VARIATION IN CELL DIMENSIONS AND FIBRIL ANGLE FOR TWO FERTILIZED EVEN-AGED LOBLOLLY PINE PLANTATIONS[1]

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ABSTRACT

Increment core samples were obtained from randomly selected, nine-year-old loblolly pine (*Pinus taeda* L.) in two even-aged plantations in Louisiana in order to determine the variation in cell dimensions and fibril angle of the sites. The Homer site is representative of the growing conditions in north Louisiana, and the Bogalusa site is typical of the conditions in southeastern Louisiana. Both sites were subjected to similar site preparation and weed control and were fertilized in the juvenile period. The anatomical properties that were measured include: fiber length, cell-wall thickness, and microfibril angle (MFA). Observations were made in order to compare corewood (rings 2–4) and outerwood (rings 7–9) and also between earlywood and latewood. For both plantations, the statistical analysis revealed that cell-wall thickness and fiber length were significantly greater in outerwood and latewood than in corewood and earlywood, respectively. Microfibril angle was found to be significantly higher in corewood than in outerwood for both plantations. The anatomical properties were found to be more acceptable from an end-use perspective on the Homer site, which experienced slower diameter growth than the Bogalusa site.

Keywords: cell-wall thickness, fiber length, microfibril angle, specific gravity.

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INTRODUCTION

Loblolly pine (*Pinus tadea* L.), the principal timber species of the southern United States (Wahlenberg 1960), is a medium-sized to large tree 27 m to 38 m in height and 610 mm to 762 mm in diameter (maximum 55 m by 1524 mm or more) (Harlow et al. 1979). Loblolly pine will grow on a wide variety of soil types. The best growth is often exhibited on soils with deep surface layers having plenty of moisture but poor surface drainage, and fine-textured subsoil.

Loblolly pine is the timber and pulp species of choice in the South because of its ability to grow quickly and its favorable wood properties. More than half of the United States' pulpwood comes from the southern pines, with a large percentage from loblolly pine because of its typical long fibers. The timber industry favors loblolly because of its high specific gravity (SG) and favorable mechanical strength properties (Forest Products Laboratory 1987). The SG of loblolly pine varies from 0.29 to 0.34 for earlywood and from 0.63 to 0.85 for latewood (Biblis 1969; Goggans 1964; Ifju 1969; Paul 1939; Woodson and Koch 1970; Yao 1970).

The objectives of this study were to determine the variability of anatomical properties from two even-aged, fertilized loblolly pine plantations that were early fertilized. Comparisons at each site were made between corewood (growth rings 2–4) and outerwood (7–9) and earlywood/latewood (fifth growth ring). The anatomical differences between the two sites can not be absolutely attributed to the cultural treatment because of the substantial inherent differences between the sites, the different fertilizer treatments, and the lack of a control plot. Therefore, the statistical analysis focused on differences within the sites, specifically between corewood and outerwood and between earlywood and latewood.

MATERIALS AND METHODS

The Homer plantation is located on an abandoned cotton field in the north Louisiana parish of Claiborne at the Louisiana Agricultural Experiment Station's Hill Farm Research Station (approximately 32°45′N latitude and 93°04′W longitude). The soil is a well-drained, fine sandy-loam Wolfpan (loamy, siliceous, thermic Arenic Paleudalfs) (USDA Soil Conservation Service 1989). The soil is highly weathered and plagued by low fertility and a pH of 5.0–5.2 (Evans et al. 1983). The clay subsoil serves to reduce water availability and restrict tree root development at the expense of tree growth. The site index is 24 m at a base age of 50. The site was fertilized in the winter at age two with 45 kg per acre each (1:1:1) of nitrogen (N), phosphorous (P_2O_5), and potassium (K_2O). Genetically unaltered (1-0) seedlings were grown using seed collected from natural loblolly stands located in Louisiana.

The Bogalusa plantation is located on a previous agricultural pasture at the Louisiana State University Lee Memorial Forest in southeastern Louisiana's Washington parish. The site is located at approximately 30°52′N latitude and 89°59′W longitude and is a better site for growth of loblolly pine because of the milder winters, more fertile soil, and longer growing seasons. The soil on this particular plot is a Ruston fine sandy-loam (fine-loamy, siliceous, thermic Typic Paleudults) (USDA Soil Conservation Service 1991). The soil is well-drained with a pH of 4.5–4.9 (Burns et al. 1985). The site index is 30 m at age 50 (Burns 1982). It was fertilized in the spring at an age of three months with 45 kg per acre of $NH_4NO_3^-$. Nursery seedlings were grown in a similar manner as on the Homer plantation.

Five trees were randomly sampled from each plantation in January of 1994, and two increment cores were taken at breast height from each tree. One core was used for determination of SG, and the other core was utilized for anatomical analysis. The increment cores from each selected tree were taken at breast height and then immediately wrapped in Saran wrap and placed in a Ziploc sandwich bag in order to maintain the green moisture content. Samples were returned to the Forest Products Laboratory in Baton Rouge the same day for determination of SG.

The anatomical properties were measured in the green condition on the same growth ring for each sample in order to avoid between growth ring variation. All comparisons between earlywood and latewood were always made on the fifth growth ring in order to attempt to avoid the effect of sampling within the corewood or outerwood region. For the corewood, tracheid length was determined on the second growth ring and tracheid wall thickness on the third growth ring. The MFA was assessed on the fourth growth ring. For the outerwood, fiber length and cell-wall thickness were determined on the sixth and seventh growth rings, respectively. The MFA was evaluated on the eighth growth ring.

Fiber length measurements were obtained by microtoming 30-μm radial sections from the appropriate growth rings and macerating the wood in a 1:1 solution of 30% hydrogen peroxide and glacial acetic acid warmed at 50°C for three days. The macerated tissues were washed in water and finally stored in 30% alcohol and mounted on temporary slides for fiber dimension measurements. Five slides of macerated fibers were made for each of the five trees from the two sites. For each tree, 50 whole fibers were randomly selected and measured through a microscope-projector.

The cell-wall thickness was determined on 20-μm-thick radial microtome sections from the appropriate growth rings and can more appropriately be described as tangential single wall thickness. The appropriate growth rings were visually identified and removed with a sharp thin-kerf band saw. A sliding microtome was used to obtain 20-μm-thick sections, which were stained in safranin, and permanent slides were mounted in Permount.[2] A sufficient number of slides were produced in order to randomly obtain 50 tracheid cell-wall thickness values for each of five trees from each plantation. A microscope was equipped with a 250× objective and an eyepiece micrometer with 0.01-μm divisions in order to obtain cell-wall thickness data.

The MFA of each tree was measured using a method previously reported by Bailey and Vestal (1937) and later modified by Senft and Bendtsen (1985). The third (corewood) and eighth (outerwood) growth ring were oven-dried from the green condition at 100°C in order to induce checking in the cell walls. Radial sections were microtomed at a thickness of 15–20 μm and stored in 50% alcohol. Sections were dehydrated in absolute alcohol for 5 min and then briefly immersed in a 2% solution of iodine-potassium iodide and blotted dry with a paper towel. Two drops of 60% nitric acid were added to the section before a cover slip was applied. The MFA appeared as elongated, dark crystals of iodine and filled the cracks in the cell wall. Careful focusing of the microscope allowed MFA measurement on the S-2 of latewood.

The SG of each unextracted increment core was determined in accordance with ASTM D 4442 (ASTM 1993). The SG was measured only on the increment core as a whole, not on any particular growth ring or earlywood/latewood zone.

RESULTS

The mean values and Scheffé's grouping of the anatomical properties studied are summarized in Table 1. All mean values represent 250 samples, i.e., 50 samples from each of five trees for each plantation.

The five trees from the Homer site yielded a mean SG of 0.40, with a coefficient (CV) = 5.40%. The Bogalusa trees possessed a mean SG of 0.48, CV = 6.11%. Accelerated growth rates have typically led to a decrease in SG. However, the Bogalusa site experienced a greater diameter growth rate response (Fig. 1) as a result of the fertilization, yet also showed the higher SG in spite of possessing thinner cell walls for all four wood types considered. This phenomenon can be partially attributed to the fact that the Bogalusa site also displayed a greater mean annual percentage of latewood (Fig. 2).

[2] The use of trade names does not constitute endorsement by the Louisiana Forest Products Laboratory or the USDA Forest Service.

TABLE 1. *Comparison by Scheffé's test for significantly different means of anatomical properties of 9-year-old loblolly pine grown at two sites in Louisiana.*[1]

Site	Anatomical property	Location	Standard deviation	CV(%)[2]	Mean
Homer	cell-wall thickness (μm)	corewood	0.46	5.61	8.27 B
		outerwood	0.64	5.21	12.26 A
		earlywood	0.20	4.34	4.60 B
		latewood	0.27	2.06	13.08 A
	fiber length (mm)	corewood	0.28	14.00	2.00 B
		outerwood	0.27	8.08	3.34 A
		earlywood	0.22	8.56	2.57 B
		latewood	0.14	5.05	2.77 A
	microfibril angle (degrees)	corewood	3.97	10.56	37.60 A
		outerwood	3.08	10.10	30.50 B
Bogalusa	cell-wall thickness (μm)	corewood	0.37	10.42	3.55 B
		outerwood	0.39	7.10	5.49 A
		earlywood	0.30	9.20	3.26 B
		latewood	0.32	5.00	6.39 A
	fiber length (mm)	corewood	0.38	21.35	1.78 B
		outerwood	0.26	10.08	2.58 A
		earlywood	0.22	13.92	1.58 B
		latewood	0.21	7.58	2.77 A
	microfibril angle (degrees)	corewood	4.93	11.56	42.69 A
		outerwood	4.12	10.58	38.92 B

[1] Comparisons were made only between both (corewood and outerwood) and (earlywood and latewood) for a given anatomical property within each site. Values with the same letter are not significantly different at the $\alpha = 0.05$ level.

[2] CV = Coefficient of variation.

Previous research by the USDA Forest Service (1965) has shown that the loblolly pine from the Bogalusa and Homer areas should have a specific gravity of 0.49 and 0.47, respectively. The SG values for this project are lower than these standard values because the trees studied in this project were still juvenile and fairly recently fertilized. Loblolly pine will naturally have a lower SG in the juvenile period than the mature period. Also, fertilization has been shown to stimulate growth but lead to thinner cell walls and lower SG (Megraw 1985).

Cell-wall thickness

Cell-wall thickness was found to be significantly higher in outerwood than in corewood (Table 1). It was also significantly greater in

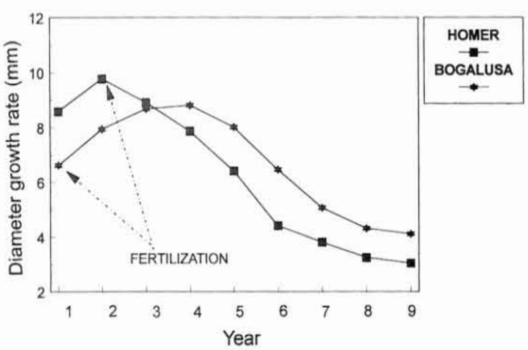

FIG. 1. Mean diameter growth rate of 9-year-old loblolly pine from Bogalusa and Homer, Louisiana.

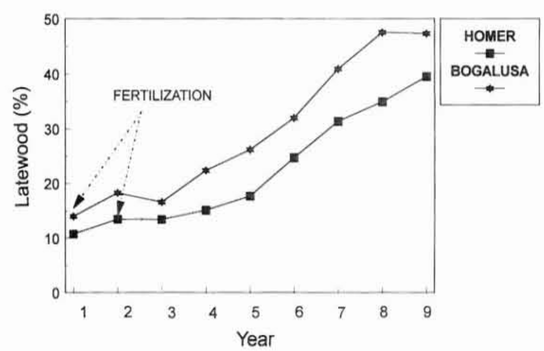

FIG. 2. Mean latewood percentage of 9-year-old loblolly pine from Bogalusa and Homer, Louisiana.

latewood than in earlywood (Table 1). It is interesting to note that the Homer site displayed much higher cell-wall thickness values for all four wood types considered (corewood, outerwood, earlywood, and latewood) than the corresponding values from the Bogalusa site. Possible explanations for these site differences include type and timing of fertilization and soil moisture variation.

The Bogalusa site has traditionally been considered a much more favorable location for loblolly pine. As a result, growth was expected to be more favorable on this site. Trees respond favorably to nitrogen application because it tends to stimulate both crown and root development. As a result, a cell division is stimulated and stem diameter and height are increased. Larson (1969) and Brown (1970) have speculated that cambial cell division is largely under the influence of auxin supply. Auxins are known to be produced in the crown and translocated downward through the stem to areas of active growth (Kramer and Kozlowski 1979).

Nitrogen application leads to a larger crown that is capable of producing more auxins, which results in an increase in cambial cell division. The enlarged crown also produces more photosynthate, which enlarges the additional cells (Kramer and Kozlowski 1979). With regard to cell-wall thickness, a more abundant auxin supply has been associated with larger cell size and thinner walls (Megraw 1985). In short, there is a shorter time period in which the cell wall can thicken. The Bogalusa site was fertilized exclusively with a nitrogen-based compound, and the trees showed thinner tracheid cell walls.

In addition, the two plantations are subject to two distinctly different soil moisture regimes. The Homer site averages 1300 mm (1016 mm–1902 mm) of precipitation per year but is subject to frequent and prolonged summer droughts. The overall mean monthly precipitation is 107 mm at Homer but only 74 mm for August (18 mm–146 mm) (Fig. 3) (Clason 1994). A reduction in precipitation late in the growing season will signal the cambium to slow cell division. These cells now have an extended period in which to lignify and thicken. There are fewer cells in the latewood zone, but these cells have a greater cell-wall thickness. The Bogalusa site receives an average of 1524 mm of precipitation per year, well distributed throughout the growing season (Fig. 3), and there is rarely a prolonged drought (Burns et al. 1985). Consequently, the Bogalusa site experienced a greater percentage of latewood (Fig. 2), but mean cell-wall thickness values were greater for the corewood and outerwood of the slower-grown Homer site. It is curious to note that the Homer average cell-wall thicknesses of earlywood (4.60 μm) and latewood (13.08 μm) are greater than the corresponding values from Bogalusa for earlywood (3.26 μm) and latewood (6.39 μm). Direct comparisons between sites are unadvisable because of the inherent differences in sites and cultural treatments.

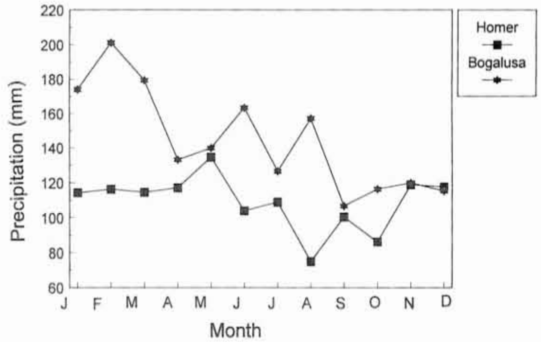

FIG. 3. Mean monthly precipitation at Bogalusa and Homer, Louisiana.

Fiber length

Fiber length showed a similar pattern to that displayed by cell-wall thickness in that outerwood measurements were significantly greater than corewood, and latewood values were significantly greater than earlywood, for both sites (Table 1). The accelerated growth on the Bogalusa site had the same declining effect on tracheid length as it did on tracheid wall thickness. A possible explanation to this scenario can be obtained by a more thorough study by Bannan (1967), who revealed the interrelationships between an increase in diameter growth, an increase in the number of anticlinal cell divisions, and shorter tracheid length. Basically, when tree growth is accelerated, there is a greater frequency of anticlinal cell divisions necessary in order to allow for an increase in stem diameter. The increasing number of cambial initials are allowed insufficient time to elongate during the cell division process and therefore are only partially elongated at the time they are dividing periclinally (Bannan 1967; Megraw 1985). This process serves to reduce fiber length during periods of accelerated growth.

Research by Linnartz et al. (1970) on 4-year-old loblolly pine grown in central Louisiana showed that fertilization has an insignificant effect on tracheid length. These researchers found a 1.73-mm mean fiber length on a plot that received no fertilizer and a 1.78-mm mean fiber length on a plot that received 90 kg per acre each of N-P_2O_5-K_2O. Moreover, research by Choong et al. (1970) on 7-year-old loblolly pine grown at Bogalusa found that faster growth rate, as a result of irrigation and fertilization or fertilization, resulted in longer tracheid lengths. Choong et al. (1970) found that the mean tracheid length of four plots at Bogalusa ranged from 2.01 mm–2.24 mm. Taylor and Burton (1982) found the average tracheid length of 11-year-old, rapidly grown loblolly pine to be 2.81 mm. These researchers accelerated tree growth on their southern Arkansas plots by thinning, pruning, and controlling understory competition. Bendtsen and Senft (1986) found that the average tracheid length of the first nine growth rings of 30-year-old loblolly pine increased from 1.57 mm to 3.03 mm. The trees for this study came from a North Carolina plantation of unspecified silvicultural history.

Most researchers have studied the effects of accelerated growth due to fertilization rather than irrigation and have observed similar results to those obtained from this study—an increase in growth rate following fertilization will lead to a corresponding reduction in tracheid length (Zobel 1961; Posey 1964; Megraw 1985). Koch (1972) suggested that much of the confounding data and viewpoints on the effect of growth rate on specific gravity and fiber length are due to an inadequate understanding of the patterns of variation within individual trees. Confusion has also arisen because of the tendency to group silvicultural treatments such as irrigation and fertilization together as "growth accelerating treatments." These treatments are distinctly different and will both serve to increase diameter growth but will have a differing effect on wood properties.

This study has shown latewood fiber length to be significantly longer than earlywood fiber length. There has been considerable disagreement in the literature concerning the relationship between tracheid length within an individual growth ring. Latewood tracheids have been reported to be longer, shorter, and the same length as earlywood tracheids. Jackson and Morse (1965) found no significant difference in the length of earlywood and latwood tracheids in the same growth ring of 30-year-old loblolly pines of unspecified silvicultural history. Taylor and Moore (1981) observed similar results in that tracheid length for 21-year-old plantation-grown loblolly pine was neither consistently longer nor shorter for the latewood portion of growth rings.

Microfibril angle

The microfibril angle (MFA) was assessed only between latewood tracheid corewood and outerwood for both sites. The thin S-2 layer of the earlywood made comparisons between earlywood and latewood extremely difficult. Previous research has established the relationship that shorter tracheids tend to have larger fibril angles (Megraw 1985). The Bogalusa site, which did have shorter tracheid lengths, displayed higher MFAs than the Homer site (Table 1). For both plantations, the corewood values were significantly higher than that of the outerwood (Table 1). These values are higher than those reported for loblolly pine by McMillin (1973). In growth rings 1–10, he reported earlywood MFAs ranging from 32.8°–34.3°. The trees in McMillin's study were from a mature stand that had never been silviculturally altered. Bendtsen and Senft (1986) found the first nine rings of plantation-grown loblolly pine to show a MFA ranging from a high of 39.3° for the third ring to a 24.5° for the ninth growth ring.

Although all three of these anatomical properties are important in terms of end-usage of lumber, MFA is perhaps the most critical. Bendtsen and Senft (1986) showed that microfibrillar orientation has a significant influence on tensile strength, stiffness, and shrinkage of small-sized loblolly pine and cottonwood specimens. Although the relationship between MFA and lumber mechanical properties has not been absolutely established, there is a clear relationship between juvenile wood (i.e., wood with high MFAs) and excessive longitudinal shrinkage and warp of kiln-dried lumber (Forest Products Lab 1987; Megraw 1985). Innerwood has been shown to contain larger MFAs than outerwood (McMillin 1973). The concern is that by fertilizing young plantations, the juvenile period is extended further than the standard 5–20 years (Bendtsen 1978) of open-grown stands. This research has shown that cultural treatment applied to young loblolly pine can lead to a significantly lower MFA in the outerwood than corewood even after fertilization two years (Homer site) or three months (Bogalusa site) after stand establishment. Further research is needed in order to determine the MFA of each growth ring of these stands at age 20–30 and determine what effect this early fertilization truly had on the length of the juvenile period.

CONCLUSIONS

This research was initiated in order to evaluate the differences in the anatomical properties of two even-aged, fertilized loblolly pine plantations in Louisiana. These results have shown that diameter growth was greater at the Bogalusa site, but anatomical properties were more favorable, from an end-use perspective, at the Homer site. Also, these findings confirm the traditional belief that anatomical properties are more favorable in latewood than earlywood and better in outerwood than corewood. While these trees were only 9-years-old, and the wood is theoretically comprised entirely of juvenile wood, there were significant differences observed between the corewood (rings 2–4) and outerwood (rings 7–9). This is not meant to imply that the juvenile period for loblolly pine ends somewhere before the seventh growth ring, but merely that it is interesting to note that there are substantial differences in the wood quality of juvenile corewood and outerwood even at age 9. Bendtsen (1978) described the gradual improvement of several anatomical, physical, and mechanical properties that occur during the juvenile period and also illustrated that the juvenile period can end anywhere from the fifth to the twentieth growth ring. Hence, the differences in the anatomical properties observed in this project can be attributed to the gradual improvements that naturally occur in the juvenile period that Bendtsen (1978) described. It is extremely unlikely that the first three growth rings represent juvenile wood and the seventh through ninth growth rings are suddenly mature wood.

Future research is recommended to determine the actual amount of between-site variation that can be attributed to the fertilizer and to the site itself. A control plot is recommended for future researchers as a basis for comparison within the sites. It is necessary to continue to monitor the plantations in order to determine if the anatomical properties continue to improve or if they remain constant and signal that mature wood production has started.

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