

ABSTRACT

CUMBIE, WILLIAM PATRICK. Variation of wood density traits in rooted cuttings and seedlings of loblolly pine. (Under the direction of Drs. Bailian Li and Barry Goldfarb)

Wood samples were collected from 10-year-old loblolly pine (*Pinus taeda* L.) rooted cuttings and seedlings from nine full-sib families resulting from a 3x3 factorial mating design. The field design consisted of two sites with six blocks per site in a randomized complete block design. In the spring of 2001, 12 mm increment cores were taken from approximately 1600 trees, and measurements of height and diameter were taken at the age of 10½ years. No significant differences were found between rooted cuttings and seedlings for specific gravity or growth traits, but sites significantly differed for growth traits. Significant family variation was found for both growth and specific gravity. Genetic parameters were estimated for wood specific gravity and growth traits for both seedlings and rooted cuttings. Heritabilities for specific gravity were generally high, and estimates from rooted cuttings were higher than from seedlings. Specific gravity was found to be negatively correlated with height. Clones were less variable than full-sib seedlings for specific gravity. These results suggest that gains in specific gravity could be made in breeding programs through the use of clonal testing during breeding and the deployment of superior clones.

Wood strips from the increment cores were then measured using x-ray densitometry. Seedlings and rooted cuttings did not differ significantly for overall latewood density, earlywood density or latewood percentage of the whole core, but overall wood density did differ significantly based on seven growth rings. Half-sib and full-sib loblolly pine

families did not display significant variation, but clones within families differed significantly in wood density, latewood density, and latewood percentage, indicating the greater potential for gains from clonal selection. Heritabilities for composite ring density traits were found to be moderate to high, indicating the potential for gains in wood density through selection of families or clones. Individual ring analysis revealed that the wood density of rings 1-4 was highly correlated with wood density through ring 7, suggesting that selection of juvenile wood density could be made at an early age.

VARIATION OF WOOD DENSITY TRAITS IN ROOTED CUTTINGS AND
SEEDLINGS OF LOBLOLLY PINE

by

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BIOGRAPHY

William Patrick Cumbie was born in April of 1978 to Peter and Nancy Cumbie in Charlotte, North Carolina. Patrick attended Myers Park High School where he graduated from the International Baccalaureate program in 1996. Patrick has been interested in the outdoors since childhood. Hiking, camping, and fishing with his father and brother helped to develop his interest in forestry. As the son of a wildlife biologist, Patrick often received lessons on trees and wildlife during family camping trips to the mountains.

When Patrick realized during his freshman year at North Carolina State University that he did not want to become an engineer, he pursued a long-time interest in forestry by transferring to the forest management curriculum. Forestry summer camp in 1998 and his experiences working under Larry Jervis on the college forests were an important part of Patrick's development as a forester. After working for International Paper Co. as a forestry intern in Burgaw, NC during the summer of 1999, Patrick decided to pursue a master's degree in forestry.

After graduating with a B.S. degree in forest management with high honors in the spring of 2000, Patrick began his graduate studies in the fall under the direction of Drs. Barry Goldfarb and Bailian Li. During his second year of graduate school, Patrick married Sarah Efird, who never stopped encouraging and supporting Patrick during his time in school.

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Some of the earliest advice from a professor was not to get married until after I finished graduate school. At the time, I thought this advice had nothing to do with me, but during my first year of graduate school I began dating the love of my life, and during the second year I married her. Being engaged and married during graduate school was certainly more difficult than being single, but the rewards were far greater. It was not easy, but Sarah never stopped encouraging me. I am forever thankful for her support.

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General Introduction

As the demand for wood and paper products increases, ensuring the wood supply for the future becomes increasingly important. With urban and suburban areas spreading into formerly rural areas, forestland in the southern United States is predicted to decrease slightly over the next 40 years (Wear and Greis 2001). Thus, existing timberlands must be used as efficiently as possible. Loblolly pine, *Pinus taeda* L., is the most important commercial timber species in the southeastern United States (Baker and Langdon 1990). The total acreage of pine plantations in the southeastern U.S. was 32 million acres in 1999, and is projected to increase to 54 million acres by 2040. The intensity of management of loblolly pine has increased, resulting in yields up to 65% greater than traditional management (Wear and Greis 2001). Since the cost of wood is the major cost involved in production of pulp (Arnold 1995) and solid wood products, increasing wood production in loblolly pine plantations will most likely continue.

Shorter rotations and increased growth rates are causing changes in the properties of wood produced in loblolly plantations, because harvested trees contain higher proportions of juvenile wood (Zobel and Talbert 1984). Juvenile wood has physical properties that differ from those of more mature wood, including shorter tracheids, lower specific gravity, thinner cell walls, lower overall wood strength and a higher amount of compression wood (Zobel and Talbert 1984; Megraw 1985). Because an increasing proportion of the loblolly pine wood supply is now coming from trees that are grown in intensively managed plantations, the potential for improvements in wood quality through

genetic selection techniques is becoming increasingly important to offset the less desirable characteristics associated with juvenile wood.

Wood specific gravity, the ratio of oven-dry weight of a given volume of wood to the weight of an equal volume of water (Zobel and Talbert 1984), is considered to be a good indicator of wood quality, because it is correlated with strength properties of lumber and to wood pulping properties (Einspahr et al. 1969; van Buijtenen 1969). Wood density, the weight of wood per unit volume, is another measure of the amount of wood material in a tree and the two are often used interchangeably. Wood density, however, should be reported at a certain moisture content, so it is only equal to specific gravity at 0% moisture content. Wood density (specific gravity) is the product of several other traits within a tree including cell diameter, cell wall thickness, and the amount of latewood produced by the tree (Zobel and Talbert 1984). Within-ring variation is also an important influence on overall wood density. The variation in earlywood and latewood density can be the largest source of variation in a tree (Zobel and van Buijtenen 1989). Earlywood is generally produced during the period of active leader growth in the first part of the growing season. Latewood production occurs later in the growing season, during and after bud resting (Kennedy 1971; Zobel and van Buijtenen 1989). Past research has shown that the proportion of latewood to earlywood influences the density, as does the variation in the density of earlywood and latewood (Zobel and van Buijtenen 1989).

Another within-tree characteristic that influences the overall wood density of a tree is the transition from juvenile to mature wood production. This transition is an important issue

affecting wood quality and end products (Sauter et al. 1999). The transition point is not a clearly defined point in a tree and varies depending on the wood characteristic used (Bendtsen and Senft 1986). Important wood traits that have been previously used include tracheid length, fibril angle, longitudinal shrinkage, lignin content, and wood density (Sauter et al. 1999). While most hard pines and Douglas-fir display fairly distinct transitions from juvenile to mature, other species do not have a distinct transition (Hoadley 1990).

Wood density or specific gravity varies among trees and among geographic locations. Among-tree variation accounts for a large portion of the variation of specific gravity in loblolly pine and this variation has been attributed to genetic differences among trees within a stand (Megraw 1985). Northern and inland areas of loblolly pine tend to be lower in specific gravity than coastal and southern areas (Zobel and van Buijtenen 1989). A strong trend of increasing specific gravity from northwest to southeast was also reported (Mitchell 1964).

The genetic variation in wood density characteristics has been studied in several species of pine, but has not been incorporated into breeding programs to the same extent as growth or disease resistance. A provenance study of loblolly pine revealed that provenances were not significantly different in wood density of early rings (3-5) while families within provenances did differ significantly (Belonger 1998). Trees on different sites produced significantly different ring density for early rings, accounting for about

75% of the total phenotypic variance. Individual tree heritabilities for early rings were low to moderate, varying from 0.18 to 0.23 (Belonger 1998). Similar individual-tree heritability estimates were reported by Hodge and Purnell (1993) for individual rings of slash pine (*Pinus elliottii* Engelm.). Individual heritabilities were also low to moderate in slash pine for earlywood density and transition age based on latewood percentage, latewood density, and ring density in a study of 56 open-pollinated families (Hodge and Purnell 1993). Although Hodge and Purnell (1993) found little useful genetic variation in wood density among half-sib families for slash pine, earlywood density varied significantly among clones of radiata pine (*Pinus radiata* D.Don.) (Donaldson et al. 1996). A study of genetic variation of transition age in loblolly pine of east Texas revealed significant differences in transition age among families when transition age is based upon a specific wood characteristic such as specific gravity or wood density (Loo et al. 1985). Half-sib families varied in the age of transition from 9.8 to 13.0 years, based on specific gravity. Information is lacking, however, on variation among full-sib families of loblolly pine for within-ring wood-density traits.

Heritability estimates of wood density (and wood specific gravity) in individual trees and half-sib families of loblolly pine have been found to be moderately high to high (Zobel et al. 1978; Talbert et al. 1983; Loo et al. 1984; Balocchi 1990; Williams and Megraw 1994; Belonger 1998; Gwaze et al. 2001). Genetic correlations between wood density and growth traits in loblolly pine vary from slightly negative (Loo et al. 1984) to slightly positive (Stonecypher et al. 1973; Williams and Megraw 1994). Both positive and

negative genetic correlations between growth rates and wood densities have been reported in other forest tree species (Zobel and Talbert 1984).

Increases in production can, in part, be attributed to the genetic improvement of loblolly pine. Forest tree breeding and tree improvement have made significant impacts on growth, rust, and stem straightness. The NCSU-Industry Cooperative Tree Improvement Program has completed over 46 years of genetic improvement for loblolly pine. First-generation improvements resulted in 7% to 12% increases in volume per acre at harvest and second-generation gains are estimated to be 13% to 21% over unimproved sources. Rogued second-generation seed orchards are expected to have a 26% to 35% increase in volume over unimproved check stock (Li et al. 1999). While improvements have been made for growth and disease resistance, little has been done to improve the wood properties of loblolly pine in breeding programs

The use of open-pollinated seeds from orchards limits improvement because of pollen contamination and low selection intensity. Controlled pollination and vegetative propagation are two alternatives for increasing gain. Controlled pollination would allow desired crosses to be made while minimizing pollen contamination. Vegetative propagation could be used in deployment to capture elite genotypes, or could be used in progeny testing to estimate the performance of genotypes. The use of full-sib seedlings or rooted cuttings may allow gains in growth and disease resistance, but little is known about the effect that propagule types will have on wood density characteristics.

The use of rooted cuttings as an alternative to seedlings for regeneration of loblolly pine has been studied by several investigators (Stelzer and Goldfarb 1997). Early growth and survival of rooted cuttings have been reported to be similar to those of seedlings in loblolly pine (Frampton et al. 2000). One study found no significant difference in five-year growth of rooted cuttings when compared to seedlings (McRae et al. 1993). Donor-plant age was a factor that affected performance of rooted cuttings of loblolly pine rooted cuttings (Foster et al. 1987). It is not known what impact rooted cuttings will have on the wood density of loblolly pine.

While little information on wood properties of loblolly pine rooted cuttings is available, studies of radiata pine showed little difference between micro-propagated plantlets and seedlings for wood density at age 7 (Cown et al. 1989). Physiological age was found to have a significant impact on wood density in rooted cuttings (Lausberg et al. 1995). A study of radiata pine clones from micro-propagules at 16 years of field growth revealed lower density values when compared to seedlings (Donaldson et al. 1996). This was attributed to age of the donor material.

One of the potential benefits of using rooted cuttings is that vegetative propagation could permit clonal forestry. Gains in production from clonal forestry result from both increased frequency of superior genotypes and production of more uniform stands. The use of individual clones offers the possibility of producing wood with more uniform

physical properties and structural quality in commercial plantations. A clonal propagation trial of loblolly pine revealed that clones vary significantly in growth (Foster et al. 1987). Another study showed that growth rate increases from the use of rooted loblolly pine cuttings are possible because of higher within-family heritabilities (Isik et al. 2002b). While the gain in growth through the deployment of clones of loblolly pine has been examined, little is known concerning the possible gains in wood density through the deployment of clones of loblolly pine.

Clones of radiata pine have been found to differ significantly in wood density. While trials in several species have revealed variation among clones and families that could be used as a basis for achieving increased growth and wood production (Mullin et al. 1992; Paul et al. 1993; Lambeth et al. 1994; Orlovic et al. 1998; Osorio et al. 2001), variation in specific gravity among clones versus full-sib seedlings has not been fully described. It is, thus, useful to investigate the extent of variation of wood density traits among clones and full-sib families of loblolly pine.

A greater understanding of how clones differ in wood density or specific gravity is a necessary topic for research if the enhancement of wood through uniformity and increased density is to be incorporated into tree improvement programs. A 10-year-old trial of rooted cuttings and seedlings from nine full-sib loblolly pine families at two sites (Frampton et al. 2000) formed the basis for this study of variation of wood specific gravity and growth by the different propagule types. Whole-core specific gravity and

growth traits were analyzed in Chapter 1, while within-ring traits were analyzed in Chapter 2.

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Chapter 1

Genetic Variation and Parameter Estimates of Wood Specific Gravity of Rooted Cuttings and Seedlings of Loblolly Pine.

Abstract

Wood samples were collected from 10-year-old loblolly pine (*Pinus taeda* L.) rooted cuttings and seedlings from nine full-sib families resulting from a 3x3 factorial mating design. The field design consisted of two sites with six blocks per site in a randomized complete block design. In the spring of 2001, 12-mm increment cores were taken from approximately 1600 trees, and measurements of height and diameter were taken at the age of 10½ years. No significant differences were found between rooted cuttings and seedlings for specific gravity or growth traits, but sites significantly differed for growth traits. Significant family variation was found for both growth and specific gravity. Genetic parameters were estimated for wood specific gravity and growth traits for both seedlings and rooted cuttings. Heritabilities for specific gravity were generally high, and estimates from rooted cuttings were higher than from seedlings. Specific gravity was found to be negatively correlated with height. Ramets of clones were less variable than seedlings of a full-sib family for specific gravity. These results suggest that gains in specific gravity could be made in breeding programs through the use of clonal testing during breeding and the deployment of superior clones.

Introduction

Loblolly pine, *Pinus taeda* L., is one of the most important commercial timber species in the United States (Baker and Langdon 1990). Shorter rotations and increased growth rates are causing changes in the properties of wood produced in loblolly plantations, because higher proportions of juvenile wood are harvested from younger trees (Zobel and

Talbert 1984). Juvenile wood has physical properties that differ from those of more mature wood, including shorter tracheids, lower specific gravity, thinner cell walls, lower overall wood strength and a higher amount of compression wood (Zobel and Talbert 1984; Megraw 1985). Because an increasing proportion of the loblolly pine wood supply is now coming from trees that are grown in intensively managed plantations, the potential for improvements in wood quality through genetic selection is becoming increasingly important to offset the less desirable characteristics associated with juvenile wood.

Wood specific gravity, the ratio of the dry weight of a given volume of wood to the weight of an equal volume of water (Zobel and Talbert 1984), is considered to be a good indicator of wood quality because it is correlated with strength properties of lumber and to wood pulping properties (Einspahr et al. 1969; van Buijtenen 1969). Heritabilities of wood density (and wood specific gravity) in individual trees and half-sib families of loblolly pine have been found to be high to moderately high (Zobel et al. 1978; Talbert et al. 1983; Loo et al. 1984; Balocchi 1990; Williams and Megraw 1994; Belonger 1998; Gwaze et al. 2001). Genetic correlations between wood density and growth traits in loblolly pine vary from slightly negative (Loo et al. 1984) to slightly positive (Stonecypher et al. 1973; Williams and Megraw 1994). Both positive and negative genetic correlations between growth rates and wood densities have been reported in other forest tree species (Zobel and Talbert 1984).

Genetic improvements may be accelerated by methods of controlled pollination and/or vegetative propagation. These strategies can enhance the quality of reforestation stock by eliminating inferior propagules that would otherwise result from pollen contamination from trees with non-desired traits. Wood quality can also be improved by increasing the intensity of selection for desirable properties full-sib families or clones. While potential improvements for both growth and disease resistance using full-sibs and clonal rooted cuttings have been demonstrated (Stelzer et al. 1998; Frampton et al. 2000), only limited data are available on potential improvements of wood properties.

The use of rooted cuttings as an alternative to bare-root seedlings for regeneration of loblolly pine has been studied by several investigators (Stelzer and Goldfarb 1997). Early growth and survival of rooted cuttings have been reported to be similar to those of seedlings in loblolly pine (Frampton et al. 2000). One study found no significant difference in five-year growth of rooted cuttings when compared to seedlings (McRae et al. 1993). A comparison of loblolly pine rooted cutting growth to seedling growth at age 10 also showed little difference in growth between the propagule types (Stelzer et al. 1998). Donor-plant age was a factor that affected performance during maturation of loblolly pine rooted cuttings (Foster et al. 1987).

One of the potential benefits of using rooted cuttings is that vegetative propagation could permit clonal forestry. The use of individual clones offers the possibility of producing wood with more uniform physical properties and structural quality in commercial

plantations. Gains in production from clonal forestry practices result from both increased frequency of superior genotypes and generation of more uniform wood and tree characteristics. A clonal propagation trial of loblolly pine revealed that clones vary significantly in growth (Foster et al. 1987). One analysis of growth rate increases related to selection through the use of loblolly pine clones demonstrated a potential for useful gains in production through higher within-family heritabilities as compared to within-family heritability estimates from seedlings (Isik et al. 2002b). Differences in early growth of rooted cuttings and seedlings of loblolly pine have not been significant, and genetic variance components were similar between types (Foster et al. 1987; McRae et al. 1993). While clonal propagation trials in other species have also revealed variation among clones and families that could be used as a basis for achieving increased growth and wood production (Mullin et al. 1992; Paul et al. 1993; Lambeth et al. 1994; Orlovic et al. 1998; Osorio et al. 2001), variation in specific gravity among clones versus full-sib seedlings has not been fully described. It is thus useful to investigate the extent of variation of specific gravity among clones and full-sib families of loblolly pine.

Studies of radiata pine, *Pinus radiata* D. Don, show little difference in micropropagated plantlets and seedlings for wood density at age 7 (Cown et al. 1989). Physiological age was found to have a significant impact on wood density in rooted cuttings of *Pinus radiata* (Lausberg et al. 1995). Clones of radiata pine have been found to be significantly different in their wood density (Donaldson et al. 1995). Little information is available concerning the wood properties of rooted cuttings in loblolly pine.

A ten-year-old trial of rooted cuttings and seedlings from nine full-sib loblolly pine families at two sites (Frampton et al. 2000) formed the basis for this study of variation of wood specific gravity and growth by the different propagule types. The objectives of this study were to: (1) determine if differences occur in specific gravity and growth traits due to propagation as seedlings and rooted cuttings; (2) determine variations in wood specific gravity and growth traits among and within families and across sites; (3) estimate genetic parameters for specific gravity and growth traits; and (4) compare uniformity of specific gravity and growth traits in trees planted as seedling families versus clones.

Materials and Methods

Experimental Design

The experimental design for this field study was described in detail by Frampton et al. (2000). Briefly, a split-plot design was employed with propagule type as the whole-plot factor (used in this study to compare properties of wood cores from propagule types). The study included two sites, Monroe Co., Alabama and Nassau Co., Florida, with six complete blocks within each site. The mating design was a 3 by 3 factorial creating 9 full-sib families. In seedling main plots, 3 sub-plots were established per family with two seedlings per plot. In rooted cutting main plots, 5 to 9 clonal sub-plots were established per family, with each sub-plot consisting of two ramets. A single border row surrounded the propagule main plots with the appropriate propagule type in each replication to

prevent interactions between propagule types. A total of 1110 rooted cuttings and 512 seedlings were analyzed in this study.

After the 9th (Florida) and 10th (Alabama) growing season, wood cores were collected at each site during March (Alabama) and May (Florida) 2001 using a 12-mm increment borer powered by an electric drill. Increment cores were taken at approximately 4.5 feet (breast height) above the ground from each tree in the study. Trees deemed to be atypical in form or severely infected by fusiform rust were excluded from sampling. Adjustments were made to avoid branches, knots, or defects; leaning trees or trees with sweep were cored perpendicular to the direction of the lean or bend, to minimize the amount of compression wood in the core; and fusiform rust galls were avoided by sampling higher or lower than 4.5 feet. Specific gravity of wood samples was determined using the gravimetric method (ASTM 1985) using the following equation:

$$\text{Specific Gravity} = \text{oven dry wood weight (g)} / \text{weight of displaced water (g)}$$

Growth measurements were recorded in March 2002 at age 10 years in Florida and age 11 years in Alabama. Height was measured to the nearest 1/2 foot and diameter at breast height (DBH) was measured to the nearest 1/10 of an inch. Volume was estimated using the outside-bark volume equation for southern pines (Goebel and Warner 1966).

Statistical Analysis

An analysis of variance was performed, using the SAS GLM procedure (SAS 1989). Data analyses for rooted cuttings and seedlings were performed for four traits: specific gravity, total tree height (feet), DBH at breast height (inches), and total tree volume (feet³). The linear model used for this analysis was similar to that used by Frampton et al. (2000) and is as follows:

$$[1] \quad Y_{ijkpqn} = \mu + S_i + R(S)_{j(i)} + T_k + RT_{jk} + ST_{ik} + F_p + M_q + SF_{ip} + SM_{iq} + SFM_{ipq} + FM_{pq} + STFM_{ikpq} + E_{ijkpqn}$$

where S_i is the effect of i -th site; $R(S)_{j(i)}$ is the effect of the j -th block in the i -th site; T_k is the effect of the k -th type; RT_{jk} is the interaction between the j -th block and the k -th type; ST_{ik} is the interaction between the i -th site and the k -th type; F_p is the effect of the p -th female; M_q is the effect of the q -th male; FM_{pq} is the interaction between the p -th female and the q -th male; SF_{ip} is the interaction between the i -th site and p -th female; SM_{iq} is the interaction between the i -th site and the q -th male; SFM_{ipq} is the interaction between the i -th site, the p -th female and the q -th male; $STFM_{ikpq}$ is the interaction between the i -th site, the k -th type, the p -th female and the q -th male; and E_{ijkpqn} is the within plot error plus random experimental error.

Site, type, and replication were treated as fixed effects, while other effects and interactions were treated as random using the random option in the GLM procedure. To test the significance of the main-plot effects (type) in the split-plot analysis, the site by

type interaction was used as the error (a) term for the F test. The appropriate error (b) term for each sub-plot effect was determined by SAS with the random test option in the GLM procedure. Least square means (LS means) and standard errors were generated from the GLM analysis.

For genetic variance component estimates, separate analyses of variance were then conducted for rooted cutting- and seedling-grown tree sample data using a factorial mating design similar to (Isik et al. 2002a). The variance and covariance estimates were generated from the MIXED procedure in SAS, where site and replication were treated as fixed effects, and all other effects were treated as random. The linear models used for this analysis were:

Rooted Cuttings:

$$[2] Y_{ijkpqn} = \mu + F_p + M_q + FM_{pq} + C(FM)_{k(pq)} + S_i + SF_{ip} + SM_{iq} + SFM_{ipq} + SC(FM)_{ik(pq)} + R(S)_{j(i)} + R(S)F_{j(i)p} + R(S)M_{j(i)q} + R(S)FM_{j(i)pq} + R(S)C(FM)_{j(i)k(pq)} + E_{ijkpqn}$$

where F_p is the effect of the p-th female; M_q is the effect of the q-th male; FM_{pq} is the interaction between the p-th female and the q-th male; $C(FM)_{k(pq)}$ is the effect of the k-th clone within the pq-th family; S_i is the effect of i-th site; SF_{ip} is the interaction between the i-th site and p-th female; SM_{iq} is the interaction between the i-th site and the q-th male; SFM_{ipq} is the interaction between the i-th site, the p-th female and the q-th male; $R(S)_{j(i)}$ is the effect of the j-th block in the i-th site; $R(S)F_{j(i)p}$ is the interaction between the j-th block within the i-th site and the p-th female; $R(S)M_{j(i)q}$ is the interaction between the j-th block within the i-th site and the q-th male. $R(S)FM_{j(i)pq}$ is the interaction between the j-th

block within the i-th site and the pq-th family; $R(S)C(FM)_{j(i)k(pq)}$ is the interaction between the j-th block within the i-th site and the k-th clone in the pq-th family; and $E_{l(k(j)(i))}$ is the within plot error plus random experimental error.

Seedlings:

$$[3] Y_{ijkpqn} = \mu + F_p + M_q + FM_{pq} + S_i + SF_{ip} + SM_{iq} + SFM_{ipq} + R(S)_{j(i)} + R(S)F_{j(i)p} + R(S)M_{j(i)q} + R(S)FM_{j(i)pq} + E_{ijkpqn}$$

where F_p is the effect of the p-th female; M_q is the effect of the q-th male; FM_{pq} is the interaction between the p-th female and the q-th male; S_i is the effect of i-th site; SF_{ip} is the interaction between the i-th site and p-th female; SM_{iq} is the interaction between the i-th site and the q-th male; SFM_{ipq} is the interaction between the i-th site, the p-th female and the q-th male; $R(S)_{j(i)}$ is the effect of the j-th block in the i-th site; $R(S)F_{j(i)p}$ is the interaction between the j-th block within the i-th site and the p-th female; $R(S)M_{j(i)q}$ is the interaction between the j-th block within the i-th site and the q-th male. $R(S)FM_{j(i)pq}$ is the interaction between the j-th block within the i-th site and the pq-th family; and E_{ijkpqn} is the within plot error plus random experimental error. For both the combined and separate analyses of propagule types, a 95% confidence level F-test was used for significant differences among types, parents, and sites.

Heritability

Variance component estimates of seedlings and rooted cuttings were made using a program in the SAS MIXED and IML procedures (Xiang and Li 2001). Standard errors were estimated using the delta method (Lynch and Walsh 1997). Heritability formulas

were adapted from an earlier analysis of growth of the same trial (Isik et al. 2002a). Narrow-sense individual tree heritability (h^2_i), half-sib family mean heritability (h^2_{HS}), and full-sib family mean heritability (h^2_{FS}) were estimated for both seedlings and rooted cuttings. Within-family heritabilities (h^2_{wHS} , h^2_{wFS}) were estimated for seedlings, while narrow-sense clone mean within-family heritabilities ($h^2_{c_HS}$, $h^2_{c_FS}$) were estimated for rooted cuttings. A broad-sense clone mean (H^2_{CM}) was calculated from the rooted cuttings.

Individual Tree Heritability

$$[4] \quad h^2 = (2 * (\sigma^2_f + \sigma^2_m)) / \sigma^2_i$$

Seedling σ^2_i

$$[5] \quad \sigma^2_i = \sigma^2_f + \sigma^2_m + \sigma^2_{fm} + \sigma^2_{sf} + \sigma^2_{sm} + \sigma^2_{sfm} + \sigma^2_{r(s)f} + \sigma^2_{r(s)m} + \sigma^2_{r(s)fm} + \sigma^2_e$$

Cutting σ^2_i

$$[6] \quad \sigma^2_i = \sigma^2_f + \sigma^2_m + \sigma^2_{fm} + \sigma^2_{c(fm)} + \sigma^2_{sf} + \sigma^2_{sm} + \sigma^2_{sfm} + \sigma^2_{sc(fm)} + \sigma^2_{r(s)f} + \sigma^2_{r(s)m} + \sigma^2_{r(s)fm} + \sigma^2_{r(s)c(fm)} + \sigma^2_e$$

Half-sib Family Mean Heritability

$$[7] \quad h^2_{HS} = (0.5(\sigma^2_f + \sigma^2_m)) / \sigma^2_{HS}$$

Seedling σ^2_{HS}

$$[8] \quad \sigma^2_{HS} = (\sigma^2_f + \sigma^2_m) / 2 + \sigma^2_{sf/s} + \sigma^2_{sm/s} + \sigma^2_{sfm/s} + \sigma^2_{r(s)f/sb} + \sigma^2_{r(s)m/sb} + \sigma^2_{r(s)fm/sb} + \sigma^2_e/sbn$$

Cutting σ^2_{HS}

$$[9] \quad \sigma^2_{HS} = (\sigma^2_f + \sigma^2_m) / 2 + \sigma^2_{c(fm)/c} + \sigma^2_{sf/s} + \sigma^2_{sm/s} + \sigma^2_{sfm/s} + \sigma^2_{sc(fm)/s} + \sigma^2_{r(s)f/sb} + \sigma^2_{r(s)m/sb} + \sigma^2_{r(s)fm/sb} + \sigma^2_{r(s)c(fm)/sbc} + \sigma^2_e/sbcn$$

Full-sib Family Mean Heritability

$$[10] \quad h^2_{FS} = (\sigma^2_f + \sigma^2_m) / \sigma^2_{FS}$$

Seedling σ^2_{FS}

$$[11] \quad \sigma^2_{FS} = \sigma^2_f + \sigma^2_m + \sigma^2_{fm} + \sigma^2_{sf/s} + \sigma^2_{sm/s} + \sigma^2_{sfm/s} + \sigma^2_{r(s)f/sb} + \sigma^2_{r(s)m/sb} + \sigma^2_{r(s)fm/sb} + \sigma^2_e/sbn$$

Cutting σ^2_{FS}

$$[12] \quad \sigma^2_{FS} = \sigma^2_f + \sigma^2_m + \sigma^2_{fm} + \sigma^2_{c(fm)/c} + \sigma^2_{sf/s} + \sigma^2_{sm/s} + \sigma^2_{sfm/s} + \sigma^2_{sc(fm)/s} + \sigma^2_{r(s)f/sb} + \sigma^2_{r(s)m/sb} + \sigma^2_{r(s)fm/sb} + \sigma^2_{r(s)c(fm)/sbc} + \sigma^2_e/sbcn$$

Within Half-Sib Family Heritability

$$[13] \quad h^2_{WHS} = 1.5(\sigma^2_f + \sigma^2_m) / \sigma^2_{WHS}$$

$$[14] \quad \sigma^2_{WHS} = (s-1)/s (\sigma^2_{sf} + \sigma^2_{sm}) + (sb-1)/sb (\sigma^2_{r(s)f} + \sigma^2_{r(s)m} + \sigma^2_{r(s)fm}) + (sbn-1)/sbn \sigma^2_e$$

Within Full-Sib Family Heritability

$$[15] \quad h^2_{WFS} = (\sigma^2_f + \sigma^2_m) / \sigma^2_{WFS}$$

$$[16] \quad \sigma^2_{WFS} = (s-1)/s (\sigma^2_{sf} + \sigma^2_{sm} + \sigma^2_{sfm}) + (sb-1)/sb (\sigma^2_{r(s)f} + \sigma^2_{r(s)m} + \sigma^2_{r(s)fm}) + (sbcn-1)/sbcn \sigma^2_e$$

Within Half-sib Family Clone Mean Heritability

$$[17] \quad h^2_{C_HS} = 1.5 (\sigma^2_f + \sigma^2_m) / \sigma^2_{C_HS}$$

$$[18] \quad \sigma^2_{C_HS} = (c-1)/c (\sigma^2_{c(fm)} + 1/bt \sigma^2_{r(s)c(fm)} + 1/c \sigma^2_e)$$

Within Full-sib Family Clone Mean Heritability

$$[19] \quad h^2_{C_FS} = (\sigma^2_f + \sigma^2_m) / \sigma^2_{C_FS}$$

$$[20] \quad \sigma^2_{C_FS} = (c-1)/c (\sigma^2_{c(fm)} + 1/s \sigma^2_{sc(fm)} + 1/sb \sigma^2_{r(s)c(fm)} + 1/c \sigma^2_e)$$

Clone Mean Heritability

$$[21] \quad H^2_{CM} = (\sigma^2_f + \sigma^2_m + \sigma^2_{fm} + \sigma^2_{c(fm)}) / \sigma^2_{CM}$$

$$[22] \quad \sigma^2_{CM} = \sigma^2_f + \sigma^2_m + \sigma^2_{fm} + \sigma^2_{c(fm)} + 1/s (\sigma^2_{sf} + \sigma^2_{sm} + \sigma^2_{sfm} + \sigma^2_{sc(fm)}) + 1/sb (\sigma^2_{r(s)f} + \sigma^2_{r(s)m} + \sigma^2_{r(s)fm}) + \sigma^2_{r(s)c(fm)}/sbc + \sigma^2_e/sbcn$$

Where:

σ^2_f = variance due to differences among female parents

σ^2_m = variance due to differences among male parents

σ^2_{fm} = variance due to female by male interaction

$\sigma^2_{c(fm)}$ = variance due to clones within female by male interaction

σ^2_{sf} = variance due to site by female interaction

σ^2_{sm} = variance due to site by male interaction

σ^2_{sfm} = variance due to site by female by male interaction

$\sigma^2_{sc(fm)}$ = variance due to site by clone within female by male interaction

$\sigma^2_{r(s)f}$ = variance due to replications within sites

$\sigma^2_{r(s)m}$ = variance due to replications within sites by male interaction

$\sigma^2_{r(s)fm}$ = variance due to replications within sites by female by male interaction

$\sigma^2_{r(s)c(fm)}$ = variance due to replications within sites by clones within female by male interaction

σ^2_e = variance within plot

Because of slightly unbalanced data, the number of sites, blocks, trees, clones, and ramets were fractions estimated by the SAS MIXED procedure where:

s number of sites (1.99)

b number of blocks (5.99)

c clones per family (4.6)

n number of trees per family (seedlings) (4.41)

n number of ramets per clone (rooted cuttings) (1.58)

Correlations

The phenotypic correlations among specific gravity and tree height for rooted cuttings and seedlings was estimated using the correlation procedure in SAS, and additive genetic

correlations and standard errors were estimated using the following equations (Falconer 1989):

$$[23] \quad \mathbf{r}_g = \frac{\sigma^2_{xy}}{(\sigma^2_x \sigma^2_y)^{1/2}}$$

$$[24] \quad \text{Standard Error } (\mathbf{r}_g) = \left(\frac{1 - r_g^2}{\sqrt{2}} \right) \sqrt{\left[\frac{\sigma(h_x^2) \sigma(h_y^2)}{h_x^2 h_y^2} \right]}$$

where σ^2_{xy} is the additive genetic covariance between traits x and y; σ^2_x is the additive variance of trait x; σ^2_y is the additive variance of trait y; $\sigma^2_{(h^2_x)}$ is the standard error of the heritability of trait x; $\sigma^2_{(h^2_y)}$ is the standard error of the heritability of trait y; h^2_x is the heritability of trait x; and h^2_y is the heritability of trait y.

Genetic values

$$[25] \quad \text{GV} = \bar{x} + \text{GCA}_f + \text{GCA}_m + \text{SCA}_{fm}$$

where \bar{x} is the test mean of a trait; GCA_f is the general combining ability of the female parent; GCA_m is the general combining ability of the male parent; and SCA_{fm} is the specific combining ability of the full-sib cross between the female parent f and the male parent m. The general combining ability for each parent was calculated by averaging the mean of each cross involving that parent and subtracting the test mean. The specific combining ability for each full-sib cross was calculated by subtracting the GCA for each parent and the test mean from the full-sib family mean.

Coefficients of variation

Coefficients of variation were calculated to compare uniformity of clones to full-sib families. CV's were calculated for each clone and full-sib family on each site, and results were reported as means for clones and full-sib families on each site to simulate clonal blocks of rooted cuttings and full-sib family blocks of seedlings.

$$[26] \quad CV (\%) = \frac{100s}{\bar{x}}$$

where s is the standard deviation and \bar{x} is the mean of clone means from rooted cuttings or full-sib family means from seedlings.

Results

Combined Analysis to Compare Propagule Types

Wood specific gravity did not differ significantly between propagule types or sites. Tree growth differed significantly between the two sites ($p < 0.02$), but not between the two propagule types (Table 1). The greatest differences in growth were between sites (Table 2). Trees (seedlings and rooted cuttings combined) on the Alabama site were on average 8.7 feet taller and 2.3 inches greater in DBH than those at the Florida site, producing more than twice as much wood volume. This difference includes the effect of one additional growing season at the Alabama site.

Interaction terms among several characteristics were significant in the analysis of variance, but the differences were small. The site by type interaction was significant only for specific gravity (Table 1). In Alabama, seedlings had greater SG, but lower height

than rooted cuttings (Table 2). DBH and volume differences between seedlings and rooted cuttings were not significant. In Florida, SG was slightly higher in rooted cuttings, but height, DBH, and volume were not significantly different between propagule types.

The female by male interaction was significant for height, DBH, and volume, indicating a significant SCA effect for growth traits. The female parent was significant for specific gravity and the male parent was significant for height. The site by male interaction was significant for DBH and volume and the type by female interaction was significant for height.

Separate Analyses of Rooted Cuttings and Seedlings

Site and Replication Effects

Significant differences for specific gravity, diameter, height, and volume were detected between sites in the separate analyses of the two propagule types. The replications within sites were significantly different for height, diameter, and volume, but not for specific gravity.

Genetic Effects

For each trait, estimates of genetic effects from rooted cuttings and seedlings were similar, with rooted cuttings slightly higher for all traits (Table 3). Both seedlings and rooted cuttings exhibited significant differences among female parents for specific

gravity. Rooted cuttings displayed a significant difference among males for tree height. The variance due to the female parent for specific gravity was much higher than the variance due to the male parent, and was similar in magnitude for both rooted cuttings and seedlings (Table 3). Height, DBH, and volume had much lower female variance component estimates. Estimates of the variance due to male parents were low for both propagule types for all traits. There was a significant full-sib interaction in the seedling analysis for height, DBH, and volume. Full-sib families accounted for low percentages of variance in all traits, but were slightly greater for variations in DBH and volume than for variations of height and specific gravity. In the rooted-cutting analysis, the clone-within-full-sibs component was significant for all traits. In the analysis of rooted cuttings, clones accounted for a larger portion of the total variance in specific gravity than in growth traits. However, for growth traits, the clone component contributed similar if not greater amounts of variance than the parent or family components.

Genotype x Environment Interactions

Some interactions including site, replication, and genetic components were significant for measured characteristics, but these interactions accounted for small proportions of the total variances observed. The female by site interaction was significant for specific gravity only in seedlings, but the clone by site interaction in rooted cuttings was significant for specific gravity, DBH, and volume. The family by site interactions (half-sibs and full-sibs), in both seedlings and rooted cuttings were smaller than the clone by site interaction for all traits except specific gravity. Volume and DBH exhibited the

largest clone by site variance components in rooted cuttings, while wood specific gravity in seedlings exhibited the largest family by site variance component. For specific gravity, the half-sib (female) by site and the full-sib family by site interactions were similar to the clone by site interaction in percentage of total variance, but in growth traits the clone by site interaction was greater than family by site interactions, with the greatest difference in volume (Table 3).

Heritability Estimates

Individual-tree heritabilities were higher for rooted cuttings for all traits (Table 4). Standard errors for individual tree heritabilities were also higher in rooted cuttings for all traits, but were a lower percentage of the heritability estimate as compared to seedling estimates. For all individual-tree heritability estimates, the standard errors were greater than half the value of the heritability and, in some cases, standard errors were larger than the heritability estimates. The broad-sense clone mean heritabilities were high for all traits, varying from 0.73 in volume to 0.96 in specific gravity.

Half-sib family mean heritability estimates were also higher for rooted cuttings than for seedlings for all traits. Specific gravity heritability estimates were similar for rooted cuttings and seedlings (0.62 and 0.47, respectively). Height heritability estimates for seedlings were slightly lower than corresponding heritability estimates for the rooted cuttings (0.57 and 0.63, respectively), but seedling heritability estimates were considerably lower than rooted cutting heritability estimates for DBH and volume.

Standard errors of heritability estimates were lower (less than half the heritability estimate value) for specific gravity and for height in both propagule types, while heritability standard errors for volume and DBH were greater than the estimate values themselves. Broad-sense clone-mean heritabilities were highest in specific gravity, and were the highest estimates for all traits.

Full-sib family mean heritability estimates varied by trait and propagule type. For specific gravity and height, full-sib family mean heritabilities were higher than half-sib family mean heritabilities, but full-sib DBH heritabilities were lower than those of half sibs. For volume, the full-sib heritability estimate was less than the half-sib estimate for rooted cutting-grown trees, but for seedlings, the full-sib estimate was greater than the half-sib estimate.

Within-family heritability estimates for rooted cuttings were larger than corresponding estimates for seedlings. Clone-mean heritabilities within full-sibs were higher than for clone-means within half-sibs for specific gravity and height, but were lower for DBH and volume. The within half-sib family seedling tree heritabilities were higher than the within full-sib seedling tree heritabilities for all traits.

Genetic Values

The general combining ability (GCA) estimates for the six parents were similar for each trait in rooted cuttings and seedlings, however some rank changes were found (Table 5).

For all traits, the parents with the highest GCA as rooted cuttings also had the highest GCA as seedlings. The two parents with the highest GCA values for specific gravity also had the lowest GCA values for volume and DBH. Parents with the highest GCA values for height also had the highest GCA values for DBH and volume, but had the second-lowest values for specific gravity.

The genetic values for full-sib families were similar to the pattern of GCA values (Figures 1 and 2). The total genetic values for each trait for full-sib families (GCA + SCA) showed that the families with the highest specific gravity had the lowest value for volume and the family with the greatest volume had the lowest wood specific gravity (Figure 1).

Correlations

Genetic correlations between specific gravity and height were similar for rooted cuttings and seedlings (-0.502 and -0.515, respectively), while the phenotypic correlation was slightly more negative for rooted cuttings than seedlings (-0.448 and -0.330, respectively). The standard error for the genetic correlation from rooted cuttings was lower than the standard error from seedlings (0.344 and 0.955, respectively).

Coefficients of Variation

The coefficients of variation (CVs) for clones were lower than those of full-sib seedlings for all traits (Table 6). For SG on both sites, the average of the clone mean CV's was 1.5

percentage points lower than the average of the full-sib family CV's from seedling-grown trees. Differences in CV's between clones and full-sib seedlings were more dramatic for growth traits. The greatest difference on both sites was in volume. Clonal mean volume CV's were 6.7 and 6.1 percentage points lower than full-sib family seedling volume CV's in trees from the Florida and Alabama study sites, respectively. The clone CV's appeared to vary more than the full-sib family CV's, suggesting that selected clones may be more uniform than families (Figure 2).

Discussion

No significant difference in specific gravity was observed between trees from seedlings and rooted cuttings of nine full-sib families across two sites at similar stand ages. In radiata pine, propagules from young donor plants produced wood of similar specific gravity as seedlings as long as the physiological age of donor plants was 5 years or younger (Lausberg et al. 1995). The rooted cuttings in this study came from hedged donor plants 2 to 3 years from seed (Anderson et al. 1999). These results show that for loblolly pine, rooted cuttings from juvenile hedges will not show the reduced density characteristics of propagules from mature donor plants.

There were also no significant differences between rooted cutting and seedling propagules for height, DBH and volume at age 10 (and 11) years. This is consistent with earlier results from the same study, where no differences were found in growth traits

between propagule types after six growing seasons (Frampton et al. 2000). The lack of differences between rooted cuttings and seedlings in growth at ten years agrees with results from other studies reporting no differences in growth traits as long as the rooted cuttings come from relatively juvenile donor plants (Foster et al. 1987; Stelzer et al. 1998).

The differences in site characteristics affected the specific gravity between the two sites. In the split-plot analysis of sites and types, sites were marginally significant ($p < 0.10$), but significant differences were observed in the separate analyses of propagule types. The split-plot design was not powerful for testing differences between sites (as a main plot effect). The Alabama site was located in the upper coastal plain on an old-field site that was disked and subsoiled for site preparation. There was very little understory competition at the time of measurement, and the site was relatively uniform. The Florida site, a flatwoods site that was high-bedded, was more variable in vegetation than the Alabama site. The growth difference between the two sites was perhaps due to nutrient availability since the Alabama site was previously in agriculture and produced trees nearly three times greater in volume than the Florida site. While trees on the Florida site produced a higher mean specific gravity and lower volume, one should not conclude that slower growing trees are the solution to improving wood specific gravity. The relationship between fast growth and specific gravity has been studied, but results have varied. Zobel and van Buijtenen (1989) reviewed literature reporting genetic and phenotypic correlations varying from negative to weakly positive. One study reported a

very small decrease in specific gravity with increased growth in hard pines, which includes loblolly pine (Zhang 1995).

There was a site by propagule type interaction for specific gravity, but the differences were small. On the Florida site, rooted cuttings had slightly higher specific gravity than seedlings (0.446 versus 0.442, respectively), while on the Alabama site seedlings had higher specific gravity (0.417 versus 0.412). Early growth measurements showed significant site by type interactions in this study at ages 4 and 6 for height, diameter, and volume (Frampton et al. 2000), however, no significant site by type interactions for height ($p < 0.0821$), DBH ($p < 0.0552$), or volume ($p < 0.1086$) were found at age 10. Further study of site specificity incorporating more clones and families across several sites, including different site qualities and climatic conditions, may be necessary to determine if site by type interactions truly exist for specific gravity during a full rotation period. The significance of the site by type interaction may also be due to the error in the experimental design. A more powerful test might be necessary to better analyze this interaction.

The moderately unfavorable genetic correlation (negative) between height and specific gravity suggests that selecting for height would decrease the specific gravity, while selecting for specific gravity would decrease height. The correlations found in this study may be due to its small population of six parents. Genetic and phenotypic correlations are more negative than those reported by Gwaze et al. (2001) (-0.33 to 0.28) for age 10

heights versus wood density. In other studies with larger population sizes, low to moderately positive correlations were found between growth and specific gravity (Stonecypher et al. 1973; Bridgwater et al. 1983; Talbert et al. 1983). Although there was a negative correlation between growth and specific gravity in this study, if the true correlation is weaker (positive or negative), then genetics could be used to ameliorate an expected site effect on specific gravity, but the amount of gain is not clear. The families in this study varied from 0.41 to 0.46 in specific gravity, suggesting that a site with a lower expected specific gravity, could be ameliorated by selecting a higher density family.

Genetic variances for specific gravity were similar in trees grown from seedlings and from rooted cuttings, but site and residual variance estimates differed. Error terms were lower for rooted cuttings, suggesting that with a more uniform genotype (ramets of clones) variation can be partitioned into those that reflect genetic versus environmental factors. Variance components for seedlings at age 6 were also similar to results in this study for site and error in height (Isik et al. 2002a). With lower residual variance values, rooted cuttings could be used in progeny testing for efficient selection.

The significance of genetic factors for growth traits differed from those for specific gravity. The variance components from half-sib, full-sibs, and clones for specific gravity were greater than for growth traits. The clonal (within full-sibs) variance term was significant for all traits for rooted cuttings and, in some cases, accounted for more of the

total variance than either parent. The clonal (within full-sibs) variance was nearly four times greater for specific gravity than for growth traits. This is, perhaps, because specific gravity is under greater genetic control and less influenced by site. From this study, it appears that selected clones, and to some extent families, of loblolly pine could be used to increase wood specific gravity at the expense of decreased height growth.

Heritability estimates were generally higher and more precise for rooted cuttings than seedlings. Similar magnitudes of heritability among traits were reported by Gwaze et al. (2001) for seedlings. Heritability for height was higher than heritability of DBH, as also reported by Gwaze et al. (2001). Clone mean within-family heritabilities for half-sibs and full-sibs were higher than seedling within-family heritabilities for all traits. Although these heritability values may not be comparable to those that would be found in a breeding population, because of the low number of parents, the seedling heritability estimates are similar to those reported by Gwaze et al (2001) and Talbert (1983). Rooted cutting heritability estimates were higher than similar estimates for seedlings, suggesting that if rooted cuttings were used in progeny testing, greater gains could be achieved for specific gravity. The higher values for clone-mean within family narrow-sense heritabilities suggest that gains could be made from clonal progeny testing since a greater amount of additive genetic variation can be captured using clones. With clones repeated across replications and sites, a better estimate of site and environmental effects is achieved, reducing the residual (error) variance. This results in a smaller denominator in heritability estimates and higher heritability estimates. The broad-sense clone-mean

heritability values suggest that clonal selection for deployment could be used to make gains in specific gravity and growth.

When compared to growth traits, specific gravity is under strong additive genetic control, which has also been reported by Stonecypher et al. (1973) and Talbert et al. (1983). The low SCA variance suggests that dominance has little effect on specific gravity, but could be different in a larger population. The GCA's of the two parents or a mid-parent value could accurately assess the full-sib performance, as suggested in Stonecypher et al. (1973). Selecting parents with high GCA values may not account for a possible SCA effect, but could be used in the selection of parents from existing orchards for control pollination.

Clonal coefficients of variation (CV's) from rooted cuttings were, on average, lower than full-sib family CV's from seedlings for all traits on both sites. Thus, a potential exists to achieve greater uniformity by the use of clones. The CV's for some clones were as low as 1.2% (Figure 2), suggesting that some genotypes may produce trees with more uniform wood density. Similar improvements in uniformity can be achieved for height, DBH, and wood volume through clones selected and deployed as clonal blocks. The lower CV values in clones suggest that uniformity could be used in the selection of clones for deployment to increase the uniformity of a stand, however, a clonal block test would provide a more definitive answer to the issue of stand uniformity of clones. From this study, however, improvement in uniformity due to cloning versus vegetative

propagation could not be distinguished. C-effects were not accounted for in the production of rooted cuttings, but vegetative propagation could produce more uniform planting stock due factors other than genetics.

Limitations and Assumptions

While this study provided an opportunity to compare the specific gravity of rooted cuttings and seedlings from nine full-sib families, limitations of this study do exist. The split-plot experimental design is to somewhat limited in testing the difference between main plots of seedlings and rooted cuttings as well as site differences due to a low number of degrees of freedom. The parents in this study were selected for a range of growth and disease resistance. The relationship between growth and wood properties may not reflect a larger population of loblolly pine. With only six parents and nine full-sib families, variance component estimates and heritability estimates do not necessarily reflect what would be found in a larger breeding population. Although a small number of parents were used in this study, the population was assumed to be normally distributed and effects were assumed to be independent of one another in the analyses of variance. C-effects of the clones and families were not accounted for in this study and were assumed to be negligible, but could have affected the growth or density of the trees.

Conclusion

Wood specific gravity of loblolly pine rooted cuttings from a 10-year-old stand was similar to the specific gravity of seedlings. Parents and families ranked similarly between

propagule types and across two sites. The use of rooted cuttings in commercial plantations should not have an adverse impact on specific gravity. Heritability estimates were higher from rooted cuttings and had lower standard errors for specific gravity. Clonal testing could allow greater gains in wood specific gravity because of better genetic parameter estimates. The deployment of rooted cuttings could allow clones with desirable wood specific gravity to be utilized in plantations, but a larger scale study of families and clones is needed to further evaluate specific gravity in clones of loblolly pine.

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Table 1. F-values and significance levels from the combined analysis of variance of specific gravity, tree height, diameter, and volume of loblolly pine seedling and rooted cuttings on two sites.

Source	DF	Specific Gravity		Height		Diameter		Volume	
		F	Pr > F	F	Pr > F	F	Pr > F	F	Pr > F
Site	1	39.33	0.1007	812.6	0.0223*	609.29	0.0258*	620.56	0.0255*
Rep (Site)	5	1.17	0.3222	73.21	<.0001***	19.18	<.0001***	20.22	<.0001***
Type	1	0.01	0.9361	4.92	0.2697	0.98	0.5027	0.41	0.6383
Rep x Type	5	2.29	0.0441*	2.92	0.0126*	3.02	0.0102*	1.43	0.2116
Site x Type	5	8.32	0.01*	4.04	0.0592	3.3	0.0851	2.18	0.1575
Female	2	19.68	0.0071**	1.48	0.3114	1.74	0.2707	0.93	0.4528
Male	2	6.63	0.0883	9.74	0.0279*	1.3	0.3443	1.84	0.2543
Site x Female	2	2.39	0.1205	0.75	0.4854	1.82	0.1905	2.61	0.1021
Site x Male	2	2.39	0.1205	2.23	0.1352	8.62	0.0022**	6.87	0.0062**
Female x Male	4	3.32	0.344	11.39	<.0001***	15.64	<.0001***	10.52	0.0002***
Site x Type x Female x Male	16	1.37	0.1471	0.87	0.6023	0.86	0.6174	1.39	0.1365

Significance of mean square F-test at 95%(*), 99%(**), and 99.9%(***).

Table 2. Least Square Means (standard errors) for specific gravity (S.G.), height, diameter, and volume for 10-year-old loblolly pine rooted cuttings and seedlings on two sites.

Site	Type	S.G.	Height (ft.)	Diameter (in.)	Volume (ft. ³)
Florida	Cuttings	0.446 (0.0010) a	38.24 (0.120) a	5.92 (0.041) a	2.79 (0.059) a
	Seedlings	0.442 (0.00147) b	37.27 (0.175) a	5.92 (0.059) a	2.74 (0.087) a
Alabama	Cuttings	0.412 (0.0011) a	46.59 (0.129) a	8.10 (0.044) a	6.21 (0.064) a
	Seedlings	0.417 (0.00157) b	46.22 (0.184) a	8.28 (0.062) a	6.44 (0.091) a
Combined Sites	Cuttings	0.4290 (0.00075) a	42.42 (0.088) a	7.008 (0.030) a	4.499 (0.044) a
	Seedlings	0.4295 (0.0011) a	41.74 (0.127) a	7.099 (0.043) a	4.591 (0.063) a

Letters indicates significant difference (95%) between propagule types or sites.

Table 3. Variance Component estimates (% of total phenotypic variance) for specific gravity, height, diameter, and volume based on the combined analysis of 2 sites.

Term	Specific Gravity		Height (ft.)		Diameter (in.)		Volume (ft. ³)	
	Cutting	Seedling	Cutting	Seedling	Cutting	Seedling	Cutting	Seedling
Fem	30%*	20%*	3%	0%	9%	0%	7%	0%
Male	1%	4%	20%*	12%	3%	1%	6%	3%
Fem*Male	0%	1%	4%	6%*	5%	7%*	4%	5%*
Clone(Fem*Male)	21%*	-	12%*	-	13%*	-	12%*	-
Site	-*	-*	-*	-*	-*	-*	-*	-*
Rep(Site)	-	-	-*	-*	-*	-*	-*	-*
Fem*Site	0%	2%*	0%	0%	0%	0%	1%	0%
Male*Site	0%	0%	2%	0%	2%	2%	2%	2%
Fem*Male*Site	0%	1%	0%	0%	0%	0%	2%	0%
Clone*Site(Fem*Male)	3%*	-	2%	-	8%*	-	12%*	-
Fem*Rep(Site)	0%	1%	1%	1%	1%	1%	1%*	1%*
Male*Rep(Site)	0%	0%	1%	0%	0%*	0%	0%*	2%
Fem*Male*Rep(Site)	0%	0%	1%	4%*	0%	0%	0%	0%
Clone(Fem*Male)*Rep(Site)	2%	-	18%*	-	7%*	-	6%*	-
Error	44%	72%	36%	77%	52%	89%	48%	87%

* F-test of means is significant at 95% level.

Table 4. Heritability estimates (standard error) for specific gravity, height, diameter, and volume for rooted cuttings and seedlings.

Heritability Estimate	Specific Gravity		Height		Diameter		Volume	
	Cutting	Seedling	Cutting	Seedling	Cutting	Seedling	Cutting	Seedling
h^2_i	0.62 (0.45)	0.47 (0.35)	0.46 (0.37)	0.25 (0.26)	0.24 (0.25)	0.02 (0.14)	0.25 (0.26)	0.06 (0.14)
h^2_{HS}	0.71 (0.04)	0.68 (0.08)	0.63 (0.13)	0.57 (0.19)	0.53 (0.23)	0.12 (0.74)	0.52 (0.24)	0.29 (0.45)
h^2_{FS}	0.83 (0.16)	0.89 (0.13)	0.70 (0.25)	0.64 (0.33)	0.49 (0.34)	0.11 (0.70)	0.45 (0.33)	0.30 (0.53)
$h^2_{C_wHS}$	0.67 (0.13)	-	0.48 (0.10)	-	0.42 (0.11)	-	0.43 (0.14)	-
$h^2_{C_wFS}$	1.08 (0.09)	-	0.68 (0.41)	-	0.47 (0.47)	-	0.53 (0.53)	-
h^2_w	-	0.43 (0.37)	-	0.21 (0.24)	-	0.02 (0.11)	-	0.05 (0.11)
h^2_{wf}	-	0.33 (0.31)	-	0.15 (0.19)	-	0.01 (0.08)	-	0.03 (0.08)
H^2_{CM}	0.96 (0.03)	-	0.93 (0.06)	-	0.84 (0.09)	-	0.75 (0.13)	-

Note: h^2_i = individual heritability; h^2_{HS} = Half-sib family mean heritability; h^2_{FS} = Full-sib family mean heritability; $h^2_{C_wHS}$ = clone mean heritability within half-sib families; $h^2_{C_wFS}$ = clone mean heritability within full-sib families; h^2_w = within half-sib family heritability; h^2_{wf} = within full-sib family heritability; and H^2_{CM} = clone mean heritability.

Table 5. General Combining Ability of six parents for specific gravity, height, diameter and volume for rooted cuttings and seedlings.

Parent	<u>Specific Gravity</u>		<u>Height (ft.)</u>		<u>Diameter (in.)</u>		<u>Volume (ft³)</u>	
	Cutting	Seedling	Cutting	Seedling	Cutting	Seedling	Cutting	Seedling
1	0.439	0.437	40.891	40.501	6.704	6.760	3.993	4.045
2	0.449	0.446	41.110	41.300	6.582	6.856	3.882	4.266
3	0.427	0.425	43.715	42.205	7.045	7.003	4.679	4.509
4	0.429	0.430	41.720	40.851	6.907	7.051	4.340	4.463
5	0.423	0.423	44.142	43.252	7.318	7.323	5.040	5.016
6	0.415	0.419	41.927	41.098	7.301	7.275	4.812	4.749

Table 6. Coefficients of variation for specific gravity, height, diameter, and volume for clone means of rooted cuttings and full-sib family seedling means on two sites.

Site	Type	Average CV(%)			
		S.G.	Height (ft.)	Diameter (in.)	Volume (ft.3)
Florida	Cuttings	4.3	9.4	14.5	34.10
	Seedlings	5.4	12.3	15.9	40.80
Alabama	Cuttings	4.25	5.3	10.7	23.50
	Seedlings	6.2	6	13.8	29.60

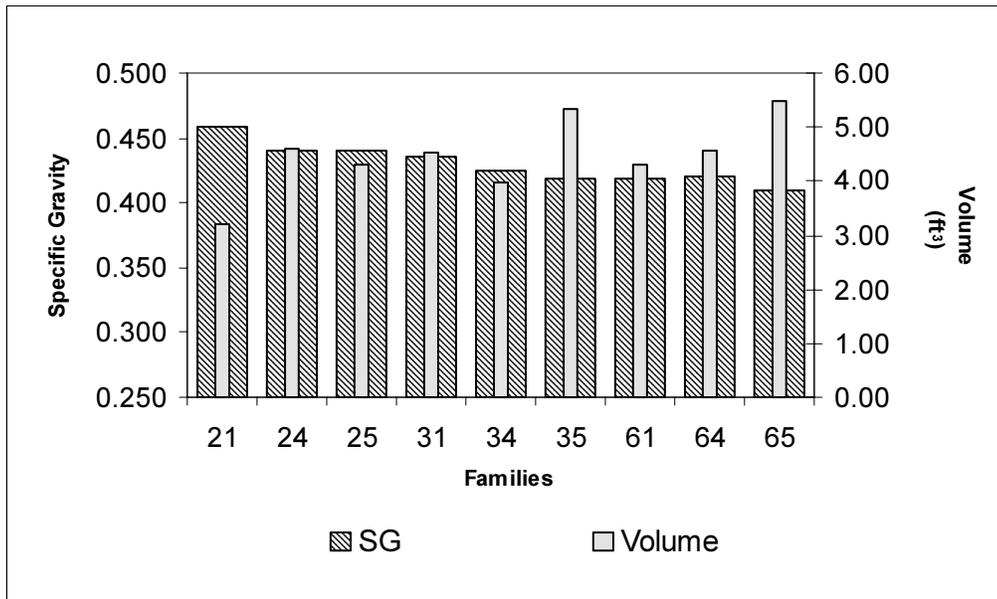


Figure 1a. Full-sib family genetic values for specific gravity and volume.

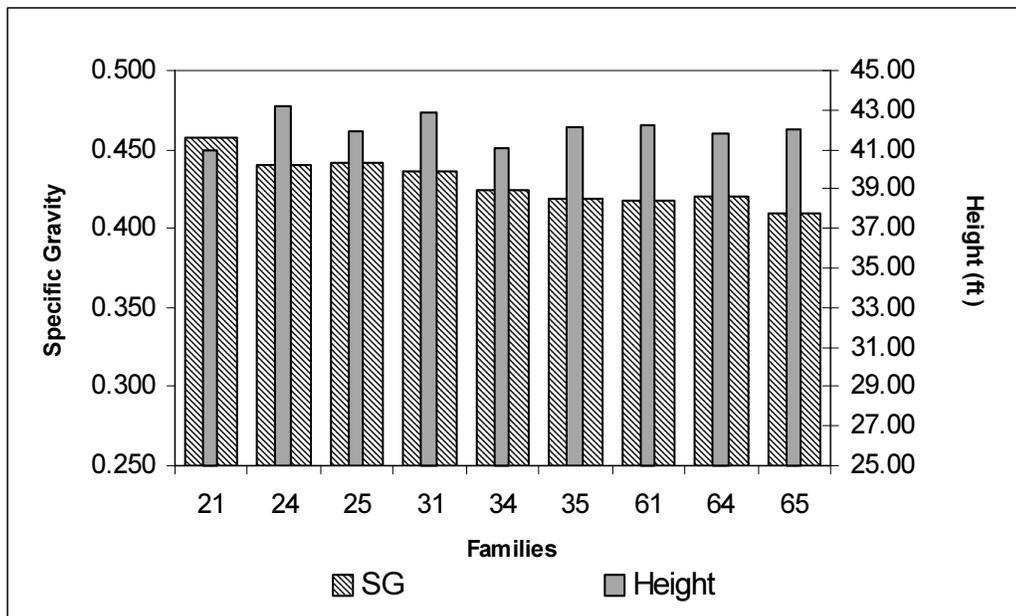


Figure 1b. Full-sib family genetic values for specific gravity and height.

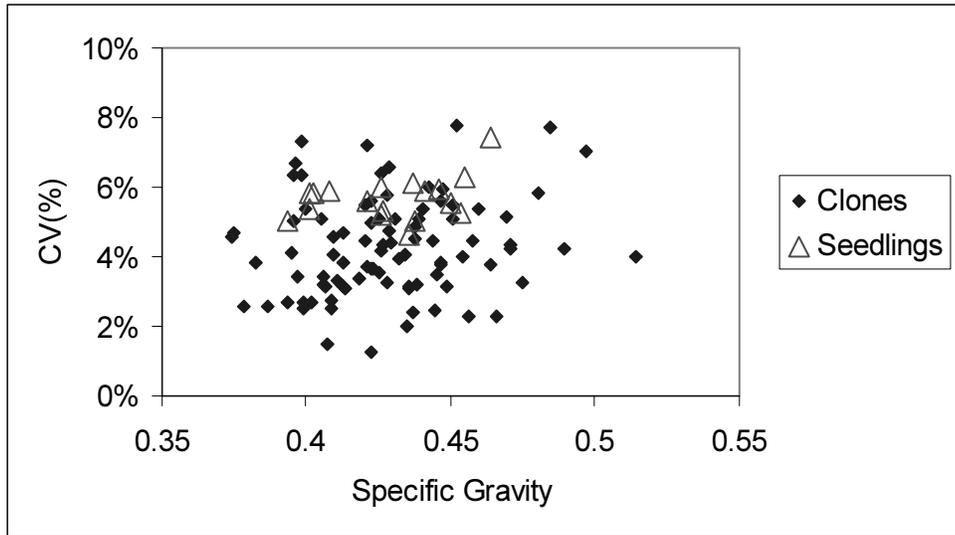


Figure 2. Clone-mean and full-sib family CV (%) values on two sites.

Chapter 2

Variation of Wood Density Components in Loblolly Pine

Seedlings and Rooted Cuttings

Abstract

Wood density components of rooted cuttings and seedlings from nine full-sib families of loblolly pine (*Pinus taeda* L.) at two sites were measured using x-ray densitometry. Seedlings and rooted cuttings did not differ significantly for latewood density, earlywood density or latewood percentage, but overall wood density did differ significantly based on seven growth rings. Half-sib and full-sib loblolly pine families did not display significant variation, but clones within families differed significantly in wood density, latewood density, and latewood percentage, indicating the potential for gains in wood density from clonal selection. Heritabilities for wood density components were found to be moderate to high, indicating the potential for gains in wood density through selection of families or clones. Individual ring analysis revealed that the wood density of rings 1-4 was highly correlated with wood density through ring 7, suggesting that selection of juvenile wood density could be made at an early age.

Introduction

Genetic improvement of loblolly pine has been ongoing during the past 46 years, and significant gains in growth, disease resistance and stem straightness have been achieved (Li et al. 1999). The current deployment method of seedlings derived from wind-pollinated seed orchards limits the potential for improvement due to pollen contamination and low selection intensity. While improvements have been made in growth and disease resistance, little has been done to improve the wood properties of loblolly pine in breeding programs. As growth rates increase and rotations are shortened, juvenile wood

becomes more prevalent in harvested trees, changing the properties of the wood produced in plantations (Zobel et al. 1978). The use of full-sib seedlings or rooted cuttings for propagation may produce gains in desirable wood properties, but, thus far, little is known about the effect that these propagule types will have on wood density characteristics.

Wood density, the weight of wood per unit volume (g/cm^3), is a measure of the amount of solid wood material in a tree and is an important characteristic that is related to wood strength and pulping yield (Mitchell 1964). Wood density is influenced by several other wood traits, including cell diameter, cell wall thickness, tracheid length, and the amount of latewood produced by the tree (Zobel and Talbert 1984). Within-ring variation in wood characteristics also influences overall wood density. The variation between earlywood and latewood density can be the largest source of variation within a tree (Zobel and van Buijtenen 1989). Earlywood is generally produced during the period of active leader growth in the early growing season. Latewood production occurs in the latter part of the growing season, during and after the resting bud stage (Kennedy 1971; Zobel and van Buijtenen 1989). Previous research has shown that the proportion of latewood to earlywood, as well as the variation in density of earlywood and latewood, influence overall wood density in individual trees (Zobel and van Buijtenen 1989).

The transition from juvenile to mature wood production is another within-tree characteristic that influences overall wood density. Juvenile wood differs from mature wood in its structural properties, including shorter tracheid length, lower density, thinner

cell walls, lower strength and increased prevalence of compression wood (Megraw 1985). The timing of transition from juvenile to mature growth, determined by the age of the cambium, has a significant effect on wood quality and end-product utility (Sauter et al. 1999). The transition is not clearly defined in a tree and varies depending on the wood characteristic used to identify it (Bendtsen and Senft 1986). Wood traits that have previously been used to determine the transition include tracheid length, fibril angle, longitudinal shrinkage, lignin content and wood density (Sauter et al. 1999). While most hard pines and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) display distinct transitions from juvenile to mature growth, other species do not show distinct transitions (Hoadley 1990).

Variation in wood density characteristics has been studied in several species of pine, but wood density has not been used as a selection criterion in breeding programs to the same extent as growth or disease resistance characteristics. A provenance study of loblolly pine found that provenances did not differ significantly in wood density of early rings (3 to 5), while families within provenances did differ (Belonger 1998). Trees on different sites produced significantly different wood density in early rings, and this accounted for about 75% of the total phenotypic variance for wood density. Individual-tree heritabilities for the wood density of early rings were low to moderate, varying from 0.179 to 0.234 (Belonger 1998). Similar individual-tree heritability estimates were reported by Hodge and Purnell (1993) for wood density of individual rings in slash pine (*Pinus elliottii* Engelm.) in a study of 56 open-pollinated families of slash pine.

Individual-tree heritabilities for earlywood density and transition age based on latewood percentage, latewood density, and ring wood density were also low to moderate (Hodge and Purnell 1993). There was no useful genetic variation in earlywood density among half-sib families for slash pine, but it did vary significantly among clones of *Pinus radiata* D. Don. (Donaldson et al. 1996). A study of genetic variation in transition age of loblolly pine from east Texas found significant differences in transition age among families when based on a specific wood characteristic, such as specific gravity or wood density (Loo et al. 1985). Transition ages based on wood specific gravity ranged from 9.8 to 13 years in half-sib families. There is little available information on variation among full-sib families of loblolly pine for within-ring wood density components.

The use of rooted cuttings for loblolly pine regeneration is presently being studied (Stelzer and Goldfarb 1997). Early growth and survival of rooted cuttings have been reported to be similar to those of seedlings in loblolly pine (Frampton et al. 2000). A clonal study of *Pinus radiata* at 16 years of age found that cloned propagules had lower wood density compared to seedlings. This difference was attributed to the age of the donor material, which was 5 years old (Donaldson et al. 1996). Seedlings and rooted cuttings of loblolly pine from juvenile hedged donor plants did not differ significantly in a comparison of whole-core specific gravity at ten years of age (see Chapter 1). Little is known about possible differences between seedlings and rooted cuttings on individual ring density characteristics in loblolly pine.

Clonal forestry continues to be an objective in loblolly pine research because of the potential large gains in growth rate and disease resistance (Stelzer and Goldfarb 1997). Clones of *Pinus radiata* were analyzed using x-ray densitometry and results demonstrated significant differences among clones for earlywood density and latewood density, but not for latewood percentage. Earlywood density had a major influence on overall density since it was the dominant component of each ring (Donaldson et al. 1996).

In a previous study of rooted cuttings and seedlings from nine full-sib families on two sites, significant differences in specific gravity were observed among families and clones (see Chapter 1). A greater understanding of how clones differ in ring density and other components of wood-core density is needed if the enhancement of wood quality through increased uniformity and density is to be incorporated into tree improvement programs for the improvement of wood quality. This study uses an analysis of individual-ring density traits from seedlings and rooted cuttings of nine full-sib families of loblolly pine at 10 years of age using x-ray densitometry to explore density variation. The objectives of the study were; (1) to determine the correlation of ring density traits and composite traits to overall wood density; (2) to determine the differences between rooted cuttings and seedlings for wood density components; (3) to estimate genetic parameters for wood density components; and (4) to compare the uniformity of wood density components of clones and full-sib seedlings.

Materials and Methods

Plant Material

The experimental design for this study is based on the field trial study design of Frampton et al. (2000) as described in Chapter 1. Briefly, 12-mm wood cores were collected in 2001 from an existing field trial of rooted cuttings and seedlings loblolly pine from nine full-sib families at two sites located in Monroe County, Alabama, and Nassau County, Florida. Wood cores were mounted on yellow poplar strips and sectioned longitudinally using a double-bladed table saw to produce a 2-mm-thick strip from the center of each wood core, exposing the radial face of the core. These strips were examined using Quintek Measurement Systems™ Density Profiler x-ray densitometers at the University of Georgia and USDA Forest Service Southern Forest Research Station in Athens, GA. The cores were scanned and analyzed for ring density (kg/m^3), earlywood density (kg/m^3), latewood density (kg/m^3), percentage of latewood, and ring width (mm).

Although the trees were 9 and 10 years of age (Florida and Alabama, respectively) most wood cores had only 7 rings. Two to three year's growth was missing from the center of the cores because they were taken at breast height (4.5 ft). Therefore, only rings 1-7 of all cores were analyzed. Approximately 558 rooted cuttings and 366 seedlings from four replications per site were used in this analysis.

Composite-Ring Traits

Individual-ring trait data were combined to form composite whole-core estimates of earlywood density, latewood density and latewood percent. A fourth trait, called LW40, was based on identification of the ring in which the proportion of latewood reached 40%. This trait was used to determine if trees vary in the time they take to produce rings with an increased proportion of latewood. Earlywood and latewood production were measured by calculating a weighted average of earlywood or latewood density against the width of the corresponding ring segment. To determine the overall latewood percentage of a core, the latewood widths were summed for the core and divided by the total core width.

Core Segments

Core segments beginning with ring 1 (nearest to the pith) and incrementally increasing by one outer ring (ring 1, rings 1-2, rings 1-3, rings 1-4, rings 1-5, rings 1-6, and rings 1-7) were used to estimate wood density for younger-aged cores. To estimate the density of each core segment, the ring density values were weighted according to the width of the rings.

Statistical Analysis

An analysis of variance for the observed characteristics was performed using the GLM procedure (SAS 1989). The combined analysis for both rooted cuttings and seedlings was performed for five composite wood traits: wood core density (WD), earlywood

density (EWD), latewood density (LWD), latewood percentage (LWP) and LW40. The model used for this analysis was as presented by equation [1] in Chapter 1, where site, replication, and type were treated as fixed and all remaining terms were treated as random using the random test statement in the GLM procedure.

Separate analyses of variance were then conducted for rooted cuttings and seedlings using a factorial mating design, as described in equations [2] and [3] of Chapter 1. Variance and covariance estimates were generated from the MIXED procedure in SAS. In the separate analysis of seedlings and cuttings, site and replication were treated as fixed effects, while all remaining terms in the model were treated as random.

Three types of correlations were calculated using the CORR procedure in SAS. Phenotypic correlations were estimated for EWD, LWD, and LWP for individual rings to observe the changes in correlations across individual rings. Phenotypic correlations between WD and the composite traits EWD, LWD, LWP, and LW40 were also calculated. Finally, correlations between core segments and overall wood density were determined to compare younger-aged core segment densities with the overall wood density estimate for the core.

Heritability

Heritability estimates for the five wood density components were calculated separately from the variance component estimates for seedlings and rooted cuttings using a program

with the SAS MIXED and IML procedures (Xiang and Li 2001), using formulae described in Chapter 1. Heritability estimates were also calculated for wood density based on the core segment data. Narrow-sense individual-tree heritability (h^2_i), half-sib family-mean heritabilities (h^2_{HS}), and full-sib family-mean heritabilities (h^2_{FS}) were estimated for both seedlings and rooted cuttings. For seedlings, within-family heritabilities (h^2_{wHS} , h^2_{wFS}) were estimated, while narrow-sense clone-mean within-family heritabilities ($h^2_{c_HS}$, $h^2_{c_FS}$) were estimated for rooted cuttings. A broad-sense clone-mean heritability (H^2_{CM}) was also calculated for rooted cuttings (see Chapter 1).

Coefficients of Variation

Coefficients of variation (CV's) were calculated as described in Chapter 1 for WD, EWD, LWD, LWP, and LW40 for rooted cuttings and seedlings. For clones, all ramets on a site were averaged to determine the CV for each clone. For full-sib families, a CV was calculated from each seedling on the site. CV values for clones and full-sib families were then averaged on each site to compare what level of uniformity might be expected in full-sib family blocks as compared to clonal blocks.

Results

Correlations

Phenotypic correlations of density components with overall wood-core density were variable (Table 1). LWP was the most highly correlated component with WD (0.84), while correlations for LW40 (-0.58), EWD (0.48), and LWD (0.23) were weaker.

Correlations between ring density and EWD, LWD, and LWP changed as the rings became more distant from the pith (Figure 1). Rings closer to the pith had a higher correlation between wood density and earlywood density and this correlation decreased in rings more distant from the pith. Correlations between latewood density and total wood density, while not as strong as those between earlywood density and total wood density, increased with distance from the pith. The correlation between latewood percent and ring wood density was consistently high in all rings.

Individual and family-mean phenotypic correlations were similar for seedlings and rooted cuttings for composite ring traits (Table 1). LWD was weakly correlated with WD in both seedlings (0.21) and rooted cuttings (0.24). EWD was more highly correlated with WD than LWD in both propagule types, based on individuals and family means. LWP had a high positive correlation with WD in both seedlings (0.82) and cuttings (0.86), while LW40 exhibited a moderately strong negative correlation with WD in both propagule types (-0.58). Family-mean correlations were slightly higher than phenotypic correlations with WD for LWD and LW40. The LW40 family-mean correlation with density was strongly negative.

Combined Analysis of Rooted Cuttings and Seedlings

Differences between sites were significant for several component traits, while differences between propagule types were significant only for WD (Table 2). WD, LWP, and LW40 differed significantly across the two sites in the split-plot test, but the differences were

small for least square (LS) means of all traits across sites (Table 3). Average WD was 423.7 kg/m³ in Florida and 394.4 kg/m³ in Alabama. LWP was higher in Florida with an average of 27.6% as compared to 24.9% in Alabama. LW40 was lower in Florida (4.5 rings) than in Alabama (6.4 rings), indicating a difference between sites for the ring in which latewood reached 40%. Trees on the Florida site also appeared to reach 50% latewood during the fifth ring while trees on the Alabama site did not reach 50% latewood through the seventh ring (Figure 2a). Individual ring density also differed between sites, but not between propagule types (Figure 2b). Neither LWD nor EWD differed significantly between sites or propagule types based on the split-plot analysis, but small differences were observed in the LS means (Figure 3, Table 2). While EWD and LWD were slightly higher in trees on the Florida site in certain rings, the overall earlywood density and latewood density did not differ significantly between sites or between propagule types in the split-plot analysis.

In the combined analysis of sites and types, genetic effects were generally not significant (Table 3). However, females differed significantly for density ($p > 0.0073$) and the female by site interaction was significant ($p < 0.0444$) for density. The site by male interaction and the replication by type interaction were significant for LW40 ($p < 0.0019$ and $p < 0.022$, respectively). Genetic effects were not significant for LWD, but the female effect was significant ($p < 0.001$) for EWD.

While neither male nor female parent was found to contribute significantly to differences detected in the combined analyses of seedlings and rooted cuttings, variation was observed among full-sib families on the two sites for ring density and ring latewood percentage (Figure 4). Although the differences were not significant for composite values from all rings, families differed by as much as 14% in latewood percentage and 60 kg/m³ in density in individual rings. The trees on the Alabama site appeared to exhibit more variation among families for both ring density and latewood percentage than those on the Florida site (Figure 4).

Separate Analyses of Rooted Cuttings and Seedlings

In the separate analyses of rooted cutting and seedlings, few genetic effects (half-sibs, full-sibs, or clones) were significant in density components for either propagule type. The female parent effect was significant for LW40 in rooted cuttings ($p < 0.0136$) (Table 4.), but neither the male parent effect nor the female by male interaction were significant for any traits in either propagule type. In the rooted cutting analysis, the clone within full-sib family was significant for WD ($p < 0.0001$), LWP ($p < 0.005$) and LWD ($p < 0.0352$), but not for LW40 or EWD.

While few genetic effects were significant, the site effect was significant for WD ($p < 0.0012$) and LW40 ($p < 0.0001$) in seedlings and for LW40 ($p < 0.0059$) and LWD ($p < 0.0001$) in rooted cuttings. The replication within site effect was significant for WD ($p < 0.0256$) in rooted cuttings. The female by site interaction was significant for density

($p < 0.0329$) in seedlings and for LW40 ($p < 0.0001$) in rooted cuttings. The male by site, female by male by site, and clone (within female by male) by site interactions were not significant for any traits in the separate analyses of propagule types.

Heritability Estimates

Heritability estimates for wood density components were higher for rooted cuttings in WD, LWP, and LW40, but higher for seedlings in EWD and LWD (Table 5). Standard errors of individual-tree heritabilities were high for cuttings and seedlings. Half-sib and full-sib family mean heritabilities were similar between rooted cuttings and seedlings, except for EWD and LWD, where seedlings heritabilities were higher.

Within-family heritability estimates were higher in clonal rooted cuttings than in full-sib seedlings. Within-family heritabilities were slightly higher in clone-mean within half-sib family estimates than in within-family seedling estimates except for EWD and LW40, where the seedling-within-family estimates were higher. Clone-mean within full-sib heritabilities were higher than within full-sib seedling heritabilities for all traits. The clone-mean within full-sib estimates varied from 0.81 to 1.10, while seedling within full-sib estimates varied from 0.10 to 0.43.

LWP exhibited the highest heritability for the traits related to latewood production. WD exhibited similarly high family-mean heritabilities in both rooted cuttings and seedlings.

LW40 exhibited the lowest individual-tree heritabilities in both rooted cuttings and seedlings (0.22 and 0.17, respectively).

Coefficients of Variation

Coefficients of variation (CV's) for WD and LWP were lower in a simulated clonal block of rooted cuttings than in a block of full-sib seedlings in both the Florida and Alabama sites (Table 6). The LWD CV was lower for clones than for full-sib seedlings in Florida, but the two types had similar values in Alabama. On the Florida site, the clonal LW40 CV was slightly higher than that of seedlings, but in Alabama the clonal CV was lower than for seedlings. CV's were lowest for WD and highest for LW40, indicating that there may be more variability in LW40 than in WD in full-sib families and clones.

Core Segments

The correlation between the WD of core segments and whole-core WD increased as rings were added (Figure 5). Seedlings and rooted cuttings produced similar results for segments 1-3 through 1-7. The correlation between WD of core segments and whole-core WD reached 0.90 when ring 4 was incorporated. The most dramatic increase was between rings 1 and rings 1-2, where the correlation increased from below 0.7 to 0.82 in both propagule types followed by a smaller but steady increase as outer rings were added.

Heritability estimates for ring groups increased as outer rings were added (Table 7). Individual-tree heritability estimates were higher in rooted cuttings for all ring groups,

but standard errors were also high for both propagule types. Half-sib family mean heritabilities were slightly higher in rooted cuttings for all ring groups while full-sib family mean heritabilities were higher in seedlings for all ring groups. Standard errors of heritability estimates were higher in younger rings, but decreased as outer rings were added. Family-mean heritabilities (half-sib and full-sib) were 0.60 or greater for ring groups 1-2 to rings 1-7.

Discussion

In this study, EWD, LWD, LWP, and LW40 did not differ significantly between propagule types, but a significant difference was seen in WD using the split-plot design. The LS means also showed a small, but significant, difference between types for WD and EWD. No significant difference was expected in this study because the whole-core specific gravity analysis in Chapter 1 revealed no difference between propagule types. The difference in significance could be due to the different methods of measuring wood density, the change in the sample (this study was a sub-set of the whole-core analysis), or the strength of the experimental design. The donor plants (hedges) from which the rooted cuttings in this study were taken were less than three years old (Anderson et al. 1999). If older hedges or more mature trees were used as parent material, a greater impact on wood density in trees grown from rooted cuttings might have resulted. In radiata pine, rooted cuttings from older donor plants (4 to 5 years old) may produce wood with reduced density (Lausberg et al. 1995). From this study it appears that wood density components

in loblolly pine would decrease slightly, but the difference would be very small as long as they are produced from relatively juvenile hedges.

The differences observed in WD, LWP and LW40 between sites were likely due to the effects of climate and soil fertility on tree growth. Using the split-plot design, sites were significantly different for WD and LW40, while the LS means also showed the Florida site slightly higher in LWP, EWD, and LWD. The values for EWD and LWD were very similar between the two sites, suggesting that the amount of latewood produced is the most important factor for whole-core density. An earlier study reported a trend of increasing specific gravity moving southward from Maryland to Florida (Zobel and van Buijtenen 1989) while another trend was observed increasing from northwest to southeast across the range of loblolly pine (Mitchell 1964). Greater proportions of latewood in loblolly in Florida may be due to differences in rainfall amounts and distribution (Zobel and van Buijtenen 1989). In this study, this effect may have been confounded by slower growth on the Florida site. Though results from previous research are not conclusive, slower growing trees may produce higher density wood (Zobel and van Buijtenen 1989; Zhang 1995). The Alabama site was previously an agricultural field, which tends to have higher soil fertility than cut-over forest sites, such as the Florida site. The volume produced by trees on the Alabama site was nearly three times greater than that produced by trees on the Florida site (see Chapter 1), suggesting that the most important difference between sites was soil fertility.

The separate analyses of seedlings and rooted cuttings across two sites revealed few genetic factors that had significant effects on measured wood density components. While family terms were not significant, the clonal (within full-sib family) terms were significant for density, LWP, and LWD in rooted cuttings. The lack of differences between families could be due to the low number of parents used in this study, or to a greater amount of variation within than among families. The method of measuring wood density, as well as the decrease in sample size could also have affected the results. This is in contrast to the results in Chapter 1 where half-sibs and clones varied significantly for whole-core specific gravity. Site by female and site by clone interactions were also significant for whole-core specific gravity, but not in the wood density components of this study. The number of observations was lower in the x-ray analysis due to only using four replications on each site and a reduced number of clones, which may have influenced the results due to fewer degrees of freedom. An earlier study of slash pine revealed little useful variation in earlywood density among families (Hodge and Purnell, 1993). A similar outcome was seen in this study, in half-sib and full-sib families as well as clones.

Latewood production, although heritable, appears to be significantly influenced by climate and geography. A large, multi-location study would be required to characterize site specificity and density gains that could be achieved by clonal deployment. While there were no significant clone by site interactions in this study, a larger number of clones across several sites would be needed for a more definitive answer.

An earlier study of loblolly pine found that a small improvement in reduced proportions of juvenile wood could be achieved through family selection (Loo et al. 1985). Similarly, latewood production varies among families, but greater gains in wood density associated with latewood production could be made through clonal selection. The use of selected clones in loblolly pine plantation forestry could increase latewood density and latewood percent, thus, increasing wood density.

This study found that EWD was more highly correlated with the juvenile-wood core density than LWD. This is perhaps due to the fact that LWP is not more than 30% for the core, thus the core is 70% earlywood. In our study, LWP was the only trait that had a high correlation with ring density in all rings, and was also strongly correlated with WD on an individual tree and family basis. This suggests that the amount of latewood in a ring, rather than the actual density of the latewood, had a strong influence on the overall wood density of the core. LW40 was highly correlated with WD on a family mean basis (-0.88), suggesting that selections of families or clones for LW40 could reduce the number of rings required to reach 40% latewood. LW40, or a similar measure, could be used as an indicator of transition age. While regression techniques have been used in the past to determine the point of transition between juvenile wood and mature wood, a threshold latewood percentage is also commonly used. Loo et al. (1985) reported transition ages based on specific gravity from 9 to 13 years, which are higher than the values from the LW40 trait in this study. A value of 50 percent latewood has been used

in the past, but this may not be an adequate indicator across the geographic range of loblolly pine because some trees may never produce rings with 50% latewood (Clark personal communication). The difference between sites for 40% latewood production in individual rings (about 2 years) has been observed in another study in similar locations, though the transition (defined by 50% latewood) was reached in later rings in comparison to this study (Belonger 1998). In this study, a definitive transition age cannot precisely be defined because overall density and LWP were still increasing, but there was a difference between sites in the time required to reach LW40.

The lack of a strong correlation between wood density and latewood density or earlywood density may reflect limited variation among sites, types, and families for latewood density and earlywood density in this study. The composite earlywood density trait from this study was found to be more highly heritable than the earlywood density trait in slash pine (0.13) by Hodge and Purnell (1993). These authors also found that latewood density and latewood percentage were moderately to highly heritable in all rings, an observation similar to those made in this study for the composite traits of latewood percentage and latewood density.

Clones and full-sib seedlings differed slightly for CV's of wood traits. WD, EWD, and LWP were less variable in clonal blocks than in seedling blocks on both sites, suggesting that deployment of clones in blocks would be somewhat more uniform than seedlings deployed in full-sib blocks. LWP and LW40 were more variable (phenotypically) than

WD, EWD, or LWD within clones and full-sib families. Planting full-sib seedling or clonal blocks may be one method of increasing the uniformity of wood, but a test involving blocks of clones or full-sib families to compare with seed orchard mixes and half-sib family blocks is needed to better estimate this increase in uniformity.

Heritabilities for all traits were moderate to high for individual trees, but standard errors for these heritabilities were all greater than half the heritability estimate. Individual-tree heritabilities were much higher for the composite traits of latewood percentage, latewood density, and earlywood density than was found in a study of slash pine (Hodge and Purnell 1993), where estimates of overall wood density and earlywood density were low (0.33 and 0.13, respectively). In slash pine, latewood percentage was less heritable than wood density (Hodge and Purnell 1993), but in this study heritability estimates for overall wood density and LWP were similar and these were the two most highly heritable traits investigated. The clone mean heritabilities were high for all traits, but greater than 0.90 for WD and LWP, indicating the potential for increased gains in wood density through clonal selection.

Moderate to high heritability estimates for core segments indicate that selection for improved juvenile wood density may be possible based on juvenile wood density at age 3 to 5 years. A earlier study of loblolly pine found that early selection for increased wood specific gravity could be more efficient than selection based on growth traits (Williams and Megraw 1994). Both rooted cuttings and seedlings revealed high correlations

between composite rings 1-3 and 1-4 and overall wood density, indicating that results of selection based on 3 or 4 rings would be similar to selection based on 7 rings. However, mature wood is not present in this study, so a comparison between juvenile wood density and rotation age wood density cannot be made.

Limitations and Assumptions

This study explored the differences in wood density components for rooted cuttings and seedlings of nine full-sib families. With only nine families from six parents, the variance components and heritability estimates may be biased due to genetic drift of a small population size. The parents of this study were not selected for their wood properties, but instead for their range of growth and disease resistance. Therefore, the range of values for wood density components in this study may not reflect the range of values in a larger population. While this study showed differences among clones for certain traits, a larger study across multiple sites including a greater number of clones from more families would be needed to estimate reliable gains in wood density for clonal deployment. The wood strips in this study came from a single core, which may not be representative of the wood in an entire tree (Megraw 1985). The ring data were collected from an x-ray densitometer on a limited number of individuals, which may have introduced bias into this study.

Conclusions

The results of this study indicate that rooted cuttings and seedlings from the same full-sib families do not exhibit dramatic differences in wood density, latewood density, earlywood density, latewood percentage, or in the onset of 40% latewood production (LW40). Site differences were significant for WD, LWP and LW40, supporting the conclusion that latewood production is an important contributor to overall wood density. Whole-core wood density and latewood percentage were the most highly heritable traits. Plantations of clonal blocks would be slightly more uniform than those of full-sib seedling blocks. The significance of the clonal terms for wood density and latewood percentage suggests that increases in wood density could be achieved through the use of clonal rooted cuttings for propagation of loblolly pine.

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Table 1. Phenotypic (r_p) and family mean (r_{family}) correlations (Prob > |r| under H0) of earlywood density (EWD), latewood density (LWD), latewood percentage (LWP) and LW40 with overall wood density (WD) across two sites for seedlings and rooted cuttings.

Type	Correlation with WD			
	EWD	LWD	LWP	LW40
All Trees r_p	0.48 (<.0001)	0.23 (<.0001)	0.84 (<.0001)	-0.58 (<.0001)
Seedling r_p	0.56 (<.0001)	0.21 (<.0001)	0.82 (<.0001)	-0.58 (<.0001)
Cutting r_p	0.40 (<.0001)	0.24 (<.0001)	0.86 (<.0001)	-0.58 (<.0001)
Seedling r_{family}	0.81 (0.0086)	0.60 (0.0847)	0.85 (0.0039)	-0.89 (0.0014)
Cutting r_{family}	0.62 (0.0764)	0.37 (0.3261)	0.95 (0.0001)	-0.88 (0.0014)

Table 2. Means (standard errors) for overall wood density (WD), earlywood density (EWD), latewood density (LWD), latewood percentage (LWP), and LW40 for rooted cuttings in the Florida and Alabama sites.

Site	Type	Density	EWD	LWD	LWP	LW40
Florida	Cuttings	421.42 (1.51) A	339.4 (1.02) A	667.23 (2.76) A	0.2765 (0.0032) A	4.47 (0.068) A
	Seedlings	425.94 (1.87) A	344.6 (1.26) B	661.30 (3.40) A	0.2761 (0.0039) A	4.48 (0.085) A
Alabama	Cuttings	393.3 (1.45) A	319.6 (0.97) A	654.67 (2.63) A	0.2457 (0.0031) A	6.47 (0.069) A
	Seedlings	395.5 (1.78) A	319.3 (1.21) A	658.08 (3.25) A	0.2524 (0.0037) A	6.34 (0.082) A
Combined	Florida	423.7 (1.20) A	342.0 (0.81) A	664.3 (2.19) A	0.2763 (0.0025) A	4.47 (0.054) A
	Alabama	394.4 (1.15) B	319.5 (0.78) B	656.4 (2.11) B	0.2491 (0.0025) B	6.41 (0.054) B
Combined	Cuttings	407.3 (1.04) A	329.5 (0.70) A	660.9 (1.89) A	0.2611 (0.0022) A	5.46 (0.048) A
	Seedlings	410.7 (1.29) B	331.9 (0.87) B	659.7 (2.35) A	0.2642 (0.0027) A	5.41 (0.059) A

Letters denote significant difference between propagule type within or across sites at 95% level

LW40 given in percent and all other means given in kg/m³

Table 3. F ratios and significance levels for combined analysis of variance of wood density (WD), latewood density (LWD), latewood percentage (LWP), LW40, and earlywood density (EWD).

Source	DF	<u>WD</u>		<u>LWD</u>		<u>LWP</u>		<u>LW40</u>		<u>EWD</u>	
		F	Pr > F	F	Pr > F	F	Pr > F	F	Pr > F	F	Pr > F
Site	1	1097929	0.0006***	7.32	0.2254	25.48	0.1245	468.65	0.0294*	99.16	0.0637
Rep (Site)	3	9.53	<.0001***	5.71	0.0007***	2	0.1119	4.49	0.0039**	1.88	0.1315
Type	1	1982	0.0143*	0.35	0.6586	0.04	0.8772	0.02	0.9117	0.76	0.5446
Rep x Type	5	2.72	0.019*	2.09	0.0645	1.51	0.1839	2.65	0.022*	3.52	0.0037**
Site x Type	1	0	0.9885	1.7	0.2041	1.34	0.2587	1.62	0.212	2.32	0.1406
Female	2	24.58	0.0444*	1.59	0.3314	12.9	0.1012	16.71	0.1159	29.67	0.1647
Male	2	10.5	0.1597	0.68	0.6011	34.82	0.3259	1.27	0.4123	1.24	0.6984
Site x Female	2	3.08	0.0709	1.89	0.18	2.05	0.158	3.01	0.072	2.85	0.0843
Site x Male	2	2.18	0.1415	1.97	0.1687	1.76	0.1999	8.75	0.0019**	0.83	0.4518
Female x Male	4	0.65	0.6334	2.04	0.134	0.48	0.7514	1.62	0.2108	0.35	0.8405
Site x Type x Female x Male	16	1.11	0.3395	1.35	0.1624	1.28	0.2009	0.58	0.8987	1.36	0.1568

Means of the effects were significantly different at 95%(*), 99%(**), and 99.9%(***)

Table 4. Variance Component estimates for overall wood density (WD), earlywood density (EWD), latewood density (LWD), latewood percentage (LWP), and LW40 based on the combined analysis of 2 sites.

Term	<u>Density</u>		<u>EWD</u>		<u>LWD</u>		<u>LWP</u>		<u>LW40</u>	
	Cutting	Seedling	Cutting	Seedling	Cutting	Seedling	Cutting	Seedling	Cutting	Seedling
Fem	241.23	178.49	129.20	186.69	112.640	127.89	0.000627	0.00013	0.1085*	0.0894
Male	24.79	47.26	18.55	0	8.401	1.42	0.000245	0.00041	0.0217	0.0093
Fem*Male	0	5.30E-16	0.00	9.56E-17	0.000	0.00	0.000000	0.00000	0.0000	0.0000
Clone(Fem*Male)	138.01*	-	53.92	-	128.63*	-	0.000371*	-	0.0278	-
Site	-	-*	-	-	-*	-	-	-	-*	-*
Rep(Site)	-*	-	-	-	-	-	-	-	-	-
Fem*Site	0	24.71*	4.11	0	35.509	0.00	0.000000	0.00018*	0*	0.0214
Male*Site	0	20.52	0.00	1.23E-16	0.000	0.00	0.000000	0.00001	0.0194	0.0217
Fem*Male*Site	0	0	0.00	0	0.000	0.00	0.000000	0.00000	0.0000	0.0000
Clone*Site(Fem*Male)	3.68	-	32.85	-	52.950	-	0.000132	-	0.0356	-
Fem*Rep(Site)	7.02E-36	1.70	16.26	0	0.000	4.29	0.000059	0.00000	0.0000	0.0000
Male*Rep(Site)	4.89	5.30	35.41*	0	14.200	0.00	0.000000	0.00000	0.0217	0.0348
Fem*Male*Rep(Site)	3.77	12.50	0.00	2.13E-15	0.000	0.00	0.000000	0.00000	0.0013	0.0000
Clone(Fem*Male)*Rep(Site)	4.20	-	7.82	-	0.000	-	0.000016	-	0.1078	-
Residual	317.99	495.84	483.15	675.01	506.900	729.00	0.001894	0.00270	0.8428	0.9560

* Means of the effects were significant at the 95% level. Site and Rep(Site) are assumed to be fixed, so there is no variance for this estimate.

Table 5. Heritability estimates (standard error) for overall wood density (WD), earlywood density (EWD), latewood density (LWD), latewood percentage (LWP), and LW40, for rooted cuttings and seedlings separately.

Heritability	WD		EWD		LWD		LWP		LW40	
	Cutting	Seedling	Cutting	Seedling	Cutting	Seedling	Cutting	Seedling	Cutting	Seedling
h^2_i	0.72 (0.48)	0.57 (0.37)	0.38 (0.31)	0.43 (0.35)	0.28 (0.30)	0.30 (0.27)	0.52 (0.33)	0.32 (0.26)	0.22 (0.20)	0.17 (0.19)
h^2_{HS}	0.72 (0.03)	0.67 (0.09)	0.69 (0.07)	0.72 (0.03)	0.60 (0.19)	0.71 (0.04)	0.72 (0.03)	0.61 (0.16)	0.66 (0.13)	0.56 (0.24)
h^2_{FS}	0.91 (0.09)	0.89 (0.12)	0.79 (0.18)	0.98 (0.02)	0.63 (0.31)	0.96 (0.04)	0.85 (0.12)	0.82 (0.22)	0.71 (0.24)	0.76 (0.32)
$h^2_{C_wHS}$	0.63 (0.13)	-	0.22 (0.13)	-	0.44 (0.13)	-	0.36 (0.13)	-	0.07 (0.11)	-
$h^2_{C_wFS}$	1.10 (0.07)	-	0.99 (0.16)	-	0.95 (0.23)	-	1.04 (0.10)	-	0.81 (0.25)	-
H^2_{CM}	0.98 (0.018)	-	0.82 (0.093)	-	0.86 (0.10)	-	0.92 (0.05)	-	0.77 (0.19)	-
h^2_w	-	0.55 (0.43)	-	0.38 (0.36)	-	0.25 (0.25)	-	0.27 (0.25)	-	0.14 (0.17)
h^2_{wf}	-	0.43 (0.38)	-	0.28 (0.29)	-	0.18 (0.19)	-	0.19 (0.19)	-	0.10 (0.12)

Note: h^2_i = individual heritability; h^2_{HS} = Half-sib family mean heritability; h^2_{FS} = Full-sib family mean heritability; $h^2_{C_wHS}$ = clone mean heritability within half-sib families; $h^2_{C_wFS}$ = clone mean heritability within full-sib families; h^2_w = within half-sib family heritability; h^2_{wf} = within full-sib family heritability; and H^2_{CM} = clone mean heritability.

Table 6. Coefficients of Variation for wood density (WD), earlywood density (EWD), latewood density (LWD), latewood percentage (LWP), and LW40 for clone means of rooted cuttings and full-sib family seedling means.

Site	Type	Average CV(%)				
		Density	EWD	LWD	LWP	LW40
Florida	Cuttings	0.048	0.069	0.053	0.162	0.200
	Seedlings	0.060	0.082	0.072	0.199	0.192
Alabama	Cuttings	0.041	0.061	0.063	0.143	0.157
	Seedlings	0.060	0.071	0.068	0.172	0.185

Table 7. Heritability estimates for core segment wood density across two sites for rooted cuttings and seedlings.

Rooted Cutting	Core segment						
	1	1-2	1-3	1-4	1-5	1-6	1-7
h^2_i	0.16 (0.18)	0.29 (0.28)	0.38 (0.33)	0.48 (0.33)	0.59 (0.41)	0.64 (0.42)	0.61 (0.41)
h^2_{HS}	0.65 (0.11)	0.68 (0.07)	0.70 (0.05)	0.71 (0.04)	0.71 (0.04)	0.72 (0.03)	0.71 (0.04)
h^2_{FS}	0.58 (0.31)	0.69 (0.25)	0.73 (0.21)	0.80 (0.16)	0.86 (0.12)	0.88 (0.10)	0.88 (0.11)
$h^2_{C_wHS}$	0.20 (0.11)	0.33 (0.13)	0.39 (0.14)	0.47 (0.18)	0.57 (0.1)	0.59 (0.13)	0.60 (0.13)
$h^2_{C_wFS}$	0.74 (0.34)	0.93 (0.22)	0.99 (0.16)	1.04 (0.11)	1.07 (0.09)	1.08 (0.08)	1.07 (0.09)
Seedling							
h^2_i	0.05 (0.07)	0.19 (0.17)	0.35 (0.27)	0.46 (0.33)	0.54 (0.37)	0.55 (0.37)	0.56 (0.38)
h^2_{HS}	0.48 (0.30)	0.60 (0.19)	0.64 (0.13)	0.65 (0.11)	0.66 (0.10)	0.67 (0.09)	0.67 (0.09)
h^2_{FS}	0.64 (0.48)	0.81 (0.25)	0.86 (0.17)	0.88 (0.15)	0.89 (0.14)	0.90 (0.12)	0.90 (0.12)
h^2_w	0.03 (0.05)	0.16 (0.15)	0.31 (0.27)	0.42 (0.35)	0.51 (0.42)	0.52 (0.42)	0.53 (0.44)
h^2_{wf}	0.02 (0.04)	0.11 (0.11)	0.23 (0.21)	0.31 (0.28)	0.38 (0.35)	0.39 (0.36)	0.40 (0.37)

Note: h^2_i = individual heritability; h^2_{HS} = Half-sib family mean heritability; h^2_{FS} = Full-sib family mean heritability; $h^2_{C_wHS}$ = clone mean heritability within half-sib families; $h^2_{C_wFS}$ = clone mean heritability within full-sib families; h^2_w = within half-sib family heritability; and h^2_{wf} = within full-sib family heritability.

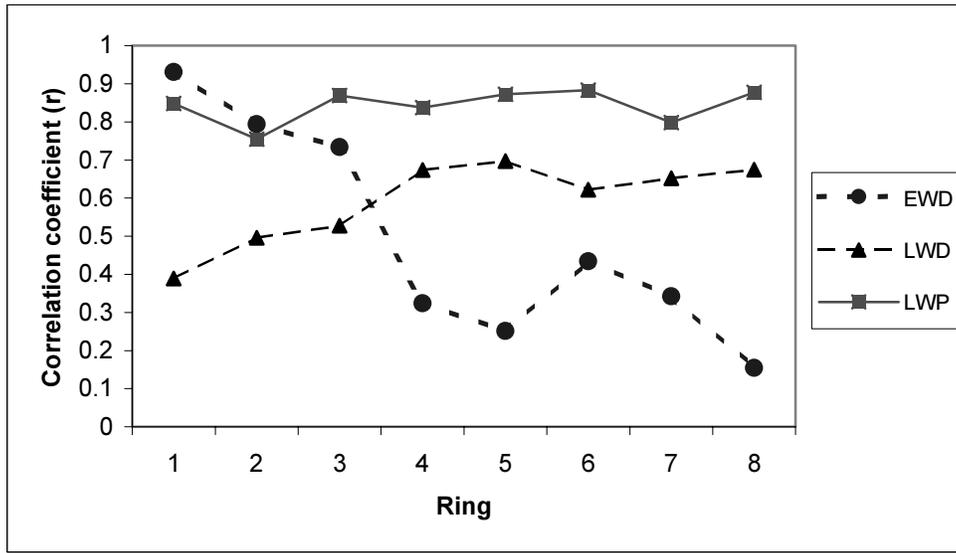


Figure 1. Correlations of individual ring values for earlywood density (EWD), latewood density (LWD), and latewood percentage (LWP) with ring density.

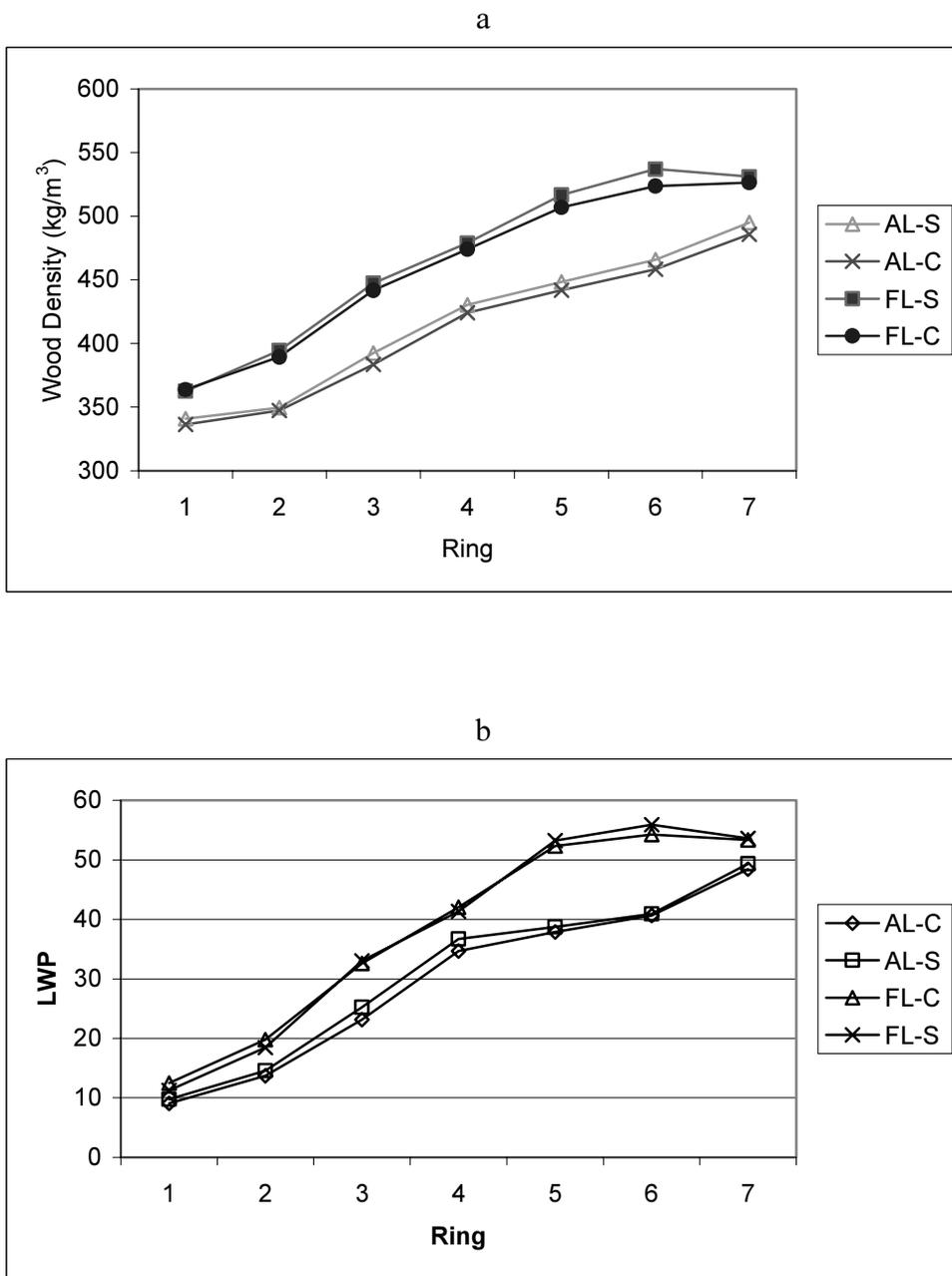


Figure 2. Ring density (a) and latewood percentage (b) by propagule type (C =rooted cutting, S=seedling) and site (AL = Alabama, FL = Florida).

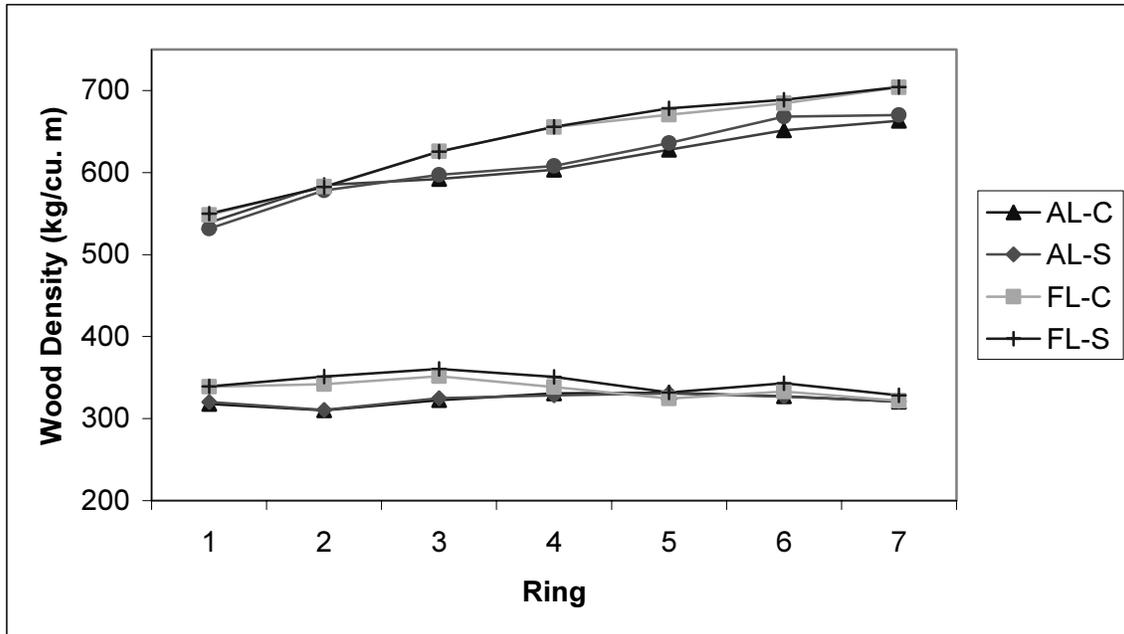


Figure 3. Latewood density and earlywood density by propagule type (C=rooted cutting, S=seedling) and site (AL=Alabama, FL=Florida).

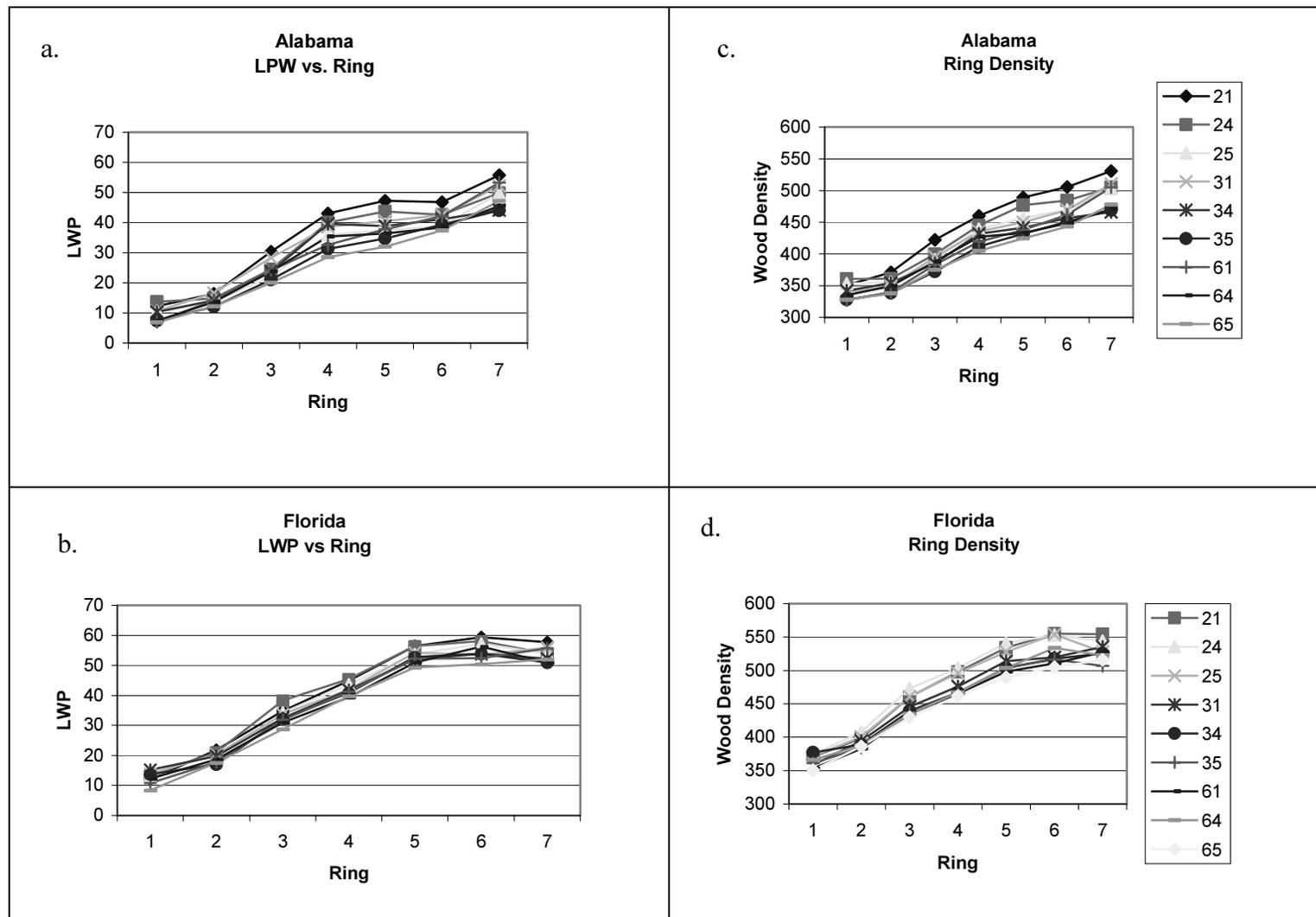


Figure 4. Latewood percentage by full-sib family and ring in Alabama (a) and Florida (b) and wood density by full-sib family and ring in Alabama (c) and Florida (d).

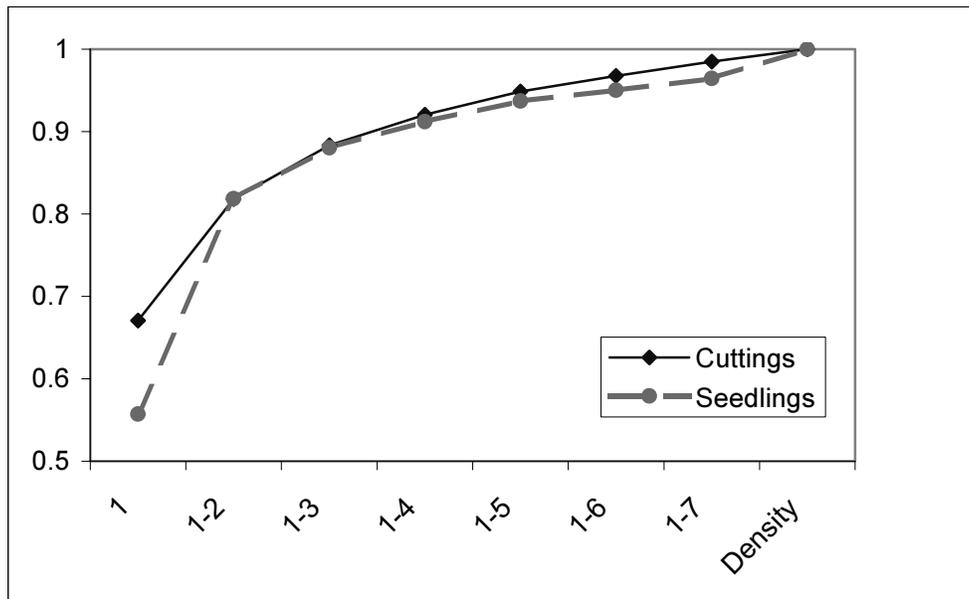


Figure 5. Core segment (1, 1-2, ..., 1-7) density correlations with whole-core density by propagule type (rooted cuttings and seedlings).

Conclusions and Implications

No dramatic differences were observed between rooted cuttings and seedlings in this study of nine full-sib families for specific gravity, earlywood density, latewood density, latewood percentage, LW40, or growth traits. The only significant difference between propagule types was observed in overall wood density from the x-ray densitometry analysis in Chapter 2, which may be due to the reduced sample size. Specific gravity (wood density) and latewood percentage did vary among clones and both were highly heritable, suggesting that gains in increased specific gravity could be made in loblolly pine through the use of clones. Clones also appeared to be more uniform in whole-core specific gravity (Chapter 1) and overall wood density (Chapter 2) than full-sib families, suggesting that the deployment of clones may contribute to increased wood uniformity if planted in blocks of very few clones. The results from this limited study of nine full-sib families on two sites, as well as previous research, suggest that the wood density of loblolly pine could be improved, though perhaps not as dramatically as improvements in growth characteristics have been since the total variance of specific gravity and density traits is relatively low. The highest density clone or full-sib family was between 5% and 10% above the test mean, suggesting that if a few desired genotypes were used, gains could be made in specific gravity. Several questions must be addressed, however, before improvements in wood density become feasible. The issues of making wood density improvement economically valuable and incorporating wood density into tree improvement programs are the two most challenging tasks. Future research on wood quality on a large population size is also important to utilize the variation in wood density of loblolly pine in a breeding program.

The value of higher density trees

Perhaps the most important issue dealing with the improvement of wood density is the economic value of higher density trees. Variation in wood density has been seen in several studies of loblolly pine, but the value of increased wood density is unknown. Currently, high-density trees do not have a higher stumpage value than low-density trees, and this will continue until mills are willing to pay higher prices for higher density trees. Wood is generally purchased by weight, so heavier trees have a higher value, but this could be due to increased density or moisture content. This raises the question of how to keep track of higher density trees. Will the origin or genetics of stands be documented so that higher density clones or families can be sorted in the wood yard? If wood is bought from private landowners, a major source of wood in the south, will landowners have access to the proper documentation sources so they know what type of wood they are selling? If forest products companies were self-sufficient in supplying their wood needs, documentation within the company would be less complex, but there are companies now that own mills and have no land. They are dependent on buying wood on the open market. One alternative to using the clone or family identification is to incorporate a wood density measurement to the timber cruise prior to a harvest. Higher prices could be paid for stands with higher wood density regardless of the genetic source. The present practice of buying wood by weight may be compatible with increased value of high-density trees because these trees will weigh more.

Wood density in a Tree Improvement Program

If a higher value is not placed on higher density trees, incorporating wood density into tree improvement programs is likely not feasible. If there is little or no economic value attached to a trait, the effort to incorporate that additional trait into a tree improvement program will not produce a monetary return. Variation and the potential for improvement of specific gravity has been researched during the last several decades, but it still has not been incorporated into the tree improvement programs for loblolly pine. Specific gravity has generally been recorded for parent trees in breeding programs, but this data may not be adequate for determining higher density parents if wood density were incorporated into the breeding program. The specific gravity of selections from wild stands may not reflect what that genotype would produce in a plantation environment. Based on the results of this study, wood density (specific gravity) is affected by site differences. Specific gravity measurements from progeny tests may not reflect what these same genotypes could produce under modern silvicultural regimes. New sampling and data collection may be required to obtain accurate specific gravity values for trees in breeding programs.

The relative value of specific gravity to other existing traits in a selection index would also be an issue for incorporating specific gravity into a tree improvement program. Is specific gravity equal to growth? Growth and specific gravity could be combined into a measure of yield, but the measure of yield might be for a specific end use such as pulp or

dimension lumber. The weight of specific gravity in the index would depend upon its economic value and the amount of genetic variation.

While this study and previous research shows variation among and within families for specific gravity, some may question the value of this genetic variation as a component of a breeding program. If site differences, including soil fertility and climate, significantly affect specific gravity, is there enough genetic variation to justify improvement? It appears that there is adequate variation. The two sites of this study differed in their mean specific gravity values, but clones also differed in their mean specific gravity. If a region or site is known for low wood specific gravity, clones could be deployed to ameliorate the environmental effects. If gains in specific gravity could be correlated to gains in wood strength of solid wood products or gains in pulp yield, then perhaps a percentage gain could be targeted for specific gravity. The cost of processing and the market value of the timber could, however, affect whether a given percentage gain was justified. It is possible that the northern part of the loblolly pine range could produce specific gravity values more typical to the middle of the range, perhaps increasing productivity in northern mills. In this study, the range of specific gravity values among families was greater than the difference between the two sites, suggesting that while sites and silvicultural practices will always affect specific gravity, genetics could still be used to increase specific gravity for a particular plantation.

Future Research

Further research is needed to quantify how clonal blocks and full-sib seedling blocks compare to current half-sib family blocks or seed orchard mixes. Clones from the best families need to be evaluated on a large scale across several sites to identify the best clones for deployment and determine the uniformity of wood properties. Specific gravity (density) was the primary trait investigated in this study, but other wood properties, both physical and chemical, are important and need to be assessed. The relationship between specific gravity and growth seems to be somewhat controversial with studies providing a variety of results, but further research of this relationship is needed in a large population, as the deployment of full-sibs or clones of loblolly pine becomes an alternative to planting half-sibs.

Although there are issues limiting the incorporation of wood specific gravity improvement in a breeding program for loblolly pine, the potential for making gains through family or clonal selection does exist. When the obstacles of placing a value on increased density and properly identifying high-density trees in the field are overcome, the application of the results from this study may become possible.