# VARIATION AND INHERITANCE OF SELECTED ANATOMICAL CHARACTERISTICS OF EASTERN COTTONWOOD

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## PREFACE

This thesis reports variation and inheritance of certain wood and growth characteristics of cottonwood from the Red River of Oklahoma. Forty-three clones, representing seven geographic sources, were selected for study. Height, diameter, degree of lean, and number of limbs were recorded for four ramets of each clone. Wood samples were taken from each of the 172 plants. Each sample was studied for amount of gelatinous fibers, fiber diameter, fiber length, and microfibril angle. Analyses of variance for the eight factors were computed. All possible linear correlations between study variables and selected environmental variables were computed. The effect of gelatinous fibers upon the other wood traits was established and broad sense heritability estimates for six of the study variables were computed. Financial assistance for this study was provided through a $4,000 grant from the Southern Forest Experiment Station, U. S. Forest Service.

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# CHAPTER I

## INTRODUCTION

Increasing demands for forest products make it essential to improve both the quality and quantity of timber produced in this country. The problems encountered in the use of wood as a raw material must be defined and possible solutions to these problems explored. It is necessary that the range of variation for certain commercially important characteristics of wood be explored and an estimate of their heritability be obtained before programs aimed at increasing timber production from a genetic standpoint can be obtained.

Oklahoma contains thousands of acres of stream bottom lands which are suited to the production of eastern cottonwood (Populus deltoides Bartr.). This species is the most important poplar in America today. Among the many reasons for its current high demand are its light weight, ease of nailing, resistance to splitting, good color for printing, and good pulping properties. At present, approximately 50,000 cords per year are being harvested within the state.

This study was made in an effort to determine the amount of variation encountered in four commercially important anatomical traits of eastern cottonwood. These traits are amount of gelatinous fibers, fiber length, fiber diameter, and microfibril angle. In addition, four growth variables were studied. The plants used in the study were one-year-old cottonwood trees which were vegetatively propagated from

cuttings. The cuttings were collected in natural stands along the Red River from the eastern edge of Oklahoma to the headwaters of the river in the Panhandle area of Texas. An analysis of variance was made on each study variable to help determine which sources of variation contribute most to the total variation. In order to determine how the study variables vary with one another and with certain environmental factors, all possible simple correlations were computed. Estimates of the coefficients of heritability for each of the anatomical traits and certain growth characters were also computed.

# CHAPTER II

# LITERATURE REVIEW

## Fiber Length

Fiber length has been found to be a very important wood character, particularly in papermaking (5), (12), (14), (42). The length of fiber desired depends upon type of product manufactured. Where tear resistance is desired in paper above other qualities, long fibers are desirable. The Forest Biology Subcommittee No. 2 On Tests and Quality Objectives (14) reported that longer average fiber length is generally associated with an increase in tear resistance and also a slight increase in burst and tensile strength and fold endurance. Dadswell, et al. (12) reported a linear relationship between fiber length and tear resistance in Eucalyptus spp.

A number of factors such as age from pith, growth rate, height along stem, etc. have been found to influence cell length; but the most important is probably age from pith. Kaeiser (23) and Kaeiser and Stewart (26) found fiber length to be greater in the outer growth rings than in the inner growth rings at the same level in the trunk. They also found that fiber lengths were greater for the outer rings at a height of 56 feet than at 4.5 feet. The range in mean fiber length which was encountered by Kaeiser was 0.76 mm to 1.24 mm and that found by Kaeiser and Stewart was 0.90 mm to 1.20 mm. These figures

represented mean fiber lengths of mature trees. The increase in fiber length from pith to bark was further substantiated by Kennedy (28).

Growth rate has also been shown to have significant effects upon fiber length. Boyce and Kaeiser (7) found that 50 percent of the total variation in fiber length in the trees they studied could be accounted for by the number of rings from the pith and the diameter of the tree. Kennedy (28) and Kennedy and Smith (27) showed that in one-year-old sprouts of black cottonwood (Populus trichocarpa Torr. & Gray) faster growth resulted in longer fibers. The range in fiber lengths which was reported by Kennedy and Smith (27) was .475 mm for slow grown sprouts to .544 mm for fast grown sprouts. The overall average fiber length which they found in one-year-old sprouts of black cottonwood was .497 mm. This figure is considerably lower than that generally reported for Populus spp. and reflects the increase in length of fiber with age from pith.

A few studies have been conducted in an attempt to show what effect amount of lean in the stem of the tree has on length of fiber or the effect of varying amounts of tension wood upon fiber length. The literature, however, seems somewhat contradictory on the subject. Kaeiser and Stewart (26) found no significant differences in fiber length which could be correlated with either lean of the tree or concentration of gelatinous fibers in the stem. Kaeiser (23), on the other hand, reported a trend for greater fiber length to be shown by trees having a greater amount of lean.

## Fiber Diameter

Very little work has been done on cell diameter per se, mainly because other morphological factors of the cell structure are of much

greater importance, namely cell wall thickness and lumen diameter. Many investigations have dealt with cell diameter in a round-about manner in conjunction with studies of cell wall thickness. According to a report by the Forest Biology Subcommittee No. 2 On Tests and Quality Objectives (14), fiber diameter has an important effect upon sheet formation, fiber bonding, and fiber rigidity. The smaller the average fiber diameter of the pulp, the finer the finish of paper which can be formed from the pulp. This is very desirable in some particular types of products such as high quality writing papers. On the other hand, better bonding between fibers can be obtained from larger diameter fibers due to the increased surface area of the cell available for bonding. Holding cell wall thickness constant, it can be seen that the smaller the diameter of the cell, the more rigid it will be and the greater the resistance to folding of paper made from such fibers. If good sheet formation and fiber bonding are desired, relatively small diameter, thin-walled cells are desirable (14). Runkel (37) stated that thin-walled fibers where $2w/l<1$ (where w = wall thickness and l = lumen diameter) are the most desirable for papermaking since they collapse into ribbon-like strands offering a large surface area for bonding which results in high tensile and burst strengths; however, thick-walled fibers are necessary to increase the tearing strength of the paper. It is necessary to arrive at some desirable diameter somewhere between the two extremes since both very thin and very thick walled fibers reduce paper strength, thin-walled fibers reducing tearing strength and very thick-walled fibers reducing tensile and bursting strengths (6).

Within tree variation of cell diameter was studied by Wheeler et al. (45). He found cell diameter to increase from the pith outward in loblolly pine (Pinus taeda L.) and also to increase with height in the stem up to a point below the crown. A trend was reported in which longer fibers on the average tended to be wider tangentially than shorter fibers. This same trend was also reported by Graff (16) and Heinig (18) for a number of southern and western conifers. Bannan (1), (3) also found cell width to increase from the pith outward, but not at a proportionate rate with cell length. This causes the cell length to width ratio to increase with age. Tangential diameter was found to vary less than any other cell dimension in a range-wide study of Douglas fir (Pseudotsuga menziesii Franco), a difference of only 9 percent being found between the maximum and minimum value (2).

## Microfibril Angle

Microfibril angle has been widely studied in most of the commercially important southern pines and other conifers; however, little work has been done on microfibril angle of hardwoods. To the best of my knowledge, microfibril angle has not been studied in eastern cottonwood.

The normal cell wall is composed of four layers, the primary wall and the $S_1$, $S_2$, and $S_3$ layers of the secondary wall. Of these layers, the $S_2$ is normally the thickest and therefore contributes most to the characteristics of the cell wall and consequently the cell. The $S_2$ layer is made up of long, parallel chains of cellulose called microfibrils which are laid down in a helical manner similar to threads on a screw. The angular orientation of these microfibrils to the longitudinal axis of the cell is known as the microfibril angle (32).

Microfibril angle has been shown to affect certain strength characteristics of wood and wood products. Pillow, Chidester, and Bray (36) found that loblolly pine wood which had a high microfibril angle (30° to 45°) yielded pulp with 18 percent less bursting strength than normal pulp. They reported also that wood with high summerwood microfibril angle tested 20 to 25 percent below normal in tear resistance. Kraemer (29) found that very strong negative correlations existed between microfibril angle and modulus of rupture (MOR) and microfibril angle and modulus of elasticity (MOE) in red pine (Pinus resinosa Ait.). He reported correlation coefficients of -.782 for microfibril angle vs. MOR and -.783 for microfibril angle vs. MOE. A correlation coefficient of -.832 between the sine of the microfibril angle and tensile strength of pitch pine (Pinus rigida Mill.) was reported by Garland (15). These findings indicated an inverse relationship between microfibril angle and the three strength factors just mentioned, i.e. as microfibril angle increases, MOR, MOE, and tensile strength all decrease. Tamolang et al. (39) found that 88.8 percent of the variation in fiber strength per unit area of cell wall could be accounted for by the cosine of the microfibril angle.

Pillow et al. (33) and Hiller (21) found microfibril angle to decrease in successive rings from the pith toward the bark in loblolly and slash pine (Pinus elliottii Engelm.). Within an annual ring, microfibril angle appears to be highest in the first formed earlywood and decrease through the latewood zone. Ordinarily the mean microfibril angle of the first formed earlywood is higher than the mean microfibril angle of the last formed latewood (20). To my knowledge, variation in microfibril angle with height in the stem has not been reported.

Indications are, however, that microfibril angle decreases from the base of the tree to a point just below the crown. Evidence to support this view was offered by Wardrop (44) and Echols (13) when they found microfibril angle to decrease with increasing fiber length. Since fiber length increases from the base of the stem to a point just below the crown (26) it is reasonable to assume that microfibril angle decreases from the base of the stem toward the crown.

Growth rate has been shown to have a pronounced effect upon microfibril angle. Hiller (21) stated that fast growing trees in general had larger microfibril angles than did slow growing trees. Microfibril angle was found to decrease in slow growing trees during the first ten years and then tended to remain constant. However, in fast growing trees the period of years over which the microfibril angle decreased was much longer and in some cases exceeded 20 years before leveling off. Pillow et al. (33) reported that closely spaced trees generally have smaller microfibril angles than do widely spaced trees. They also reported that releasing overtopped pines resulted in larger microfibril angles.

In conclusion, microfibril angle has been shown to have significant effects upon many strength characteristics of wood and pulp. Microfibril angle decreases from pith outward and although not proved, indications are that it also decreases from the base of the tree toward the crown. Factors affecting the growth rate and general vigor of the tree may also affect the size of the microfibril angle.

## Gelatinous Fibers

A major defect which occurs to some extent in all hardwood species is that of so-called "tension wood." Tension wood is a type of reaction wood formed in hardwood species in response to internal stresses in the stem and which is composed of varying amounts of abnormal fibers characterized by the presence of a gelatinous layer on the innermost surface of the cell wall. These abnormal cells are commonly called "gelatinous" or tension wood fibers.

Wardrop and Dadswell (43) found that the gelatinous layer may be present in addition to all three normal layers of the secondary wall; or that it may replace the $S_3$ layer of the secondary wall; or that it may replace both the $S_3$ and $S_2$ layers. They further reported that the gelatinous layer was completely unlignified and that it is probably composed of a form of cellulose of exceptional purity. The findings of Chow (8) supported this observation. In general, tension wood is characterized by having a higher cellulose content and a lower lignin content than normal wood.

The name tension wood seems to have been applied to this abnormal tissue because it is commonly found in greatest amounts on the upper or tension side of the stem of leaning trees. Gelatinous fibers were found on all sides of two quaking aspen (Populus tremuloides Michx.) logs from leaning trees by Terrell (40). However, the largest amounts of these fibers were located on the tension side of the logs. At breast height in leaning cottonwood trees, Kaeiser (24) and Kaeiser and Pillow (25) found that near the middle of the stem, gelatinous fibers were distributed nearly evenly on all four sides of the tree and at the upper heights of the stem, the lower or compression side

frequently contained the greatest amounts of gelatinous fibers. The amount of gelatinous fibers present in the wood was reported to increase with increasing lean in the stem. The tendency for gelatinous fibers to occur in greater amounts on the tension side of leaning trees was further substantiated by Wahlgren (41) and Clarke (10).

Many defects attributable to the occurrence of tension wood have been reported. Pillow (34), (35) found warping of hardwood lumber containing tension wood to be a frequent occurrence. This was a result of unequal changes in length of the two types of wood during drying. Lumber containing tension wood frequently collapsed during drying, particularly heartwood. Buckling or splitting of veneer is also common. Increasing amounts of gelatinous fibers were found to increase the amount of longitudinal shrinkage in cottonwood (35), (41). Clark (9) reported gelatinous fibers resulted in severe fuzzy surfaces and excessive checking of sawn and planed lumber.

Several strength characteristics have been reported to be affected by the amount of tension wood present. These include tension perpendicular to the grain and compression parallel to the grain, both of which were found to be lower in wood containing gelatinous fibers than in normal wood (17), (30). Wood containing gelatinous fibers was found to be stronger than normal wood when tested in shear and was also found to have higher toughness and average modulus of elasticity value (17), (30). Kaeiser and Boyce( 22) reported that increases in the amount of gelatinous fibers present in a piece of wood were accompanied by a decrease in size of rays, vessels, and normal fibers. Therefore, the adverse physical properties of reaction wood should be attributed to the interaction of these structural differences and not merely to the presence of gelatinous fibers.

Tension wood has been reported to occur in at least three different ways and possibly four. It may occur as solitary gelatinous fibers, groups or clusters of such fibers, or as tangential bands of gelatinous fibers (41). In addition, some authors feel that the occurrence of abnormal unlignified fibers and partly lignified fibers where no gelatinous layers are evident may also be a form of tension wood formation (4).

# CHAPTER III

## METHODS

The area from which the plant material for this study came is along the Red River from the southeastern corner of Oklahoma to the headwaters of the river in the Panhandle area of Texas. There is a wide range in environmental factors from one end of the study area to the other, as can be seen from Table I. For example, average annual rainfall varies from 43.7 inches in the east to 17.9 inches in the west. Elevation varies from 310 feet above sea level at the eastern end of the river system to 1,820 feet above sea level on the western end. It was hypothesized that these and other environmental factors might have exerted different selection pressures upon the natural population from one end of the river to the other, resulting in genetic differences.

Seven plots were located along the Red River approximately 60 miles apart, as shown in Figure 1. These plots were located in the best natural stands of cottonwood that could be found in the area. Ten dominant or codominant trees were selected as study trees from each plot or stand, and 20 vegetative cuttings 18 to 20 inches long were collected from each study tree in the fall and winter of 1966. These cuttings were treated with fermate and stored in polyethylene bags at 38°F until March of 1967. The cuttings were then planted at the State Forest Tree Nursery in Norman, Oklahoma, in a split plot

TABLE I

RANGE OF ENVIRONMENTAL FACTORS AT SEVEN GEOGRAPHIC SOURCES OF EASTERN COTTONWOOD

| Source | Longitude | Latitude | Elevation (Feet) | Average Annual Rainfall (Inches) | Average Mean Daily Minimum Temperature (January) |
|---|---|---|---|---|---|
| 1 | 94°30' | 33°45' | 0310 | 43.7 | 33 |
| 2 | 95°30' | 34°00' | 0410 | 48.3 | 33 |
| 3 | 96°30' | 33°45' | 0500 | 32.8 | 32 |
| 4 | 97°15' | 34°00' | 0680 | 28.7 | 30 |
| 5 | 98°30' | 34°15' | 0940 | 29.3 | 29 |
| 6 | 99°15' | 34°30' | 1230 | 23.0 | 28 |
| 7 | 100°30' | 34°30' | 1820 | 17.9 | 26 |

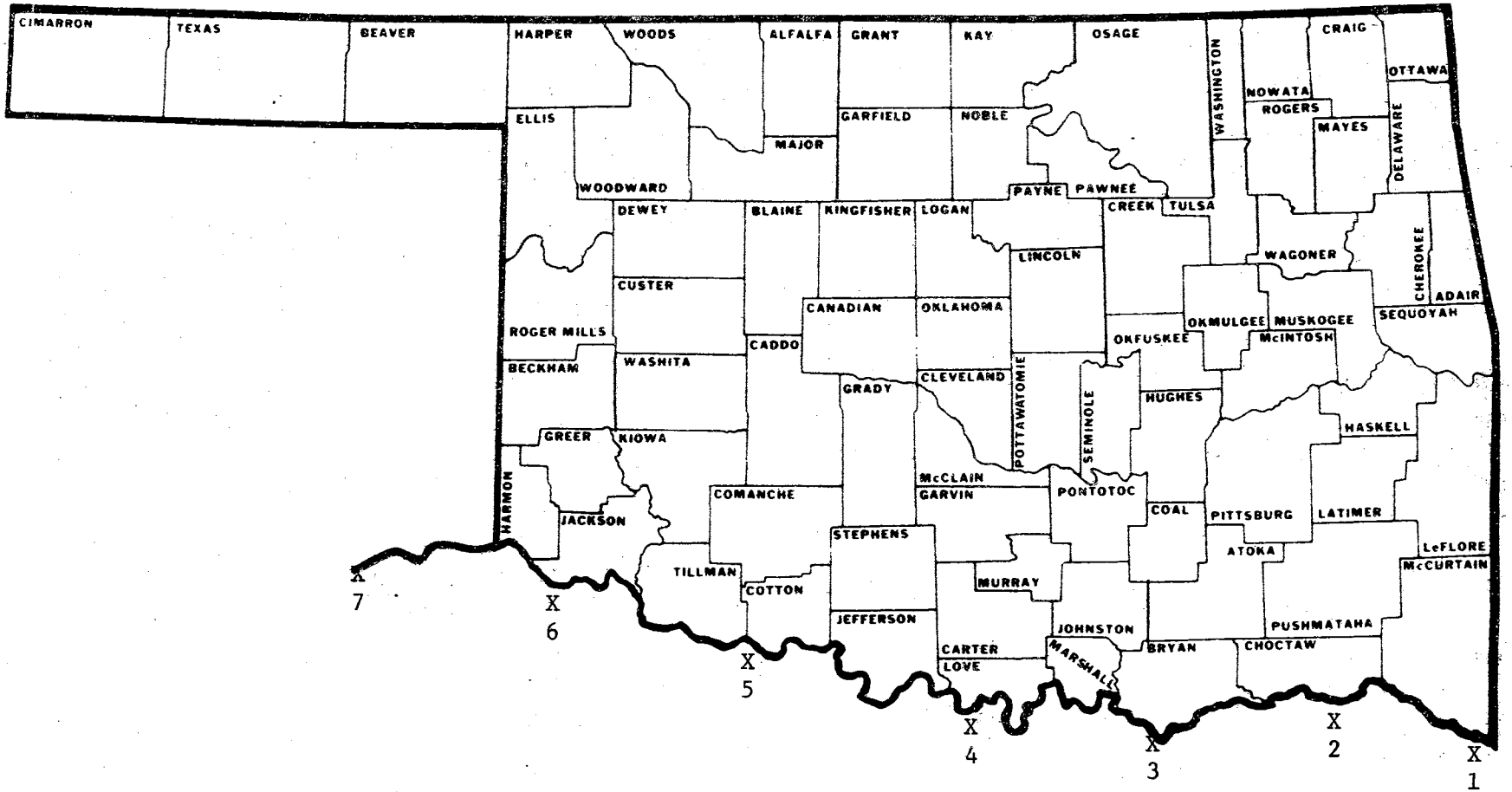


Figure 1. Locations of the Seven Geographic Sources of Eastern Cottonwood

design, with four replications. Geographic sources or stands were the main plot treatments, and parent trees or clones were the sub-plot treatments. The cuttings were planted in five-tree row plots at a spacing of two feet by two feet.

From the seven sources, 43 clones were selected for use in this study. Seven clones came from each source with the exception of sources 1 and 7, from which only four clones each were selected due to poor survival. Four ramets per parent tree were sampled, one from each replication where possible. However, due to poor survival, it was sometimes necessary to take more than one ramet from a given replication and none from another.

Total height, lean, and number of limbs were recorded for each ramet and the tension side of the stem marked with weatherproof pencil before they were cut down in January of 1968.

Total height was measured to the nearest 0.1 foot by means of a telescoping fiberglass measuring rod. Degree of lean was determined by measuring the horizontal distance from the base of the stem to the point at which a vertical line, extended from the tip of the stem downward, intersected the ground. Using this horizontal distance and the height of the tree, it was possible to arrive at the lean in degrees of the stem by means of the tangent function. The plumb bob device consisted of the height measuring rod with a bulls-eye level attached to it. The rod was held at the tip of the stem and positioned vertically by means of the level. Total number of limbs on each ramet was recorded and later converted to number of limbs per foot of height for analysis. The tension side of the stem was taken to be the opposite side of the stem from the direction of lean and was so marked regardless

of local crooks in the stem. On subsequent examination of the samples for amount of gelatinous fibers, there was some indication that local crooks should have been considered.

A section of the stem about two inches long was removed from each ramet at nine inches above ground line, labeled, and stored in water.

Once in the laboratory, the diameter was recorded while the samples were still in a green condition. The samples were then boiled in water for about five minutes to facilitate bark removal.

## Fiber Length

A thin disc about one-quarter inch thick was sawn from one end of each of the samples. Two small pie-shaped wedges were removed from each of these discs, one from the tension side and one from the compression side. These were then macerated, using Franklin's technique (32). This involves placing the chips of wood in a small vial containing enough of an equal mixture of glacial acetic acid and 30 percent hydrogen peroxide to cover the chips well and then heating the vials at 55°C until the wood turns silvery white in color. This required about 24 hours for cottonwood.

The acid is then removed and the vials shaken vigorously with a small amount of water in them to break the chips down into individual fibers for easy mounting on slides.

The fibers were stained with basic fuchsin and mounted in Karo syrup. Two slides were prepared and labeled from each vial, one slide from fibers in the upper portion of the vial and the other from fibers near the bottom of the vial.

Fiber length measurements were made to the nearest 0.025 mm on 15 whole fibers from each slide at 100X magnification, using a bioscope and a bulls-eye target. A total of 240 fibers was measured per clone, 15 each on four slides per ramet, and four ramets per clone.

## Fiber Diameter

At the outset of this study, it was planned to investigate cell wall thickness, lumen diameter, and cell diameter; however, during preliminary investigations it was found that in the one-year-old material which was being used in the study, there was not sufficient variation in cell wall thickness to justify the time and expense required to make a thorough study on the trait. Also, the cell walls were so thin in the one-year-old material that precise measurements were very difficult to make. For these reasons it was decided to simply measure the cell diameter of fiber tracheids.

Fiber diameter measurements were made to the nearest 0.2μ on 20 fibers from the same slides that cell length measurements were made. The measurements were made at 400X magnification using a Zeiss Standard Universal model microscope equipped with a mechanical stage and an eyepiece micrometer. Diameter measurements were made at the widest point along the length of the fiber so that average maximum cell diameter was obtained. Measurements for both fiber diameter and fiber length were always made from the first whole fibers encountered as the slide was traversed from the upper right hand corner toward the left. This was done in order to have both measurements made on some of the same fibers so that the correlations between these variables

would be more accurate. A total of 320 measurements was made per clone, 20 each on four slides per ramet and four ramets per clone.

## Microfibril Angle

A second disc about one-quarter inch thick was cut from the same end of the original sample that the disc for cell dimension measurements was removed from. This section was then cut in half along a line from the tension side through the pith to the compression side, exposing a radial surface. A thin radial section was then cut from each side of one of the two halves of the disc with a razor blade. This produced two radial sections for examination, one each from the tension and compression sides. A staining technique similar to that described by Marts (31) was used to prepare the sections for examination. They were placed in 1.0 percent Auramine 0 solution for five minutes, rinsed in water for about five seconds, and dried for 15 minutes at 195°C. The use of a flourescent dye allowed the examination of the sections under a flourescent lighting system, and the high temperature drying resulted in the development of cleavage planes in the cell walls of the fibers. A Zeiss Standard Universal model microscope equipped with a mercury-arc light source and a mechanical stage was used to examine the sections. A BG38 and BG12 exciter filter combination was used to produce light waves of 360A° length. The sections were placed on a microscope slide after drying and examined at 800X magnification. No cover slip was used.

The angular deviation of either the cleavage planes or the elongated pit apertures from the longitudinal axis of the cell was used to approximate the microfibril angle. It is commonly believed

that these cleavage planes and pit apertures closely approximate the orientation of the fibrils in the $S_2$ layer of the secondary wall (19). Twenty-five measurements were made to the nearest five minutes on each sample of each ramet for a total of 200 measurements per parent tree. The first 25 fibers which exhibited either elongated pit apertures or cleavage planes were selected for measurement as the section was traversed from the outside toward the pith. Being only one-year-old wood from the pith, it was sometimes very difficult to cause the development of cleavage planes. This has been reported by several other authors (19), (33). Occasionally, it was necessary to traverse all the way to the pith in order to find 25 fibers upon which microfibril angle measurements could be made.

## Gelatinous Fibers

In order to examine the samples for amount of gelatinous fibers, a rotary microtome was used to obtain a transverse section of wood approximately 100 to 150 microns thick from the same end of the sample that fiber dimension measurements were made on.

The sections were stained with a chloride of zinc solution as described by Sass (38), which was made by the following formula:

water - 14.0 cc.

zinc chloride - 30.0 g.

potassium iodide - 5.0 g.

iodine - 0.9 g.

The solution was prepared in the following manner: (1) the water and zinc chloride were mixed together and placed in a refrigerator due to

the heat which is given off in the reaction; (2) the potassium iodide and iodine were mixed; and (3) when both reactions were complete, the two solutions were mixed together, allowed to react, and then filtered.

The sections were placed on slides, covered with a few drops of the chloride of zinc solution, and allowed to stand for two minutes. The chloride of zinc solution was drained off, a new drop added, and a cover slip placed over the section. Since chloride of zinc is a cellulose staining material, the gelatinous layer of tension wood fibers was stained a deep reddish brown and normal cell walls a pale yellow color, making it relatively easy to pick out the regions in which gelatinous fibers occurred.

The measurements were made along a line from the tension side to the compression side passing through the pith. A binocular microscope having a 25X magnification with a dial micrometer stage and a crosshair eyepiece was used to make the examination. The reading was simply recorded each time a transition zone was reached between tension wood and normal wood. Later the tension wood zones were summed for each side of the section and converted to a percent of the total width of the respective side.

# CHAPTER IV

## STATISTICAL ANALYSIS

The design of the experiment was a split plot with geographic sources randomized in each replication and parent trees randomized within geographic sources. The five ramets per parent tree were planted in five tree row plots.

From the seven geographic sources, a total of 43 parent trees or clones were chosen for analysis. Four ramets were chosen to represent each parent tree, one from each replication when possible. However, due to the complete loss of some parent trees in some replications, it was sometimes necessary to take more than one ramet from a given replication and none from another. This would have made it impossible to obtain an analysis of variance with a component for replications. Therefore, the assumption was made to treat the four ramets from each clone as if they had come from each of the four replications. This is probably a valid assumption since the area on which the material was grown is fairly homogeneous; also, preliminary tests in which each of the samples was taken from a different replication indicated there were no significant differences among replications.

To test for significant differences, two different heirarchal analyses of variance (AOV) were used for each trait and the information from the two AOV's pooled. This was necessary in order to get estimates of the sums of squares for all the sources of variation

which were to be tested. In the first AOV, geographic sources (sources) were used as the treatment source of variation; and in the second AOV, replications were the treatment source of variation. From the first AOV, estimates of the sum of squares for sources and clones in sources (C in S) were obtained. From the second AOV, estimates of the sum of squares for replications were obtained. Estimates for the replication X source interaction ( R x S) were obtained by subtracting the sum of squares estimate for sources, obtained in the first AOV, from the sources in replications sum of squares in the second AOV. Since the sources in replications classification contains variation due to differences among sources and also variation due to the R x S interaction, the remainder after subtraction is an estimate of the R x S interaction. A similar procedure was used for obtaining an estimate of the clone X replication in sources classification (C x R in S), which was used as error b in the classical split-plot analysis. To get this estimate, the sum of squares for the clones in sources classification from the first AOV was subtracted from the C in S in R classification from the second AOV. From the two AOV's a pooled AOV was constructed with sources of variation and degrees of freedom as shown in Table II.

This would be the normal split-plot analysis of variance with the R x S interaction being error a and the C x R in S classification being error b. Table III shows an example of the two separate AOV's used and the pooled AOV which was constructed from them.

It was necessary, however, to construct a special error term like that described by Cochran (11) for testing differences due to sources. This was necessary because the expected mean square (Table IV) for the

TABLE II

SOURCES OF VARIATION AND DEGREES OF FREEDOM FOR POOLED ANALYSIS OF VARIANCE

| Source of Variation | Degrees of Freedom |
|---|---|
| Total | 171 |
| Reps | 3 |
| Sources | 6 |
| R x S | 18 |
| C in S | 36 |
| C x R in S | 108 |

TABLE III

CONSTRUCTION OF ANALYSIS OF VARIANCE
TABLE FOR FIBER LENGTH

| | Source | d.f. | SS | MS |
|---|---|---|---|---|
| | Heirarchal Analysis of Variance with Sources as Treatments | | | |
| | Total | 171 | 0.217446 | |
| $L_1$ | Sources | 6 | 0.018386 | 0.003064 |
| $L_2$ | Clones in Sources | 36 | 0.099609 | 0.002766 |
| $L_3$ | Reps in Clones in Sources | 129 | 0.099449 | 0.000770 |
| | Heirarchal Analysis of Variance with Replications as Treatments | | | |
| | Total | 171 | 0.217446 | |
| $L_4$ | Reps | 3 | 0.000489 | 0.000163 |
| $L_5$ | Sources in Reps | 24 | 0.037485 | 0.001561 |
| $L_6$ | Clones in Sources in Reps | 144 | 0.179471 | 0.001246 |
| | Pooled Heirarchal Analysis of Variance | | | |
| | Total | 171 | 0.217446 | |
| $L_4$ | Reps | 3 | 0.000489 | 0.000163 |
| $L_1$ | Sources | 6 | 0.018386 | 0.003064 |
| $L_5-L_1$ | Reps x Sources | 18 | 0.019099 | 0.001061 |
| $L_2$ | Clones in Sources | 36 | 0.099609 | 0.002766 |
| $L_6-L_2$ | Clones x Reps in Sources | 108 | 0.079861 | 0.000739 |

TABLE IV

COEFFICIENTS OF EXPECTED MEAN SQUARES
FOR THE ANALYSIS OF VARIANCE

| Source | d.f. | EMS |
|---|---|---|
| Reps | (r-1) | $\sigma^2_\varepsilon + 4\,\sigma^2_{RxS} + 28\,\sigma^2_R$ |
| Sources | (s-1) | $\sigma^2_\varepsilon + 4\,\sigma^2_{RxS} + 4\,\sigma^2_{C(S)} + 16\,\sigma^2_S$ |
| R x S | (r-1)(s-1) | $\sigma^2_\varepsilon + 4\,\sigma^2_{RxS}$ |
| Clones in S | s(c-1) | $\sigma^2_\varepsilon + 4\,\sigma^2_{C(S)}$ |
| C x R in S | s(c-1)(r-1) | $\sigma^2_\varepsilon$ |

R x S interaction (error a in a classical split-plot analysis) did not contain a term for clones in sources and therefore could not be used for testing differences among sources. The special error term was constructed by adding the mean squares for the R x S interaction and the C in S term from the pooled AOV, and subtracting the mean square for the C x R in S. This special error term was then used for making the standard "F" test for differences among geographic sources. The degrees of freedom for the special error term (54) were obtained by taking the sum of the degrees of freedom for the R x S and C in S terms. Using expected mean squares from Table IV, the construction of the special error term may be demonstrated in the following manner:

$$
\begin{array}{rl}
R \times S = & \sigma^2_\varepsilon + 4\,\sigma^2_{RxS} \\
+\ C \text{ in } S = & \sigma^2_\varepsilon + 4\,\sigma^2_{C(S)} \\
\hline
 & 2\,\sigma^2_\varepsilon + 4\,\sigma^2_{RxS} + 4\,\sigma^2_{C(S)} \\
- \ C \times R \text{ in } S = & \sigma^2_\varepsilon \\
\hline
 & \sigma^2_\varepsilon + 4\,\sigma^2_{RxS} + 4\,\sigma^2_{C(S)}
\end{array}
$$

The expected mean squares were obtained from a separate analysis than the one used for testing for significant differences. This was done to facilitate ease of computation of the variance components and to increase their precision. Expected mean squares for the complete experiment could have been computed but since there was not perfect balance in the design, i.e. varying numbers of clones per source, it was decided to run a separate analysis for the computation of the variance components. This was done using only four parent trees or clones per geographic source. Perfect balance all the way through the

experiment was thus obtained. In those five sources which contained seven clones each, four clones were selected at random to be used in the analysis for obtaining variance components. It was again necessary to run two separate heirarchal AOV's in order to obtain estimates of the sum of squares for all sources of variation. This was done in exactly the same manner as was described previously for the pooled AOV for testing differences.

Simple linear correlations were computed between certain site factors and study variables. The correlations were run on both a clone mean and a source mean basis. The site factors, however, were run against the other study variables on a source mean basis only since the site information pertained to geographic sources only and not to clones in sources. The degrees of freedom for testing for significance in the source mean correlations was critical since there were only seven geographic sources. This made it very difficult to declare significance even though several correlation coefficients were fairly large, 0.60 or larger. Just the opposite situation existed with the clone mean correlations. Here there were 170 degrees of freedom for testing, which meant that relatively small r values were declared statistically significant when from a practical standpoint they may mean little, if anything.

# CHAPTER V

# RESULTS AND DISCUSSION

## "F" Tests

A standard "F" test was calculated for the data of each variable. The replication differences were tested by the use of the R x S interaction. Source differences were tested with the special error term; and C in S differences, as well as the R x S interaction, were tested with the C x R in S term of the pooled AOV.

### Fiber Length

Fiber length showed less variation than any other variable studied. The greatest variation was found among clones in sources rather than among sources. From Table V it can be seen that the highest clone mean was 0.668 mm while the lowest was 0.511. These two clone means were located in source number 2 and source number 5 respectively. Table VI shows the highest source mean was that of source number 2, 0.579 mm, and the lowest was that of source number 7, 0.549 mm. Overall mean fiber length was 0.562 mm.

The analysis of variance (Table VII) did not reveal any significant differences due to geographic sources. Clones in sources, however, were significant at the 1 percent level. One should keep in mind that essentially the "F" test in the AOV is testing for genetic differences since all plants were propogated asexually and grown in a rather

TABLE V

MAXIMUM - MINIMUM SOURCE AND CLONE MEANS FOR EIGHT VARIABLES FROM SEVEN SOURCES OF EASTERN COTTONWOOD IN OKLAHOMA

| Variables | Source | | | Clone | | |
|---|---|---|---|---|---|---|
| | Maximum | Minimum | Diff. | Maximum | Minimum | Diff. |
| F. Lgth. (mm) | 0.579 | 0.549 | 0.030 | 0.668 | 0.511 | 0.157 |
| F. Dia. (μ) | 19.779 | 18.914 | 0.865 | 21.234 | 17.427 | 3.807 |
| M.F. Angle (Deg.) | 23.39 | 20.13 | 3.26 | 26.91 | 17.18 | 9.73 |
| % G.F. | 30.11 | 21.38 | 8.73 | 39.33 | 14.56 | 24.77 |
| Lean (Deg.) | 15.38 | 4.51 | 10.87 | 28.04 | 2.24 | 25.81 |
| Height (Ft.) | 8.84 | 6.89 | 1.95 | 11.12 | 5.34 | 5.78 |
| R.G. (In.) | 0.9734 | 0.7266 | 0.2468 | 1.3063 | 0.6000 | 0.7063 |
| Limbs/Ft. | 2.6416 | 1.2019 | 1.4397 | 3.9837 | 0.1342 | 3.8495 |

TABLE VI

MEAN VALUES FOR THE STUDY VARIABLES FROM SEVEN SOURCES OF EASTERN COTTONWOOD IN OKLAHOMA

| Variables | Source | | | | | | | Overall Mean |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | |
| F. Lgth. (mm) | 0.576 | 0.579 | 0.561 | 0.554 | 0.553 | 0.561 | 0.549 | 0.562 |
| F. Dia. (μ) | 19.8 | 19.7 | 19.4 | 19.2 | 19.0 | 18.9 | 19.7 | 19.3 |
| M.F. Angle (Deg.) | 20.1 | 20.6 | 20.4 | 20.3 | 21.0 | 22.0 | 23.4 | 21.0 |
| % G.F. | 23.55 | 21.38 | 29.68 | 29.11 | 25.64 | 30.11 | 28.64 | 27.00 |
| Lean (Deg.) | 4.51 | 5.60 | 6.96 | 4.90 | 6.53 | 8.20 | 15.38 | 7.09 |
| Height (Ft.) | 8.12 | 8.65 | 7.83 | 8.84 | 7.76 | 7.81 | 6.89 | 8.05 |
| R.G. (In.) | 0.973 | 0.950 | 0.934 | 0.973 | 0.813 | 0.968 | 0.727 | 0.913 |
| Limbs/Ft. | 2.02 | 1.20 | 1.90 | 2.09 | 2.04 | 2.64 | 1.52 | 1.94 |

TABLE VII

ANALYSIS OF VARIANCE FOR FIBER LENGTH FROM SEVEN SOURCES OF EASTERN COTTONWOOD IN OKLAHOMA

| Source | d.f. | SS | MS | F[1] |
|---|---|---|---|---|
| Total | 171 | 0.21744611 | | |
| Reps | 3 | 0.00048936 | 0.00016312 | 0.154 |
| Source | 6 | 0.01838641 | 0.00306440 | 0.992 |
| R x S | 18 | 0.01909933 | 0.00106107 | 1.452 |
| Error[2] | 54 | | 0.00308856 | |
| Clones in S | 36 | 0.09960995 | 0.00276694 | 3.742** |
| C x R in S | 108 | 0.07986104 | 0.00073945 | |

* = significant at 5 percent level
** = significant at 1 percent level

[1]"F" Tests = Clones in S and R x S with C x R in S
Sources with Error
Reps with R x S

[2]Error = (MS of R x S + MS of Clones in S) - MS of C x R in S

homogeneous environment. The only possible way environmental effects might have been carried over is by the effect it might have had upon formation of the wood in the cuttings.

Fiber Diameter

Mean fiber diameter was again much more variable among clones in sources than among geographic sources. Fiber diameter on a clone mean basis ranged from 17.4μ to 21.2μ. The lowest clone was found in source number 7 and the highest clone was in source number 3. The difference between the lowest and highest clone mean was 3.8μ. On a source mean basis, much less variation was found. The range in fiber diameters on a source mean basis was 18.9μ to 19.8μ, or a difference between highest and lowest of 0.9μ. The highest source mean was that of source number 1 and the lowest was that of source number 6. As can be seen in Table VI, fiber diameter was highest at the eastern end of the river system and declined steadily toward the west except for source number 7. No explanation could be found for the sudden rise in fiber diameter for source number 7. Overall mean fiber diameter was found to be 19.3μ.

The analysis of variance (Table VIII) revealed no significant differences in fiber diameter due to sources; however, differences due to clones in sources were significant at the 1 percent level. This test indicates that more emphasis in selection should be placed upon good individuals regardless of geographic source rather than placing heavy emphasis upon geographic source.

TABLE VIII

ANALYSIS OF VARIANCE FOR FIBER DIAMETER FROM SEVEN SOURCES OF EASTERN COTTONWOOD IN OKLAHOMA

| Source | d.f. | SS | MS | F[1] |
|---|---|---|---|---|
| Total | 171 | 0.02756517 | | |
| Reps | 3 | 0.00052168 | 0.00017389 | 2.633 |
| Sources | 6 | 0.00171117 | 0.00028519 | 0.803 |
| R x S | 18 | 0.00118892 | 0.00006605 | 0.693 |
| Error[2] | 54 | | 0.00035533 | |
| Clones in S | 36 | 0.01384648 | 0.00038462 | 4.034** |
| C x R in S | 108 | 0.01029689 | 0.00009534 | |

* = significant at 5 percent level
** = significant at 1 percent level

[1]"F" Tests = Clones in S and R x S with C x R in S
Sources with Error
Reps with R x S

[2]Error = (MS of R x S + MS of Clones in S) - MS of C x R in S

## Microfibril Angle

Great variation was apparent in mean microfibril angle among clones. The range was from 17.2° for one of the clones in source number 4 to 26.9° for a clone in source number 7. There was very little variation in mean microfibril angle on a source mean basis except for source number 7 which had a mean microfibril angle much larger than the other sources. The lowest source mean was found in source number 1 with a mean microfibril angle of 20.1°, and the highest was found in source number 7 with a mean microfibril angle of 23.4°. The overall mean microfibril angle was 21.0°; however, if source number 7 were excluded, this figure dropped to 20.1°.

The analysis of variance for microfibril angle (Table IX) revealed that only clones in sources was a significant source of variation, being significant at the 1 percent level. This is what one would expect from the small differences in mean microfibril angle between sources. This variable follows the general trend of the other anatomical traits in that it would appear that individual tree selection with little regard to source is the manner in which future selection work should be done.

## Percent Gelatinous Fibers

A tremendous amount of variation was encountered in percent gelatinous fibers, both on a clone mean basis and on a source mean basis. The range in percent gelatinous fibers on a clone mean basis was 14.56 percent for one of the clones in source number 2 to 39.33 percent for a clone in source number 4. The difference between the highest and lowest clone for percent gelatinous fibers was 24.77

TABLE IX

ANALYSIS OF VARIANCE FOR MICROFIBRIL ANGLE FROM SEVEN SOURCES OF EASTERN COTTONWOOD IN OKLAHOMA

| Source | d.f. | SS | MS | F[1] |
|---|---|---|---|---|
| Total | 171 | 1607.06675884 | | |
| Reps | 3 | 2.78271726 | 0.92757242 | 0.129 |
| Sources | 6 | 159.28800390 | 26.54800065 | 1.383 |
| R x S | 18 | 129.00856880 | 7.16714271 | 1.168 |
| Error[2] | 54 | | 19.18903265 | |
| Clones in S | 36 | 653.58789580 | 18.15521932 | 2.960** |
| C x R in S | 108 | 662.39957306 | 6.13332938 | |

* = significant at 5 percent level
** = significant at 1 percent level

[1]"F" Tests = Clones in S and R x S with C x R in S
Sources with Error
Reps with R x S

[2]Error = (MS of R x S + MS of Clones in S) - MS of C x R in S

percent. The range in percent gelatinous fibers on a source mean basis was 21.38 percent in source number 2 to 30.11 percent in source number 6. The difference between highest and lowest source was 8.73 percent. The overall mean for percent gelatinous fibers was 27.00 percent.

The analysis of variance for percent gelatinous fibers (Table X) showed quite a different pattern of variation than did the ones for the characters discussed previously. Geographic sources were found to be significant at the 1 percent level while clones in sources were not significant even at the 5 percent level. This was the only character studied which showed no significant variation among clones in sources. Although no heritability estimates were computed for percent gelatinous fibers, as will be explained later, these findings indicate that there are genetic differences among geographic sources. If in subsequent studies this is proved to be so, the most rapid gains in reducing the amount of gelatinous fibers in cottonwood may be made by making selections for breeding purposes from areas having low amounts of gelatinous fibers. This test alone, however, is not conclusive evidence. Further studies will have to be made in which reliable heritability estimates for percent gelatinous fibers are computed before this can be accepted as fact.

## Growth Variables

The growth characters which were measured in this study will be discussed together since they were measured mainly for the purpose of providing more information concerning anatomical traits and the manner in which they vary. These growth factors include amount of lean,

TABLE X

ANALYSIS OF VARIANCE FOR PERCENT GELATINOUS FIBERS FROM SEVEN SOURCES OF EASTERN COTTONWOOD IN OKLAHOMA

| Source | d.f. | SS | MS | F[1] |
|---|---|---|---|---|
| Total | 171 | 23908.96792472 | | |
| Reps | 3 | 488.17608736 | 162.72536245 | 2.409 |
| Sources | 6 | 1766.73695427 | 294.45615904 | 4.512** |
| R x S | 18 | 1216.07906704 | 67.55994816 | 0.474 |
| Error[2] | 54 | | 65.27108835 | |
| Clones in S | 36 | 5047.69473919 | 140.21374275 | 0.984 |
| C x R in S | 108 | 15390.28107684 | 142.50260256 | |

* = significant at 5 percent level
** = significant at 1 percent level

[1]"F" Tests = Clones in S and R x S with C x R in S
Sources with Error
Reps with R x S

[2]Error = (MS of R x S + MS of Clones in S) - MS of C x R in S

number of limbs per foot of height, one-year height growth, and one-year diameter or radial growth. Tables XI, XII, XIII, and XIV show the analysis of variance for each of these characters respectively.

From the analyses of variance, it was found that clones in sources was a significant source of variation at the 1 percent level for all four characters. However, geographic source was statistically significant for only one character, amount of lean. The F value for geographic source was significant at the 5 percent level for amount of lean.

The range for these characters was fairly large in all cases. Amount of lean varied from 2.24° to 28.04° on a clone mean basis and from 4.51° to 15.38° on a source mean basis. One of the clones in source number 4 had the lowest amount of lean of any clone and one in source number 7 had the highest. The highest amount of lean on a source mean basis was in source number 7, 15.38°, and the lowest was in source number 1, 4.51°.

Height varied from 6.89 feet in source number 7 to 8.84 feet in source number 4. The maximum and minimum values of clone means were 11.12 feet and 5.34 feet respectively. The difference between the extremes on a source mean basis was 1.95 feet. This is a tremendous difference when one considers that this is only one-year height growth. The tallest source was, on the average, 28 percent taller at the end of one year's growth than the shortest source and nearly 10 percent taller than the average of all sources, which was 8.05 feet.

Radial growth in inches on a source mean basis ranged from 0.727 inches in source number 7 to 0.973 inches in source number 1. The highest clone mean for radial growth was 1.306 inches and the smallest

TABLE XI

ANALYSIS OF VARIANCE FOR LEAN FROM SEVEN SOURCES OF EASTERN COTTONWOOD IN OKLAHOMA

| Source | d.f. | SS | MS | F[1] |
|---|---|---|---|---|
| Total | 171 | 20879653.69186046 | | |
| Reps | 3 | 44042.85465116 | 14680.95155038 | 0.153 |
| Sources | 6 | 5204689.26328903 | 867448.21054817 | 3.671* |
| R x S | 18 | 1724870.00249168 | 95826.11124953 | 1.559 |
| Error[2] | 54 | | 236288.36257228 | |
| Clones in S | 36 | 7268993.67857142 | 201916.49107142 | 3.286** |
| C x R in S | 108 | 6637057.89285714 | 61454.23974867 | |

* = significant at 5 percent level
** = significant at 1 percent level

[1]"F" Tests = Clones in S and R x S with C x R in S
Sources with Error
Reps with R x S

[2]Error = (MS of R x S + MS of Clones in S) - MS of C x R in S

TABLE XII

ANALYSIS OF VARIANCE FOR NUMBER OF LIMBS PER FOOT OF HEIGHT FROM SEVEN SOURCES OF EASTERN COTTONWOOD IN OKLAHOMA

| Source | d.f. | SS | MS | F[1] |
|---|---|---|---|---|
| Total | 171 | 238.36433153 | | |
| Reps | 3 | 1.14010538 | 0.38003512 | 0.443 |
| Sources | 6 | 33.00822849 | 5.50137141 | 1.381 |
| R x S | 18 | 15.43722905 | 0.85762383 | 1.619 |
| Error[2] | 54 | | 3.98365224 | |
| Clones in S | 36 | 131.59745905 | 3.65548497 | 6.904** |
| C x R in S | 108 | 57.18130953 | 0.52945656 | |

* = significant at 5 percent level
** = significant at 1 percent level

[1]"F" Tests = Clones in S and R x S with C x R in S
Sources with Error
Reps with R x S

[2]Error = (MS of R x S + MS of Clones in S) - MS of C x R in S

TABLE XIII

ANALYSIS OF VARIANCE FOR ONE-YEAR HEIGHT GROWTH FROM SEVEN SOURCES OF EASTERN COTTONWOOD IN OKLAHOMA

| Source | d.f. | SS | MS | F[1] |
|---|---|---|---|---|
| Total | 171 | 632.67483469 | | |
| Reps | 3 | 2.72711720 | 0.90903906 | 0.329 |
| Sources | 6 | 54.24501438 | 9.04083573 | 1.207 |
| R x S | 18 | 49.80273968 | 2.76681887 | 1.119 |
| Error[2] | 54 | | 7.49189246 | |
| Clones in S | 36 | 259.05197792 | 7.19588827 | 2.912** |
| C x R in S | 108 | 266.84798548 | 2.47081468 | |

* = significant at 5 percent level
** = significant at 1 percent level

[1]"F" Tests = Clones in S and R x S with C x R in S
Sources with Error
Reps with R x S

[2]Error = (MS of R x S + MS of Clones in S) - MS of C x R in S

TABLE XIV

ANALYSIS OF VARIANCE FOR RADIAL GROWTH FROM SEVEN SOURCES OF EASTERN COTTONWOOD IN OKLAHOMA

| Source | d.f. | SS | MS | F[1] |
|---|---|---|---|---|
| Total | 171 | 13.33173137 | | |
| Reps | 3 | 0.25383735 | 0.08461245 | 1.652 |
| Sources | 6 | 1.13150863 | 0.18858477 | 1.479 |
| R x S | 18 | 0.92219950 | 0.05123330 | 0.891 |
| Error[2] | 54 | | 0.12751091 | |
| Clones in S | 36 | 4.81554210 | 0.13376505 | 2.327** |
| C x R in S | 108 | 6.20864378 | 0.05748744 | |

* = significant at 5 percent level
** = significant at 1 percent level

[1]"F" Tests = Clones in S and R x S with C x R in S
Sources with Error
Reps with R x S

[2]Error = (MS of R x S + MS of Clones in S) - MS of C x R in S

was 0.600 inches. Source number 7, the highest scoring source for radial growth, was 34 percent greater in diameter than the lowest scoring source, but only 6 percent larger than the overall mean diameter of the experiment, 0.913 inches.

On a source mean basis, number of limbs per foot of stem was smallest in source number 2, with an average of 1.20 and largest in source number 6, with 2.64. On a clone mean basis, the range was from .13 to 3.98 limbs per foot of stem. Overall average number of limbs per foot of stem was 1.94. The source having the fewest number of limbs per foot of stem had 61 percent fewer limbs than the average for all sources. It should be noted here that source numbers 2 and 6 were the lowest and highest sources respectively for percent gelatinous fibers as well as for number of limbs per foot of stem. This suggests that percent gelatinous fibers increases as number of limbs per foot increases.

## Correlations

Simple linear correlations between the study variables and certain site factors representing the areas in which the parent trees are located were computed. All possible combinations were computed on a source mean basis. In addition, all possible simple linear correlations among the eight study variables were run on a clone mean basis. In interpreting these correlations, one should keep in mind that correlations do not imply cause and effect relationships; they simply demonstrate the manner in which two factors vary together.

Fiber Length

From Table XV fiber length is seen to be significantly correlated with three environmental variables on a source mean basis. Fiber length was found to be significantly correlated with longitude and average mean daily minimum temperature during the month of January (AMDM temp.) at the 5 percent level. The correlation coefficient (r) for fiber length vs. longitude was -.851, and for AMDM temp. (r) was +.842. Fiber length was significantly correlated with average annual rainfall (AAR) at the 1 percent level. The correlation coefficient for these two variables was +.916.

Since AAR and AMDM temp. both increase from west to east, these three correlations may be summed up by saying that environmental factors are such that one can expect increases in fiber length in eastern cottonwood from west to east in southern Oklahoma. This may be due to both genetic differences and environmental differences. However, it would seem logical to assume that it is due to genetic differences since all sources were grown under essentially the same environment.

Fiber length was not significantly correlated with height or radial growth; however, the correlation coefficient for radial growth, +.645, was fairly large. This seems to be in agreement with previous work by Boyce and Kaeiser (7), Kennedy (28), and Kennedy and Smith (27) which indicated that fiber length increases with increasing rate of growth. Fiber length was found to be significantly correlated with only one of the anatomical traits on a source mean basis, that being percent gelatinous fibers. The correlation coefficient (r) for these two variables was -.765 and it was significant at the 5 percent level.

TABLE XV

CORRELATION COEFFICIENTS AMONG STUDY VARIABLES AND SITE FACTORS BASED ON SOURCE MEANS

| Variables | | Correlation Coefficient | Variables | | Correlation Coefficient |
|---|---|---|---|---|---|
| F. Lgth. | vs. Long. | = -.851* | % G.F. | vs. R.G. | = -.149 |
| | vs. Lat. | = -.522 | | vs. Hght. | = -.161 |
| | vs. Elev. | = -.744 | | vs. Lean | = +.399 |
| | vs. A.A.R. | = +.916** | Lean | vs. Long. | = +.788* |
| | vs. A.M.D.M. | = +.842* | | vs. Lat. | = +.537 |
| | vs. Lmbs./Ft. | = -.266 | | vs. Elev. | = +.909** |
| | vs. R.G. | = +.645 | | vs. A.A.R. | = -.715 |
| | vs. Hght. | = +.361 | | vs. A.M.D.M. | = -.798* |
| | vs. Lean | = -.588 | | vs. Lmbs./Ft. | = -.380 |
| | vs. % G.F. | = -.765* | | vs. R.G. | = -.810* |
| | vs. Mic. Angle | = -.594 | | vs. Hght. | = -.873* |
| | vs. F. Dia. | = +.480 | Hght. | vs. Long. | = -.598 |
| F. Dia. | vs. Long. | = -.451 | | vs. Lat. | = -.338 |
| | vs. Lat. | = -.416 | | vs. Elev. | = -.731 |
| | vs. Elev. | = -.192 | | vs. A.A.R. | = +.480 |
| | vs. A.A.R. | = +.472 | | vs. A.M.D.M. | = +.587 |
| | vs. A.M.D.M. | = +.375 | | vs. Lmbs./Ft. | = +.449 |
| | vs. Lmbs./Ft. | = -.757* | | vs. R.G. | = +.809* |
| | vs. R.G. | = -.126 | R.G. | vs. Long. | = -.678 |
| | vs. Hght. | = -.204 | | vs. Lat. | = -.480 |
| | vs. Lean | = +.162 | | vs. Elev. | = -.754* |
| | vs. % G.F. | = -.564 | | vs. A.A.R. | = +.560 |
| | vs. Mic. Angle | = +.004 | | vs. A.M.D.M. | = +.691 |
| Mic. Angle | vs. Long. | = +.670 | | vs. Lmbs./Ft. | = +.489 |
| | vs. Lat. | = +.801* | Lmbs./Ft. | vs. Long. | = +.143 |
| | vs. Elev. | = +.795* | | vs. Lat. | = +.086 |
| | vs. A.A.R. | = -.469 | | vs. Elev. | = -.043 |
| | vs. A.M.D.M. | = -.704 | | vs. A.A.R. | = -.305 |
| | vs. Lmbs./Ft. | = -.068 | | vs. A.M.D.M. | = -.145 |
| | vs. R.G. | = -.744 | A.M.D.M. | vs. Long. | = -.982** |
| | vs. Hght. | = -.819* | | vs. Lat. | = -.799* |
| | vs. Lean | = +.957** | | vs. Elev. | = -.971** |
| | vs. % G.F. | = +.387 | | vs. A.A.R. | = +.939** |
| % G.F. | vs. Long. | = +.656 | A.A.R. | vs. Long. | = -.935** |
| | vs. Lat. | = +.231 | | vs. Lat. | = -.604 |
| | vs. Elev. | = +.528 | | vs. Elev. | = -.877** |
| | vs. A.A.R. | = -.848* | Elev. | vs. Long. | = +.955** |
| | vs. A.M.D.M. | = -.623 | | vs. Lat. | = +.774* |
| | vs. Lmbs./Ft. | = +.592 | Lat. | vs. Long. | = +.813* |

*Significant value of r at the 5 percent level = .754
**Significant value of r at the 1 percent level = .874

On a clone mean basis (Table XVI) fiber length was significantly correlated with four variables, fiber diameter, microfibril angle, height, and radial growth. All four correlation coefficients were significant at the 1 percent level except microfibril angle, which was significant at the 5 percent level. All correlations were positive except the one with microfibril angle. None of the correlation coefficients between these four variables and fiber length were significant even at the 5 percent level on a source mean basis. However, the general trends were the same and some of the r values were fairly large, i.e. r for fiber length vs. radial growth on a source mean basis was +.645. The two correlations for percent gelatinous fibers vs. fiber length were somewhat contradictory, since on a source mean basis it was significant and on a clone mean basis, where it was easier to declare significance, it was not. However, the fact that amount of gelatinous fibers had little effect upon length of fiber seems to be in agreement with the work done by Kaeiser and Stewart (26).

These various correlations may be summed up in this manner: (1) fiber length increases as longitude decreases in Oklahoma, (2) fiber length and microfibril angle vary inversely with one another, and (3) fiber length increases with increasing growth rate, i.e. one-year height and radial growth.

Fiber Diameter

On a source mean basis, fiber diameter was found to be significantly correlated with only one factor; and that was number of limbs per foot of stem. The correlation coefficient (r) between fiber

TABLE XVI

CORRELATION COEFFICIENTS AMONG STUDY VARIABLES
BASED ON CLONE MEANS

| Variable | Lmbs/ Ft. | R.G. | Hght. | Lean | % G.F. | Mic. Angle | F. Dia. | F. Lgth. |
|---|---|---|---|---|---|---|---|---|
| Lmbs/Ft. | | +.420** | +.257** | -.224** | -.043 | +.123 | +.224** | +.057 |
| R.G. | | | +.841** | -.435** | -.014 | -.178* | +.457** | +.381** |
| Hght. | | | | -.531** | -.001 | -.228** | +.454** | +.327** |
| Lean | | | | | +.160* | +.236** | -.278** | -.125 |
| % G.F. | | | | | | +.076 | -.168* | -.040 |
| Mic. Angle | | | | | | | +.010 | -.177* |
| F. Dia. | | | | | | | | +.360** |
| F. Lgth. | | | | | | | | |

*Significant value of r at the 5 percent level = .149
**Significant value of r at the 1 percent level = .194

diameter and number of limbs was -.757 and was significant at the 5 percent level. The meaning of this correlation is difficult to interpret. Because large amounts of gelatinous fibers are generally found in the vicinity of limbs, the correlation is probably an indirect reflection of the effect of gelatinous fibers upon fiber diameter. That is, as percent gelatinous fibers increases, mean fiber diameter decreases. A rather strong though not significant positive correlation existed between fiber length and fiber diameter. The correlation coefficient between these variables was +.480. Wheeler et al. (45), Graff (16), and Heinig (18) reported this same relationship.

The correlation ($r = -.451$) between fiber diameter and longitude was not significant. However, a definite east-west trend is evident from the data in Table VI. Mean fiber diameter decreases steadily from east to west except for source number 7.

On a clone mean basis, fiber diameter was correlated with all variables at the 1 percent level except percent gelatinous fibers and microfibril angle. It was correlated with percent gelatinous fibers at the 5 percent level. Fiber diameter was significantly correlated with none of these variables except limbs per foot on a source mean basis. In fact, the r values for these correlations were very small except for the ones with fiber length and percent gelatinous fibers, which were +.480 and -.564 respectively.

These correlations indicate the following about the manner in which fiber diameter is related to the other variables: (1) fiber diameter decreases with an increase in percent gelatinous fibers, and (2) fiber diameter and fiber length increase together.

Microfibril Angle

On a source mean basis, microfibril angle was found to be significantly correlated with two environmental factors, latitude and elevation. Both correlation coefficients were significant at the 5 percent level. The significant correlation with latitude, r = +.801, was rather surprising considering the small amount of variation in latitude encountered from one end of the river system to the other, the range being only $33^{o}45'$ to $34^{o}30'$. Though microfibril angle was not significantly correlated with longitude, r = +.670, a definite east-west trend was evident in the source means. Mean microfibril angle increased fairly steadily from east to west with a sudden sharp rise in size of microfibril angle on the west end of the river system. Since both elevation and latitude are significantly correlated with longitude, it is safe to say that mean microfibril angle increases from east to west within the geographic area studied.

Microfibril angle was also significantly correlated with two growth traits, lean and one-year height. The correlation coefficient with lean, r = +.957, was significant at the 1 percent level, while the one with one-year height, r = -.819, was significant at the 5 percent level. Although not significant, microfibril angle was strongly correlated with radial growth, r = -.744, and fiber length, r = -.594.

The strong negative correlation with radial growth does not agree with the work done by Hiller (21) and Pillow et al. (33). They found microfibril angle to increase with rate of growth. The negative relationship between microfibril angle and fiber length substantiates the work done by Wardrop (44) and Echols (13) in which both reported microfibril angle to decrease with increasing cell length.

On a clone mean basis, microfibril angle was significantly correlated with four other variables, lean and height at the 1 percent level and fiber length and radial growth at the 5 percent level.

On the basis of these correlations, these general trends between microfibril angle and other variables may be identified: (1) microfibril angle increases with increases in latitude, (2) microfibril angle increases as amount of lean increases, and (3) microfibril angle increases as growth rate decreases.

Percent Gelatinous Fibers

The correlation between percent gelatinous fibers and fiber length has been discussed previously under the analysis of fiber length. The only other variable which was significantly correlated with percent gelatinous fibers was average annual rainfall (AAR). The correlation coefficient for these two variables was -.848 and it was significant at the 5 percent level. This is another correlation which is difficult if not impossible to explain without further work being done. Percent gelatinous fibers was not strongly enough correlated to any other variables to allow significance to be declared; however, it was fairly strongly correlated with fiber diameter, $r = -.564$, and number of limbs per foot of stem, $r = +.592$. Kaeiser and Boyce (22) also reported that gelatinous fibers tend to decrease mean fiber diameter. Percent gelatinous fibers was also strongly correlated with two environmental factors; AMDM temp., $r = -.623$, and longitude, $r = +.656$. Since AAR and AMDM temp. are both reflections of longitude, it may be said that percent gelatinous fibers increases with increasing longitude.

On a clone mean basis, percent gelatinous fibers was significantly correlated with only two variables, fiber diameter and lean; and then only at the 5 percent level. The correlation between percent gelatinous fibers and fiber diameter has been discussed previously. The correlation coefficient (r) between percent gelatinous fibers and amount of lean was +.160, indicating that the presence of large amounts of such tissue is related to the amount of lean in the stem. This is what one would expect and agrees with the work of other authors on the subject (10), (24), (35), (40), (41).

The lack of significance for the correlation between lean and percent gelatinous fibers on a source mean basis and the fact that it was significant only at the 5 percent level on a clone mean basis indicated that perhaps total lean of the stem was not an accurate enough predictor of where the highest percentage of gelatinous fibers would be located. Perhaps it would have been better to have marked the tension side of the stem as being the opposite side of any basal crook when such was present rather than simply the opposite side of the direction of lean of the total stem.

In conclusion, the correlations involving percent gelatinous fibers indicate: (1) percent gelatinous fibers increases with increases in longitude, and (2) percent gelatinous fibers has a slight effect upon fiber diameter, tending to decrease that cell dimension.

Growth Variables

There were only seven significant correlations involving growth variables and environmental factors. All but one of these were

significant at the 5 percent level. Height was positively correlated with radial growth, r = +.809, as one would expect. Lean was found to be negatively correlated with both height and radial growth, r = -.873 and -.810 respectively. Lean was found to be positively correlated with longitude, r = +.788, and elevation, r = +.909. These correlations indicate: (1) a direct relationship exists between radial growth and height, and (2) lean is inversely related to growth and directly related to longitude.

## Paired "t" Tests

In order to try to determine what effect the occurrence of gelatinous fibers had upon the other three anatomical variables, paired "t" tests were run on all four of these variables. Since all anatomical measurements had been made on both sides of the stem; i.e. tension and compression sides, and since equal numbers of measurements had been made on each side, it was possible to run this test. The results of the test are shown in Table XVII, and the means for each side of the anatomical traits are shown in Table XVIII. A calculated value of "t" was computed as follows:

$$t = \frac{\bar{d}}{S\bar{d}}$$

where: $\bar{d}$ = the mean of the differences between the two sides

$S\bar{d}$ = the variance of the differences between the two sides

$S\bar{d}$ was computed in the following manner:

$$S\bar{d} = \sqrt{\frac{\Sigma D^2 - (\Sigma D)^2/N}{N\ (N-1)}}$$

TABLE XVII

PAIRED "t" TESTS FOR ANATOMICAL TRAITS OF EASTERN COTTONWOOD[1]

| Formula Components | Per Cent Gelatinous Fibers | Fiber Length | Fiber Diameter | Microfibril Angle |
|---|---|---|---|---|
| $\Sigma D$ | 5200.560 | 0.78830 | -0.73480 | 101.06 |
| $\Sigma D^2$ | 236699.6 | 0.24647 | 0.08164 | 1828.7202 |
| $(\Sigma D)^2$ | 27045824.3136 | 0.62142 | 0.53993 | 10213.1236 |
| N | 172 | 172 | 172 | 172 |
| $S\bar{d}$ | 1.644 | 0.002887 | 0.001633 | 0.2453 |
| $\bar{d}$ | 30.235813 | 0.0045831 | -0.004272 | 0.58755 |
| "t" Tabulated | 3.291 | 1.282 | 2.576 | 2.326 |
| "t" Calculated | 18.396*[4] | 1.595*[1] | -2.615*[3] | 2.395*[2] |

*[1] = significant at the 10 percent level
*[2] = significant at the 1 percent level
*[3] = significant at the .5 percent level
*[4] = significant at the .05 percent level

[1] $S\bar{d} = \sqrt{\frac{\Sigma D^2 - (\Sigma D)^2/N}{N\ (N-1)}}$, $t = \frac{\bar{d}}{S\bar{d}}$

TABLE XVIII

MEANS OF THE TENSION AND COMPRESSION SIDES FOR THE ANATOMICAL TRAITS OF EASTERN COTTONWOOD

| Variable | $\bar{X}$ Tension Side | $\bar{X}$ Compression Side |
|---|---|---|
| Gelatinous Fibers (Percent) | 42.103 | 11.867 |
| Fiber Length (mm) | 0.56415 | 0.55957 |
| Fiber Diameter (μ) | 31.285 | 31.712 |
| Microfibril Angle (Degree) | 21.2568 | 20.5229 |

where: $\Sigma D^2$ = the sum of the squares of the differences between the two sides

$(\Sigma D)^2$ = the sum of the differences between the two sides squared

N = the number of pairs

Percent Gelatinous Fibers

The paired "t" test which was run on percent gelatinous fibers simply proved that indeed gelatinous fibers do occur in larger percentages on the tension side of a leaning stem than on the compression side. The test for gelatinous fibers showed that the means of the two sides were significantly different from one another at the 0.05 percent level. The mean percent gelatinous fibers for the tension side was 42.103 and for the compression side, 11.867.

Fiber Length

The test on fiber length failed to show significant differences between the two sides sampled, even at the 5 percent level. The mean fiber length of the tension side was 0.56415 and for the compression side, 0.55957. From this test and the rather weak and conflicting correlations between fiber length and percent gelatinous fibers, it is necessary to conclude that percent gelatinous fibers had little if any effect upon length of fiber in this study.

Fiber Diameter

The paired "t" test on fiber diameter indicated that the mean fiber diameter values for the tension and compression sides were significantly different from one another at the 0.5 percent level.

Mean fiber diameter was smaller on the tension side, 31.285μ, than on the compression side, 31.712μ. In this experiment, then, the occurrence of gelatinous fibers had the effect of decreasing fiber diameter. The difference in the means for the tension and compression sides was very small, however, being only 0.427μ. The correlations between fiber diameter and percent gelatinous fibers did agree with the results of this test. The correlation coefficient between these two factors was -.564 on a source mean basis and -.168 on a clone mean basis. Of the two correlations, only the one based on clone means was significant, being significant at the 5 percent level. From the two tests, it can be concluded that percent gelatinous fibers did have a definite, though small, effect upon fiber diameter. This effect was to reduce the mean fiber diameter in this experiment.

Microfibril Angle

The paired "t" test which was performed for microfibril angle showed mean microfibril angle to be significantly different at the 1 percent level on the two sides sampled. Mean microfibril angle for the tension side of the stem was 21.2568° and 20.5229° for the compression side. Although the correlations between microfibril angle and percent gelatinous fibers were not significant, this test seems to imply that the occurrence of gelatinous fibers has the effect of raising the mean microfibril angle.

## Heritabilities

Broad sense heritability estimates were computed for six of the study variables. These were fiber length, fiber diameter, microfibril

angle, lean, height, and number of limbs per foot. The two variables for which heritabilities were not computed were percent gelatinous fibers and radial growth. The reason heritabilities were not computed for these two traits was that the estimate of the variance component for clones in sources for each of these traits was negative (Tables XIX and XX) making it impossible to compute a sufficiently accurate estimate of heritability.

Broad sense heritabilities were computed as follows:

$$H = \frac{\sigma^2_{C(S)} + \sigma^2_S}{\sigma^2_R + \sigma^2_S + \sigma^2_{RxS} + \sigma^2_{C(S)} + \sigma^2_\varepsilon}$$

where: $\sigma^2_{C(S)}$ = variance due to clones in sources

$\sigma^2_S$ = variance due to sources

$\sigma^2_R$ = variance due to replications

$\sigma^2_{RxS}$ = variance due to rep and source interaction

$\sigma^2_\varepsilon$ = error

From Table XXI it can be seen that three traits showed rather high degrees of heritability in this study, microfibril angle, H = .591; lean, H = .508; and number of limbs per foot, H = .463. The other two anatomical traits exhibited heritabilities which seem somewhat low in comparison to some of the reports published to date. It should be kept in mind, however, that heritability estimates are just that, estimates, and may vary a great deal depending upon the age of material used in the study, type of heritability (broad sense or narrow sense), and how the heritability estimate was computed.

Microfibril angle would seem to be the anatomical trait upon which most rapid gains could be made by selection. Since microfibril angle

TABLE XIX

ESTIMATES OF COMPONENTS OF VARIANCE FOR THE ANALYSIS OF VARIANCE

| Variable | Reps | Sources | R x S | C in S | C x R in S |
|---|---|---|---|---|---|
| Fiber Length | 0.00000000* | 0.00006196 | 0.00008058 | 0.00017850 | 0.00081420 |
| Fiber Diameter | 0.00000923 | 0.00001431 | 0.00000000* | 0.00003810 | 0.00010832 |
| Microfibril Angle | 0.00000000* | 0.16695679 | 0.94500844 | 3.87018281 | 1.85149626 |
| % Gelatinous Fibers | 1.72741224 | 4.18089786 | 0.00000000* | 0.00000000* | 139.88158453 |
| Lean | 0.00000000* | 33036.63442460 | 1049.28373016 | 48262.27976190 | 77719.41666666 |
| One-Year Height | 0.00000000* | 0.18348619 | 0.28624068 | 0.25263376 | 2.74047781 |
| Radial Growth | 0.00024941 | 0.00986823 | 0.00000000* | 0.00000000* | 0.06667280 |
| Limbs Per Foot | 0.00000000* | 0.20889224 | 0.07001844 | 0.29491203 | 0.51403928 |

*Negative values for which the best estimate is zero

TABLE XX

ESTIMATES OF COMPONENTS OF VARIANCE EXPRESSED AS PERCENT OF TOTAL EXCLUDING C x R IN S

| Variable | Reps | Sources | R x S | C in S |
|---|---|---|---|---|
| Fiber Length | 00.0* | 19.2 | 25.0 | 55.6 |
| Fiber Diameter | 14.9 | 23.2 | 00.0* | 61.8 |
| Microfibril Angle | 00.0* | 3.3 | 18.9 | 77.6 |
| % Gelatinous Fibers | 29.2 | 70.7 | 00.0* | 00.0* |
| Lean | 00.0* | 40.1 | 1.2 | 58.6 |
| One-Year Height | 00.0* | 25.4 | 39.6 | 34.9 |
| Radial Growth | 2.4 | 97.5 | 00.0* | 00.0* |
| Limbs Per Foot | 00.0* | 36.4 | 12.2 | 51.3 |

*Negative value for which the best estimate is zero

TABLE XXI

BROAD SENSE COEFFICIENTS OF HERITABILITY FOR THE EIGHT STUDY VARIABLES[1]

| Variable | $\sigma^2_G$ | $\sigma^2_T$ | H |
|---|---|---|---|
| Fiber Length | 0.00024046 | 0.00113524 | 0.212 |
| Fiber Diameter | 0.00005241 | 0.00016996 | 0.308 |
| Microfibril Angle | 4.03713960 | 6.83364430 | 0.591 |
| Gelatinous Fibers* | | | |
| Lean | 81298.913 | 160067.612 | 0.508 |
| One-Year Height | 0.43611995 | 3.42713869 | 0.127 |
| Radial Growth* | | | |
| Limbs Per Foot | 0.50380427 | 1.08786199 | 0.463 |

*It was impossible to compute heritability estimates for these variables due to negative estimates of the clones in sources variance component

[1] $$H = \frac{\sigma^2_{C(S)} + \sigma^2_S}{\sigma^2_R + \sigma^2_S + \sigma^2_{RxS} + \sigma^2_{C(S)} + \sigma^2_\varepsilon} = \frac{\sigma^2_G}{\sigma^2_T}$$

where: $\sigma^2_{C(S)}$ = variance due to clones in sources

$\sigma^2_S$ = variance due to sources

$\sigma^2_R$ = variance due to replications

$\sigma^2_{RxS}$ = variance due to rep x source interaction

$\sigma^2_\varepsilon$ = error

and fiber length are negatively correlated, gains would also be made upon fiber length at the same time, although at a less rapid rate since the heritability estimate for fiber length is lower.

Fairly rapid gains through selection should also be attainable for fewer numbers of limbs per foot of stem and amount of lean. Both these factors are very important from a commercial standpoint since both affect the amount of tension wood one would expect to find in the stem.

Slight gains could be made in mean fiber diameter through selection; however, these gains would be slow and would have to be selected for independently of selections for microfibril angle, since they do not seem to vary together.

# CHAPTER VI

## SUMMARY AND CONCLUSIONS

This study succeeded in defining the amount of variation one should expect in one-year-old eastern cottonwood from the entire length of southern Oklahoma. Within the geographical area studied, it was established that for most of the anatomical traits considered in the study, individual tree selection should receive the major emphasis in future selections of parent trees for breeding work; however, geographic sources must not be ignored completely since they do contribute a considerable amount to the total variation, as Table XX shows. It appears that greater emphasis should be placed upon geographic source when selecting for the growth variables than when selecting for the anatomical variables.

Heritability estimates for six of the eight variables used in this study were computed. It was unfortunate but unavoidable that heritability estimates for the other two traits, percent gelatinous fibers and radial growth, could not be obtained. Three of the heritability estimates which were obtained were very strong; namely, microfibril angle, lean, and number of limbs per foot of stem.

Several important conclusions were drawn from information obtained from the various statistical tests, including the following:

(1) Fiber length decreases and percent gelatinous fibers increases with increases in longitude.

(2) Fiber length increases and microfibril angle decreases with increasing growth rate, i.e. height growth and radial growth.

(3) Fiber length is directly related to fiber diameter and inversely related to microfibril angle.

(4) Mean fiber diameter is slightly lower than normal, and microfibril angle is slightly higher when found in association with gelatinous fibers.

(5) Fiber length is apparently affected very little by the presence of gelatinous fibers.

(6) Microfibril angle increases with increases in latitude.

(7) Degree of lean increases with increasing longitude.

(8) Increased growth rate is significantly negatively correlated with degree of lean.

The findings of this study should be helpful to researchers in the fields of forest genetics, forest management, wood technology, silviculture, and forest economics.

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