was measured to the nearest .001 of an inch. Rings per inch was then calculated for each segment by dividing the number of rings in the segment by segment length. The same method was used to obtain rings per inch for the total core.

$$\text{Number of Rings Per Inch} = \frac{\text{number of rings}}{\text{length of core segments}} \qquad (3.2)$$

<u>Percent Summerwood</u>

Summerwood ring widths were measured to the nearest .001 of an inch. The measurements were obtained by using a dissecting scope equipped with vernier calipers. Summerwood rings were highlighted by staining the core with a one part hydrochloric acid, one part water solution (Holz, 1959).

False rings were measured and included as summerwood in this study. False rings are indistinguishable from normal summerwood rings unless observed with the proper equipment. The density of a false ring produced by a tree is about the same as the summerwood produced by the same tree (Panshin and deZeeuw, 1980). After considering these facts, it was decided that false rings would be included as summerwood. This decision made measuring summerwood more efficient and may have improved the correlation of percent summerwood with specific gravity.

The percent summerwood for each core segment and whole core was computed by dividing the summed widths of summerwood rings by the total core segment length, then multiplying by 100.

$$\text{Percent Summerwood} = \frac{\text{summerwood ring widths}}{\text{segment length}} \times 100 \qquad (3.3)$$

Tracheid Length

Tracheids were obtained from the summerwood in the fifth and twelfth growth rings. The summerwood from the fifth growth rings in the B and C core segments were sliced into thin disks and placed in separate vials. The same was done for the twelfth growth rings in the A and D core segments. It was discovered that core segments that had been heavily stained with the hydrocholoric acid solution used when measuring percent summerwood were easier to slice.

The summerwood disks were macerated in the vials by the use of a procedure described by Buxton (1970). Each vial was filled approximately one-third full with a 1 to 1 solution of hydrogen peroxide and glacial acetic acid. The vials were then placed in an oven set at 66 degrees centigrade. The vials remained in the oven until the summerwood disks took on a silvery appearance. The vials were removed from the oven and the hydrogen peroxide-glacial acetic acid solution was removed. Water was used as a rinse to remove any remaining hydrogen peroxide-glacial acetic acid from the summerwood. The vials were next filled one-half full with water and ten drops of Safranin O dye were added. The vials were then shaken to separate the tracheids.

One wet slide was made from each vial, and 20 whole tracheids were measured per slide. The tracheid lengths from a slide were next averaged together. This produced an average tracheid length for each core segment. The average tracheid length for segments A and D of the same tree were then averaged. The same was done for segments B and C in the same tree core sample. These averages produced one tracheid length for the fifth growth ring and one tracheid length for the twelfth growth ring in a core sample. This was done to obtain an estimate of the mean tracheid length for the growth rings in question for each tree.

The measuring of tracheid lengths was performed with the aid of a bioscope and a calibrated ruler. The bioscope projected the tracheids onto a screen. The tracheids were then measured on the screen with a ruler which was calibrated to convert the projected tracheid lengths into acutal tracheid lengths. The tracheids were measured to the nearest .01 of a millimeter.

## Data Analysis

### Analysis of Variance

A hierarchal analysis of variance (Snedecor and Cochran, 1967) was computed for all six wood properties for each segment age by location. A pooled analysis of variance was computed for each wood property and age by the analysis of variance over locations. Tests for significant differences among stands, among families in stands, stand by location interaction, and family in stand by location interaction, were computed using the F-test. The analysis of variance tables were also used to estimate components of variance for the calculation of half sib heritabilities and genetic correlations (Table I and Table II).

### Genetic Correlations

Genetic correlations are used to estimate the response to selection of one trait on the genotypic variation of another trait. Genetic correlations were computed for all possible combinations of wood properties measured in the study. The genetic correlations were derived by the use of the half sib progeny data from each location and from the

TABLE I

COMPONENTS OF VARIANCE FROM ANALYSIS OF VARIANCE TABLE FOR A SINGLE LOCATION

| Source of Variation | df | Expected Mean Squares | Actual Mean Squares |
|---|---|---|---|
| Stand | 11 | $\sigma_e^2 + S\sigma_{fs}^2 + fs\sigma_s^2$ | $MS_s$ |
| Family (stand) | 44 | $\sigma_e^2 + S\sigma_{fs}^2$ | $MS_{fs}$ |
| Error | 269 | $\sigma_e^2$ | $MS_e$ |

$\sigma_s^2$ = stand variance component

$\sigma_{fs}^2$ = family in stand variance component

$\sigma_e^2$ = error variance component

S, fs are respective coefficients of the expected mean squares

$MS_s$, $MS_{fs}$, $MS_e$ are respective actual mean squares

TABLE II

COMPONENTS OF VARIANCE FROM ANALYSIS OF VARIANCE TABLE FOR POOLED DATA

| Source of Variation | df | Expected Mean Squares | Actual Mean Squares |
|---|---|---|---|
| Stand | 11 | $\sigma^2_e + S\sigma^2_{fxs} + ls\sigma^2_{fs} + fs\sigma^2_{sxl} + fs\sigma^2_s$ | $MS_{sc}$ |
| Stand x location | 11 | $\sigma^2_e + S\sigma^2_{fxs} + ls\sigma^2_{fs} + fs\sigma^2_{sxl}$ | $MS_{sxl}$ |
| Family (stand) | 44 | $\sigma^2_e + S\sigma^2_{fxs} + ls\sigma^2_{fs}$ | $MS_{fsc}$ |
| Family (stand) x location | 44 | $\sigma^2_e + S\sigma^2_{fxs}$ | $MS_{fxs}$ |
| Error | 550 | $\sigma^2_e$ | $MS_{ec}$ |

$\sigma^2_s$ = Stand variance component

$\sigma^2_{sxl}$ = Stand by location interaction variance component

$\sigma^2_{fs}$ = Family in stand variance component

$\sigma^2_{fxs}$ = Family in stand by location interaction variance component

$\sigma^2_e$ = Experimental error variance component

S, ls, fs are respective coefficients of the expected mean squares

$MS_{sc}$, $MS_{sxl}$, $MS_{fsc}$, $MS_{fxs}$, $MS_{ec}$ are respective actual mean squares pooled analysis. The formula used to calculate the half sib genetic correlations is:

$$\Gamma g = \frac{MP_{fs} - MP_{e}}{\sqrt{\hat{\sigma}^2_{fs1} \times \hat{\sigma}^2_{fs2}}} \qquad (3.4)$$

$\Gamma g$ = Genetic Correlation between trait 1 and trait 2.

$MP_{fs}$ = The family (stand) mean cross product for traits 1 and 2.

$MP_{e}$ = The residual mean cross product for traits 1 and 2.

$\hat{\sigma}^2_{fs1}$ = Family (stand) variance component estimate for trait 1.

$\hat{\sigma}^2_{fs2}$ = Family (stand) variance component estimate for trait 2.

Genetic correlations were also estimated by a procedure involving all possible combinations of progeny on parent regression coefficients for two traits. The formula used to calculate the parent progeny regression genetic correlations is:

$$\Gamma g = \frac{\sqrt{b_{O_1P_2} \times b_{O_2P_1}}}{b_{O_1P_1} \times b_{O_2P_2}} \qquad (3.5)$$

$\Gamma g$ = Genetic correlation between trait 1 and trait 2.

$b_{O_1P_2}$ = Regression coefficient of progeny trait 1 on parent trait 2.

$b_{O_2P_1}$ = Regression coefficient of progeny trait 2 on parent trait 1.

$b_{O_1P_1}$ = Regression coefficient of progeny trait 1 on parent trait 1.

$b_{O_2P_2}$ = Regression coefficient of progeny trait 2 on parent trait 2.

## Narrow Sense Heritability

Heritability is a measure of the proportion of phenotypic variation among individuals that is under genetic control. Narrow sense heritability estimates the proportion of phenotypic variation due to additive gene action. Additive gene action is the cause of similarities between parents and offspring. The proportion of genetic control due to additive gene action is a function of the difference in frequencies of certain alleles among individuals within a population (Falconer, 1960).

Narrow sense heritability was computed for each wood property using two methods, half sib correlations and parent progeny regression. It must be realized that the progeny in these tests are not true half sibs. They are open pollinated progeny of a parent tree in a natural stand. If there are enough progeny in the study that are really full sibs the variance of families within stands will contain more than the assumed one-fourth additive variance. This would inflate the half sib heritability estimates. It was assumed in this study that open pollinated progeny are true half sibs.

The half sib correlation method for estimating heritability uses the components for variance from the analysis of variance shown in Table I (Falconer, 1960). Heritabilities were estimated using both single location and pooled location analysis of variance. The equation used to calculate heritability at one location is shown below.

$$h^2 = \frac{4\ (\hat{\sigma}^2_{fs})}{\hat{\sigma}^2_e + \hat{\sigma}^2_{fs}} \qquad (3.6)$$

$h^2$ = Narrow sense heritability

$\hat{\sigma}^2_{fs}$ = Family (stand) component of variance estimate

$\hat{\sigma}^2_e$ = Error component of variance estimate

The one parent progeny regression method estimates heritability estimates by multiplying the regression coefficient of progeny on parents by two (Falconer, 1960). The regression coefficient of progeny data on parent data produces an estimate of one half the additive genetic variation over the phenotypic variation.

$$h^2 = 2 \cdot \frac{\Sigma\, xy}{\Sigma\, x^2} \tag{3.7}$$

x = independent variable, parent measurements

y = dependent variable, family average

Due to skewness in the percent summerwood parent data, the parent and progeny data were transformed using the arcsine transformation (Snedecor and Cochran, 1967). It must also be noted that the parent tree data for the older core segments covers a ten year growth period, while in the progeny, it covered a three year period. When studying the parent progeny regression heritability estimates it will be important to keep in mind the affects of tree age on wood properties and the amount of environmental variation that may be added by seven extra years of growth.

# CHAPTER IV

# RESULTS AND DISCUSSION

## Environment

The two progeny test locations used in this study represent two contrasting sites found in the shortleaf pine range of Oklahoma. The Broken Bow site is located on a small ridge in the coastal plain at about 850 feet above sea level. The soil type at the location is a deep sandy loam, which receives approximately 52 inches of rain annually. The Stilwell site is located at over 1000 feet above sea level in the Quachita mountains on a shallow silt loam soil. The Stilwell planting is in the flood plain of a small creek. The Stilwell area receives about 45 inches of rain per year. In a study by Tauer and McNew (In press), of the same two progeny tests the difference between the two environments manifested itself in terms of survival. The Broken Bow location had a high survival of 90 percent. The Stilwell location survival was much lower at 60 percent. The shallow soil and dry mountainous climate of the Stilwell location seemed to be a harsher environment for shortleaf pine than that found at the Broken Bow location.

In this study, percent survival added another dimension to the environmental effects. Only families which had no missing plot at either location were sampled in order to provide a balanced experimental design. The effects of different spacing on the sampled plots due to the difference in survival at the two locations may cause added environmental variation in the pooled data.

## Specific Gravity and Percent Extractives

Significant variation among families for unextracted and extracted specific gravity was found at the Broken Bow location. The variation was significant for both mature wood and juvenile wood (Appendix A, Table V and Table VI). Many researchers have reported similar results for among tree variation of specific gravity (Dadswell et al., 1961; Echols, 1958; Goggans, 1962; McCullough, 1972). No significant difference among stands was found.

The Stilwell location, like Broken Bow, possessed significant among family variation for unextracted and extracted specific gravity in both mature and juvenile wood. The Stilwell location also exhibited, in the mature wood, significant variation among stands for unextracted and extracted specific gravity. Stands from dry areas of Oklahoma may possess increased drought tolerance or the ability to grow better under dry conditions. The bulk of rain received at Stilwell during the shortleaf pine growing season is in the late spring and early summer followed by two to three months of drought conditions. The shallow soil and the rainfall distribution does not allow for large increments of dense summerwood to be formed. Families from stands located in dry environments possess the ability to produce more summerwood growth during periods of drought than those families from less droughty areas (Larson, 1957; Zobel and McElwee, 1958). This was found to be true for the families examined in this study. When stand means for percent summerwood and specific gravity are compared, stands from the drier areas have a larger percentage of summerwood and a higher specific gravity (Appendix B, Table XII, Table XIII, and Table XV).

The pooled over location data contained variation among families and among stands for both unextracted and extracted specific gravity (Appendix A, Table V and Table VI) of the juvenile wood. As stated previously, significant variation among families in the juvenile wood agrees with the documented significant tree to tree variation in specific gravity reported by others. In the juvenile wood for both unextracted and extracted specific gravity, stands performed similarly at both locations (Appendix B, Table XII and Table XIII). Based on the information from the pooled data, genetic gains may be increased for junvenile wood specific gravity if selections are made first among stands and then among individuals in the best stands.

In older trees, percent extractives might make up an important part of the phenotypic variation found in specific gravity. However, due to the young age of the trees in this study, the amount of percent extractives was small (Appendix B, Table VII). There was no significant genetic variation in percent extractives at either location or in the pooled data for mature and juvenile wood (Appendix A, Table VIII). Most of the variation in percent extractives at an individual location was among replications. In the pooled data the bulk of the variation for percent extractives is due to the differences between location. The presence of a large proportion of variation among replications and between locations is an indication that the environment plays an important role in the variation of percent extractives found in shortleaf pine.

A significant genotype by environment interaction was detected in the mature wood for unextracted and extracted specific gravity pooled data (Appendix A, Table V and Table VI). This genotype by environment interaction was not detected in any of the juvenile wood data. The significant variation found in the family x location interaction may have two causes. The first is the difference in the magnitude of both the unextracted and the extracted specific gravity estimates between the two locations. The difference in magnitude can easily be seen when comparing location means (Table III).

TABLE III

LOCATION MEANS FOR UNEXTRACTED AND EXTRACTED SPECIFIC GRAVITY

| | Broken Bow | Stilwell |
|---|---|---|
| Unextracted Specific Gravity | .447 | .377 |
| Extracted Specific Gravity | .424 | .346 |

The other possible cause for family x location interaction is the significant interchange of family rankings noted between location. The significant difference in family performance at the two locations may cause an averaging effect when the data is pooled. This averaging effect would hide significant variation among families.

Narrow sense heritability estimates for unextracted specific gravity, extracted specific gravity, and percent extractive content were calculated by use of half sib correlations and parent progeny regression for both the mature wood and the juvenile wood (Table IV). The half sib correlation procedure of calculating heritability was used to obtain heritability estimates for each location and for the pooled data. The parent progeny regression was used to obtain heritability estimates by regressing the pooled data family means on the parent tree data.

The mature wood heritability estimates for the Broken Bow location were .364 for unextracted specific gravity, .345 for extracted specific gravity, and .109 for percent extractives. An unextracted specific gravity heritability estimate higher than the extracted specific gravity heritability estimate was unexpected. With the removal of extractives from the mature wood core segments a reduction of phenotypic variation is expected. The reduction in phenotypic variation due to the removal of extractives would produce a higher heritability estimate for extracted specific gravity. Apparently because the mature wood core segments from Broken Bow contained an extremely small amount of extractives, (Appendix B, Table XI) the slight difference between unextracted and extracted specific gravity heritability estimates is due to sample variation in the data.

The juvenile wood heritability estimates from Broken Bow followed an expected pattern. The unextracted specific gravity heritability estimate of .320 is lower than the extracted specific gravity heritability estimate of .417. The percent extractives heritability estimate at .06 did not vary much from the heritability calculated for the mature wood core segments for the same trait.

Heritability estimates for the mature wood core segments from Stilwell are .446 for unextracted specific gravity, .501 for extracted

TABLE IV

NARROW SENSE HERITABILITY ESTIMATES

| | Unextracted Specific Gravity | | Extracted Specific Gravity | | Percent Extractives | | Number of Rings Per Inch | | Percent Summerwood | | Tracheid Length | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $h^2$ | s.e. | $h^2$ | s.e. | $h^2$ | s.e. | $h^2$ | s.e. | $h^2$ | s.e. | $h^2$ | s.e. |
| <u>Mature Wood</u> | | | | | | | | | | | | |
| Pooled Data Half Sibs | .100 | .157 | .145 | .147 | -.060 | .117 | .194 | .132 | .038 | .105 | .147 | .124 |
| Broken Bow Half Sibs | .364 | .205 | .345 | .211 | .109 | .173 | .263 | .192 | .066 | .168 | .350 | .206 |
| Stilwell Half Sibs | .446 | .217 | .501 | .223 | .229 | .168 | .124 | .173 | .100 | .139 | .331 | .203 |
| Parent Progeny Regression | .033 | .033 | .190 | .080 | .015 | .021 | .081 | .261 | .382 | .385 | .382 | .400 |
| <u>Juvenile Wood</u> | | | | | | | | | | | | |
| Pooled Data Half Sibs | .346 | .156 | .242 | .165 | .012 | .086 | .312 | .129 | -.039 | .104 | .230 | .137 |
| Broken Bow Half Sibs | .320 | .202 | .417 | .197 | -.065 | .145 | .250 | .194 | -.001 | .104 | .271 | .191 |
| Stilwell Half Sibs | .545 | .194 | .567 | .227 | .282 | .144 | .161 | .182 | -.060 | .149 | .279 | .199 |
| Parent Progeny Regression | .037 | .054 | .190 | .086 | .013 | .024 | -.240 | .282 | .360 | .757 | - | - |

specific gravity, and .229 for percent extractives. The heritability estimates for the juvenile wood core segments are .545 for unextracted specific gravity, .567 for extracted specific gravity, and .282 for percent extractives.

In general, the half sib heritability estimates for specific gravity calculated by locations are very similar to those obtained by other researchers for other southern pines (Namkoong et al., 1969; Squillace et al., 1962; van Buijtenen, 1962). The heritability estimates for percent extractives at each location are quite high. The effect of a common environment within a location may be one reason for the high heritability estimates for percent extractives. It is a known fact that environment and age strongly influence the extractive content in a tree (Ifju and Labesky, 1972; Kurth, 1933; Posey and Robinson, 1969).

The unextracted specific gravity, extracted specific gravity, and percent extractives heritability estimates calculated from the Stilwell data are larger than those obtained from the Broken Bow data. If it is assummed that the additive genetic variance of the trees at the two locations are the same, then the phenotypic variation at Broken Bow is greater than that at Stilwell. The difference in variation can be observed when comparing the replication mean squares of the two locations in Table VII.

The half sib heritability estimates from the pooled data for the mature wood are considerably lower than those estimated at either location. As discussed previously, there is significant genotype by environment interaction and non-significant among family variation in the pooled specific gravity data. The averaging effect caused by pooling the data of families which performed significantly different between locations reduces the among family variation. The reduction of variation among families indicates the degree of resemblance among half sibs is not very good. This leads to a reduction in the estimation of additive genetic variance. The half sib heritability estimates for the pooled mature wood core segment data is .100 for unextracted specific gravity, .145 for extracted specific gravity, and -.060 for percent extractives. The negative percent extractive heritability estimate possesses a large standard error (Table IV). When the percent extractive data was pooled, the effect of the common environment within a location was lost. With the loss of the common environment effect the estimate of additive genetic variance was reduced while the estimate of phenotypic variation was increased. The pooled data suggest that heritability estimates calculated with data from only one location may be inflated due to the confounding of the family in stand variance component by the genotype by environmental interaction component.

In the juvenile wood, the heritability estimates for unextracted and extracted specific gravity are only slightly smaller than those calculated for each location. The unextracted specific gravity heritability estimate is .346 which is larger than the extracted specific gravity heritability estimate of .242. Both unextracted and extracted heritability estimates have large standard errors (Table IV), so the most probable reason for the difference in the heritability estimates is the sampling error in the pooled data. The heritability estimate for percent extractives in the juvenile wood core segments is .012. The magnitude of reduction in the heritability estimates for extractive percent in juvenile wood is similar to that found in the mature wood.

The pooled half sib heritability estimates for specific gravity were lower than expected. Variation due to genotype by environment interaction can be accounted for in the analysis of variance for the pooled data. In the analysis of variance for a single location the variation caused by differences in the ability to perform in certain environments is confounded in the family in stand variance component. This inflates the family in stand variance component which is used as an estimate of additive genetic variation in the calculation of half sib heritability estimates. Therefore, specific gravity heritability estimates calculated with data from only one location may be inflated.

Heritabilities estimated by use of parent progeny regression were expected to be lower than those calculated using half sibs. The parent data was collected from trees in their natural stands. McCullough (1972) reported significant variation among the stands from which the parent tree data was obtained. The added environmental variation in the parents, due to the significant among stand variation, increased the denominator in the parent progeny regression formula (3.7). This increase in the denominator, or phenotypic variation, is the cause for the lower parent progeny regression heritability estimates observed (Table IV). However, the distortion that may be caused by the significant environmental variation in the parent progeny regression heritability estimates are not as large for traits which have low additive genetic variance. In the case of percent extractives the parent progeny regression heritability estimates vary little from those calculated using half sib family means.

Genetic correlations were calculated for extracted and unextracted specific gravity with all the other measured traits in the study.

Unfortunately, due to the presence of negative variance components, only a few correlations were obtained (Appendix C).

The mature wood genetic correlations for percent summerwood with unextracted specific gravity (Appendix C, Table XVII) and extracted specific gravity (Appendix C, Table XVIII) were estimated only in the pooled data. Neither of these correlations was significant. Juvenile wood genetic correlations for percent summerwood with unextracted and extracted specific gravity were only computable for the Broken Bow data. These correlations, like those of the mature wood core segments, are non-significant. However, it was noted that all these genetic correlations of specific gravity with percent summerwood were positive. This trend is in agreement with findings of other researchers (Ifju and Labesky, 1972; Jayne, 1958; Larson, 1957).

The relationship between diameter growth and specific gravity has been of interest for decades. Therefore, genetic correlations of unextracted and extracted specific gravity with number of rings per inch were computed for both the mature and juvenile wood data (Appendix C, Table XVII and Table XVIII). All the mature wood correlations were positive. Only one was significant, but it was a theoretically impossible 1.2. Since number of rings per inch is an inverse measure of diameter growth, these data suggest that diameter growth and specific gravity in mature wood have a negative genetic correlation. The juvenile wood core segments produced an opposite result for genetic correlations of diameter growth with specific gravity, except at the Broken Bow location. These juvenile wood genetic correlations are not only non-significant, they fail to give any possible insight on the direction of the correlations. The ambiguous results of the correlation of juvenile wood specific gravity with number of rings per inch exemplifies the controversy surrounding this particular correlation. These data suggest that, at least for juvenile wood, no relationship exists.

## Number of Rings Per Inch

There was no significant variation in number of rings per inch observed at either location or in the pooled data for the mature wood (Appendix A, Table VIII). The lack of significant variation among families indicates that the variation in number of rings per inch can be attributed to factors other than additive genetic influences. The analysis of variance shows that the bulk of the variation in the pooled data for the number of rings per inch in mature wood is due to difference between locations.

The juvenile wood number of rings per inch data contained significant among family variation at the Broken Bow location and in the pooled data (Appendix A, Table VIII). Apparently, the relatively good site at Broken Bow allowed for the expression of genetic variation in diameter growth while Stilwell did not. At Stilwell where there was only 60 percent survival, the environmental conditions seem to mask the expression of genetic variation in diameter growth. The significant among family variation in the pooled data suggest that genetic control is an important factor in diameter growth rate of juvenile shortleaf pine.

The half sib heritability estimates for the mature wood number of rings per inch are .194 for the pooled data, .263 for Broken Bow, and .124 for Stilwell (Table VIII). These heritability estimates do not vary greatly from those reported by other researchers for other southern pines (Stonecypher and Zobel, 1966; Rousseau, 1980).

The half sib heritability estimates for the juvenile wood are higher than those for the mature wood core segments (Table IV). An increase in heritability for diameter growth for younger material over those found for older material from the same tree has been found before (Rousseau, 1980). The heritability estimates for the juvenile wood number of rings per inch seem reasonable when compared to other heritability estimates reported on the trait. However, these estimates are low when compared to narrow sense heritability estimates calculated by Tauer (in press) for diameter growth of trees from the same progeny test. The heritabilities estimated by Tauer may be inflated somewhat due to the use of families with missing plots.

The parent progeny regression heritability estimates varied greatly between the mature wood core segments and the juvenile wood core segments. The mature wood parent progeny regression heritability estimate was .081, which is lower than the heritability estimates produced by the half sib family mean procedure of estimating heritability. The reason for the low parent progeny regression heritability estimate is possibly the fact that the parent tree data was collected from natural stands and possesses a large amount of environmental variation. In the juvenile wood the parent progeny regression gave the lowest heritability estimate reported in this study, -.240. Again, the cause of the extremely low heritabilities produced by the parent progeny regression lies in the large amount of environmental variation present in the parent data. If the parent progeny regression heritability estimates are considered unreliable and only the half sib heritability estimates are taken into account for both the mature and juvenile wood, some gains in diameter growth rate may be obtained through selection.

A few genetic correlations were computed for number of rings per inch and percent summerwood in both mature wood and juvenile wood (Appendix C, Table XIX). These genetic correlations were nonsignificant, but they did suggest a definite positive trend.

Number of rings per inch was not genetically correlated with any of the other traits measured, except for the previously discussed relationship with specific gravity.

## Percent Summerwood

There was no significant genetic variation in percent summerwood at either location or in the pooled data for the juvenile and mature wood (Appendix A, Table IX). The lack of genetic variation in percent summerwood was not expected. Previous studies have demonstrated a strong environmental influence on percent summerwood in other southern pines (Larson, 1975; Squillace et al., 1962).

The half sib heritability estimates calculated for percent summerwood are low (Table IV). The mature wood produced slightly higher heritability estimates than the juvenile wood. The low heritability estimates were expected. The lack of variation among families and stands indicates a minimal amount of additive genetic variation. McCullough (1972) found that his percent summerwood data were skewed, and used an arcsine of the square root of the percent summerwood transformation as a correction factor. The same transformation was tried on the progeny data, but the transformation had no real effect on the distribution of the progeny data. The half sib heritability estimates changed little with the use of the transformation. The transformation was used on both the parent and progeny data for the calculation of parent progeny regression heritability. The parent progeny regression heritability estimates are higher than the half sib heritability estimates. The transformation reduced the amount of phenotypic variation in the parent data which is the denominator in the parent progeny regression heritability equation (3.7). Also, the magnitude of the regression of the progeny data onto the parent data may have been increased by the transformation. The effects of the transformation on the distribution of both the parent and progeny data may be the cause for the parent progeny regression heritability estimates to be higher than those calculated by use of half sib family means. The half sib heritability estimates appear to be the most reliable.

All genetic correlations of interest for percent summerwood, and their implications, have been discussed previously.

## Tracheid Length

It would have been impossible to obtain tracheid length estimates for all the juvenile and mature wood growth rings in the time period in which this study was performed. Therefore, the fifth growth ring was chosen to represent the juvenile wood and the twelfth growth ring was chosen for the mature wood. The analysis of variance for tracheid length by location and pooled data for the fifth and twelfth growth rings shows an unexpected large amount of environmental influence (Appendix A, Table X). Work reported on other pines has produced evidence that tracheid lengths are under predominantly genetic control (Dadswell et al., 1961; Goggans, 1962; Jackson and Greene, 1958). Some indications of genetic influence on shortleaf pine tracheid lengths were detected in the Broken Bow data for both growth rings sampled. The genetic control is in the form of variation among families. Significant among family variation suggests the presence of additive genetic variation. In the pooled data for the juvenile wood tracheid lengths significant among stand variation was found. McCullough (1972) discovered significant among stand variation in the parent trees. The significant among stand variation may be at least partly attributed to differences in the contents of the stand gene pools. However, the overriding evidence in these data suggest a significant amount of variation in shortleaf pine tracheid lengths is due to non-additive and environmental influences.

The mature wood tracheid length half sib heritability estimates of .350 for Broken Bow and .331 for Stilwell are relatively similar (Table IV). The half sib heritability estimate for the pooled data of .147 is somewhat lower than the individual location heritability estimates. Significant variation between locations is the cause for the small heritability estimate for tracheid length in the pooled data. The parent progeny regression heritability estimate could only be calculated for the mature wood because only tracheid lengths for mature wood were available from McCullough's data. The heritability calculated by use of a parent progeny regression is .382. This heritability estimate is similar to those calculated for the mature wood tracheid length using half sib family means. The parent data obtained by McCullough (1972) consisted of the averaging of tracheid length measurements from the eleventh, fifteenth, and twentieth growth ring summerwood segments. The twelfth growth ring pooled progeny data was then regressed on McCullough's parent data to obtain a mature wood core segment heritability estimate. If one accepts all of Sanio's (1892) laws then the parent progeny regression heritability estimate is valid. If Sanio's (1892) laws are considered false, then the parent progeny regression heritability estimate contains added phenotypic variation caused by variation among growth rings in the mature wood.

The juvenile wood tracheid length half sib heritability estimates are lower than those calculated for the mature wood (Table IV). Like the mature wood heritability estimates, the juvenile wood heritability estimates are grouped close together. Even the pooled data half sib heritability estimate for the juvenile wood is close in magnitude to those calculated for the individual locations.

All the heritability estimates calculated for tracheid length in this study are considered low when compared to tracheid length heritability estimates for other pines. However, the precision of the groupings of the heritability estimates in the study may indicate that the amount of additive genetic control of tracheid length in shortleaf pine is less than that found in other pines. Still, these heritability estimates are of a sufficient magnitude to allow adequate genetic gains in a selection program.

# CHAPTER V

## SUMMARY AND CONCLUSIONS

The objective of this study was to estimate genetic variation in six wood properties of shortleaf pine in southeastern Oklahoma. The variation components estimated for unextracted specific gravity, extracted specific gravity, percent extractives, number of rings per inch, percent summerwood, and tracheid lengths were used to compute narrow sense heritability and genetic correlations.

The trees used in this study are open pollinated progeny of measurement trees used in a study of geographic variation in Oklahoma shortleaf pine reported by McCullough (1972). The parent trees are located in natural stands throughout the shortleaf pine range in southeastern Oklahoma. The open pollinated progeny were planted at two contrasting sites in the shortleaf pine range of southeastern Oklahoma. A randomized complete block design consisting of six replications each constructed of 100 four tree family row plots were used at both locations. The fifty-six unrelated half sib families without missing plots at both locations were sampled. The experimental design was balanced. The wood sample from a tree was divided into two main segments; the mature wood segment consisting of growth rings (11-13), and the juvenile wood segment consisting of growth rings (1-10). Analysis of variance for each wood property was computed within each growth segment group.

Heritability estimates were calculated by use of half sib family means and parent progeny regression. The half sib heritability procedure was performed for each wood property within growth segment groups for individual locations and pooled data. The parent progeny regression method for calculating heritability was used only with the pooled progeny data for both growth segment groups.

The half sib heritability estimates calculated in this study by location for unextracted and extracted specific gravity of shortleaf pine are similar to those reported for other pines. The pooled half sib heritability estimates are similar to each other, but they are lower than those calculated for individual locations. The parent progeny heritability estimates are considerably lower than the half sib heritability estimates, probably due to a large amount of environmental variation in the parent data. On the average, the extracted specific gravity heritability estimates are higher than those calculated for the unextracted specific gravity. The removal of extractives from the core samples reduces the amount of phenotypic variation present without much effect on the amount of additive genetic variation. The trend found between juvenile and mature wood heritability estimates suggests that specific gravity in juvenile wood may be slightly more heritable than specific gravity in mature wood. However, there is a possibility that some of the variation discovered in the mature wood may be due to the fact that not all trees were producing mature wood at ages 11 through 13. It seems probable, based on this study's data, that heritability for specific gravity is of an adequate size to achieve acceptable genetic gains through selection for specific gravity.

Narrow sense heritability estimates for extractive content varied greatly. In most cases the standard error of the heritability estimate was larger than the heritability estimate itself. Generally, heritability estimates produced from individual location data were high, and those estimated from pooled data and by parent progeny regression were low. Even though it is difficult to give definite values for the expected heritability of extractive content, it is apparent that heritability is fairly low. Factors such as age and site appear to have a great influence on the extractive content of a shortleaf pine.

Percent summerwood heritability estimates increased from juvenile wood to mature wood; however, all the half sib percent summerwood heritability estimates were extremely low and have large standard errors. The parent progeny regression heritability estimates were of a moderate magnitude but the standard error of the heritability estimates did not improve over that of the half sibs. It would be very risky to make any interpretations about the nature of the genetic variance of percent summerwood found in this study due to the over-riding environmental influences.

The number of rings per inch half sib heritability estimates were fairly similar between locations and between wood segment age groups. The Stilwell location produced slightly lower half sib heritability estimates due to large environmental variations which may be the result of low survival. The heritability estimates produced for number of rings per inch by using half sib families are similar to those reported for other pines. The probable cause of an extremely low heritability estimate produced by the parent progeny regression is the large amount of environmental variation in the parent data.

The heritabilities calculated for tracheid lengths are higher for the mature wood than for juvenile wood. Both mature wood and juvenile wood tracheid length heritability estimates are low when compared to heritability estimates for tracheid lengths of other southern pines reported in the literature. Although the heritability estimates for tracheid lengths estimated in this study are comparatively low, they are of sufficient size to indicate that an adequate amount of genetic gain can be obtained through selection.

The genetic correlations estimated in this study have large standard errors, and at best, can only provide some idea of the direction of the relationships. For both tracheid length and percent extractives, no correlations of interest were observed. Weak positive genetic correlations were found for specific gravity with percent summerwood. Stronger positive correlations were observed for number of rings per inch with percent summerwood. Positive genetic correlations were also found for specific gravity with number of rings per inch in all of the mature data and in the juvenile data from Broken Bow. The rest of the juvenile data produced negative specific gravity with number of rings per inch genetic correlations. It is improbable, using the genetic correlations calculated in this study, to obtain accurate estimates of genetic response of one wood property to selection for another.

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# APPENDIXES

# APPENDIX A

# ANALYSIS OF VARIANCE TABLES

TABLE V

ANALYSIS OF VARIANCE BY LOCATIONS AND POOLED DATA FOR UNEXTRACTED SPECIFIC GRAVITY

| | Mature Wood | | | Juvenile Wood | | |
|---|---|---|---|---|---|---|
| **Pooled Data** | | | | | | |
| Source | D.F. | Mean Squares | F-Test | D.F. | Mean Squares | F-Test |
| Location | 1 | 0.81914 | | 1 | 0.00076 | |
| Replication (Loc.) | 10 | 0.00168 | | 10 | 0.00296 | |
| Stand | 11 | 0.00350 | 2.279 | 11 | 0.00204 | 3.643* |
| Stand x Loc. | 11 | 0.00154 | .990 | 11 | 0.0056 | .776 |
| Family (Stand) | 44 | 0.00191 | 1.266 | 44 | 0.00136 | 1.863* |
| Family (Stand) x Loc | 44 | 0.00156 | 1.604* | 44 | 0.00073 | 1.196 |
| Error | 550 | 0.0097 | | 550 | 0.0061 | |
| Total | 671 | | | 671 | | |
| **Broken Bow** | | | | | | |
| Source | | | | | | |
| Replication | 5 | 0.00897 | | 5 | 0.00908 | |
| Batch (Rep.) | 6 | 0.03145 | | 6 | 0.01345 | |
| Stand | 11 | 0.01604 | .941 | 11 | 0.01100 | 1.410 |
| Family (Stand) | 44 | 0.01763 | 1.513* | 44 | 0.00781 | 1.592* |
| Error | 269 | 0.01170 | | 269 | 0.00490 | |
| Total | 335 | | | 335 | | |
| **Stilwell** | | | | | | |
| Source | | | | | | |
| Replication | 5 | 0.01802 | | 5 | 0.03739 | |
| Batch (Rep.) | 6 | 0.01129 | | 6 | 0.00489 | |
| Stand | 11 | 0.02460 | 2.46* | 11 | 0.0853 | 1.036 |
| Family (Stand) | 44 | 0.01004 | 1.923* | 44 | 0.00822 | 1.74* |
| Error | 269 | 0.00521 | | 269 | 0.00473 | |
| Total | 335 | | | 335 | | |

*Significance at the .05 level.

TABLE VI

ANALYSIS OF VARIANCE BY LOCATIONS AND POOLED DATA FOR EXTRACTED SPECIFIC GRAVITY

| | Mature Wood | | | Juvenile Wood | | |
|---|---|---|---|---|---|---|
| **Pooled Data** | | | | | | |
| Source | D.F. | Mean Squares | F-Test | D.F. | Mean Squares | F-Test |
| Location | 1 | 1.02890 | | 1 | 0.02704 | |
| Replication (Loc.) | 10 | 0.00196 | | 10 | 0.00127 | |
| Stand | 11 | 0.00345 | 2.447 | 11 | 0.00205 | 4.578* |
| Stand x Loc. | 11 | 0.00140 | 1.052 | 11 | 0.00045 | .7680 |
| Family (Stand) | 44 | 0.00167 | 1.307 | 44 | 0.00100 | 1.724* |
| Family (Stand) x Loc | 44 | 0.00134 | 1.672* | 44 | 0.00058 | 1.275 |
| Error | 550 | 0.00080 | | 550 | 0.00046 | |
| Total | 671 | | | 671 | | |
| **Broken Bow** | | | | | | |
| Source | | | | | | |
| Replication | 5 | 0.02688 | | 5 | 0.01566 | |
| Batch (Rep.) | 6 | 0.00411 | | 6 | 0.00472 | |
| Stand | 11 | 0.01781 | 1.171 | 11 | 0.00923 | 1.640 |
| Family (Stand) | 44 | 0.01523 | 1.692* | 44 | 0.00569 | 1.555* |
| Error | 269 | 0.00905 | | 269 | 0.00366 | |
| Total | 335 | | | 335 | | |
| **Stilwell** | | | | | | |
| Source | | | | | | |
| Replication | 5 | 0.00484 | | 5 | 0.00196 | |
| Batch (Rep.) | 6 | 0.00985 | | 6 | 0.00456 | |
| Stand | 11 | 0.01840 | 2.424* | 11 | 0.00796 | 1.588 |
| Family (Stand) | 44 | 0.00768 | 1.974* | 44 | 0.00501 | 1.851* |
| Error | 269 | 0.00391 | | 269 | 0.00272 | |
| Total | 335 | | | 335 | | |

*Significance at the .05 level.

TABLE VII

ANALYSIS OF VARIANCE BY LOCATIONS AND POOLED DATA FOR PERCENT EXTRACTIVES

| | Mature Wood | | | Juvenile Wood | | |
|---|---|---|---|---|---|---|
| **Pooled Data** | | | | | | |
| Source | D.F. | Mean Squares | F-Test | D.F. | Mean Squares | F-Test |
| Location | 1 | 17711.00 | | 1 | 2227.30 | |
| Replication (Loc.) | 10 | 94.8729 | | 10 | 125.490 | |
| Stand | 11 | 2.61226 | .510 | 11 | 2.90539 | .772 |
| Stand x Loc. | 11 | 5.12479 | 1.082 | 11 | 3.76530 | .586 |
| Family (Stand) | 44 | 3.84201 | .809 | 44 | 6.22853 | .969 |
| Family (Stand) x Loc | 44 | 4.73607 | .901 | 550 | 5.28345 | 1.216 |
| Error | 550 | 5.15226 | | 671 | | |
| Total | 671 | | | | | |
| **Broken Bow** | | | | | | |
| Source | | | | | | |
| Replication | 5 | 171.360 | | 5 | 90.4816 | |
| Batch (Rep.) | 6 | 215.876 | | 6 | 125.453 | |
| Stand | 11 | 7.97314 | .779 | 11 | 4.70866 | .588 |
| Family (Stand) | 44 | 10.2190 | 1.144 | 44 | 8.02925 | 1.155 |
| Error | 269 | 8.93361 | | 269 | 6.95530 | |
| Total | 335 | | | | | |
| **Stilwell** | | | | | | |
| Source | | | | | | |
| Replication | 5 | 61.7065 | | 5 | 329.960 | |
| Bat. (Rep) | 6 | 56.1728 | | 6 | 74.8943 | |
| Stand | 11 | 5.09461 | 1.899 | 11 | 6.66810 | .865 |
| Family (Stand) | 44 | 2.67679 | .613 | 44 | 0.84509 | .613 |
| Error | 269 | 4.37055 | | 269 | 7.25365 | |
| Total | 335 | | | 335 | | |

*Significance at the .05 level.

TABLE VIII

ANALYSIS OF VARIANCE BY LOCATIONS AND POOLED DATA FOR NUMBER OF RINGS PER INCH

| | Mature Wood | | | Juvenile Wood | | |
|---|---|---|---|---|---|---|
| **Pooled Data** | | | | | | |
| Source | D.F. | Mean Squares | F-Test | D.F. | Mean Squares | F-Test |
| Location | 1 | 382.527 | | 1 | 2.48768 | |
| Replication (Loc.) | 10 | 2.92906 | | 10 | 4.32770 | |
| Stand | 11 | 0.84300 | .477 | 11 | 0.82297 | .637 |
| Stand x Loc. | 11 | 1.76076 | 1.475 | 11 | 1.22339 | 1.631 |
| Family (Stand) | 44 | 1.90010 | 1.583 | 44 | 1.60576 | 2.141* |
| Family (Stand) x Loc | 44 | 1.19401 | 1.040 | 44 | 0.75003 | .871 |
| Error | 550 | 1.14863 | | 550 | 0.86090 | |
| Total | 671 | | | 671 | | |
| **Broken Bow** | | | | | | |
| Source | | | | | | |
| Replication | 5 | 1.94220 | | 5 | 1.32405 | |
| Batch (Rep.) | 6 | 1.41089 | | 6 | 0.78124 | |
| Stand | 11 | 1.98525 | 1.070 | 11 | 0.91055 | .798 |
| Family (Stand) | 44 | 1.85560 | 1.392 | 44 | 1.14292 | 1.829* |
| Error | 269 | 1.33355 | | 269 | 0.62456 | |
| Total | 335 | | | 335 | | |
| **Stilwell** | | | | | | |
| Source | | | | | | |
| Replication | 5 | 3.91592 | | 5 | 7.33136 | |
| Batch (Rep.) | 6 | 1.41430 | | 6 | 0.88987 | |
| Stand | 11 | 0.64398 | .538 | 11 | 1.09640 | .865 |
| Family (Stand) | 44 | 1.19447 | 1.239 | 44 | 1.26999 | 1.165 |
| Error | 269 | 0.95810 | | 269 | 1.09063 | |
| Total | 335 | | | 335 | | |

*Significance at the .05 level.

TABLE IX

ANALYSIS OF VARIANCE BY LOCATIONS AND POOLED DATA FOR PERCENT SUMMERWOOD

| | Mature Wood | | | Juvenile Wood | | |
|---|---|---|---|---|---|---|
| **Pooled Data** | | | | | | |
| Source | D.F. | Mean Squares | F-Test | D.F. | Mean Squares | F-Test |
| Location | 1 | 14079.4 | | 1 | 26530.8 | |
| Replication (Loc.) | 10 | 108.417 | | 10 | 117.806 | |
| Stand | 11 | 18.0021 | 1.617 | 11 | 44.2214 | .425 |
| Stand x Loc. | 11 | 11.1229 | .427 | 11 | 104.031 | 1.517 |
| Family (Stand) | 44 | 23.2635 | .898 | 44 | 76.7234 | 1.118 |
| Family (Stand) x Loc | 44 | 26.0340 | 1.115 | 44 | 68.5986 | .978 |
| Error | 550 | 23.3503 | | 550 | 70.1214 | |
| Total | 671 | | | 671 | | |
| **Broken Bow** | | | | | | |
| Source | | | | | | |
| Replication | 5 | 144.022 | | 5 | 133.400 | |
| Batch (Rep.) | 6 | 98.6361 | | 6 | 181.349 | |
| Stand | 11 | 14.1009 | .456 | 11 | 103.794 | .999 |
| Family (Stand) | 44 | 30.7359 | 1.098 | 44 | 103.865 | .990 |
| Error | 269 | 27.9931 | | 269 | 104.000 | |
| Total | 335 | | | 335 | | |
| **Stilwell** | | | | | | |
| Source | | | | | | |
| Replication | 5 | 72.8129 | | 5 | 102.213 | |
| Batch (Rep.) | 6 | 60.0056 | | 6 | 67.4587 | |
| Stand | 11 | 14.9751 | 1.120 | 11 | 50.6708 | 1.581 |
| Family (Stand) | 44 | 13.3591 | .764 | 44 | 32.0564 | .914 |
| Error | 269 | 17.0636 | | 269 | 35.1046 | |
| Total | 335 | | | 335 | | |

*Significance at the .05 level.

TABLE X

ANALYSIS OF VARIANCE BY LOCATIONS AND POOLED DATA FOR TRACHEID LENGTH

| | Mature Wood | | | Juvenile Wood | | |
|---|---|---|---|---|---|---|
| **Pooled Data** | | | | | | |
| Source | D.F. | Mean Squares | F-Test | D.F. | Mean Squares | F-Test |
| Location | 1 | 15.6930 | | 1 | 16.3594 | |
| Replication (Loc.) | 10 | 1.82379 | | 10 | 0.25655 | |
| Stand | 11 | 0.11614 | 1.837 | 11 | 0.09173 | 3.597* |
| Stand x Loc. | 11 | 0.06320 | .465 | 11 | 0.02549 | .311 |
| Family (Stand) | 44 | 0.13581 | 1.257 | 44 | 0.08161 | 1.437 |
| Family (Stand) x Loc | 44 | 0.10806 | 1.029 | 44 | 0.05681 | 1.059 |
| Error | 550 | 0.10497 | | 550 | 0.05365 | |
| Total | 671 | | | 671 | | |
| **Broken Bow** | | | | | | |
| Source | | | | | | |
| Replication | 5 | 2.12749 | | 5 | 0.30570 | |
| Batch (Rep.) | 6 | 0.41166 | | 6 | 0.06528 | |
| Stand | 11 | 0.05085 | .406 | 11 | 0.04227 | .489 |
| Family (Stand) | 44 | 0.12522 | 1.563* | 44 | 0.08638 | 1.425* |
| Error | 269 | 0.08009 | | 269 | 0.06063 | |
| Total | 335 | | | 335 | | |
| **Stilwell** | | | | | | |
| Source | | | | | | |
| Replication | 5 | 1.52010 | | 5 | 0.20740 | |
| Batch (Rep.) | 6 | 0.61357 | | 6 | 0.08782 | |
| Stand | 11 | 0.11152 | .951 | 11 | 0.08660 | 1.814 |
| Family (Stand) | 44 | 0.11733 | 1.045 | 44 | 0.04775 | 1.041 |
| Error | 269 | 0.11261 | | 269 | 0.04587 | |
| Total | 335 | | | 335 | | |

*Significance at the .05 level.

APPENDIX B

STAND MEAN TABLES

## TABLE XI

## STAND MEANS OF PERCENT EXTRACTIVES

| Stand | Juvenile Wood | | | Mature Wood | | |
|---|---|---|---|---|---|---|
| | Pooled | Broken Bow | Stilwell | Pooled | Broken Bow | Stilwell |
| 1 | 10.5 | 8.52 | 12.65 | 6.69 | 5.54 | 7.55 |
| 3 | 10.3 | 8.07 | 12.69 | 6.49 | 6.16 | 8.60 |
| 6 | 10.0 | 8.60 | 11.46 | 6.92 | 5.50 | 8.34 |
| 7 | 10.0 | 8.38 | 11.68 | 6.73 | 5.64 | 8.22 |
| 15 | 9.78 | 7.83 | 11.72 | 6.71 | 6.14 | 8.65 |
| 16 | 9.91 | 8.20 | 11.62 | 6.40 | 5.28 | 8.20 |
| 23 | 9.89 | 8.03 | 11.76 | 6.65 | 5.88 | 8.30 |
| 26 | 9.73 | 8.02 | 11.44 | 6.36 | 5.54 | 7.55 |
| 39 | 10.0 | 8.10 | 12.06 | 6.34 | 5.96 | 7.97 |
| 45 | 10.1 | 8.66 | 11.73 | 6.71 | 5.91 | 8.37 |
| 47 | 9.93 | 7.95 | 11.91 | 6.68 | 5.59 | 8.08 |
| 49 | 9.79 | 8.42 | 11.17 | 6.11 | 5.98 | 7.91 |

TABLE XII

STAND MEANS OF UNEXTRACTED SPECIFIC GRAVITY

| Stand | Juvenile Wood | | | Mature Wood | | |
|---|---|---|---|---|---|---|
| | Pooled | Broken Bow | Stilwell | Pooled | Broken Bow | Stilwell |
| 1 | 0.379 | 0.375 | 0.384 | 0.393 | 0.431 | 0.356 |
| 3 | 0.392 | 0.386 | 0.391 | 0.409 | 0.439 | 0.378 |
| 6 | 0.395 | 0.399 | 0.391 | 0.413 | 0.449 | 0.376 |
| 7 | 0.396 | 0.393 | 0.400 | 0.408 | 0.437 | 0.379 |
| 15 | 0.394 | 0.398 | 0.390 | 0.409 | 0.454 | 0.364 |
| 16 | 0.401 | 0.401 | 0.402 | 0.417 | 0.449 | 0.385 |
| 23 | 0.396 | 0.395 | 0.397 | 0.420 | 0.454 | 0.385 |
| 26 | 0.404 | 0.406 | 0.402 | 0.414 | 0.450 | 0.378 |
| 39 | 0.394 | 0.394 | 0.395 | 0.412 | 0.451 | 0.373 |
| 45 | 0.402 | 0.399 | 0.404 | 0.415 | 0.448 | 0.382 |
| 47 | 0.391 | 0.388 | 0.393 | 0.403 | 0.436 | 0.369 |
| 49 | 0.405 | 0.401 | 0.409 | 0.427 | 0.452 | 0.401 |

TABLE XIII

STAND MEANS OF EXTRACTED SPECIFIC GRAVITY

| Stand | Juvenile Wood | | | Mature Wood | | |
|---|---|---|---|---|---|---|
| | Pooled | Broken Bow | Stilwell | Pooled | Broken Bow | Stilwell |
| 1 | 0.339 | 0.343 | 0.335 | 0.367 | 0.405 | 0.329 |
| 3 | 0.351 | 0.355 | 0.347 | 0.383 | 0.419 | 0.345 |
| 6 | 0.355 | 0.364 | 0.346 | 0.384 | 0.424 | 0.344 |
| 7 | 0.356 | 0.359 | 0.353 | 0.381 | 0.414 | 0.348 |
| 15 | 0.356 | 0.367 | 0.344 | 0.382 | 0.431 | 0.332 |
| 16 | 0.361 | 0.368 | 0.355 | 0.390 | 0.428 | 0.353 |
| 23 | 0.357 | 0.363 | 0.350 | 0.392 | 0.431 | 0.353 |
| 26 | 0.365 | 0.374 | 0.356 | 0.388 | 0.426 | 0.350 |
| 39 | 0.354 | 0.362 | 0.347 | 0.386 | 0.429 | 0.343 |
| 45 | 0.360 | 0.364 | 0.357 | 0.388 | 0.425 | 0.350 |
| 47 | 0.351 | 0.357 | 0.346 | 0.376 | 0.413 | 0.339 |
| 49 | 0.365 | 0.367 | 0.363 | 0.400 | 0.432 | 0.369 |

TABLE XIV

STAND MEANS OF NUMBER OF RINGS PER INCH

| Stand | Juvenile Wood Pooled | Juvenile Wood Broken Bow | Juvenile Wood Stilwell | Mature Wood Pooled | Mature Wood Broken Bow | Mature Wood Stilwell |
|---|---|---|---|---|---|---|
| 1 | 4.78 | 4.53 | 5.02 | 5.02 | 5.42 | 4.49 |
| 3 | 4.94 | 4.82 | 5.06 | 5.30 | 5.52 | 4.43 |
| 6 | 4.82 | 4.73 | 4.90 | 4.92 | 5.39 | 4.34 |
| 7 | 4.67 | 4.76 | 4.58 | 4.93 | 5.37 | 4.22 |
| 15 | 4.97 | 5.04 | 4.91 | 5.16 | 5.79 | 4.18 |
| 16 | 4.83 | 4.67 | 4.98 | 4.97 | 5.32 | 4.67 |
| 23 | 4.88 | 4.90 | 4.86 | 5.02 | 5.45 | 4.15 |
| 26 | 4.69 | 4.49 | 4.88 | 4.95 | 5.58 | 4.36 |
| 39 | 5.06 | 5.00 | 5.13 | 5.16 | 5.52 | 4.37 |
| 45 | 4.78 | 4.78 | 4.78 | 5.03 | 5.64 | 4.15 |
| 47 | 4.89 | 4.58 | 5.21 | 4.89 | 5.44 | 4.18 |
| 49 | 4.84 | 5.03 | 4.65 | 5.07 | 5.54 | 4.15 |

TABLE XV

STAND MEANS OF PERCENT SUMMERWOOD

| Stand | Juvenile Wood Pooled | Juvenile Wood Broken Bow | Juvenile Wood Stilwell | Mature Wood Pooled | Mature Wood Broken Bow | Mature Wood Stilwell |
|---|---|---|---|---|---|---|
| 1 | 20.32 | 25.34 | 15.31 | 25.61 | 29.98 | 21.23 |
| 3 | 19.37 | 23.99 | 14.76 | 24.50 | 30.96 | 18.05 |
| 6 | 18.79 | 23.57 | 14.01 | 23.55 | 29.64 | 17.45 |
| 7 | 19.38 | 24.16 | 14.59 | 25.15 | 29.43 | 20.88 |
| 15 | 20.19 | 24.49 | 15.89 | 26.61 | 35.55 | 17.67 |
| 16 | 20.15 | 23.61 | 16.70 | 23.42 | 28.67 | 18.31 |
| 23 | 19.42 | 23.58 | 15.26 | 25.00 | 30.16 | 19.83 |
| 26 | 18.77 | 23.08 | 14.47 | 25.18 | 32.70 | 17.65 |
| 39 | 18.83 | 23.72 | 13.93 | 24.57 | 31.17 | 17.96 |
| 45 | 19.78 | 24.04 | 15.52 | 24.84 | 31.56 | 18.12 |
| 47 | 18.84 | 23.67 | 14.01 | 23.86 | 30.70 | 17.02 |
| 49 | 19.87 | 25.17 | 14.56 | 25.18 | 31.21 | 19.16 |

TABLE XVI

STAND MEANS OF TRACHEID LENGTH

| Stand | Juvenile Wood | | | Mature Wood | | |
|---|---|---|---|---|---|---|
| | Pooled | Broken Bow | Stilwell | Pooled | Broken Bow | Stilwell |
| 1 | 2.0 | 2.2 | 1.8 | 3.0 | 3.2 | 2.8 |
| 3 | 1.9 | 2.1 | 1.8 | 3.0 | 3.2 | 2.8 |
| 6 | 2.0 | 2.2 | 1.9 | 3.0 | 3.1 | 2.8 |
| 7 | 1.9 | 2.1 | 1.8 | 3.0 | 3.2 | 2.8 |
| 15 | 2.0 | 2.2 | 1.9 | 3.0 | 3.1 | 2.9 |
| 16 | 2.0 | 2.2 | 1.9 | 3.0 | 3.1 | 3.0 |
| 23 | 2.0 | 2.1 | 1.8 | 3.0 | 3.1 | 2.8 |
| 26 | 1.9 | 2.1 | 1.8 | 3.1 | 3.2 | 2.9 |
| 39 | 1.9 | 2.1 | 1.8 | 3.0 | 3.1 | 2.9 |
| 45 | 2.0 | 2.2 | 1.8 | 2.9 | 3.2 | 2.7 |
| 47 | 2.0 | 2.1 | 1.8 | 3.0 | 3.1 | 2.8 |
| 49 | 2.0 | 2.1 | 1.8 | 2.9 | 3.1 | 2.7 |

# APPENDIX C

# GENETIC CORRELATION TABLES

TABLE XVII

GENETIC CORRELATIONS OF UNEXTRACTED SPECIFIC GRAVITY
WITH ALL MEASURED WOOD PROPERTIES

| | Juvenile Wood | | | | | | | Mature Wood | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Pooled | | Broken Bow | | Stilwell | | Parent Progeny Regression | Pooled | | Broken Bow | | Stilwell | | Parent Progeny Regression |
| | rg | s.e. | rg | s.e. | rg | s.e. | rg | rg | s.e. | rg | s.e. | rg | s.e. | rg |
| Extracted Specific Gravity | .99 | .03 | .96 | .04 | .96 | .04 | .29 | .90 | .15 | .99 | .02 | .99 | .01 | 1.09 |
| Percent Extractives | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Number of Rings per Inch | -.06 | .34 | 1.16 | 2.34 | -.26 | .63 | -1.25 | .91 | .99 | .32 | .51 | .11 | .51 | - |
| Percent Summerwood | - | - | .31 | .87 | - | - | - | .10 | 1.45 | - | - | - | - | - |
| Tracheid Length | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

TABLE XVIII

GENETIC CORRELATIONS OF EXTRACTED SPECIFIC GRAVITY
WITH ALL MEASURED WOOD PROPERTIES

| | Juvenile Wood | | | | | | | Mature Wood | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Pooled | | Broken Bow | | Stilwell | | Parent Progeny Regression | Pooled | | Broken Bow | | Stilwell | | Parent Progeny Regression |
| | rg | s.e. | rg | s.e. | rg | s.e. | rg | rg | s.e. | rg | s.e. | rg | s.e. | rg |
| Unextracted Specific Gravity | .99 | .03 | .96 | .04 | .96 | .04 | .79 | .90 | .15 | .99 | .03 | .99 | .01 | 1.09 |
| Percent Extractives | - | - | .32 | .78 | - | - | - | - | - | - | - | - | - | - |
| Number of Rings per Inch | -.15 | .36 | .23 | .40 | -.32 | .62 | -.37 | 1.22 | 1.10 | - | - | .18 | .50 | - |
| Percent Summerwood | - | - | .55 | .96 | - | - | -.06 | .29 | 1.37 | - | - | - | - | - |
| Tracheid Length | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

TABLE XIX

GENETIC CORRELATIONS OF NUMBER OF RINGS PER INCH WITH ALL MEASURED WOOD PROPERTIES

| | Juvenile Wood | | | | | | | Mature Wood | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Pooled | | Broken Bow | | Stilwell | | Parent Progeny Regression | Pooled | | Broken Bow | | Stilwell | | Parent Progeny Regression |
| | rg | s.e. | rg | s.e. | rg | s.e. | rg | rg | s.e. | rg | s.e. | rg | s.e. | rg |
| Unextracted Specific Gravity | -.06 | .34 | 1.16 | 2.34 | -.26 | .63 | -1.25 | .91 | .99 | .32 | .51 | .11 | .51 | - |
| Extracted Specific Gravity | -.15 | .37 | .33 | .40 | -.32 | .62 | -.367 | 1.22 | 1.09 | - | - | .18 | .51 | - |
| Percent Extractives | - | - | .13 | .63 | - | - | - | - | - | - | - | - | - | - |
| Percent Summerwood | - | - | 1.19 | 1.25 | - | - | - | - | - | - | - | - | - | - |
| Tracheid Length | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

TABLE XX

GENETIC CORRELATIONS OF PERCENT SUMMERWOOD
WITH ALL MEASURED WOOD PROPERTIES

| | Juvenile Wood | | | | | | | Mature Wood | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Pooled | | Broken Bow | | Stilwell | | Parent Progeny Regression | Pooled | | Broken Bow | | Stilwell | | Parent Progeny Regression |
| | rg | s.e. | rg | s.e. | rg | s.e. | rg | rg | s.e. | rg | s.e. | rg | s.e. | rg |
| Unextracted Specific Gravity | - | - | .31 | .87 | - | - | - | .10 | 1.45 | - | - | - | - | - |
| Extracted Specific Gravity | - | - | .55 | .96 | - | - | -.06 | .29 | 1.37 | - | - | - | - | - |
| Percent Extractive | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Number of Rings per Inch | - | - | 1.19 | 1.25 | - | - | - | .56 | .77 | - | - | - | - | - |
| Tracheid Length | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

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