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I am submitting herewith a thesis written by Donald Holt Ross entitled "The Effect of Nitrogen Fertilization on Yellow-Poplar Wood Density as Measured by the Gamma Densitometry Technique." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

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THE EFFECT OF NITROGEN FERTILIZATION ON YELLOW-POPLAR WOOD DENSITY AS MEASURED BY THE GAMMA DENSITOMETRY TECHNIQUE

A Thesis

Presented for the

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Degree

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ABSTRACT

This study was designed to measure the possible changes in yellow-poplar (Liriodendron tulipifera L.) wood density following the application of an ammonium nitrate fertilizer to a plantation. Increment core samples were taken from a yellow-poplar plantation which had been divided into 16 plots which provided for 4 replications for testing 3 levels of elemental N against a control in 1966 and 1969. The gamma densitometry technique was used to determine the relative density of wood samples following the two applications of N at levels ranging from 40 to 640 pounds per acre. Relative wood density decreased with increased levels of N, while diameter growth increased with increased levels. A density response curve was described for each application.

Two conventional methods (maximum moisture content and volumetric measurement) for measuring wood density were compared with the gamma densitometry technique. Low correlation between the results of the three techniques suggest that measuring the density of small wood samples by any method is difficult and subject to error.

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CHAPTER I

INTRODUCTION

In recent years silviculturists have been experimenting with forest fertilization to increase wood yields. Changes in wood density as a result of fertilization have never been a major consideration in the cost-benefit analysis for these investments. The increasing cost of fertilizer and money has tended to make forest fertilization a more economically marginal operation. Interest in the effect of fertilization on wood density has increased. Wood density, more than any other single characteristic, is related to hardness, shrinkage, strength and cellulose yield. Changes in wood density as a result of fertilization may have economic ramifications which may either offset or add to the economic benefits of fertilization. The purpose of this study was to measure possible changes in yellow-poplar (Liriodendron tulipifera L.) wood density (as measured by the gamma densitometry technique) following the application of an ammonium nitrate fertilizer.

CHAPTER II

LITERATURE REVIEW

I. EARLY RESEARCH ON SPECIFIC GRAVITY IN YELLOW-POPLAR WOOD

Investigations into the silvicultural control of wood density began in Europe nearly a century ago. Hartig is cited by Paul (1930) as having formulated what he termed the nourishment theory. His theory was formulated from the results of 20 years' research on the effect of climate and soil fertility on the weight of dry wood. With regard to specific gravity, Paul interprets Hartig's theory to say "that the specific gravity of wood is dependent upon the relationships of soil fertility, transpiration of water by the tree crown, and assimilation." More specifically Hartig thought that the ratio of transpiration to production of wood substance determined the amount of porous tissue formed and, hence, the wood density. Under this theory density was maximized when assimilation was greatest and accompanied by moderate transpiration.

Around the turn of the century, Ciesler and Janka (1902) investigated the relationship between growth rate and specific gravity of dominant and codominant spruce trees. Paul (1930) cites their results: the more rapidly growing trees produced wood of lower density than did the slower growing trees, and the wood of higher density . . contained a greater proportion of summerwood. Later Janka (1913)

investigated the same relationship in larch wood. He could not demonstrate a relation between specific gravity and growth rate, but he did conclude "that the weight depended upon the relative proportion of summerwood in the annual rings" (cited from Paul, 1930).

By the time investigations on the influence of environment on wood quality were started in the United States in 1922, Europeans had already found that the relationship between growth rate and specific gravity was difficult to define. They did, however, document the strong relationship between density and the proportion of summerwood in the annual ring (Ciesler and Janka, 1902; Janka, 1913).

The U. S. Forest Service Forest Products Laboratory at Madison, Wisconsin, spearheaded the first American effort to understand the factors controlling specific gravity of wood. Paul (1930) reported the results of this experimentation. With regard to yellow-poplar, he found that when growth was suppressed for a prolonged length of time, "the severity of the suppression was reflected in a lowering of the specific gravity of wood." An increase in specific gravity from releasing old-growth trees by thinning was also reported. Paul concluded that continuation of adverse growing conditions resulted in the formation of narrower rings and an increase in the proportion of springwood. Later Paul and Norton (1936) found no close relationship between growth rate and specific gravity. Nevertheless, they maintained that growth rate would be a useful indicator of wood density.

Erickson (1949) used 345 wood blocks from 23 yellow-poplar trees in an attempt to clarify the growth rate-specific gravity enigma. He was

the first to recognize the need for rigorous statistical analysis to test the hypothesized relationships between these variables. Specific gravity was found to vary directly with growth rate, but the association was weak. Only 23 percent of the variation in specific gravity could be explained by growth rate. Erickson concluded,

> This indicates that the tree means of specific gravity do not change regularly with mean rings per inch, but are definitely erratic. . . . Evidently, other biological forces influence the average specific gravity of a tree more than does the average growth rate within the range studied.

He attributed the variation in specific gravity to "inherent or heriditary characteristics" but completely ignored the relationship between specific gravity and proportion of summerwood in the annual ring.

Erickson's work also laid a solid foundation for subsequent research strategies. He demonstrated that there was no difference with respect to specific gravity between north and south sides of a tree per se, that wood near the pith is lower in specific gravity than wood farther out, and that there is no significant difference in specific gravity between heartwood and sapwood. The latter result corroborates that of Stern (1944) who reports "only a 2 percent greater average specific gravity of sapwood over heartwood" in yellow-poplar.

Erickson's assertion that hereditary characteristics play an important role in determining the specific gravity of yellow-poplar stimulated interest in tree breeding programs to look further into the variance components of wood density. Thorbjornsen (1961) compared wood samples from "superior" phenotypes of yellow-poplar and dominant

yellow-poplar crop trees occurring on the same 1/5-acre plot as the "superior" trees. His samples came from east Tennessee and southeast Kentucky at elevations between 1500 and 2000 feet. Thorbjornsen confirmed Erickson's (1949) and Stern's (1944) conclusion that there were no important differences between the density of heartwood and sapwood. He also found that about 70 percent of the total variation in density was attributable to differences among trees within plots and that there was no significant difference in density between plots. Because of the small number of plots (10) and the site uniformity inherent in the selection process (a phenotypically superior tree and 5 dominant crop trees growing on the same 1/5-acre plot comprised a sample plot), Thorbjornsen's results probably underestimated between-plot variation as a proportion of the total variation. If so, within-plot variation was necessarily overestimated because all the variation has to be partitioned in the analysis of variance procedure.

Barefoot (1963) found that density decreased with an increase in site index and Sluder (1972) has recently corroborated the conclusion. Taylor (1965) studied natural variation in specific gravity within yellow-poplar trees, between trees, and between 3 geographic areas of North Carolina. He found considerable variation both within trees and between trees, but only negligible variation between geographic areas. His work conflicts with that of Barefoot (1963) and Sluder (1972) but corroborates Erickson's (1949) conclusions that specific gravity is not affected by cardinal direction and only a weak association exists between growth rate and specific gravity.

The fact that specific gravity is independent of growth rate per se appears to have been established, but Taylor's conclusion that specific gravity could not be affected by silvicultural methods which control growth rate may have been premature. As the early workers noted, specific gravity variation may be influenced more by the proportion of summerwood in the annual ring than by growth rate per se. Some contemporary workers have suggested that this approach might explain the relationship between specific gravity and growth rate (Bethel, 1943; van Eck and Woessner, 1964; Sluder, 1972).

Sluder (1972) has shown that 24 percent of the specific gravity variation in yellow-poplar is due to site index alone. This result is similar to that of Erickson (1949), except that Sluder found density to be inversely related to site index in yellow-poplar. His analysis also demonstrated that "growth rate [ring width] has no effect on specific gravity independent of the effect of site index." Sluder commented on the relationship between ring width and specific gravity:

> One critical distinction is whether wide growth rings are produced by rapid growth per se or by a sustained growth period. The transition from springwood to summerwood production is also involved.

Wooten et al. (1973) found that the effect of tree release on yellow-poplar wood density was to increase it. However, they had insufficient data to show a statistical difference in density between released and unreleased trees.

Research has advanced to the point of trying to correlate percent summerwood in the annual ring with growth rate, but no suitable technique

has been developed for demarcating the springwood/summerwood transition in diffuse porous woods such as yellow-poplar.

II. EFFECTS OF FERTILIZATION ON WOOD SPECIFIC GRAVITY

Numerous workers have reported that the wood of fertilized trees generally has lower density than that of trees of the same species grown without fertilization (Williams and Hamilton, 1961; Zobel et al., 1961; Posey, 1964; Siddiqui et al., 1972; Gladstone and Gray, 1972). Paul and Marts (1954) found that application of a complete fertilizer on longleaf pine resulted in a decrease in the proportion of summerwood in the annual ring and, hence, a decrease in wood density. However, when fertilization was concomitant with irrigation, they found an increase in the proportion of summerwood with the corresponding increase in density. They also reported an increase in wood density with the application of nitrogen alone. As Zobel et al. (1961) point out, "opposite results may be obtained if additional environmental factors are brought to bear." Their observation suggests the synergistic effect of the factors controlling tree growth.

Working with Douglas-fir, Gladstone and Gray (1972) found that fertilization not only resulted in lower density wood, but that the wood was more uniform in cell wall structure. Fiber cell walls in springwood were found to be thicker following treatment with a complete fertilizer, while summerwood fiber cell walls were found to be thinner. They substantiated Paul and Marts' (1954) finding that fertilization produced a decrease in the proportion of summerwood.

While the preponderance of evidence points to a decrease in specific gravity as a result of fertilization, some work has shown the contrary to be the case. Smith et al. (1972) found that neither fertilization nor fertilization concomitant with irrigation had any effect on the wood density of slash pine. They suggest that these results from experimentation with juvenile trees may not be typical of the response of more mature trees. Nevertheless, Gooding and Smith (1972) working with fifteen-year-old slash pine found no significant change in specific gravity following fertilization with P on a phosphorus deficient site.

III. THEORETICAL CONSIDERATIONS REGARDING WOOD DENSITY

Robert Zahner's (1970) theoretical considerations of wood density in upland hardwoods provide groundwork for research in the silvicultural control of wood density. He explains extrinsic variation in wood density in terms of "interactions between the distribution of cell types and the cell properties of size and wall thickness." With regard to diffuse porous woods, Zahner reports that trees grown on low quality sites produce wood of higher density than those grown on better sites. This relationship between site and wood density is more pronounced in species having higher wood densities. This is because the latewood of the more dense species has fewer and more scattered vessels and "thus a greater potential to increase the proportion of vessels." Diffuse porous hardwoods characterized by a specific gravity greater than 0.40 vary 10-20 percent in specific gravity depending on site, according to

Zahner, while less dense woods show less than 10 percent variation with site. Accepting these assumptions, yellow-poplar has a specific gravity of 0.38 (Zahner, 1970) and is in the less dense group of diffuse porous woods and should have low variation in density due to site.

CHAPTER III

HISTORY OF SITE AND EXPERIMENT

I. EXPERIMENTAL SITE

The experimental site is located on the University of Tennessee Cumberland Forestry Field Station in Morgan County, Tennessee. The station is about 1.5 miles south of Joyner, Tennessee at 36°2'45" north latitude and 84°29'30" west longitude at an elevation of about 1340 feet.

The experimental plots were located on a lower slope position with a southwest aspect. Slope within the plots varies from 0 to 15 percent.

Soil samples collected from the A horizon in 1974 show that the soil has an average P content of 20.5 pounds per acre and an average K content of 120.8 pounds per acre. The soil was given a rating of "medium" with regard to P and "low" with regard to K by the University of Tennessee Agricultural Extension Service. The average pH was determined to be 6.0.

The nearest United States Weather Bureau station is at Crossville, Tennessee, about 35 miles from the site. The station at Crossville has an elevation of 1810 feet. Martin (1966) has summarized climatological data from Crossville for the period 1930 through 1964. Mean annual temperature is reported to be 55.1°F for this period. Mean annual precipitation is 54.66 inches, well distributed throughout the year with the least amount in autumn. Mean annual snowfall is 11.6 inches.

Martin reports that temperature and precipitation records kept at the University of Tennessee Forestry Field Station since 1958 compare closely with those recorded at Crossville. Temperatures appear slightly above the Crossville average and precipitation slightly below.

The experimental site was used for growing annual tobacco crops in the early 1950's. Tobacco is an especially nutrient demanding crop (Janick et al., 1969). It can be reasonably assumed that after several crops of tobacco the soil nutrients, especially N, were greatly depleted. The poor soil protection provided by tobacco cropping and the sloping land surface resulted in varying degrees of erosion over the study area. The poor growth in Block 4 has been due to the loss of essentially all of the A-horizon; soil loss was less severe in the other study blocks.

In 1954 the site was planted in alternate rows (spacing = 6' x 6') of yellow-poplar and shortleaf pine. Because of the loss of topsoil, the low nutrient status and southwest exposure, shortleaf pine might be expected to compete favorably with the yellow-poplar. By the end of the seventh year (1960), both species were still viable competitors.

II. HISTORY OF THE EXPERIMENT

In 1961 the plantation was treated with low levels of ammonium nitrate. Sixteen one-tenth acre treatment plots were established to provide four replications in which to test three fertilzer levels against an untreated control (Buckner and Thor, 1974). The three levels of fertilization were 12, 24, and 48 pounds of elemental nitrogen per acre. The height growth of yellow-poplar was stimulated

by the two higher treatment levels. Shortleaf pine did not respond to treatment.

In 1966 the plantation was fertilized following the same treatment pattern with 40, 80, and 160 pounds of elemental N per acre. Again the height-growth of yellow-poplar responded to the two higher treatment levels, while shortleaf pine was not stimulated. By the end of the 1968 growing season yellow-poplar in unfertilized plots had a 4 foot height advantage over shortleaf pine, while those on the plots receiving the two higher levels of nitrogen had a 6 foot height advantage over the pine. This was sufficient to cause severe suppression of the pine.

In the spring of 1969 the alternate rows of shortleaf pine were harvested and the remaining rows of yellow-poplar were heavily thinned, leaving only 40 square feet of basal area per acre. Following the same treatment pattern as before, N was applied at increased levels: 160, 320, and 640 pounds per acre. Fifteen pounds per acre of elemental phosphorus were applied to all plots to assure that nitrogen response would not be limited by a phosphorus deficiency. This experiment was designed to determine the upper nitrogen levels to which yellow-poplar would respond where competition among trees was minimized and where no other major nutrient was limiting. Height growth response was obscured by frequent ice breakage, however, there was significant response in diameter growth to all three levels of treatment. For a more detailed treatment of these results see Buckner and Thor (1974).

CHAPTER IV

PROCEDURES

I. TREE SELECTION

Trees in each treatment plot were randomly numbered. Following ascending numerical order each tree was evaluated for its suitability as a sample tree. To be a sample, a tree had to be without defects indicating disease or mechanical damage either past or present, and its crown had to be in a dominant or codominant position. When possible, five trees were selected from each plot for sampling. One plot had only two acceptable trees, while five plots had only four.

II. INCREMENT CORE COLLECTION

From each sample tree a 12mm increment core was extracted at 4-1/2 feet above the ground. All trees were bored parallel to the land contour and from the south facing half. To retard drying and the resultant warping, extracted cores were sealed in plastic tubes and refrigerated until mounted for densitometry measurements.

III. SAMPLE PREPARATION

Extracted cores were glued with white glue between two pieces of wood each having a groove cut the shape of the core and of sufficient depth to "sandwich" the increment core without the pieces touching.

The samples were then allowed to air-dry to approximately 14.5 percent moisture content.

A section 3.2mm thick was cut using two parallel mounted, hollow-ground circular saw blades. A blade with no set was used to produce a polished surface. Samples were cut radially, resulting in a radial surface of the increment core held by two strips of mounting wood (Figure 1). This techique is a slight modification of that developed by Parker and Meleskie (1970) and has been described by Woods and Lawhon (1974).

Growth rings representing growth following two treatment periods were analyzed on each sample: (1) 1966-68, the period following the 1966 fertilizer application, and (2) 1969-72, the period following the thinning and fertilization of 1969. Each period was established by counting inward from the bark.

IV. DATA ACQUISITION

The wood density of the samples was measured using a technique developed by Woods and Lawhon (1974) which "involves moving a wood sample through a ray of highly collimated ^{55}Fe radiation (5.6 kev) which is scanned by a detector." The samples were moved by a modified hydraulic lathe through the path of the gamma rays at a constant rate of 4mm per minute.

The detector was a sodium iodide crystal encased in brass and fitted with a beryllium window. An adjustable collimator at the base of the detector restricted the scanning field to a slit 2mm by 5mm.

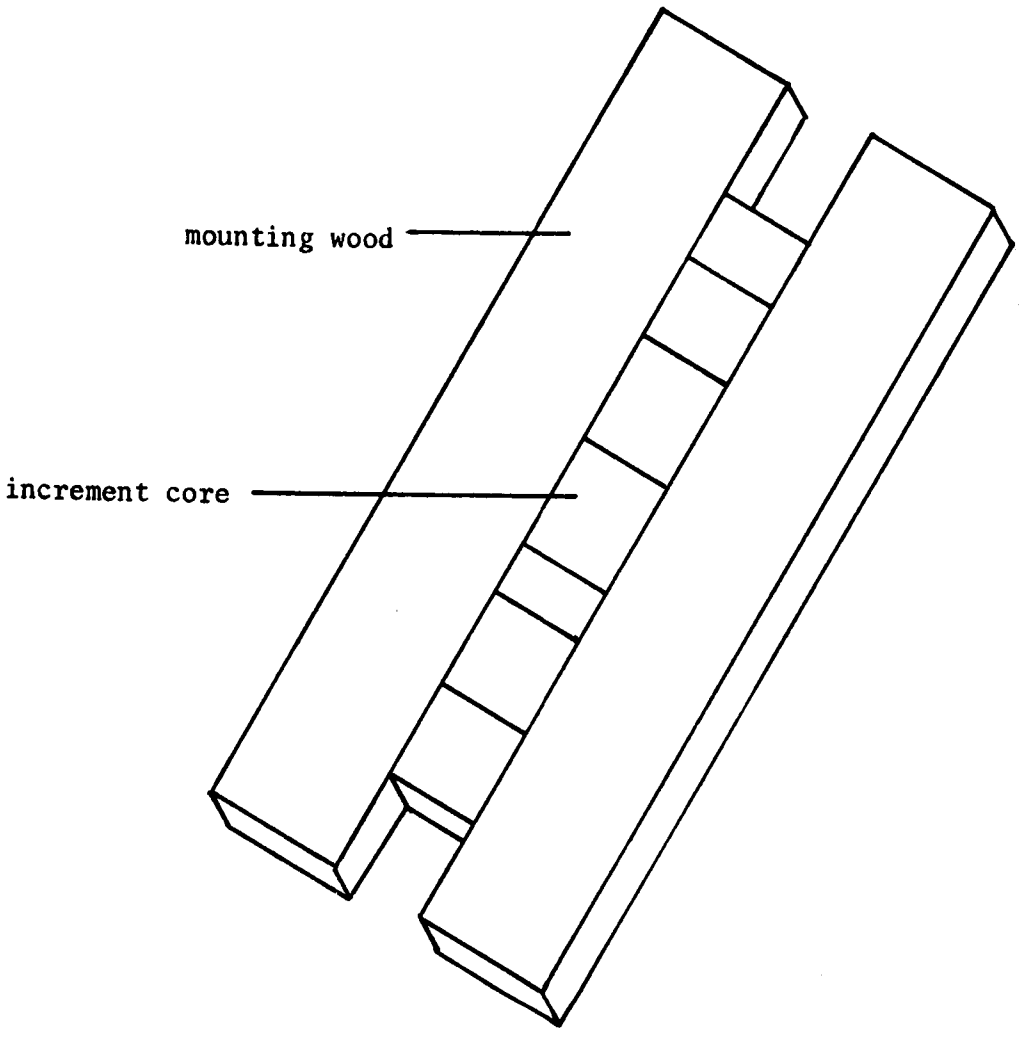


Figure 1. Radially cut increment core held by two strips of mounting wood (not to scale).

From the detector, signals passed first into a Tennelec TC 154 photo-multiplier base and then into a Tennelec TC 216 linear amplifier and single channel analyzer. From the single channel analyzer the signal was routed both to a Tennelec TC 590 ratemeter and to a Tennelec 592P digital ratemeter. From the Tennelec TC 590 ratemeter the signal went to a Tolshin Electron, model T02NL-h strip chart recorder. The graphic output from the strip chart recorder provided a convenient means of monitoring the system while in operation. The signal routed to the digital ratemeter from the single channel analyzer went to a Tennelec 570 automatic recycle control and teletype interface and then to a Teletype 33 Teletypewriter where the digital output was typed and punched on paper tape (Lawhon, 1973).

Using the Teletype 33 Teletypewriter and an acoustic coupler, the data were stored on magnetic tape using the CALL-OS System of the University of Tennessee Computing Center.

V. DATA CONVERSION

The natural log (ln) of the count rate (CR) is inversely proportional to the density of the materials contained in wood at 14.5 percent moisture content.

Each time wood samples were analyzed, a standard density curve was constructed using polyethylene filters of three different densities (0.92, 0.48, and 0.23 grams per cubic centimeter) and the same thickness (3.2mm) as the wood samples. The ln CR (natural log of the count rate) obtained for each of these filters was plotted on the ordinate against

the corresponding filter density on the abscissa. A straight line with negative slope was obtained.

The standard curve was entered into a computer program in the form

$$Y = m(X) + b$$

where Y = ln CR

m = slope of the line

X = relative density of the wood sample

b = Y-intercept of the line.

As each count rate (CR) in the data set was encountered, the computer converted the number to ln CR and solved the equation for relative density (X). Seventy-five CR values were collected from each centimeter of wood analyzed. The relative density values are $\mu_m(x\rho)$ in the following equation:

$$I = I_0 e^{-\mu m(x\rho)}$$

where I = the beam intensity of the gamma ray after passing through the wood sample

I_0 = the beam intensity of the gamma ray before passing through the wood sample

x = thickness of the wood sample in centimeters

μm = mass absorption coefficient for the wood sample

ρ = the density of the wood sample in grams per cubic centimeter (Lapp and Andrews, 1963).

Since the thickness of the samples is known to be constant and the mass absorption coefficient is assumed to differ little between wood samples, the expression in the exponent is proportional to density. The computer averaged the derived relative density values for each treatment period.

Because moisture content could not be controlled, absolute density could not be obtained without further sophistication of the technique (Woods and Lawhon, 1974). For the purposes of this experiment, relative wood density was an adequate indicator of differences in actual wood density.

VI. CONVENTIONAL ANALYSIS OF WOOD DENSITY

Since the gamma densitometry technique cannot measure absolute wood density, two conventional techniques were used to determine the absolute wood density of selected samples representing the range of relative density values measured by the new technique. The two conventional techniques were the maximum moisture content method (Smith, 1954) and ovendry weight (105°C) expressed as a ratio to the weight of water equivalent to the green volume. Knowing a range of absolute density values which correspond to a range of relative density values allows comparison with research which uses conventional techniques to measure absolute density. Moisture content was also determined.

The maximum moisture content technique for determining specific gravity of small wood samples was used because it could be carried out on the core samples used for the densitometry measurements. Twenty samples were chosen representing the range of relative density values. Samples were cut from the mounting wood and surfaced with a sharp knife to remove glue impregnated wood and crushed surface fibers. Weighings were made (1) with the samples air-dried at the same relative humidity used with the gamma densitometer, (2) in the maximum saturation condition

as described by Smith (1954), and (3) in the standard ovendry (105°C) condition.

Moisture content of the samples at 50 percent relative humidity was determined by the formula,

$$M.\ C. = \frac{m_a - m_o}{m_o}$$

where M. C. = the moisture content expressed as a percent of the ovendry mass in grams

m_a = the air-dry mass in grams at 50 percent relative humidity

m_o = the ovendry mass in grams.

Specific gravity by the maximum moisture content method was determined by the formula,

$$G_f = \frac{1}{\frac{m_m - m_o}{m_o} + \frac{1}{G_{so}}}$$

where G_f = the basic specific gravity

m_m = the mass of water-saturated wood in grams

m_o = the mass of ovendry wood in grams

G_{so} = the specific gravity of wood substance comprising the cell walls (Smith, 1954).

G_{so} was assumed to be 1.5 (Smith, 1954; Panshin and DeZeeuw, 1964). The volume of the samples used in the above method was measured while in the saturated condition. Specific gravity was determined using the formula,

$$SpG = \frac{m_o}{V_m}$$

where SpG = specific gravity

m_o = ovendry mass in grams

V_m = water mass equivalent of the green volume.

VII. STATISTICAL METHODS

The study was designed to provide answers to five basic questions: (1) are there differences in relative wood density between the three levels of fertilization treatment and the untreated control for the 1966 treatment, (2) are there similar differences in relative wood density for the 1969 treatment, (3) if there are differences between the fertilization treatment levels and the untreated control in either the 1966 or 1969 treatment periods, is there sufficient information to establish a fertilization response curve, (4) if a response curve can be established, is the major component a linear, quadratic, or cubic function, and (5) to what degree do the relative wood density values of the gamma densitometry technique correlate with the absolute values as determined by the two conventional methods.

To answer the first, second, and third questions, an analysis of variance and the F-test were used.

To answer the fourth question, the sum of squares among treatments were partitioned into the following components: linear, the partial effect of quadratic given linear, and the partial effect of cubic given linear and quadratic.

Simple linear regression was used to answer the fifth question concerning the measurement technique.

CHAPTER V

RESULTS

I. WOOD DENSITY FOLLOWING THE 1966 FERTILIZATION TREATMENT

There was a significant decrease in the relative density of wood formed following the 1966 fertilization associated with the nitrogen levels applied (Figure 2). Differences among treatment means accounted for 10.2 percent of the variation in relative wood density. Ninety-four percent of the variation due to treatment was explained by the linear component. The equation for the responsive curve is

$$R.D. = 0.8818 - 0.000511(X)$$

where R.D. = relative wood density

X = quantity of elemental N applied in pounds.

The coefficient of determination for the response equation is 0.098 (Table 1, Appendix).

II. WOOD DENSITY FOLLOWING THE 1969 FERTILIZATION TREATMENT

Again there was a significant decrease in the relative density of wood formed following the 1969 fertilization associated with the nitrogen levels applied (Figure 2). Differences among treatment means accounted for 20.5 percent of the variation in relative wood density. Again approximately 94 percent of the variation due to treatment was explained by the linear component. The equation for the response curve is

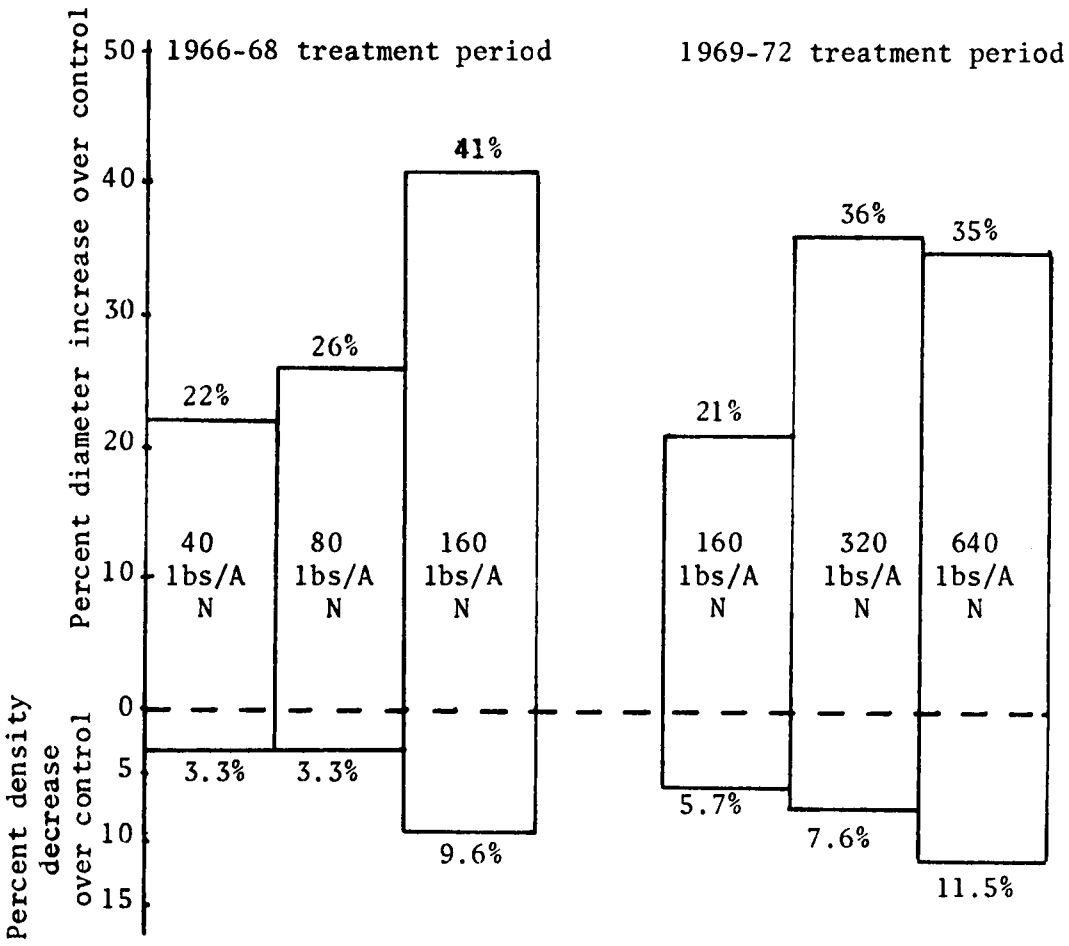


Figure 2. Diameter growth and relative density response to 1966 and 1969 fertilization treatments.

$$R.D. = 0.8991 - 0.000155(X)$$

where R.D. = relative wood density

X = quantity of elemental N applied in pounds.

The coefficient of determination for the response equation is 0.192 (Table 2, Appendix).

III. CONVENTIONAL ANALYSIS OF DENSITY FOR SELECTED SAMPLES

Density determinations from the maximum moisture content method ranged from 0.37 to 0.55 grams per cubic centimeter (Table 5, Appendix). When relative density values from the gamma densitometry technique were correlated with the absolute density values of the maximum moisture content method, a coefficient of determination of 0.36 was obtained, i.e. 36 percent of the total variation in absolute density values was explained by the relative density values.

Density determinations from the volumetric measurement method ranged from 0.28 to 0.49 grams per cubic centimeter (Table 5, Appendix). Again when relative density values were correlated with the absolute density values of the volumetric measurement method, a coefficient of determination of 0.36 was obtained. Correlation between values from the maximum moisture content method and the volumetric measurement method were only slightly better ($r^2 = 0.44$).

CHAPTER VI

DISCUSSION

I. EFFECT OF SITE ON WOOD DENSITY

The primary variables that influence wood density are the distribution of cell types and the cell properties of size and wall thickness. More fundamentally, wood density is determined by the relative proportion of lumen volume to cell wall volume in xylem tissue. In dry wood lumens are air-filled cavities, while cell wall material has a density of about 1.5 grams per cubic centimeter. Though both vessel and fiber cells have lumens and thickened secondary cell walls, most of the lumen volume in wood is found in vessel elements and most of the cell wall volume is found in fiber elements. In some species, like yellow-poplar, parenchyma cells have little effect on wood density because they are relatively scarce.

Within the physiological limits of the tree, site quality has a strong influence on the relative proportion of vessel and fiber elements in xylem tissue, the size of the lumen in these elements, and the amount of cell wall material. The effects of variation in site quality on wood density is not the same for all tree species.

The site factors which affect tree growth are numerous and complex. In the broadest sense, the extrinsic factors which affect water and nutrient availability affect food and hormone synthesis (Larson, 1964).

The concentrations of various endogenous hormones produced primarily in new foliage determine the type of wood cells initiated at any given time (Wareing et al., 1964). The number and sizes of cell types that differentiate from cambial mother cells are controlled by a combination of hormones, carbohydrate nutrition, and water relations (Zahner, 1970).

In diffuse porous woods such as yellow-poplar, new leaf production occurs throughout most of the growing season on good sites. The hormones produced by the new foilage permit the initiation of a large number of vessel cells late into the season. Since vessel cells have a lumen diameter to cell wall thickness ratio of from 200:1 to 20:1 and this ratio for fiber cells is from 20:1 to 1:1, the effect of a greater proportion of vessel elements is to produce lower density wood. On lower quality sites, new leaf production may not continue as late in the growing season and fewer vessel elements will be produced, resulting in a higher density wood than that produced on the better sites.

Once a cell has reached its maximum size, secondary cell walls are formed. The degree to which secondary wall thickening occurs is also influenced by site quality. The variation in wall thickness of vessels has little effect on density because the lumen accounts for most of the volume. In fiber elements, however, wall thickening may have a pronounced effect on wood density. Maximum thickening usually occurs on sites of intermediate quality, with the least thickening occurring on the very good and very poor sites. On good cites cell initiation is so rapid that, despite a rapid rate of food elaboration, there is competition among fiber cells for food with which to build cell walls,

and cell wall thickening is restricted. On poor sites food is limiting because insufficient water or nutrients restrict the elaboration of the needed carbohydrates. On intermediate sites there appears to be adequate food for complete cell development since the initiation of new cells appears to be restricted more than is the capacity to elaborate food (Zahner, 1970).

II. CHANGES IN WOOD DENSITY DUE TO FERTILIZATION TREATMENTS

In the 1966 fertilization treatment, the plots receiving the highest N level (160 pounds of N per acre) produced wood that was 9.7 percent less dense than the control plots. The steepness of the response curve ($b = -0.000511$) suggests that an N deficiency might have been limiting growth on control plots (Figure 3). This conclusion is supported by the fact that previous to the establishment of the plantation the site was used for tobacco farming, a very demanding crop from which there is little organic residue.

The effects of the 1969 fertilization on wood density were similar to those of 1966; however, some important differences are apparent. The highest fertilizer level applied in 1969 was four times greater than the highest level applied in 1966, yet the wood produced on these plots was only slightly less dense (11.5 percent compared to 9.7 percent) than was the case following the 1966 application. Secondly, the slope of the response curve ($b = -0.000155$) was less steep than that of the earlier fertilization (Figure 4).

It is interesting to note that diameter response to the 1969 fertilization continued to increase up to the 320 pounds per acre

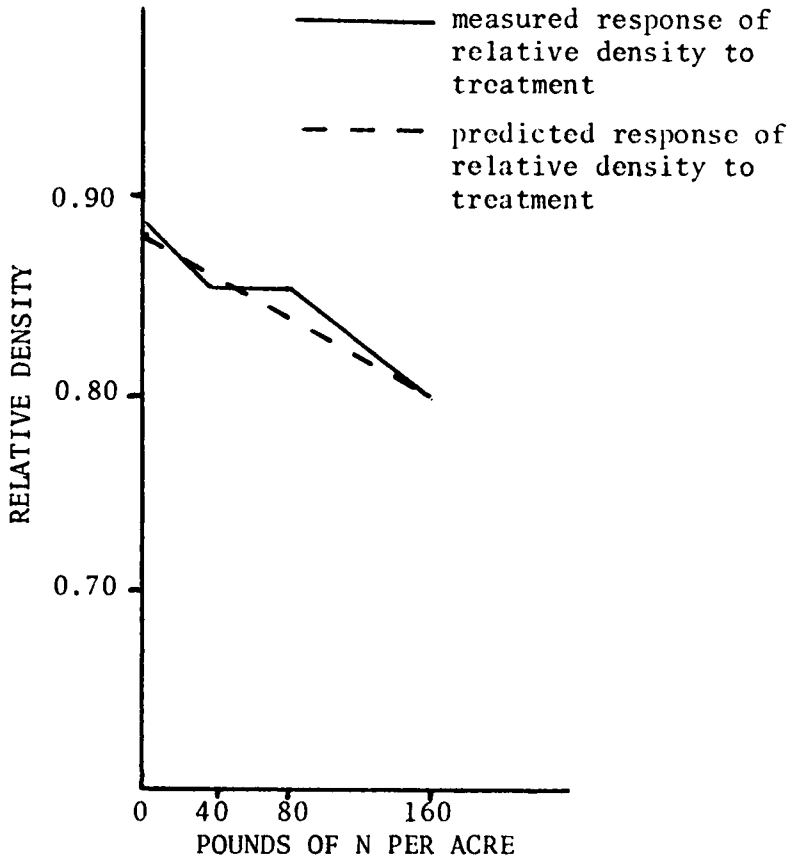


Figure 3. Response of relative wood density to 1966 fertilization treatment.

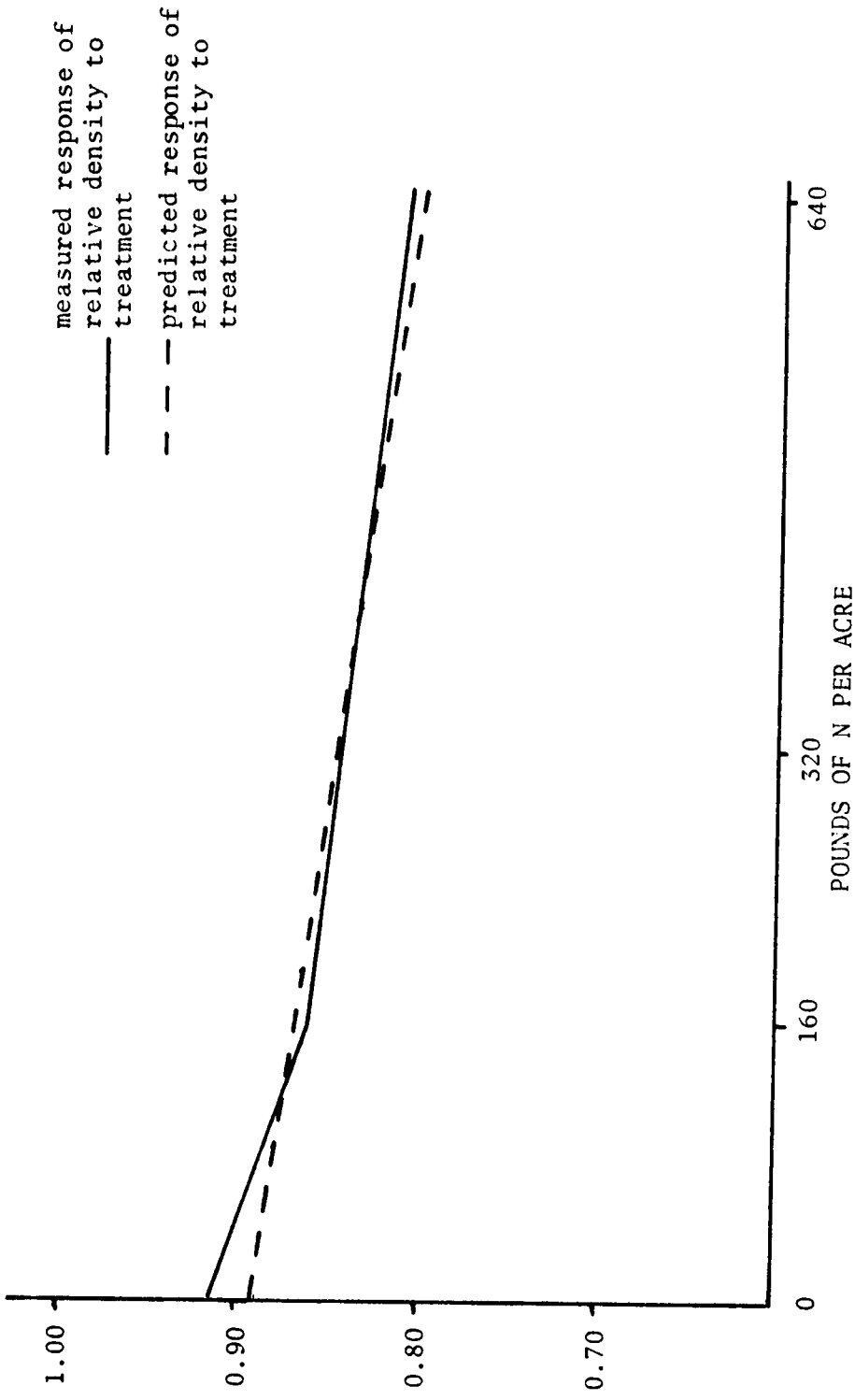


Figure 4. Response of relative wood density to 1969 fertilization treatment.

level (Table 6, Appendix), considerably above the 160 pounds per acre level where the decrease in wood density seems to approach a limit. Figure 2 (page 23) shows a comparison of diameter and density responses.

The decrease in the slope of the response curve between 1966 and 1969 fertilizations may be explained by the spatial proximity of the fertilizations. Nitrogen entered the nitrogen cycle of the plantation in relatively large quantities in 1966 through the application of ammonium nitrate. There is reason to believe that after three years some of the nitrogen could have moved via soil water into adjacent plots. Certainly some of the applied N was redistributed in the plantation through leaf fall and decay. If this argument is sound the control plots had a higher level of nitrogen in 1969 than in 1966. This could partially account for the steeper slope of the 1966 response curve.

A linear function best described the response curves for both the 1966 and 1969 fertilization treatments. However, it is recognized that if a larger number of fertilizer levels were tested that covered the response range, a nonlinear relationship could exist.

III. THE INFLUENCE OF PLOT LAYOUT ON EXPERIMENTAL RESULTS

Deficiencies in the plot layout of the original fertilization experiment probably resulted in underestimation of the amount of variation in wood density that could be attributed to the effects of fertilization. The use of one-tenth acre plots without buffer zones may have allowed a certain amount of N to move across plot borders through tree roots. An effort was made to avoid sampling border trees,

but some had to be included to obtain the desired sample number. Also, the use of a randomized complete block design on sloping land allowed the control plot in the third replication to be placed downslope from the highest treatment level for that replication. Comparison of the growth in control plots among replications clearly substantiates this contention.

Use of the randomized complete block design is most efficient when the within block variation is minimal. The effect of these layout faults is to minimize differences between treatments. The resulting increase in variation among plots decreased the sensitivity of the statistical tests to which these data were subjected.

IV. THE GAMMA DENSITOMETRY TECHNIQUE

The poor correlation obtained between the relative density values of the gamma densitometry technique and absolute density as measured by the two conventional techniques (34 percent in both cases) is difficult to explain. However, correlation between the two conventional techniques was also low ($r^2 = 0.44$), suggesting that measuring the density of small wood samples is difficult and subject to error. The gamma densitometry technique gave ranges in relative wood density similar to the range of absolute density obtained using the two conventional techniques. For the measurement of average density of small wood samples the two conventional techniques are far easier to use. The advantages of the gamma densitometry technique lie in analyzing variations in wood density within annual rings. Where there is a distinct demarcation of the

springwood/summerwood transition, the relative percentages of these two types of wood can easily be determined. However, before this information can be obtained, an improved system must be devised for passing the wood sample through the path of the gamma rays at a constant rate. Exact percentages of wood in various density categories cannot be determined as variation in the rate of movement of the hydraulic carrier is as much as 15 percent.

CHAPTER VII

CONCLUSIONS

The following conclusions have been drawn:

1. Yellow poplar wood density decreases with increasing levels of N application.
2. Response curves can be established that describe the relationship between wood density and the amount of N applied.
3. Density measurement of small wood samples is difficult and subject to error. More research is needed to develop accurate techniques.
4. The gamma densitometry technique has high potential for measuring variations in relative wood density within annual rings. Again, more work is needed to overcome the technical and theoretical problems presently limiting its use.

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APPENDIX

TABLE 1

ANALYSIS OF VARIANCE TABLE FOR 1966 FERTILIZATION TREATMENT

Source	D.F.	Sum of Squares	Mean Squares	F
Treatment	3	0.0718	0.0239	3.46*
linear	1	0.0675		9.78**
quad./linear	1	0.0000		
cubic/quad. linear	1	0.0026		
Replication	3	0.0875	0.0292	
Treatment X Replication[a]	9	0.0619	0.0069	
Residual	56	0.4812	0.0086	
Total	71	0.7022	0.0099	

[a]Treatment X Replication was deemed to be the proper error term for testing treatment effect.

*0.1 level of significance.

**0.05 level of significance.

TABLE 2

ANALYSIS OF VARIANCE TABLE FOR 1969 FERTILIZATION TREATMENT

Source	D.F.	Sum of Squares	Mean Squares	F
Treatment	3	0.1148	0.0383	4.97*
linear	1	0.1075		13.96***
quad./linear	1	0.0091		
cubic/quad., linear	1	0.0006		
Replication	3	0.1376	0.0458	
Treatment X Replication[a]	9	0.0691	0.0077	
Residual	60	0.2387	0.0040	
Total	75	0.5603	0.0075	

[a]Treatment X Replication was deemed to be the proper error term for testing treatment effect.

*0.1 level of significance.

***0.01 level of significance.

TABLE 3

RELATIVE WOOD DENSITY AFTER 1966 FERTILIZATION TREATMENT

TMT[a]	REP	N	Mean Relative Density
1	1	5	0.8135
1	2	5	1.0069
1	3	5	0.8616
1	4	5	0.8577
2	1	4	0.8271
2	2	5	0.9228
2	3	4	0.8121
2	4	4	0.8458
3	1	2	0.8070
3	2	5	0.8743
3	3	5	0.8425
3	4	5	0.8711
4	1	5	0.7959
4	2	4	0.7996
4	3	4	0.7928
4	4	5	0.8080
	1	16	0.8106
	2	19	0.9062
	3	18	0.8300
	4	19	0.8456
1		20	0.8849
2		17	0.8561
3		17	0.8561
4		18	0.7994

[a]TMT 1 = control
TMT 2 = 40 pounds of N per acre
TMT 3 = 80 pounds of N per acre
TMT 4 = 160 pounds of N per acre

TABLE 4

RELATIVE WOOD DENSITY AFTER 1969 FERTILIZATION TREATMENT

TMT[a]	REP	N	Mean Relative Density
1	1	5	0.8086
1	2	5	1.0165
1	3	5	0.8751
1	4	5	0.9494
2	1	4	0.8898
2	2	5	0.9072
2	3	5	0.7942
2	4	5	0.8552
3	1	2	0.8064
3	2	5	0.9076
3	3	5	0.7981
3	4	5	0.8381
4	1	5	0.7967
4	2	5	0.8320
4	3	5	0.7672
4	4	5	0.8322
	1	16	0.8249
	2	20	0.9158
	3	20	0.8086
	4	20	0.8687
1		20	0.9124
2		19	0.8601
3		17	0.8430
4		20	0.8070

[a]TMT 1 = control
TMT 2 = 160 pounds of N per acre
TMT 3 = 320 pounds of N per acre
TMT 4 = 640 pounds of N per acre

TABLE 5

WOOD DENSITIES AS DETERMINED BY THREE METHODS FOR 20 SELECTED SAMPLES

Block	Plot	Tree	Gamma Dens. (Relative Density)	Max. Moist. (g/cc)	Vol. Meas. (SpG)
1	3	60	0.8517	0.464	0.371
1	4	51	0.7256	0.452	0.330
1	4	53	0.8281	0.541	0.409
2	1	23	0.9780	0.503	0.394
2	1	25	1.0125	0.474	0.401
2	1	61	1.1920	0.510	0.431
2	1	64	1.0170	0.537	0.486
2	2	3	0.9162	0.443	0.388
2	2	59	0.8746	0.568	0.393
2	3	49	0.7714	0.389	0.431
2	4	50	0.7589	0.474	0.389
2	4	63	0.7898	0.410	0.357
3	2	67	0.7499	0.374	0.280
3	3	76	0.8912	0.512	0.426
3	3	40	0.6580	0.416	0.380
3	4	72	0.6093	0.405	0.306
3	4	73	0.6925	0.443	0.380
4	2	25	0.7984	0.444	0.351
4	3	49	0.8608	0.480	0.362
4	4	52	0.6681	0.453	0.332
Mean			0.8265	0.459	0.376

TABLE 6

DIAMETER GROWTH RESPONSE TO 1966 AND 1969 FERTILIZATION TREATMENTS

1966-1968 Treatment Period		1969-1972 Treatment Period	
Treatment Level (pounds N per acre)	Mean Annual DBH Growth (inches)	Treatment Level (pounds N per acre)	Mean Annual DBH Growth (inches)
0	1.15	0	1.81
40	1.41	160	2.20
80	1.45	320	2.47
160	1.63	640	2.45

VITA

Donald H. Ross was born in Memphis, Tennessee, on August 8, 1948. He was graduated from Messick High School, Memphis, in 1966 and entered The University of Tennessee the same year. In 1970 he received a B.S. degree in Forestry. After working two years in an Ecuadorian reforestation program, he returned to The University of Tennessee for study in the Graduate Program in Ecology. He received the M.S. degree in Ecology in 1975.