EFFECTS OF PLANTING DENSITY AND CULTURAL INTENSITY ON INDIVIDUAL TREE- AND STAND-LEVEL CROWN, STEM, AND GROWTH CHARACTERISTICS OF NON-THINNED AND THINNED LOBLOLLY PINE PLANTATIONS AT AGES 12 AND 13 AND DURING THE 13TH GROWING SEASON IN THE UPPER COASTAL PLAIN AND PIEDMONT OF THE SOUTHEASTERN U.S.

by

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(Under the Direction of Michael Kane)

ABSTRACT

Existing cultural intensity x planting density research installations were utilized to examine stem, crown, and growth attributes at ages 12 and 13 and during the 13th growing season in non-thinned and thinned loblolly pine plantations. Results showed that individual tree and stand-level stem and crown characteristics differed significantly by planting density, while differences between cultural intensities were minimal. This result suggests that at this stage of stand development, light limitations due to high stocking have a greater influence on growth than soil nutrient limitations for the loblolly pine plantations analyzed in this study. Interestingly, individual trees of a given DBH had similar crown characteristics regardless of the silvicultural treatments they received. For these stands, knowledge of DBH distribution appears to be a sufficient modeling tool regardless of past cultural or planting density treatment. Future research should include long-term analysis of these trends.

INDEX WORDS: Loblolly pine, Crown, Planting density, Culture, Thinning, Growth efficiency, Radiation

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B.S., West Virginia University, 2009

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2011

EFFECTS OF PLANTING DENSITY AND CULTURAL INTENSITY ON INDIVIDUAL TREE- AND STAND-LEVEL CROWN, STEM, AND GROWTH CHARACTERISITICS OF NON-THINNED AND THINNED LOBLOLLY PINE PLANTATIONS AT AGES 12 AND 13 AND DURING THE 13TH GROWING SEASON IN THE UPPER COASTAL PLAIN AND PIEDMONT OF THE SOUTHEASTERN U.S.

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December 2011

ACKNOWLEDGEMENTS

This research was possible through support from the National Science Foundation (NSF) Center for Advanced Forest Systems (CAFS) and the Plantation Management Research Cooperative (PMRC) at the University of Georgia. I wish to thank NSF CAFS and the PMRC for funding support and the PMRC field crew and industrial cooperators for the installation and maintenance of this study. Thank you Chris Silcox and Colin Threlkeld for helping me sort through thousands of pine needles and Santosh Subedi for being a great office-mate. Most importantly, I wish to thank my knowledgeable and very patient advisory committee, Dr. Mike Kane, Dr. Dehai Zhao, Dr. Bob Teskey, and Dr. Dick Daniels. I truly appreciate your help.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1. Purpose of Study

Loblolly pine is a widely studied tree species due to its commercial and ecological importance. Many studies have examined the effects of silvicultural practices on loblolly pine plantation productivity. There is a notable lack, however, in research concerning the physiological mechanisms that drive productivity and how these mechanisms respond to common silvicultural practices such as planting density, cultural intensity, and thinning. The purpose of this research was to evaluate the effects of a wide range of planting densities, distinct cultural intensities, and their combination on individual tree and stand attributes of loblolly pine plantations with an emphasis on crown characteristics. No other known studies have examined crown attributes on such an extensive range of loblolly pine stand structures. Specifically, the effects of six planting densities and two levels of cultural intensity on stem, crown, and growth characteristics of non-thinned and thinned loblolly pine stands were analyzed at ages 12, 13, and during the 13^{th} growing season in the Upper Coastal Plain and Piedmont of the southeastern U.S. Results from this research will provide a better understanding of foliar development patterns which can be used to improve process-based growth and yield models and develop more appropriate silvicultural prescriptions.

2. Thesis Structure

The remainder of this chapter consists of a literature review of the main topics addressed in this thesis. Chapters 2, 3, and 4 report on individual study segments contributing to the overall

research. Specifically, Chapter 2 consists of research on non-thinned stands at the individual tree level, Chapter 3 consists of research on non-thinned stands at the stand level, and Chapter 4 consists of research on thinned stands at the stand level. Main conclusions from Chapters 2, 3, and 4 are presented in Chapter 5.

3. Literature Review

3.1 Intensive Silviculture

Because of its popularity as a commercial tree species, a substantial amount of research has focused on intensive silviculture in loblolly pine (*Pinus taeda* L.) plantations. Silvicultural practices such as fertilization, control of competing vegetation, and density control have become effective practices for manipulating growth rates in loblolly pine plantations (Borders and Bailey 2001; Fox et al. 2007b; Jokela et al. 2004; Jokela et al. 2000; Will et al. 2005). Typically, the objective of these practices is to accelerate stand growth and development by influencing the availability and/or supply of site resources to select crop trees. Because intensive forest management requires considerable planning and investment, it is critical that gains in growth and yield justify silvicultural inputs. The response of loblolly pine to common silvicultural inputs has been fairly well documented, however, the mechanisms that drive this response are not thoroughly understood (Jokela et al. 2004; King et al. 2008; Tyree et al. 2009; Will et al. 2005).

3.2 Forest Fertilization and Control of Competing Vegetation

The purpose of forest fertilization is to alleviate site nutritional deficiencies by increasing the supply of nutrients essential to tree growth. Nitrogen (N)and phosphorus (P) are the nutrients most commonly limiting to loblolly pine growth (Fox et al. 2007a). If insufficient nutrition is the factor most limiting to tree growth, mitigation through fertilizer inputs can allow trees to take advantage of other previously unusable site resources (Fox et al. 2007a; Jokela and Martin 2000).

Similarly, by reducing the presence of competing vegetation, site resources (water, nutrients, light, etc.) become more available to the crop trees. Fertilization and competition control practices (alone and combined) can significantly increase productivity in loblolly pine plantations, although the nature of the response is very site and age specific (Allen et al. 2005; Fox et al. 2007a; Jokela et al. 2004; Jokela and Martin 2000; Jokela et al. 2000; Martin and Jokela 2004b; Will et al. 2002). Borders and Bailey (2001) conducted a study of 12-year-old loblolly pine plantations near Waycross, Georgia. Results showed that control plots exhibited 122 m^3 ha^{-1} merchantable volume, while complete competition control, annual fertilization, and the combination of the competition control and fertilization treatments resulted in 206, 360, and 381 m^3 ha^{-1} merchantable volume, respectively (Borders and Bailey 2001; Will et al. 2002). Although complete competition control and annual fertilization are extreme treatments, they illustrate the ability of loblolly pine to respond to increases in site resources.

3.3 Density Management

An early and important decision for forest managers is deciding how many trees to plant per unit land area. Lower planting densities (greater space between trees) allow for increased individual tree growth rates early in the rotation due to less competition among crop trees for site resources compared to higher planting densities (less space between trees). At the stand level, however, higher planting densities result in increased stand growth rates early in the rotation. Stands planted at higher densities have the ability to utilize site resources more quickly due to the greater number of stems per unit land area. In young stands, the increase in the number of stems per unit land area makes up for the decrease in average individual tree size at higher planting densities (Albaugh et al. 2006; Barron-Gafford et al. 2003; Carlson et al. 2009; Harms et al. 2000; Will et al. 2010). The greatest annual stem growth per unit area occurs initially in higher

density stands and later in lower density stands. Total stand volume for different planting densities will eventually converge at a maximum for a given site and then begin to decline. This convergence point represents the upper limit of productivity for a given site, and is influenced by site quality, stand age, and environmental conditions (Burkes et al. 2003; Will et al. 2001). Based on these general growth trends, choosing an initial planting density should take into account the objectives for the stand. The desired products and expected management practices throughout the rotation should be considered (Huang et al. 2005).

Thinning (harvesting a portion of the stand volume) is also used to manipulate stand density. By reducing the number of trees per unit land area, site resources are more available to the crop trees left after the thinning. Similar to the effect of low initial planting densities, individual tree growth rate is increased for a period after thinning, but this usually comes at the expense of overall stand growth rate (Ginn et al. 1991; Hennessey et al. 2004; Jokela et al. 2004; Peterson et al. 1997; Russell et al. 2010). Perhaps the main benefits of thinning are that volume that would otherwise be lost due to intra-specific competition-induced mortality is removed before it is lost, and the remaining trees display higher growth rates (Ginn et al. 1991; Hennessey et al. 2004; Jokela et al. 2004).

3.4 Intercepted Photosynthetically Active Radiation, Specific Leaf Area, and Radiation Use Efficiency

Significant changes in stand growth and development can be achieved through management of nutrition and inter- and intra-specific competition, as evidenced by the silvicultural practices mentioned previously. The success of these treatments is dependent upon the relationship between site resources and stand productivity. A more detailed understanding of the processes that drive this relationship is essential to develop prescription approaches resulting

in more consistent, site-specific growth responses due to intensive forest management of loblolly pine (Jokela et al. 2004; King et al. 2008; Will et al. 2001). Many processes that influence tree growth are related to crown size, structure, and chemistry. Crown vigor has become an accepted predictor of potential tree productivity, e.g. crown classes. Although there are many ways to assess crown vigor, perhaps one of the most intrinsic is a measure of the amount of usable light coming into contact with the leaves (MacFarlane et al. 2002; Will et al. 2005). This measurement is known as intercepted photosynthetically active radiation (IPAR), and it represents photosynthetic energy capture (Will et al. 2005). Studies have shown that IPAR is positively correlated with stem growth in loblolly pine, and is often linearly related to growth for a given site (Allen et al. 2005; Chmura and Tjoelker 2008; Dalla-Tea and Jokela 1991; McCrady and Jokela 1998; Will et al. 2001; Will et al. 2005). IPAR accounts for the total amount of foliage and how that foliage is displayed and distributed within the canopy, making it a more useful measure than crown size measures (foliar biomass, leaf area, etc.) which simply represent the amount of foliage (Allen et al. 2005; Will et al. 2005). In a study conducted in the Upper Coastal Plain and Piedmont of Georgia, Will et al. (2005) found that radiation use efficiency (current annual stem volume growth per annual IPAR) was constant for 4-year old loblolly pine planted at a wide range of densities, suggesting a functional relationship between IPAR and stand growth, although no other known studies have examined the relationship between planting density and radiation use efficiency in loblolly pine.

In the Lower Coastal Plain of the southeastern U.S., Will et al. (2001) found a positive linear relationship between current annual stand volume growth and IPAR for young loblolly pine stands planted at different densities even though as stand density increased, the amount of IPAR per unit leaf area most likely decreased due to self-shading. This phenomenon was

attributed to adjustments in needle morphology in response to differences in irradiance (Will et al. 2001). Specific leaf area (SLA), defined as leaf area per unit leaf mass, is one measure of needle morphology that can adjust under different light levels (Chmura and Tjoelker 2008; McCrady and Jokela 1996; Will et al. 2001). SLA is typically greater under more light-limited conditions (increased shading), resulting in more photosynthetic surface area per unit of needle biomass (longer, thinner needles), which may help mitigate the effects of increased shading (Meir et al. 2002; Samuelson et al. 2008; Samuelson et al. 2010; Will et al. 2001). Increased shading occurs with increasing canopy depth (Chmura and Tjoelker 2008) and with increasing planting density (Will et al. 2001).

Studies that examine the effects of soil nutrient availability and IPAR relationships for loblolly pine have shown inconsistent results. In a study in the North Carolina Sandhills, Sampson and Allen (1998) found that fertilized plots had significantly lower under-canopy PAR transmittance when compared to non-fertilized plots in 12-year-old loblolly pine. Decreased canopy light transmittance in the fertilized plots was attributed to large increases in leaf area index, however, the authors noted that foliage display may influence IPAR as well (Sampson and Allen 1998). In contrast, a loblolly pine study conducted in the West Gulf Coastal Plain by Chmura and Tjoelker (2008) showed that increased levels of fertilization and competition control resulted in no significant effects on plot-level light interception compared to control plots in the fourth and fifth growing seasons.

Studies addressing the effects of cultural intensity on radiation use efficiency have shown mixed results as well. Martin and Jokela (2004a) found that IPAR and radiation use efficiency (defined by the authors as above-ground biomass production per unit IPAR) increased in response to treatments that elevated soil nutrient availability in loblolly pine stands from age 4

through 18, although stand development affected the presence and magnitude of this response over time. This study also demonstrated a decline in radiation use efficiency with age in the treated plots. This decline was attributed to decreasing above-ground woody biomass increment because variations in foliar biomass production and IPAR were not large enough to greatly influence radiation use efficiency (Martin and Jokela 2004a). Measurements of radiation use efficiency over shorter time periods, however, may show less response to resource amendments. Two separate studies conducted in the Lower Coastal Plain of the southeastern U.S. found that increases in soil nutrient availability increased PAR interception but had no significant effect on radiation use efficiency for 6-year old loblolly pine (Allen et al. 2005; Dalla-Tea and Jokela 1991).

3.5 Leaf Area Index and Growth Efficiency

Stand ability to intercept radiation is primarily regulated by the amount of leaf area in the canopy (Munger et al. 2003; Sampson and Allen 1998). Leaf area provides an essential link between environmental factors and photosynthetic processes influencing the conversion of solar energy into dry matter production (Jokela and Martin 2000). Leaf area index (LAI) is a measure of the amount of leaf area per unit ground area, and it represents the amount of photosynthetic surface area. Numerous studies have shown that loblolly pine stand productivity has a positive linear relationship with LAI (Albaugh et al. 2004; Jokela and Martin 2000; Samuelson et al. 2001; Samuelson et al. 2004; Will et al. 2005; Xiao et al. 2003b), although studies have also shown the relationship to be curvilinear (Jokela et al. 2004; McCrady and Jokela 1998; Sword Sayer et al. 2004), possibly due to increased shading within high LAI canopies (Martin and Jokela 2004a; Will et al. 2005). The slope of this relationship (stem growth or above-ground

biomass production per unit LAI) is often referred to as "growth efficiency", and there is evidence that it can be altered through silvicultural practices.

Increases in planting density have been shown to increase stand level LAI and growth efficiency until the point when canopy size reaches a peak and then declines with age (Burkes et al. 2003; Will et al. 2005). It has been suggested that enhanced efficiencies at higher densities for loblolly pine may be attributed to increased biomass partitioning to stem relative to other tree components and/or changes in canopy structure at higher densities (Burkes et al. 2003; Will et al. 2005). Thinning reduces LAI at the stand level but increases LAI of individual trees (Hennessey et al. 2004; Peterson et al. 1997; Sword Sayer et al. 2004; Yu et al. 2003). Albaugh et al. (2006) found that individual tree foliar biomass of 19-year-old loblolly pine was influenced by the relative size and proximity of neighboring trees with nearby larger neighbors reducing the amount of foliage. At the same time, stand level foliar biomass and stem biomass increment, however, were constant or increasing; exhibiting the trade-off between individual tree growth and stand level growth and the importance of competition dynamics (Albaugh et al. 2006).

Treatments that enhance soil nutrient availability, e.g. fertilization and competition control, typically increase loblolly pine LAI development (Albaugh et al. 2006; Borders et al. 2004; Maier et al. 2002; Samuelson and Stokes 2006; Sword Sayer et al. 2004; Will et al. 2002; Xiao et al. 2003b), although LAI will eventually reach a maximum value. The effects of nutrient amendments on growth efficiency have been mixed. Increased nutrient availability in loblolly pine stands has resulted in increased growth efficiency (Albaugh et al. 2004), decreased growth efficiency (Xiao et al. 2003b), or no significant growth efficiency response (Samuelson et al. 2008). Interestingly, studies have found that early increases in growth efficiency attributed to increased nutrient availability may disappear or become negative as the stands age (Colbert et al.

1990; Jokela and Martin 2000; Will et al. 2002). Will et al. (2002) reported that changes in growth efficiency related to fertilization may be confounded with changes in tree size because growth efficiency decreases as mean tree size increases. This suggests that differences in growth efficiency could be related to changes in stand development, which is influenced by resource availability. A decrease in growth efficiency with increasing tree age/size has been observed in other studies as well (Jokela and Martin 2000; Martin and Jokela 2004b). This decrease in efficiency has been attributed to increased respiration and/or increased biomass partitioning below ground relative to stem for older/larger trees (Borders et al. 2004; Will et al. 2002).

3.6 Foliar Nitrogen

Nitrogen (N) is an important component of loblolly pine crowns, as it is a major component in all proteins and pigments involved in photosynthesis (Evans 1989; Tyree et al. 2009). Increases in foliar N concentration do not lead to a consistent observable increase in photosynthetic capacity for loblolly pine (Munger et al. 2003). Additional N acquired by the foliage, however, may serve as a source for subsequent foliage development, which may consequentially drive additional stem growth (Borders et al. 2004; Munger et al. 2003; Tyree et al. 2009; Will et al. 2002). Increases in foliar N concentration have been linked to increases in soil N availability (Albaugh et al. 2004; Borders et al. 2004; Martin and Jokela 2004b). Similarly, assessments of foliar N concentration may be used to help determine the degree of plant nitrogen deficiency (Albaugh et al. 2010; Vose and Allen 1988; Xiao et al. 2003a), with foliar N concentrations below 1.10% considered nitrogen deficient for loblolly pine(Allen 1987). Because foliar N concentration is most likely important in determining future foliage development, it is not a reliable predictor of current annual increment of stem growth (Will et al. 2005).

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CHAPTER 2

EFFECTS OF PLANTING DENSITY AND CULTURAL INTENSITY ON INDIVIDUAL TREE STEM AND CROWN ATTRIBUTES OF LOBLOLLY PINE PLANTATIONS IN THE UPPER COASTAL PLAIN AND PIEDMONT OF THE SOUTHEASTERN U.S. AT AGE 12[1]

[1] Akers, M.K., Kane, M., Zhao, D., Daniels, R.F., Teskey, R.O., and Subedi, S. To be submitted to Forest Ecology and Management.

Abstract

Examining the role of foliage in stand development across a range of stand structures provides a more detailed understanding of the processes driving productivity and allows further development of process-based models for prediction. Productivity changes observed at the stand scale will be the integration of changes at the individual tree scale, but few studies have analyzed crown attributes at the individual tree level. Four Plantation Management Research Cooperative (PMRC) study installations were utilized to analyze the effects of planting density and cultural intensity on individual tree stem and crown attributes in non-thinned loblolly pine plantations in the Upper Coastal Plain and Piedmont of Georgia and Alabama. Treatments included six planting densities, ranging from 740 to 4440 trees ha^{-1}, in a factorial combination with two cultural treatments that included different levels of fertilization and competition control. Treatment effects on stem and crown attributes were analyzed at age 12 using destructive sampling techniques. Results showed that cultural intensity did not have a major influence on average individual stem and crown attributes. Lower planting density stands resulted in significantly greater average individual tree DBH, total stem height, total stem volume, and diameter at the base of the live crown and significantly less height to the live crown. Average individual tree live crown length and width, crown ratio, crown density, foliar biomass, leaf area, and foliar N content were greater for trees planted at lower densities compared to trees planted at higher densities. Interestingly, trees of a given DBH had similar crown characteristics regardless of the silvicultural treatments they received. For these stands, knowledge of DBH distribution appears to be a sufficient modeling tool regardless of past cultural or planting density treatment. Future research should include long-term analysis of these trends and the introduction of other silvicultural practices such as thinning.

1. Introduction

Loblolly pine (*Pinus taeda* L.) is the most widely planted tree species in the southeastern United States; a region that leads the world in industrial timber production (Prestemon and Abt 2002). Loblolly pine is a fast-growing plantation species that has displayed significant gains in productivity over the last sixty years due to genetic improvement and silvicultural practices (Fox et al. 2007b). Studies analyzing loblolly pine stand response to common silvicultural practices such as fertilization, control of competing vegetation, and density management are numerous, however, the physiological mechanisms that drive this response are not thoroughly understood (Jokela et al. 2004; King et al. 2008; Tyree et al. 2009; Will et al. 2005).

Leaf area provides an essential link between environmental factors and photosynthetic processes influencing the conversion of solar energy into dry matter production (Jokela and Martin 2000). Many studies have shown that loblolly pine stand productivity has a positive linear relationship with leaf area (Albaugh et al. 2004; Jokela and Martin 2000; Samuelson et al. 2001; Samuelson et al. 2004; Will et al. 2005; Xiao et al. 2003b), although studies have also shown the relationship to be curvilinear (Jokela et al. 2004; McCrady and Jokela 1998; Sword Sayer et al. 2004), possibly due to increased shading within high leaf area canopies (Martin and Jokela 2004a; Will et al. 2005). Tree crowns have become important indicators of potential tree productivity due to their fundamental relationship with growth. Treatments that enhance soil nutrient availability, e.g. fertilization and competition control, typically increase loblolly pine leaf area development (Albaugh et al. 2006; Borders et al. 2004; Maier et al. 2002; Samuelson and Stokes 2006; Sword Sayer et al. 2004; Will et al. 2002; Xiao et al. 2003b). Increases in planting density have been shown to increase stand level leaf area development until the time

when stand level leaf area reaches a peak and then declines with age (Burkes et al. 2003; Will et al. 2005).

Serving as a major component in all proteins and pigments involved in photosynthesis, nitrogen (N) is an essential nutrient for loblolly pine growth (Evans 1989; Tyree et al. 2009). Nitrogen availability is commonly limiting to loblolly pine growth and is often added to the soil through fertilizers (Fox et al. 2007a). Increases in foliar nitrogen concentration have been linked to increases in soil nitrogen availability (Albaugh et al. 2004; Borders et al. 2004; Martin and Jokela 2004b). Assessments of foliar nitrogen concentration may be used to help determine the degree of plant nitrogen deficiency (Albaugh et al. 2010; Vose and Allen 1988; Xiao et al. 2003a).

Examining the role of foliage in stand development across a range of stand structures provides a more detailed understanding of the processes driving productivity and allows further development of process-based models for prediction purposes (MacFarlane et al. 2002). Productivity changes observed at the stand scale will be the integration of changes at the individual tree scale, but few studies have analyzed crown attributes at the individual tree level (Albaugh et al. 2006). This is important from a value perspective, as trees with larger stems can be used for higher value products (Huang et al. 2005).

The objective of this study was to explore relationships between silvicultural practices, crown attributes, and tree size. Silvicultural treatments included six planting densities and two levels of cultural intensity. Treatment combinations were used to establish a range of stand structures, and these stands were analyzed at age 12 for differences in tree and crown development.

Hypotheses include:

(1a) More intensive culture will result in significantly greater individual tree stem volume.

(1b) More intensive culture will result in significantly larger individual crowns with greater leaf area and greater foliar N concentration.

(2a) Increases in planting density will result in significantly less individual tree stem volume.

(2b) Increases in planting density will result in significantly smaller individual crowns with less leaf area and less foliar N concentration.

(3) There will not be a significant cultural intensity x planting density interaction effect on the stem and crown attributes evaluated.

(4) Crown characteristics will not be significantly different for trees of a given DBH, regardless of treatment.

2. Methods

2.1 Study sites and treatments

This study utilized four permanent loblolly pine research installations maintained by the University of Georgia Plantation Management Research Cooperative (PMRC). Three installations were located in the Upper Coastal Plain region of Alabama, and one installation was located in the Piedmont region of Georgia (Table 2.1). The installations were planted in early 1998 with open-pollinated, bare root loblolly pine seedlings chosen by the PMRC cooperator for that site. Although planting material may have differed among installations, only one half-sib family was planted within each installation. Each installation was arranged in a split-plot design. Two main plots received one of two cultural treatments; termed "operational" or "maximum" (Table 2.2). The maximum treatment included very frequent fertilization and complete sustained competition control. The operational treatment included less frequent fertilization and early competition control. Six sub-plots were planted at one of six densities (740, 1480, 2220, 2960,

3700, and 4440 trees ha $^{-1}$). To ensure adequate first-year survival, planting locations were double-planted and reduced to a single surviving seedling after the first growing season. The combination of two cultural treatments and six planting densities resulted in 12 plots per installation, with a different randomly-assigned combination of cultural intensity and planting density for each plot. Plot size varied to accommodate the different planting densities (Table 2.3). Gross plots contained an interior measurement plot surrounded by an approximate 8 m wide buffer. The entire gross plot received the designated planting density and cultural regime. Measurements were obtained only from trees in the interior measurement plots.

2.2 Population stem and stand measurements

In the measurement plots, diameter at breast height (DBH) was measured on all trees and total height was measured on every other tree in the dormant season at ages 10 and 12. For the trees that were not measured for total height, estimates of total height were made using an equation fit for trees with both measured total height and DBH for each plot and measurement year using the model form: $\ln(\text{height}) = \beta 0 + \beta 1\ \text{DBH}^{-1}$. Total outside-bark stem volume was estimated for all trees using the volume equation developed by (Pienaar et al. 1987) at ages 10 and 12. Current annual increment (CAI) of volume growth per ha was estimated by subtracting the volume at age 10 from the volume at age 12 and dividing by two. Plot level basal area (m^2 ha^{-1}) and percent survival were also determined for age 12. The trees in the measurement plots were considered as the population for this study.

2.3 Destructively sampled tree stem and crown measurements

To obtain detailed age 12 stem and crown measurements, four trees per plot were destructively sampled in February 2010. The target sample consisted of two trees from the dominant and/or co-dominant crown class, one tree from the intermediate crown class, and one

suppressed tree per plot. This resulted in 192 total sampled trees with 16 sampled trees for each culture x density treatment combination. Because destructive sampling took place in the dormant season, only one foliar age class was present. DBH, total stem height, stem diameter at the base of the live crown, height to live crown, and live crown length were measured for each of the sampled trees. Stem diameters were measured at 0.61, 1.22, 2.44, 3.66, and 6.1 meters from the base and at 2.4 meter intervals after that for the destructively sampled trees. These diameter measurements were used to calculate total outside-bark stem volume for each of the destructively sampled trees using Smalian's taper formula. Crown width was measured in two directions (along the planted rows and across the planted rows) and averaged to calculate crown width for each tree. Crown ratio was calculated as live crown length divided by total stem height. Crown area was calculated as the product of live crown length and live crown width.

For each sampled tree, the crown was divided into three sections of equal length representing the lower, middle, and top portion of the crown. The total green weight of the live branches (including the foliage) was measured in the field for each crown position. Two randomly selected sub-sampled branches per crown position were weighed individually in the field. The sub-sampled branches were dried in a drying oven at 65° C to a constant weight. The dry-weight of the sub-sampled branches with and without foliage was measured in the lab. These measurements were used to estimate total foliar biomass (dry) by crown position for each sampled tree. Total foliar biomass for one foliar age class was calculated as the sum of foliar biomass for the three crown positions for each tree. Total tree foliar biomass estimates were then doubled to represent peak foliar biomass (two foliar age classes) per tree. Crown density was calculated as peak foliar biomass divided by live crown length.

Needle samples were collected for all-sided specific leaf area (SLA) measurements. SLA was measured as the ratio of needle surface area (green) to needle mass (dry) using the method by Fites and Teskey (1988). For each of the four sampled trees per plot, two branches were randomly selected from each crown position. At least five fascicles were removed from the middle of each of the two to four flushes of foliage present on each of the selected branches. Fascicles from the sample trees were combined by plot, but kept separate by crown position. For each crown position per plot, 15 to 30 needles were randomly chosen and measured to determine average SLA. SLA ratios were applied to the peak foliar biomass values to estimate individual tree peak leaf area by crown position. Leaf area for each crown position was combined to estimate total individual tree peak all-sided leaf area which were converted to peak projected leaf area by dividing by 3.14 (Grace et al. 1987). SLA values are reported as the average of the three crown positions for each treatment.

The two randomly selected branches used for SLA samples were also used for foliar N concentration samples. At least five fascicles were removed from the middle of each of the two to four flushes of foliage present on each of the selected branches. Fascicles from the three crown positions were combined, and at least 30 fascicles were randomly chosen as foliar N concentration samples for each plot. Samples were dried and ground using a Certiprep 8000-D mixer/mill (Spex, Metuchen, NJ, USA). The dry combustion method was used for foliar N concentration analysis using a CE Elantech NA2100 (CE Elantech Inc., Lakewood, NJ, USA). Foliar N content was calculated for each crown position for each tree as the product of peak foliar biomass for each crown position for each tree and foliar N concentration for the corresponding plot. Foliar N content for each crown position was combined to estimate total individual tree foliar N content.

2.4 Statistical analyses

The main effects of culture, density, and their interaction on average stem and crown characteristics were analyzed using a mixed-model approach. Each of the four installations was treated as a replication. Culture and planting density served as fixed effects and installation and installation x culture served as random effects (Littell et al. 1996). ANOVA was used to assess treatment effects on average stem attributes at age 12 for all of the trees in the measurement plots (population) and the destructively sampled trees. ANOVA was used to assess treatment effects on average crown attributes at age 12 for the destructively sampled trees. Multiple comparisons for significant treatment effects were conducted using Fisher's LSD test. For statistical analysis purposes, data transformation was performed on the percent survival measure by taking the arcsine of the square root of each value. Analyses were performed using the mixed-model procedure (proc mixed) in SAS (version 9.1.3 SAS Institute Inc., Cary, North Carolina) with a type-I error rate of 0.05.

To determine whether trees of a given DBH had similar crown characteristics, indicator variables were established for cultural level, planting density, DBH, and all interactions. Linear regression models were defined with a crown characteristic as the dependent variable and the indicator variables as the independent variables. ANOVA was used to test for independent variable significance in the regression models. Natural log transformations were performed on data as needed to ensure linearity. Analyses were performed using the regression procedure (proc reg) in SAS (version 9.1.3 SAS Institute Inc., Cary, North Carolina) with a type-I error rate of 0.05.

3. Results

3.1 Average population stem and stand characteristics

For the trees in the measurement plots (population), average DBH ($p = 0.03$), total stem volume per hectare ($p = 0.04$), and basal area per hectare ($p = 0.02$) were significantly greater for the trees grown under the maximum cultural treatment at age 12 (Tables 2.4 and 2.5). Average tree height ($p=0.06$), CAI ($p=0.3$), and percent survival ($p=0.05$) were not significantly affected by culture (Tables 2.4 and 2.5).

At age 12, average DBH, total stem height, and percent survival decreased significantly ($p<0.0001$) with increasing planting density for the trees in the measurement plots (Tables 2.4 and 2.6). Total stem volume per hectare and basal area per hectare increased significantly ($p <0.0001$) with increasing planting density, and CAI ($p=0.2$) was not significantly affected by planting density. The effect of the interaction between culture and planting density was not significant for any of the previously discussed measures for the population (Table 2.4). There was no significant effect of the interaction between culture and planting density for the average population stem and stand attributes evaluated (Table 2.4).

3.2 Average destructively sampled tree stem characteristics

At age 12, average DBH ($p=0.07$), total stem height ($p=0.06$), diameter at the base of the live crown ($p=0.3$), and height to the live crown ($p=0.2$) did not differ significantly between the two cultural treatments for the destructively sampled trees (Tables 2.7 and 2.8). Average individual tree standing stem volume, however, was significantly ($p = 0.03$) greater for plots receiving the maximum cultural treatment. The operational treatment averaged 0.13 m^3 $tree^{-1}$ stem volume while the maximum treatment averaged 0.16 m^3 $tree^{-1}$ stem volume (Tables 2.7 and 2.8).

Planting density had a significant effect on all of the average stem characteristics measured at age 12 for the destructively sampled trees (Table 2.7). DBH, total stem height, total

stem volume, and diameter at the base of the live crown decreased significantly ($p < 0.0001$) with increasing planting density. Average DBH ranged from 13.6 to 21.4 cm, and average diameter at the base of the live crown ranged from 8.7 to 15.4 cm (Table 2.9). The four lowest planting densities had significantly taller stems than the two highest planting densities. Average total stem volume ranged from 0.10 to 0.24 m^3 $tree^{-1}$. Average height to the live crown increased significantly ($p < 0.0001$) with increasing planting density and ranged from 6.3 to 8.0 m, although the four highest planting densities were not significantly different (Tables 2.7 and 2.9). The overall result was that trees planted at the lower densities had larger stems with crowns beginning lower on the stem compared to trees planted at the higher densities. The interaction between culture and planting density did not have a significant effect on the average destructively sampled tree stem attributes evaluated (Table 2.7).

3.3 Average destructively sampled tree crown characteristics

Average live crown length, live crown width, crown area, and crown ratio were not significantly affected by cultural intensity ($p > 0.05$), but decreased significantly ($p < 0.0001$) with increasing planting density for the destructively sampled trees at age 12 (Table 2.7 and 2.10). The average crown ratio was greater than one-third for all of the planting densities and greater than one-half for the 740 and 1480 trees ha^{-1} planting densities (Table 2.11). Trees planted at lower densities had longer, wider crowns that made up a larger proportion of total tree height compared to trees planted at the higher densities (Table 2.11).

Cultural intensity did not have a significant effect on average foliar biomass ($p=0.9$), SLA ($p=0.2$), leaf area ($p=0.6$), or crown density ($p=0.3$) for the destructively sampled trees at age 12 (Tables 2.7 and 2.10). Foliar biomass and leaf area showed a similar significant ($p < 0.0001$) trend in that they generally decreased with increasing planting density (Tables 2.7 and

2.11). Average foliar biomass ranged from 4.6 to 17.0 kg tree^{-1}, and average leaf area ranged from 16.6 to 58.3 m^2 tree^{-1}. Crown density decreased from 2.1 to 0.8 kg m^{-1} as planting density increased from 740 to 4440 trees ha^{-1}, although the four highest planting densities were not significantly different from each other. SLA increased significantly ($p < 0.0001$) with increasing planting density, but the pattern was not distinct for the 1480, 2220, 2960, 3700 trees ha^{-1} planting densities (Tables 2.7 and 2.11).

Average foliar N content was not significantly ($p=0.3$) different between the two levels of culture, but decreased significantly ($p < 0.0001$) with increasing planting density for the destructively sampled trees at age 12 (Table 2.7). Foliar N content ranged from 68.4 to 233.8 g tree^{-1}, although the four highest densities were not significantly different (Table 2.11). Foliar N concentration was significantly affected by culture ($p = 0.04$), planting density ($p = 0.0001$), and the culture x planting density interaction ($p < 0.0001$) (Table 2.7). Although foliar N concentration differed by planting density, there was no apparent trend (Table 2.11). Foliar N concentration averaged 1.35% for the operational treatment and 1.50% for the maximum treatment (Table 2.10). Foliar N concentration was significantly greater for the maximum treatment (compared to the operational treatment) at the 740 ($p = 0.03$), 1480 ($p < 0.0001$), and 4440 ($p < 0.0001$) trees ha^{-1} planting densities (Fig. 2.1). There was no significant difference in foliar N concentration between cultural treatments at the other planting densities: 2220, 2960, and 3700 trees ha^{-1}. With the exception of foliar N concentration, the interaction effect of culture and planting density was not significant for the crown attributes evaluated (Table 2.7).

3.4 Crown characteristics for destructively sampled trees of a given DBH

Significance status in the regression equation described in section *2.4* was used to determine whether culture and/or planting density had an effect on crown characteristics for

destructively sampled trees of a given DBH at age 12. All of the crown characteristics evaluated exhibited the same trend. DBH was significant ($p \leq 0.05$) in the model, while culture, planting density, DBH x culture, DBH x planting density, culture x planting density, and DBH x culture x planting density were not significant in the model (Table 2.12). This was the result for the following crown characteristics: diameter at the base of the live crown, live crown length, live crown width, crown ratio, height to the live crown, crown area, crown density, foliar biomass, leaf area, and N content. A graphical representation of the relationship between DBH and leaf area for a sub-set of planting densities is shown in Fig. 2.2. Specific leaf area and N concentration were not tested because they were measured at the plot level as opposed to the tree level.

4. Discussion

Based on the results from the population analysis, plots that received the maximum cultural treatment had significantly greater stem volume per hectare and basal area per hectare and greater percent mortality (although not statistically significant) compared to plots that received the operational cultural treatment, suggesting that the maximum plots were more advanced in stand development at age 12. Similarly, greater stem volume per hectare, basal area per hectare, and percent mortality for the higher planting density plots suggests that they were more advanced in stand development compared to the lower density plots. Trends for average DBH and total stem height were similar between population trees and destructively sampled trees.

Trees planted at lower densities were able to maintain larger crowns (increased live crown length, live crown width, leaf area, crown density, etc.). Less intra-specific competition in the lower planting density stands allowed for more light to reach the lower branches. Because

leaf area is representative of photosynthetic surface area, it is assumed that individual trees planted at the lower densities were intercepting more light, allowing for increases in individual stem growth at the lower planting densities. Carlson et al. (2009) and MacFarlane et al. (2002) found similar patterns for loblolly pine planted at different densities. SLA, however, was generally lower in the lower planting density stands. SLA is typically greater under more light-limited conditions, resulting in more photosynthetic surface area per unit of needle biomass (longer, thinner needles), which may help mitigate the effects of increased shading present in densely stocked stands (Samuelson et al. 2008; Samuelson et al. 2010; Will et al. 2001).

Of the average individual tree stem and crown attributes measured for the destructively sampled trees, only stem volume and foliar N concentration were significantly affected by cultural intensity at age 12. Although the maximum cultural regime provided more frequent fertilization and competition control relative to the operational cultural regime, the operational treatment still provided considerable inputs (e.g. chemical competition control at planting and three fertilizer treatments). Although average N concentration was lower for the trees grown under operational culture, it was still above the critical level of 1.10% for loblolly pine (Allen 1987), suggesting that loblolly pine nutrition was not markedly deficient for either treatment at age 12. Increases in foliar N concentration do not lead to a consistent observable increase in photosynthetic capacity for loblolly pine (Munger et al. 2003). Additional N acquired by the foliage, however, may serve as a source for subsequent foliage development, which may consequentially drive additional stem growth (Borders et al. 2004; Munger et al. 2003; Tyree et al. 2009; Will et al. 2002). Although foliar N concentration significantly differed among planting densities, there was no obvious pattern. Foliar N content per tree decreased with increasing planting density, primarily because N content is strongly related to foliar biomass.

The results suggest that trees of a given DBH had similar crown characteristics regardless of the silvicultural treatments they received. In other words, after DBH was taken into account, further variation in the crown was not explained by culture or planting density. It seems that the treatments affected tree crowns while correspondingly affecting DBH. It should be noted that this interpretation is limited to the age, genetics, locations, and treatments used in this study. Albaugh et al. (2006) found similar results for loblolly pine grown on a nutrient poor, well-drained sandy soil in the Sandhills of North Carolina. Although fertilization had a significant effect on average DBH, stem height, and foliar mass, the fertilization effect was not significant in a model predicting individual tree foliar biomass where tree size (stem volume) was an independent variable (Albaugh et al. 2006).

5. Conclusions

The cultural intensities analyzed in this study did not have a major influence on average individual tree crown attributes at age 12, but different planting densities resulted in a range of average crown dimensions and foliar development. The more intensive cultural treatment resulted in significantly greater individual tree stem volume, supporting Hypothesis 1a. It should be noted, however, that other measurements of individual tree size (DBH and total height) were not significantly affected by culture. Hypothesis 1b was not supported as cultural treatment did not affect the crown attributes analyzed (leaf area, N concentration, etc.). Hypotheses 2a and 2b were supported: increases in planting density resulted in significantly less individual tree stem volume and significantly smaller individual crowns with less leaf area and less foliar N concentration. A significant cultural intensity x planting density interaction effect was not present for the stem and crown attributes evaluated, supporting Hypothesis 3.

This study suggests that age 12 loblolly pine tree growth projections can be based on DBH along with other site and stand factors without consideration of crown traits. Because trees of a given DBH had similar crown characteristics regardless of the silvicultural treatments they received (Hypothesis 4), knowledge of DBH distribution appears to be a sufficient modeling tool regardless of past cultural or planting density treatment.

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Table 2.1. Site location and attributes for four PMRC culture x planting density study installations

County, State	Latitude	Longitude	Soil series*	Soil Taxonomy*	Physiographic region
Baldwin Co., AL	30.8330	-87.6859	Lakeland	Thermic, coated typic quartzipsamments	Upper Coastal Plain
Barbour Co., AL	31.7467	-85.6735	Orangeburg – Springhill	Fine-loamy, kaolinitic, thermic typic kandiudults and kanhapludults	Upper Coastal Plain
Escambia Co., AL	31.1954	-87.3154	Freemanville	Fine, kaolinitic, thermic plinthic kandiudults	Upper Coastal Plain
Greene Co., GA	33.6235	-83.0278	Cecil - Madison – Pacolet	Fine, kaolinitic, thermic typic kanhapludults	Piedmont

* Soils information provided by the USDA-NRCS Soil Survey Division

Table 2.2. Description of operational and maximum cultural treatments on the PMRC culture x planting density study

Treatment	Growing Season	Operational	Maximum
Site preparation		Chemical and mechanical	Chemical and mechanical
Fertilization	At planting	560 kg ha^{-1} 10-10-10	560 kg ha^{-1} 10-10-10
	2^{nd}		673 kg ha^{-1} 10-10-10 + 131 kg ha^{-1} NH_4NO_3 + micronutrients
	4^{th}		131 kg ha^{-1} NH_4NO_3
	6^{th}		336 kg ha^{-1} NH_4NO_3
	8^{th}	224 kg ha^{-1} N + 28 kg ha^{-1} P	224 kg ha^{-1} N + 28 kg ha^{-1} P
	10^{th}		224 kg ha^{-1} N + 28 kg ha^{-1} P
	12^{th}	224 kg ha^{-1} N + 28 kg ha^{-1} P	224 kg ha^{-1} N + 28 kg ha^{-1} P
Competition control (chemical)	1^{st}	280 g ha^{-1} sulfometuron-methyl banded application + glyphosate and tryclopyr direct spraying	280 g ha^{-1} sulfometuron-methyl broadcast application + glyphosate and tryclopyr direct spraying
	2^{nd}		841 g ha^{-1} imazapyr broadcast application
	3^{rd} through 12^{th}		Glyphosate and tryclopyr repeated direct spraying

Table 2.3. Plot size and spacing for different planting densities on the PMRC culture x planting density study

Planting Density (trees ha^{-1})	Original spacing (m x m)	Measurement plot size (ha)	Gross plot size (ha)
740	3.66 x 3.66	0.105	0.227
1480	2.44 x 2.74	0.053	0.150
2220	2.44 x 1.83	0.046	0.125
2960	1.83 x 1.83	0.040	0.121
3700	1.83 x 1.46	0.045	0.129
4440	1.83 x 1.22	0.040	0.125

Table 2.4. P-values for the effects of culture, planting density, and their interaction on average stem and stand attributes for all trees (population) on four PMRC loblolly pine installations at age 12

Attribute	Source		
	Culture	Planting density	Interaction
DBH	0.0260	<0.0001	0.6855
Total stem height	0.0644	<0.0001	0.5115
Total stem volume	0.0359	<0.0001	0.6375
Basal area	0.0238	<0.0001	0.8818
Percent survival	0.0526	<0.0001	0.6198
CAI stem volume	0.2651	0.1690	0.3009

Table 2.5. Mean stem and stand attributes by cultural intensity for all trees (population) on four PMRC loblolly pine installations at age 12

Culture	DBH (cm)	Total stem height (m)	Total stem volume (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Percent survival (%)	CAI stem volume (m^3 ha^{-1} $year^{-1}$)
Operational	15.1 b	13.1 a	229.2 b	35.0 b	89.0 a	30.7 a
Maximum	17.0 a	14.7 a	290.7 a	41.1 a	82.9 a	35.4 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 2.6. Mean stem and stand attributes by planting density for all trees (population) on four PMRC loblolly pine installations at age 12

Planting density (trees ha^{-1})	DBH (cm)	Total stem height (m)	Total stem volume (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Percent survival (%)	CAI stem volume (m^3 ha^{-1} $year^{-1}$)
740	23.1 a	14.9 a	204.9 a	30.2 a	94.7 a	29.3 a
1480	18.4 b	14.8 ab	255.9 b	36.6 b	90.5 a	34.2 a
2220	15.6 c	14.2 b	256.9 b	36.8 b	83.6 b	33.6 a
2960	14.2 d	13.5 c	275.7 bc	40.5 c	84.1 b	33.8 a
3700	12.9 e	13.1 c	273.7 bc	40.7 c	81.9 b	34.4 a
4440	12.2 f	13.0 c	292.5 c	43.4 d	80.8 b	33.0 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 2.7. P-values for the effects of culture, planting density, and their interaction on average stem and crown attributes for destructively sampled trees on four PMRC loblolly pine installations at age 12

Attribute	Source		
	Culture	Planting density	Interaction
Stem attributes			
DBH	0.0717	<0.0001	0.7041
Total stem height	0.0629	<0.0001	0.5438
Total stem volume	0.0278	<0.0001	0.7196
Diameter at base of live crown	0.2671	<0.0001	0.7083
Height to live crown	0.1582	<0.0001	0.1838
Crown attributes			
Live crown length	0.1123	<0.0001	0.4025
Live crown width	0.6172	<0.0001	0.4008
Crown ratio	0.4312	<0.0001	0.2738
Crown area	0.5754	<0.0001	0.2935
Crown density	0.2765	<0.0001	0.9656
Foliar biomass	0.8928	<0.0001	0.9820
SLA	0.2074	<0.0001	0.0709
Leaf area	0.6493	<0.0001	0.9496
Foliar N concentration	0.0408	0.0001	<0.0001
Foliar N content	0.3371	<0.0001	0.8395

Table 2.8 Mean tree stem attributes by cultural intensity for destructively sampled trees on four PMRC loblolly pine installations at age 12

Culture	DBH (cm)	Total stem height (m)	Total stem volume (m^3 $tree^{-1}$)	Diameter at base of live crown (cm)	Height to live crown (m)
Operational	15.9 a	13.4 a	0.13 a	10.9 a	7.8 a
Maximum	16.9 a	14.6 a	0.16 b	11.5 a	6.9 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 2.9. Mean tree stem attributes by planting density for destructively sampled trees on four PMRC loblolly pine installations at age 12

Planting density (trees ha^{-1})	DBH (cm)	Total stem height (m)	Total stem volume (m^3 $tree^{-1}$)	Diameter at base of live crown (cm)	Height to live crown (m)
740	21.4 a	14.5 a	0.24 a	15.4 a	6.3 a
1480	17.7 b	14.2 a	0.17 b	12.3 b	6.8 b
2220	15.6 c	14.2 a	0.14 c	10.5 c	7.8 c
2960	15.6 c	14.2 a	0.14 c	10.5 c	7.7 c
3700	14.5 cd	13.5 b	0.12 cd	9.6 cd	7.5 c
4440	13.6 d	13.6 b	0.10 d	8.7 d	8.0 c

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 2.10. Mean tree crown attributes by cultural intensity for destructively sampled trees on four PMRC loblolly pine installations at age 12

Culture	Live crown length (m)	Live crown width (m)	Crown ratio (%)	Crown area (m2)	Crown density (kg m^{-1})	Foliar biomass (kg $tree^{-1}$)	SLA (cm^2 g^{-1})	Leaf area (m^2 $tree^{-1}$)	Foliar N concentration (%)	Foliar N content (g $tree^{-1}$)
Operational	6.5 a	3.1 a	48.5 a	21.2 a	1.3 a	8.5 a	109.4 a	29.6 a	1.36 a	117.2 a
Maximum	6.9 a	3.0 a	46.7 a	22.1 a	1.2 a	8.6 a	112.5 a	30.6 a	1.50 b	130.4 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 2.11. Mean tree crown attributes by planting density for destructively sampled trees on four PMRC loblolly pine installations at age 12

Planting density (trees ha^{-1})	Live crown length (m)	Live crown width (m)	Crown ratio (%)	Crown area (m2)	Crown density (kg m^{-1})	Foliar biomass (kg $tree^{-1}$)	SLA (cm^2 g^{-1})	Leaf area (m^2 $tree^{-1}$)	Foliar N concentration (%)	Foliar N content (g $tree^{-1}$)
740	8.2 a	4.4 a	56.4 a	36.7 a	2.1 a	17.0 a	106.5 a	58.3 a	1.39 a	233.8 a
1480	7.4 b	3.5 b	51.8 b	26.0 b	1.4 b	10.5 b	111.1 bc	37.0 b	1.48 b	154.4 b
2220	6.4 cd	3.0 c	45.1 c	19.1 c	1.0 c	6.7 cd	110.1 b	23.4 cd	1.41 a	93.2 c
2960	6.6 c	2.7 c	46.1 c	18.2 c	1.0 c	6.9 c	112.9 d	24.5 c	1.39 a	95.0 c
3700	5.9 de	2.7 c	44.3 cd	16.1 cd	1.0 c	6.0 cd	111.9 cd	21.1 cd	1.44 ab	85.4 c
4440	5.6 e	2.3 d	41.5 d	13.1 d	0.8 c	4.6 d	113.4 d	16.6 d	1.47 b	68.4 c

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 2.12. Summary of statistical significance (p-values) of independent variables in models to predict crown attributes (dependent variables) for destructively sampled trees on four PMRC loblolly pine installations at age 12

Dependent variable	Source (independent variable)						
	DBH	Planting density	Culture	DBH x planting density	DBH x culture	Planting density x culture	DBH x planting density x culture
Diameter at base of live crown	<0.0001	0.8423	0.8168	0.7875	0.7980	0.4313	0.4306
Height to live crown*	<0.0001	0.3312	0.7346	0.2738	0.6824	0.8648	0.7709
Live crown length	0.0003	0.7490	0.4656	0.7718	0.7276	0.3369	0.5477
Live crown width	<0.0001	0.9961	0.1289	0.3942	0.2620	0.1829	0.2398
Crown ratio	0.0158	0.7791	0.8833	0.4144	0.8277	0.3907	0.4751
Crown area*	<0.0001	0.3278	0.2790	0.4887	0.2720	0.3928	0.3439
Crown density*	<0.0001	0.4093	0.5033	0.3351	0.5591	0.5936	0.5732
Foliar biomass*	<0.0001	0.3985	0.6439	0.3205	0.6536	0.9055	0.8238
Leaf area*	<0.0001	0.4677	0.6267	0.4144	0.6248	0.9559	0.8762
N content*	<0.0001	0.3312	0.7346	0.2738	0.6824	0.8648	0.7709

* log transformed variables

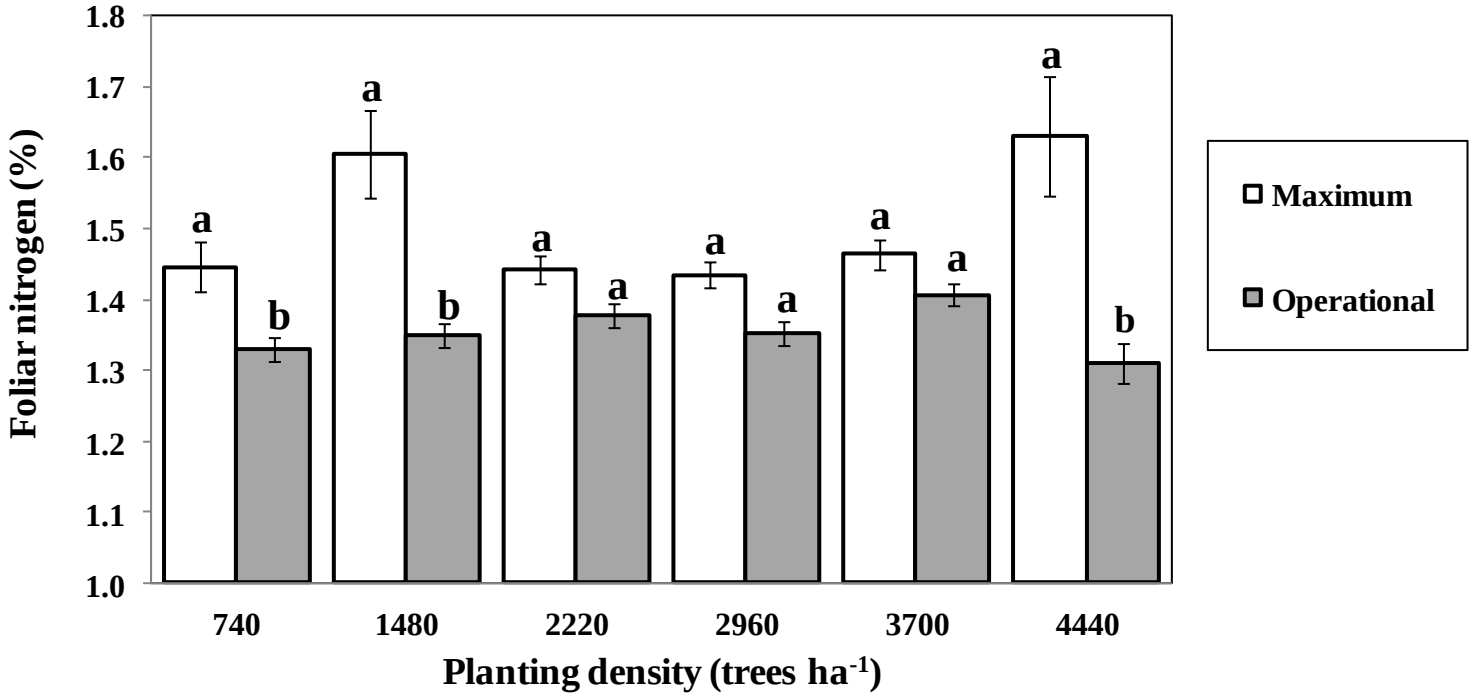

Fig. 2.1. Mean foliar N concentrations for planting density and culture treatment combinations for destructively sampled trees on four PMRC loblolly pine installations at age 12. The white columns represent the maximum cultural intensity and the gray columns represent the operational cultural intensity at each of the six planting densities. At each level of planting density, columns with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05). Bars represent the standard error of the means for each combination of planting density and cultural intensity.

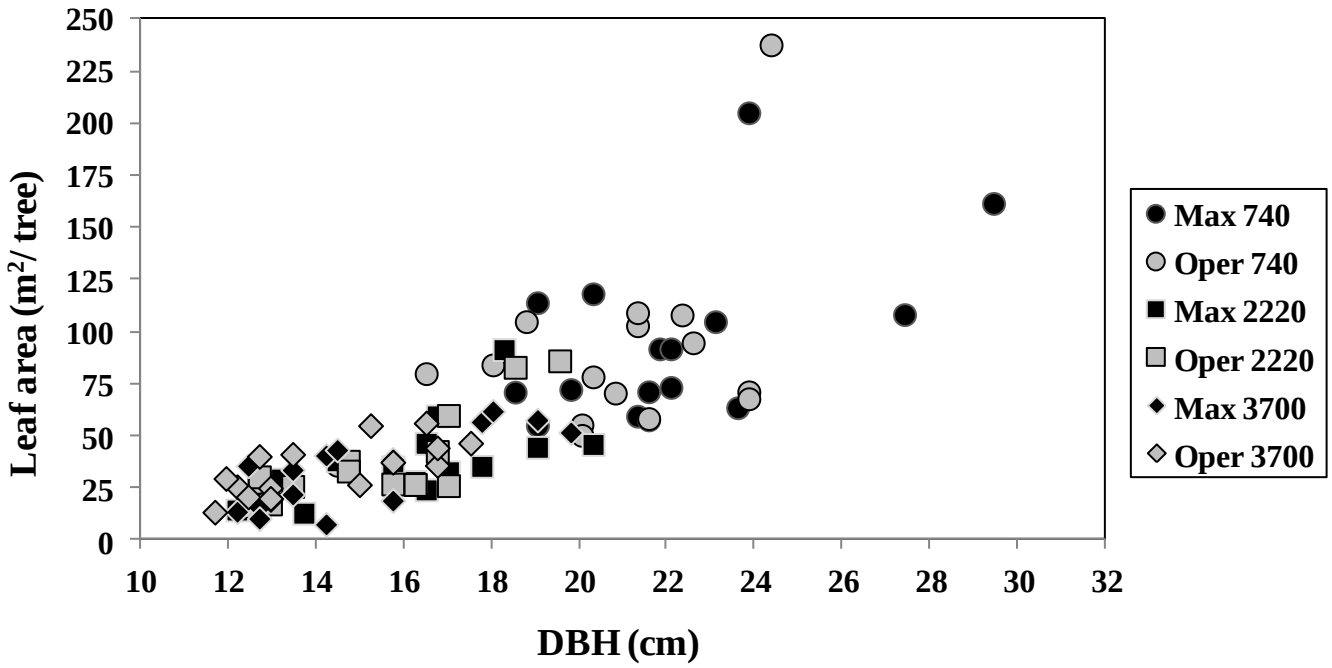

Fig. 2.2. Relationship between individual tree DBH and leaf area for destructively sampled trees on four PMRC loblolly pine installations at age 12. A sub-set of the planting density and culture treatment combinations is displayed for simplicity. The circle, square, and diamond symbols represent the 740, 2220, and 3700 trees ha^{-1} planting densities, respectively. The black symbols represent the maximum cultural intensity and the gray symbols represent the operational cultural intensity.

CHAPTER 3

EFFECTS OF PLANTING DENSITY AND CULTURAL INTENSITY ON STAND AND CROWN ATTRIBUTES IN NON-THINNED LOBLOLLY PINE PLANTATIONS DURING THE AGE 12- TO AGE 13-YEAR PERIOD IN THE UPPER COASTAL PLAIN AND PIEDMONT OF THE SOUTHEASTERN U.S. [2]

[2] Akers, M.K.., Kane, M., Zhao, D., Teskey, R.O., and Daniels, R.F. To be submitted to Forest Ecology and Management.

Abstract

The response of loblolly pine to common silvicultural inputs has been fairly well documented, however, the mechanisms that drive this response are not thoroughly understood. Four Plantation Management Research Cooperative (PMRC) study installations were utilized to analyze the effects of planting density and cultural intensity on average stand and crown attributes in non-thinned loblolly pine plantations in the Upper Coastal Plain and Piedmont of Georgia. Treatments included six planting densities, ranging from 740 to 4440 trees ha^{-1}, in a factorial combination with two cultural treatments that included different levels of fertilization and competition control. Treatment effects on average stand and crown attributes were analyzed at ages 12 and 13 and during the 13^{th} growing season. Results showed that cultural intensity did not have a major influence on average stand and crown attributes. Stands planted at lower densities resulted in significantly greater average DBH and total stem height and less standing stem volume per acre, basal area per acre, and current annual increment (CAI) stem volume growth compared to stands planted at higher densities. Average stand-level foliar biomass, peak projected leaf area index (LAI), foliar N content, specific leaf area (SLA), and intercepted photosynthetically active radiation (IPAR) were significantly greater for stands planted at higher densities, while average live crown length and crown ratio were significantly greater for stands planted at the lower densities. IPAR efficiency (CAI per IPAR) was significantly affected by planting density, with values of 0.32 to 0.42 m^3 $\%IPAR^{-1}$ for the 740 and 4440 trees ha^{-1} planting densities, respectively. It appears that at this stage of stand development, light limitations due to high stocking have a greater influence on growth than soil limitations due to poor nutrition for the loblolly pine plantations analyzed in this study. Higher density stands resulted in increased SLA and IPAR efficiency, supporting the idea that higher density stands utilize the available

light source more efficiently than lower density stands. Future research should include long-term analysis of these trends and the introduction of other silvicultural practices such as thinning.

1. Introduction

Worldwide, plantation forests represent only 4% of all forests, yet they provide 50% of all wood production (Miller et al. 2009). The high productivity of many plantation forests can be attributed to advances in silvicultural and genetic technology (Borders and Bailey 2001; McKeand et al. 2006). Almost half of all industrial forest plantations are located in the southern United States, where the most widely planted species is *Pinus taeda* L., commonly known as loblolly pine (Fox et al. 2007a; Prestemon and Abt 2002). A substantial amount of research has focused on increasing productivity in loblolly pine plantations; and silvicultural practices such as fertilization, control of competing vegetation, and density management have become effective practices for manipulating growth rates (Borders and Bailey 2001; Fox et al. 2007b; Jokela et al. 2004; Jokela et al. 2000; Will et al. 2005). The response of loblolly pine to common silvicultural inputs has been fairly well documented, however, the mechanisms that drive this response are not thoroughly understood (Jokela et al. 2004; King et al. 2008; Tyree et al. 2009; Will et al. 2005).

Many processes that influence tree growth are related to crown size, structure, and chemistry. Crown vigor, e.g. crown classes, has become an accepted predictor of potential tree productivity. Although there are many ways to assess crown vigor, perhaps one of the most intrinsic is a measure of the amount of usable light coming into contact with the leaves (MacFarlane et al. 2002; Will et al. 2005). This measurement is known as intercepted photosynthetically active radiation (IPAR), and it represents photosynthetic energy capture (Will et al. 2005). Studies have shown that IPAR is positively correlated with stem growth in loblolly

pine, and is often linearly related to growth for a given site (Allen et al. 2005; Chmura and Tjoelker 2008; Dalla-Tea and Jokela 1991; McCrady and Jokela 1998; Will et al. 2001; Will et al. 2005). IPAR accounts for the total amount of foliage and how that foliage is displayed and distributed within the canopy, making it a more useful measure than crown size measures (i.e. foliar biomass, leaf area index) which simply represent the amount of foliage (Allen et al. 2005; Will et al. 2005). In a study conducted in the Upper Coastal Plain and Piedmont of Georgia, Will et al. (2005) found that radiation use efficiency (stem growth per annual IPAR) was constant for 4-year old loblolly pine planted at a wide range of densities, suggesting a functional relationship between IPAR and stand growth, although no other known studies have examined the relationship between planting density and radiation use efficiency in loblolly pine.

Stand ability to intercept radiation is primarily regulated by the amount of leaf area in the canopy (Munger et al. 2003; Sampson and Allen 1998). Leaf area provides an essential link between environmental factors and photosynthetic processes influencing the conversion of solar energy into dry matter production (Jokela and Martin 2000). Leaf area index (LAI) is a measure of the amount of leaf area per unit ground area, and it represents the amount of photosynthetic surface area. Numerous studies have shown that loblolly pine stand productivity has a positive linear relationship with LAI (Albaugh et al. 2004; Jokela and Martin 2000; Samuelson et al. 2001; Samuelson et al. 2004; Will et al. 2005; Xiao et al. 2003b), although studies have also shown the relationship to be curvilinear (Jokela et al. 2004; McCrady and Jokela 1998; Sword Sayer et al. 2004), possibly due to increased shading within high LAI canopies (Martin and Jokela 2004a; Will et al. 2005). The slope of this relationship (stem growth or above-ground biomass production per unit LAI) is often referred to as “growth efficiency”, and there is

evidence that it can be altered through silvicultural practices (Albaugh et al. 2006; Borders et al. 2004; Burkes et al. 2003; Maier et al. 2002; Sword Sayer et al. 2004).

Nitrogen (N) is an important component of loblolly pine crowns, as it is a major component in all proteins and pigments involved in photosynthesis (Evans 1989; Tyree et al. 2009). Increases in foliar N concentration do not lead to a consistent observable increase in photosynthetic capacity for loblolly pine (Munger et al. 2003). Additional N acquired by the foliage, however, may serve as a source for subsequent foliage development, which may consequentially drive additional stem growth (Borders et al. 2004; Munger et al. 2003; Tyree et al. 2009; Will et al. 2002). Increases in foliar N concentration have been linked to increases in soil N availability (Albaugh et al. 2004; Borders et al. 2004; Martin and Jokela 2004b). Similarly, assessments of foliar N concentration may be used to help determine the degree of plant N deficiency (Albaugh et al. 2010; Vose and Allen 1988; Xiao et al. 2003a).

The objective of this study was to determine relationships between silvicultural practices, stand growth, and crown attributes. Silvicultural treatments included planting density and cultural intensity. Treatment combinations were used to establish a range of stand structures, and these stands were analyzed during the age 12- to age 13-year period for differences in average stand and crown development. Hypotheses include:

At age 12:

(1a) The more intensive cultural treatment will result in significantly greater average specific leaf area (SLA) and average foliar N concentration compared to the less intensive cultural treatment.

(1b) Lower planting density stands will result in significantly greater average foliar N concentration and significantly less average SLA compared to the stands at the higher densities.

(1c) There will not be a significant cultural intensity x planting density interaction effect on average SLA and foliar N concentration.

At ages 12 and 13:

(2a) The more intensive cultural treatment will result in significantly greater average DBH, average total stem height, standing stem volume per hectare, basal area per hectare, and live crown length and significantly less percent survival and crown ratio compared to the less intensive cultural treatment.

(2b) Lower planting density stands will result in significantly greater average DBH, average total stem height, percent survival, live crown length, and crown ratio and significantly less average standing stem volume per hectare and basal area per hectare compared to the stands planted at the higher densities.

(2c) There will not be a significant cultural intensity x planting density interaction effect on average DBH, average total stem height, standing stem volume per hectare, basal area per hectare, live crown length, or percent survival.

During the 13^{th} growing season:

(3a) The more intensive cultural treatment will result in significantly greater average current annual increment (CAI) standing stem volume per hectare, foliar biomass per hectare, leaf area index (LAI), foliar N content, intercepted photosynthetically active radiation (IPAR), growth efficiency determined using foliar biomass ($GE_{folmass}$), growth efficiency determined using LAI (GE_{LAI}), and N-use efficiency (NUE) and no significant difference in average IPAR efficiency compared to the less intensive cultural treatment.

(3b) Lower planting density stands will result in significantly less average CAI standing stem volume growth per hectare, foliar biomass per hectare, LAI, foliar N content, IPAR, $GE_{folmass}$,

GE_{LAI}, and NUE and no significant difference in average IPAR efficiency compared to stands planted at the higher densities.

(3c) There will not be a significant cultural intensity x planting density interaction on average CAI standing stem volume per hectare, foliar biomass per hectare, LAI, foliar N content, IPAR, $GE_{folmass}$, GE_{LAI}, NUE, or the IPAR efficiency.

2. Methods

2.1 Study sites and treatments

This study utilized four permanent loblolly pine research installations maintained by the University of Georgia Plantation Management Research Cooperative (PMRC). Two installations were located in the Upper Coastal Plain region of Georgia and two installations were located in the Piedmont region of Georgia (Table 3.1). The installations were planted in 1998 with open-pollinated, bare-root loblolly pine seedlings chosen by the PMRC cooperator for that site. Although planting material may have differed among installations, only one half-sib family was planted within each installation. Each installation was arranged in a split-plot design, with two main plots that received one of two cultural treatments and six sub-plots that were planted at one of six densities. The two cultural treatments were termed "operational" and "maximum" (Table 3.2). The maximum treatment included frequent fertilization and complete sustained competition control. The operational treatment included less frequent fertilization and early competition control. The six sub-plots were planted at 740, 1480, 2220, 2960, 3700, and 4440 trees ha^{-1}. To ensure adequate first-year survival, planting locations were double-planted and reduced to a single surviving seedling after the first growing season. The combination of two cultural treatments and six planting densities resulted in 12 plots per installation, with a different randomly-assigned combination of cultural intensity and planting density for each plot. Plot size

varied to accommodate the different planting densities (Table 3.3). Gross plots contained an interior measurement plot surrounded by an approximate 8 m wide buffer. The entire gross plot received the designated planting density and cultural regime. Measurements were obtained only from trees in the interior measurement plots.

2.2 Stand and crown measurements

In the measurement plots, diameter at breast height (DBH) was measured on all trees and total height and live crown length were measured on every other tree in the dormant season at age 12 and age 13. Crown ratio was calculated as live crown length divided by total stem height. For the trees that were not measured for total height, estimates of total height were made using an equation fit for trees with both measured total height and DBH for each plot and measurement year using the model form: $\ln(\text{height}) = \beta 0 + \beta 1\ DBH^{-1}$.

Total outside-bark stem volume was estimated for all trees at ages 12 and 13 using the volume equation developed by Pienaar et al. (1987). Current annual increment (CAI) of stem volume growth per hectare was estimated by subtracting total volume at age 12 from total volume at age 13. When estimating CAI, tree volume lost to mortality from age 12 to age 13 years old was included in the total volume at age 13 to ensure that CAI reflected the growth rate of the remaining trees. Basal area ($m^2\ ha^{-1}$) and percent survival were also determined at ages 12 and 13.

Leaf litter traps were used to estimate plot level foliar biomass. Circular traps (0.46 m^2) were constructed using PVC pipe as the frame, window screen as the lining, and metal wire as legs. Eight traps were randomly distributed throughout each of the plots on all four installations. Litter was collected from the traps over the course of the 13^{th} year (March 2010 – March 2011) at approximately 13 week intervals. Litter was dried in a drying oven at 65° C to a constant

weight and then hand-sorted to remove debris (bark, weeds, reproductive material, etc). Pine needles were weighed to estimate previous-year (2009) age-class foliar biomass for each plot; as loblolly in the southeastern U.S. typically retains needles for 1.5 years. Foliar biomass estimates were then doubled to represent peak foliar biomass (two foliar age classes) for each plot.

In February 2010, needle samples were collected for all-sided specific leaf area (SLA) measurements. SLA was measured as the ratio of needle surface area (green) to needle mass (dry) using the method by Fites and Teskey (1988). Because the crowns were not accessible from the ground, samples were shot from the trees. One branch was removed from the upper portion of the middle third of the crown of five trees per plot. Because sampling was performed in the dormant season, only one foliage age class was present. At least ten fascicles were removed from the middle of each of the two to four flushes of foliage present on the sampled branches. From this sample, 15 to 30 needles were randomly chosen for plot-level SLA measurements. SLA ratios were applied to the peak foliar biomass estimates to obtain plot-level leaf area estimates. Peak all-sided leaf area index (LAI) was calculated as leaf area per unit ground area and divided by 3.14 to estimate peak projected LAI (Grace et al. 1987).

The branches sampled for SLA measurements were also used for foliar nitrogen (N) measurements. For each plot, at least 30 fascicles were randomly chosen and dried to a constant weight. The samples were analyzed at Waters Agricultural Laboratories, Inc. (Camilla, GA) using the combustion method to determine N concentration (percent N). Foliar N content per hectare was estimated as the product of foliar N concentration and peak foliar biomass.

Intercepted photosynthetically active radiation (IPAR) was measured for each plot using the SunScan Canopy Analysis System (Delta-T Devices Ltd., Cambridge, UK). Solar radiation was measured under the canopy and in nearby areas receiving full sunlight to determine the

proportion of IPAR for each plot. Approximately 200 individual IPAR measurements were taken beneath the canopy of each plot along 4 transects parallel to the tree rows and 5 transects perpendicular to the tree rows. Measurements were taken around solar noon between July 23, 2010 and August 4, 2010 to capture peak leaf area and a desirable sun angle. Each installation was measured within a single day. In this study, IPAR for each treatment is reported as the percentage of total photosynthetically active radiation intercepted by the foliage.

2.3 Efficiency calculations

Efficiency calculations were used to measure stem growth (volume) per unit crown measure. Growth efficiency was measured using foliar biomass ($GE_{folmass}$) and LAI (GE_{LAI}). $GE_{folmass}$ was calculated as m^3 CAI growth per tonne of peak foliar biomass. GE_{LAI} was calculated as m^3 CAI growth per unit peak projected LAI. Nitrogen-use efficiency (NUE) was calculated as m^3 CAI growth per tonne N content. Radiation-use efficiency (RUE) could not be calculated because IPAR was only measured once during the year. Instead, IPAR efficiency was calculated as m^3 CAI per IPAR percentage.

2.4 Statistical analysis

The main effects of culture, planting density, and their interaction were analyzed using a mixed-model approach. Each of the four installations was treated as a replication. Culture and planting density served as fixed effects and installation and installation x culture served as random effects (Littell et al. 1996). ANOVA was used to assess treatment effects on average DBH, total stem height, total standing stem volume per hectare, basal area per hectare, percent survival, live crown length, and crown ratio at ages 12 and 13; SLA and N concentration at age 12; and average CAI, foliar biomass, LAI, N content, IPAR, $GE_{folmass}$, GE_{LAI}, NUE, and IPAR efficiency during the 13^{th} growing season. Least square means comparisons for significant

treatment effects were conducted using Fisher's LSD test. For statistical analysis purposes, data transformation was performed on the percent survival and IPAR measures by taking the arcsine of the square root of each value. All analyses were performed using the mixed-model procedure (proc mixed) in SAS (version 9.1.3 SAS Institute Inc., Cary, North Carolina) with a type-I error rate of 0.05.

3. Results

3.1 Stand attributes

Average DBH, total stem height, total standing stem volume per hectare, basal area per hectare, and percent survival did not significantly ($p>0.05$) differ between the two cultural treatments at age 12 (Tables 3.4 and 3.5) or age 13 (Tables 3.9 and 3.10). At age 12, average DBH and total stem height decreased with increasing planting density ($p<0.0001$), while average total standing stem volume per hectare and basal area per hectare increased as planting density increased ($p<0.0001$) (Tables 3.4 and 3.6). Percent survival was significantly ($p<0.0001$) greater for the 740 trees ha^{-1} planting density compared to the 1480 trees ha^{-1} and higher planting densities and was greater than 75 percent for all planting densities at age 12 (Table 3.6). Similarly, at age 13 planting density had a significant ($p<0.0001$) effect on average DBH, total stem height, total standing stem volume per hectare, and basal area per hectare (Table 3.9), with greater DBH and total height of average individual tree stems at the lower densities but greater stem volume and basal area per hectare at the higher densities (Table 3.11). Planting density had a significant ($p<0.0001$) effect on percent survival at age 13, with survival generally decreasing with increasing planting density (Table 3.11). Current annual increment (CAI) for the 13^{th} growing season was not significantly affected by cultural intensity ($p=0.7$), but there was a significant ($p=0.002$) planting density effect, with a general trend of increasing CAI (29.6 to 39.6

m^3 ha^{-1} $year^{-1}$) with increasing planting density (740 to 4440 trees ha^{-1}) (Tables 3.9 and 3.11). There was no significant effect of the interaction between culture and planting density for the stand attributes evaluated (Tables 3.4 and 3.9).

3.2 Crown attributes

Cultural intensity did not have a significant ($p>0.05$) effect on average live crown length or crown ratio at age 12 (Tables 3.4 and 3.7) or age 13 (Tables 3.9 and 3.12), although both were significantly ($p<0.0001$) affected by planting density. Average live crown length and crown ratio decreased with increasing planting density at age 12 (Table 3.8) and age 13 (Table 3.13). Average crown ratio was greater than one-third for all planting densities and greater than one-half for the 740 trees ha^{-1} planting density.

At age 12, SLA and foliar N concentration did not significantly ($p>0.05$) differ between the two cultural treatments (Tables 3.4 and 3.7). SLA was significantly ($p<0.0001$) affected by planting density, with the two lowest planting densities (740 and 1480 trees ha^{-1}) resulting in significantly less SLA compared to the higher planting densities (Tables 3.4 and 3.8). Foliar N concentration was not significantly affected by planting density, and averages for each planting density were above 1.65 percent (Tables 3.4 and 3.8).

During the 13^{th} growing season, average foliar biomass per hectare did not significantly ($p=0.4$) differ between the two cultural treatments (Tables 3.9 and 3.12), but average foliar biomass increased from 11.5 to 13.2 tonnes ha^{-1} as planting density increased from 740 to 4440 trees ha^{-1} ($p=0.02$) (Table 3.13). The interaction (culture x planting density) effect on foliar biomass was also significant ($p=0.04$) due to the significantly higher average foliar biomass for the plots receiving the maximum cultural treatment planted at 740 trees ha^{-1} (Fig. 3.1).

Average LAI (p=0.3) and N content (p=0.3) did not differ significantly between the two cultural treatments during the 13th growing season (Tables 3.9 and 3.12). LAI increased significantly (p<0.0001) from 3.8 to 4.8 m^2 m^{-2} as planting density increased from 740 to 4440 trees ha^{-1} (Table 3.13). N content was significantly (p=0.02) affected by planting density (Table 3.9). Foliar N content increased with increasing planting density, with the highest planting density treatment (4440 trees ha^{-1}) exhibiting an additional 27.9 kg ha^{-1} N in the crown compared to the lowest planting density (740 trees ha^{-1}) (Table 3.13). During the 13th growing season, IPAR (percent) was not significantly (p=0.2) affected by cultural regime (Table 3.9). Average IPAR values for all planting densities were above 90 percent and differed significantly (p=0.02) among planting densities (Table 3.13). The 740 and 1480 trees ha^{-1} planting densities intercepted significantly less photosynthetically active radiation than the 2220, 2960, and 4440 trees ha^{-1} planting densities. IPAR for the 3700 trees ha^{-1} planting density did not significantly differ from the other planting densities. With the exception of foliar biomass, the interaction effect of culture and planting density was not significant for the crown attributes evaluated (Tables 3.4 and 3.9).

3.3 Resource-use efficiency

$GE_{folmass}$, GE_{LAI}, and NUE were not significantly (p>0.05) affected by cultural intensity or planting density during the 13th growing season (Tables 3.9, 3.14 & 3.15). IPAR efficiency showed no significant difference between cultural treatments, but it differed significantly (p=0.008) with planting density (Table 3.9). IPAR efficiency (CAI $IPAR^{-1}$) ranged from 0.32 for the 740 trees ha^{-1} planting density to 0.42 for the 4440 trees ha^{-1} planting density (Table 3.15). IPAR efficiency for the four middle planting densities (1480, 2220, 2960, and 3700 trees ha^{-1}) did not significantly differ from each other. The interaction between culture and planting density

did not have a significant effect on the average resource-use efficiency attributes evaluated (Table 3.9).

4. Discussion

4.1 Cultural treatment

Stand and crown attributes were not significantly affected by cultural intensity for the time period analyzed. Although the maximum cultural regime provided more frequent fertilization and competition control relative to the operational cultural regime, the operational treatment still provided considerable inputs (e.g. chemical competition control at planting and three fertilization treatments). Although cultural intensity may have affected growth earlier in stand development, it appears that both stem growth and canopy size have converged for the cultural treatments. Foliar N concentration was above 1.60 percent for all cultural intensity and planting density combinations; well above the critical level of 1.10 percent for loblolly pine (Allen 1987), suggesting that loblolly pine N nutrition is not deficient for either treatment. Peak projected LAI values for all cultural intensity and planting density combinations were approaching or above the critical level of 3.5 (Fox et al. 2007a) and approaching the theoretical maximum LAI value for loblolly pine (Vose and Allen 1988). Sufficient N concentrations and high LAI values suggest that canopy development was not limited by N availability in either cultural treatment at age 12 or during the 13^{th} growing season. LAI may have reached a constant level in the plots receiving the maximum cultural treatment, thus allowing the plots receiving the operational cultural treatment to approach LAI values similar to the maximum cultural treatment plots (Allen et al. 2005). It should be noted that this result is quite different from the average findings from 22 PMRC culture x planting density study installations throughout the Piedmont and Upper Coastal Plain of the southeastern U.S. including the installations analyzed in detail in

the current study. Analysis of all 22 culture x planting density study installations showed that cultural intensity had a significant effect on average DBH, total stem height, basal area per acre, total standing stem volume per acre, percent survival, live crown length, and crown ratio at age 12 (Zhao and Kane 2010). Analyzing all 22 installations resulted in a sample size much larger than the current study (4 installations), which contributed to statistical power and may have allowed for more sensitivity to cultural differences. Similarly, results from the PMRC culture x planting density study in the Lower Coastal Plain of the southeastern U.S. (17 installations) showed that cultural intensity had a significant effect on average DBH, total stem height, basal area per acre, total standing stem volume per acre, and percent survival at age 12 (Zhao et al. 2011). The Lower Coastal Plain study sites were typically on somewhat poorly to poorly drained soils of relatively low fertility which may have contributed to the significant response to increased soil nutrient availability.

4.2 Planting density and stand attributes

Stand attributes followed traditional density relationships. Individual tree stems were larger in the lower density stands as evidenced by greater average DBH and tree height. At the stand level, greater standing stem volume per hectare, basal area per hectare, CAI, and mortality were exhibited in the higher density stands. Clearly, there was a trade-off between individual tree growth and stand growth. Lower planting densities allow for increased growth rates among individual trees due to less competition among crop trees for site resources, whereas stands planted at higher densities have the ability to utilize site resources more quickly due to the greater number of stems per unit land area. At the higher density stands, however, there is a reduction in crop tree survival due to competition-induced mortality (Albaugh et al. 2006; Barron-Gafford et al. 2003; Carlson et al. 2009; Harms et al. 2000; Will et al. 2010).

4.3 Planting density and crown attributes

Stand level foliar biomass and LAI were greater in the higher planting density stands, while live crown length and live crown ratio were greater in the lower planting density stands. This implies that foliar biomass and leaf area were denser in the higher density stands (more compact crowns). Although higher planting density resulted in more photosynthetic surface area and increased IPAR, it also led to the potential for more shading within and among crop trees. Results showed that the IPAR efficiency was greatest in the 4440 trees ha^{-1} stand, however, suggesting that despite more shaded conditions, the high density stands had more efficient use of the available light source. A possible mechanism for increased efficiency is changes to needle morphology (Meir et al. 2002; Samuelson et al. 2008; Samuelson et al. 2010; Will et al. 2001). SLA is one measurement of needle morphology that can vary under different light levels (Chmura and Tjoelker 2008; McCrady and Jokela 1996; Will et al. 2001). In this study, SLA increased with increasing planting density. This allowed for more photosynthetic surface area per unit of needle biomass (longer, thinner needles), which may help mitigate the effects of increased shading.

4.4 Planting density and nitrogen

Foliar N concentration was similar among all six planting densities and averaged 1.68%; suggesting that even the higher planting densities were not N limited (Allen 1987). Although N concentration is not a good predictor of CAI (Will et al. 2005), it may serve as a source for subsequent foliage development (Borders et al. 2004; Munger et al. 2003; Tyree et al. 2009; Will et al. 2002). Foliar N content (kg ha^{-1}) was greater in the higher planting density stands, primarily because N content is strongly related to foliar biomass.

4.5 Planting density and resource-use efficiency

Planting density did not have a significant effect on $GE_{folmass}$, GE_{LAI}, or NUE. IPAR efficiency, however, was greatest for the 4440 trees ha^{-1} planting density plots. Radiation-use efficiency (RUE) could not be calculated in this study because IPAR was only measured once during the year. Assuming that IPAR readings taken during peak leaf area are indicative of trends in average annual IPAR, the IPAR efficiency can be used as a surrogate for RUE. Efficiency estimates that include IPAR may account for more subtle changes in crown morphology compared to efficiency estimates that simply account for the amount of foliage, because IPAR accounts for the total amount of foliage and how that foliage is displayed and distributed within the canopy (Allen et al. 2005; Will et al. 2005). The significant increase in IPAR efficiency between the lowest and highest planting density corresponds with the increase in SLA with increasing planting density. It is possible that IPAR efficiency was affected by differences in needle morphology that were not reflected in the other efficiency measurements. Although not addressed in this study, another possible explanation for enhanced efficiencies at higher densities for loblolly pine may be attributed to increased biomass partitioning to stem relative to other tree components at higher densities (Burkes et al. 2003; Subedi 2011; Will et al. 2005).

5. Conclusions

Hypotheses 1a and 2a were negated, as the more intensive cultural treatment did not have a significant effect on stem and crown characteristics at ages 12 and 13. Hypothesis 1b was partially negated due to the absence of a significant planting density effect on foliar N concentration at age 12, but supported by the SLA results, which increased with increased planting density at age 12. At ages 12 and 13, lower planting density stands resulted in significantly greater average DBH, total stem height, percent survival, live crown length, and

crown ratio and significantly less average standing stem volume per hectare and basal area per hectare compared to stands planted at the higher densities, which supported Hypothesis 2b. The culture x planting density interaction effect was not significant for any of the stem and crown attributes analyzed at ages 12 and 13 supporting Hypotheses 1c and 2c.

Hypothesis 3a was partially upheld because culture had no significant affect on IPAR efficiency, and it was partially negated due to the absence of a cultural affect on the other crown and growth attributes during the 13th growing season. Hypothesis 3b was partially confirmed as lower planting density stands resulted in significantly less CAI, foliar biomass per hectare, LAI, foliar N content, and IPAR compared to stands planted at the higher densities during the 13th growing season. The predictions made about resource-use efficiency in Hypothesis 3b were not upheld as $GE_{folmass}$, GE_{LAI}, and NUE were not significantly affected by planting density, and IPAR efficiency generally increased with increasing planting density. Hypothesis 3c was supported for all crown and growth attributes during the 13th growing season with the exception of foliar biomass per hectare, which was the only attribute that was significantly affected by the interaction of cultural intensity and planting density.

In summary, stand and crown attributes were similar between the two levels of culture, but varied greatly with planting density. It appears that at this stage of stand development, light limitations due to high stocking have a greater influence on growth than soil limitations due to poor nutrition for the loblolly pine plantations analyzed in this study. Knowledge of growth limitation trends over time is important for forest management decisions regarding silvicultural prescriptions. Higher density stands resulted in increased SLA and IPAR efficiency, supporting the idea that higher density stands utilize the available light source more efficiently than lower density stands. This is of particular importance when modeling productivity based on

physiological processes, as stands grown at different densities can result in varying foliar relationships with growth.

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Table 3.1. Site location and attributes for four PMRC culture x planting density study installations

County, State	Latitude	Longitude	Soil series*	Soil Taxonomy*	Physiographic region
Burke Co., GA	33.0581	-82.2329	Tifton	Fine-loamy, kaolinitic, thermic plinthic kandiudults	Upper Coastal Plain
Burke Co., GA	33.0820	-82.2412	Tifton	Fine-loamy, kaolinitic, thermic plinthic kandiudults	Upper Coastal Plain
Hancock Co., GA	33.2730	-82.8375	Cecil - Madison - Pacolet	Fine, kaolinitic, thermic typic kanhapludults	Piedmont
Jasper Co., GA	33.3892	-83.5799	Lloyd – Pacolet	Fine kaolinitic, thermic rhodic and typic kanhapludults	Piedmont

* Soils information provided by the USDA-NRCS Soil Survey Division

Table 3.2. Description of operational and maximum cultural treatments on the PMRC culture x planting density study

Treatment	Growing Season	Operational	Maximum
Site preparation		Chemical and mechanical	Chemical and mechanical
Fertilization	At planting	560 kg ha^{-1} 10-10-10	560 kg ha^{-1} 10-10-10
	2^{nd}		673 kg ha^{-1} 10-10-10 + 131 kg ha^{-1} NH_4NO_3 + micronutrients
	4^{th}		131 kg ha^{-1} NH_4NO_3
	6^{th}		336 kg ha^{-1} NH_4NO_3
	8^{th}	224 kg ha^{-1} N + 28 kg ha^{-1} P	224 kg ha^{-1} N + 28 kg ha^{-1} P
	10^{th}		224 kg ha^{-1} N + 28 kg ha^{-1} P
	12^{th}	224 kg ha^{-1} N + 28 kg ha^{-1} P	224 kg ha^{-1} N + 28 kg ha^{-1} P
Competition control (chemical)	1^{st}	280 g ha^{-1} sulfometuron-methyl banded application + glyphosate and tryclopyr direct spraying	280 g ha^{-1} sulfometuron-methyl broadcast application + glyphosate and tryclopyr direct spraying
	2^{nd}		841 g ha^{-1} imazapyr broadcast application
	3^{rd} through 12^{th}		Glyphosate and tryclopyr repeated direct spraying

Table 3.3. Plot size and spacing for different planting densities on the PMRC culture x planting density study

Planting density (trees ha^{-1})	Original spacing (m x m)	Measurement plot size (ha)	Gross plot size (ha)
740	3.66 x 3.66	0.105	0.227
1480	2.44 x 2.74	0.053	0.150
2220	2.44 x 1.83	0.046	0.125
2960	1.83 x 1.83	0.040	0.121
3700	1.83 x 1.46	0.045	0.129
4440	1.83 x 1.22	0.040	0.125

Table 3.4. P-values for the effects of culture, planting density, and their interaction on mean stem and crown attributes on four PMRC loblolly pine installations at age 12

Attribute	Source		
	Culture	Planting density	Interaction
Stem attributes			
DBH	0.0721	<0.0001	0.2954
Total stem height	0.1864	<0.0001	0.7050
Total stem volume	0.3598	<0.0001	0.6259
Basal area	0.4519	<0.0001	0.4506
Percent survival	0.1923	<0.0001	0.7371
Crown attributes			
Live crown length	0.1952	<0.0001	0.7625
Crown ratio	0.9355	<0.0001	0.4915
SLA	0.0524	<0.0001	0.0608
Foliar N concentration	0.2816	0.6617	0.5188

Table 3.5. Mean stem attributes by culture on four PMRC loblolly pine installations at age 12

Culture	DBH (cm)	Total stem height (m)	Total standing stem volume (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Percent survival (%)
Operational	15.9 a	14.2 a	253.8 a	36.8 a	85.3 a
Maximum	16.8 a	15.0 a	278.6 a	38.8 a	81.3 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 3.6. Mean stem attributes by planting density on four PMRC loblolly pine installations at age 12

Planting density (trees ha^{-1})	DBH (cm)	Total stem height (m)	Total standing stem volume (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Percent survival (%)
740	22.7 a	15.4 a	200.5 a	28.8 a	95.8 a
1480	18.5 b	15.1 a	242.4 b	34.0 b	86.7 b
2220	16.3 c	15.0 a	270.4 c	37.6 c	79.8 c
2960	14.6 d	14.2 b	284.4 c	40.6 d	80.5 bc
3700	13.4 e	14.0 bc	287.3 c	41.1 d	76.7 c
4440	12.6 e	13.7 c	312.2 d	44.9 e	80.2 bc

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 3.7. Mean crown attributes by culture on four PMRC loblolly pine installations at age 12

Culture	Live crown length (m)	Crown ratio (%)	SLA (m^2 kg^{-1})	Foliar N concentration (%)
Operational	6.0 a	42.3 a	10.76 a	1.65 a
Maximum	6.4 a	42.1 a	11.34 a	1.71 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 3.8. Mean crown attributes by planting density on four PMRC loblolly pine installations at age 12

Planting density (trees ha^{-1})	Live crown length (m)	Crown ratio (%)	SLA (m^2 kg^{-1})	Foliar N concentration (%)
740	8.6 a	56.2 a	10.33 a	1.69 a
1480	6.6 b	44.2 b	10.67 a	1.66 a
2220	6.1 bc	40.5 bc	11.40 b	1.68 a
2960	5.5 cd	38.8 c	11.29 b	1.67 a
3700	5.1 d	36.8 c	11.17 b	1.70 a
4440	5.1 d	36.9 c	11.45 b	1.68 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 3.9. P-values for the effects of culture, planting density, and their interaction on mean stem, crown, and efficiency attributes on four PMRC loblolly pine installations at age 13 or during the 13th growing season

Attribute	Source		
	Culture	Planting density	Interaction
Stem attributes			
DBH	0.0585	<0.0001	0.4341
Total stem height	0.1598	<0.0001	0.6847
Total stem volume	0.3857	<0.0001	0.4573
Basal area	0.5511	<0.0001	0.2647
Percent survival	0.1493	<0.0001	0.7972
CAI	0.7394	0.0020	0.1149
Crown attributes			
Live crown length	0.2223	<0.0001	0.3450
Crown ratio	0.7368	<0.0001	0.3991
Foliar biomass	0.3952	0.0185	0.0427
LAI	0.2627	<0.0001	0.6126
Foliar N content	0.2920	0.0189	0.0951
IPAR	0.2103	0.0197	0.9945
Efficiency attributes			
$GE_{folmass}$	0.5493	0.1189	0.3389
GE_{LAI}	0.3893	0.6044	0.3787
NUE	0.4199	0.0646	0.2899
IPAR efficiency	0.6883	0.0084	0.1100

Table 3.10. Mean stand attributes by culture on four PMRC loblolly pine installations (DBH, height, volume, basal area, and percent survival at age 13 and current annual increment for the 13th growing season)

Culture	DBH (cm)	Total stem height (m)	Total standing stem volume (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Percent survival (%)	Current annual increment (m^3 ha^{-1} $year^{-1}$)
Operational	16.5 a	15.2 a	286.3 a	39.2 a	83.9 a	34.7 a
Maximum	17.4 a	15.9 a	306.0 a	40.5 a	78.9 a	33.1 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 3.11. Mean stand attributes by planting density on four PMRC loblolly pine installations (DBH, height, volume, basal area, and percent survival at age 13 and current annual increment for the 13th growing season)

Planting density (trees ha^{-1})	DBH (cm)	Total stem height (m)	Total standing stem volume (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Percent survival (%)	Current annual increment (m^3 ha^{-1} $year^{-1}$)
740	23.4 a	16.4 a	228.5 a	31.0 a	95.5 a	29.6 a
1480	19.2 b	16.1 ab	273.7 b	36.5 b	86.1 b	32.2 ab
2220	16.9 c	16.0 b	299.9 c	39.7 c	78.4 c	32.6 ab
2960	15.2 d	15.3 c	315.3 c	42.4 cd	77.8 c	36.1 bc
3700	13.9 e	15.0 cd	314.7 c	42.6 d	73.9 c	33.3 ab
4440	13.1 e	14.8 d	344.9 d	46.8 e	76.8 c	39.6 c

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 3.12. Mean crown attributes by culture on four PMRC loblolly pine installations (live crown length and crown ratio at age 13 and foliar biomass, LAI, foliar N content, and IPAR for the 13th growing season)

Culture	Live crown length (m)	Crown ratio (%)	Foliar biomass (tonnes ha^{-1})	Peak projected LAI (m^2 m^{-2})	Foliar N content (kg ha^{-1})	IPAR (%)
Operational	6.4 a	41.3 a	12.0 a	4.1 a	198.5 a	92.3 a
Maximum	6.6 a	40.8 a	12.9 a	4.6 a	218.5 a	93.8 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 3.13. Mean crown attributes by planting density on four PMRC loblolly pine installations (live crown length and live crown ratio at age 13 and foliar biomass, LAI, foliar N content, and IPAR for the 13th growing season)

Planting density (trees ha^{-1})	Live crown length (m)	Crown ratio (%)	Foliar biomass (tonnes ha^{-1})	Peak projected LAI (m^2 m^{-2})	Foliar N content (kg ha^{-1})	IPAR (%)
740	8.8 a	53.5 a	11.5 a	3.8 a	192.6 a	91.3 a
1480	7.1 b	44.2 b	12.2 ab	4.1 ab	202.6 a	91.1 a
2220	6.4 c	39.3 c	12.3 ab	4.5 bc	205.6 ab	94.6 b
2960	6.0 cd	38.6 cd	12.6 b	4.5 bc	208.8 ab	94.3 b
3700	5.4 cd	36.2 de	13.0 b	4.6 c	220.9 b	92.9 ab
4440	5.3 d	35.4 e	13.2 b	4.8 c	220.5 b	94.0 b

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 3.14. Mean resource-use efficiency attributes by culture on four PMRC loblolly pine installations for the 13th growing season

Culture	$GE_{folmass}$ (m^3 $tonne^{-1}$)	GE_{LAI} (m^3 LAI^{-1})	NUE (m^3 $tonne^{-1}$)	IPAR efficiency (m^3 $\%IPAR^{-1}$)
Operational	2.9 a	8.5 a	176.6 a	0.37 a
Maximum	2.6 a	7.4 a	152.9 a	0.35 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 3.15. Mean resource-use efficiency attributes by planting density on four PMRC loblolly pine installations for the 13th growing season

Planting density (trees ha^{-1})	$GE_{folmass}$ (m^3 $tonne^{-1}$)	GE_{LAI} (m^3 LAI^{-1})	NUE (m^3 $tonne^{-1}$)	IPAR efficiency (m^3 $\%IPAR^{-1}$)
740	2.6 a	7.9 a	154.1 a	0.32 a
1480	2.7 a	8.0 a	161.4 a	0.35 ab
2220	2.8 a	7.7 a	163.9 a	0.34 ab
2960	2.9 a	8.2 a	174.3 a	0.38 bc
3700	2.6 a	7.4 a	153.7 a	0.36 ab
4440	3.0 a	8.3 a	181.3 a	0.42 c

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

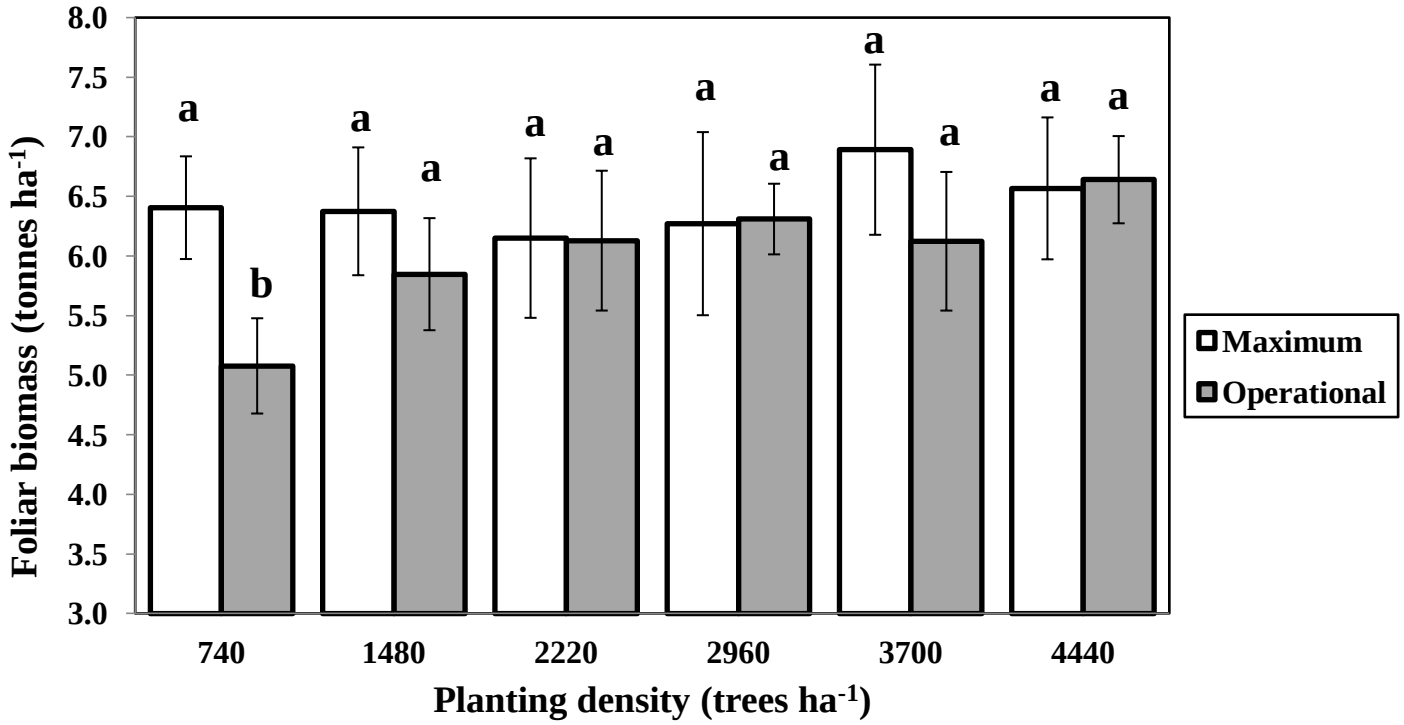

Fig. 3.1. Mean foliar biomass (tonnes ha^{-1}) for planting density and cultural intensity treatment combinations on four PMRC loblolly pine installations during the 13th growing season. The white columns represent the maximum cultural intensity and the gray columns represent the operational cultural intensity at each of the six planting densities. At each level of planting density, columns with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05). Bars represent the standard error of the means for each combination of planting density and cultural intensity.

CHAPTER 4

EFFECTS OF PLANTING DENSITY AND CULTURAL INTENSITY ON STAND AND CROWN ATTRIBUTES OF LOBLOLLY PINE PLANTATIONS THINNED AT AGE 12 DURING THE AGE 12- TO AGE 13-YEAR PERIOD IN THE UPPER COASTAL PLAIN AND PIEDMONT OF THE SOUTHEASTERN U.S. [3]

[3] Akers, M.K.., Kane, M., Zhao, D., Teskey, R.O., and Daniels, R.F. To be submitted to Forest Ecology and Management.

Abstract

Increased understanding of productivity drivers in thinned stands will lead to better growth and yield predictions and management approaches concerning thinning regimes. Thinning was implemented in three installations of an existing planting density x cultural intensity loblolly pine study in the Upper Coastal Plain and Piedmont of Georgia and Alabama. Each installation was arranged in a split-plot design, with two main plots that received one of two cultural treatments (operational or maximum) and four sub-plots that received one of four density management regimes: (1) 740 trees ha^{-1} planting density; no thinning, (2) 1480 trees ha^{-1} planting density; thinned at age 12, (3) 2220 trees ha^{-1} planting density; thinned at age 12, and (4) 2960 trees ha^{-1} planting density; thinned at age 12. All thinned plots were thinned to match the current trees ha^{-1} on the 740 trees ha^{-1} plot with the corresponding cultural treatment. Treatment effects on average stand and crown attributes were analyzed at ages 12 and 13 and during the 13^{th} growing season. Results showed that cultural intensity did not have a major influence on average stand and crown attributes before or after thinning at age 12. During the 13^{th} growing season, however, average growth efficiency calculated using leaf area index (LAI) was significantly greater for stands grown under the operational (less intensive) cultural regime. Density regime significantly affected average stem and crown attributes before and after thinning. For example, average peak projected LAI, foliar N content, and intercepted photosynthetically active radiation decreased with increasing planting density during the 13^{th} growing season (post-thinning). It appears that at this stage of stand development, light limitations due to high stocking had a greater influence on growth than soil limitations due to poor nutrition for the loblolly pine plantations analyzed in this study. It is of great interest to monitor these trends over time, as foliar development has a strong relationship with tree and

stand productivity and therefore, important implications for growth and yield modeling and management decisions.

1. Introduction

Loblolly pine (*Pinus taeda* L.) is a fast-growing plantation species that is very responsive to intensive silviculture, producing yields as high as 34 m^3 ha^{-1} $year^{-1}$ mean annual stem volume increment in its native southeastern U.S. (Borders and Bailey 2001) and even greater yields abroad (Jokela et al. 2004; Samuelson et al. 2008). Silvicultural practices such as genetic improvement, competition control, fertilization, and density management have greatly enhanced growth rates in loblolly pine plantations (Fox et al. 2007). To gain a better understanding of how these practices can influence loblolly pine growth rates, the physiological systems that drive growth should be studied in more detail (Jokela et al. 2004; King et al. 2008; Tyree et al. 2009; Will et al. 2005).

Many studies have shown that loblolly pine stand productivity has a positive linear relationship with leaf area (Albaugh et al. 2004; Jokela and Martin 2000; Samuelson et al. 2001; Samuelson et al. 2004; Will et al. 2005; Xiao et al. 2003b), although studies have also shown the relationship to be curvilinear (Jokela et al. 2004; McCrady and Jokela 1998; Sword Sayer et al. 2004), possibly due to increased shading within high leaf area canopies (Martin and Jokela 2004a; Will et al. 2005). The slope of this relationship (stem growth or above-ground biomass production per unit leaf area) is often referred to as "growth efficiency", and there is evidence that it can be altered through silvicultural practices (Albaugh et al. 2006; Borders et al. 2004; Burkes et al. 2003; Maier et al. 2002; Sword Sayer et al. 2004). Leaf area represents the amount of photosynthetic surface area, and is therefore an integral component of tree growth. Similarly, measures of intercepted photosynthetically active radiation (IPAR) represent photosynthetic

energy capture (Will et al. 2005). IPAR accounts for the total amount of foliage and how that foliage is displayed and distributed within the canopy (Allen et al. 2005; Will et al. 2005). Studies have shown that IPAR is positively correlated with stem growth in loblolly pine, and is often linearly related to growth for a given site (Allen et al. 2005; Chmura and Tjoelker 2008; Dalla-Tea and Jokela 1991; McCrady and Jokela 1998; Will et al. 2001; Will et al. 2005).

Foliar nitrogen (N) concentration has not shown a consistent observable relationship with photosynthetic capacity for loblolly pine (Munger et al. 2003), however, additional N acquired by the foliage may serve as an important source for subsequent foliage development (Borders et al. 2004; Munger et al. 2003; Tyree et al. 2009; Will et al. 2002). Increases in foliar N concentration have been linked to increases in soil N availability (Albaugh et al. 2004; Borders et al. 2004; Martin and Jokela 2004b), and assessments of foliar N concentration may be used to help determine the degree of loblolly pine N deficiency, a common limitation to productivity (Albaugh et al. 2010; Vose and Allen 1988; Xiao et al. 2003a).

Stand and crown development response to thinning is of great interest, as thinning can be used as a tool to remove stand volume that would otherwise be lost due to intra-specific competition-induced mortality while increasing the growth rate of the remaining trees (Ginn et al. 1991; Jokela et al. 2004). Studies have shown that reducing stand density through thinning results in less stand level leaf area and greater average live crown length compared to high density non-thinned control stands (Hennessey et al. 2004; Sword Sayer et al. 2004). Results from these studies showed that thinning had no consistent effect on growth efficiency from year to year, although it was suggested that thinned stands may better endure poor growing conditions due to drought (Hennessey et al. 2004; Sword Sayer et al. 2004).

Increased understanding of productivity drivers in thinned stands will lead to better growth and yield predictions and management approaches concerning thinning regimes. In this study, thinning was implemented in three installations of an existing planting density x cultural intensity loblolly pine study. Each installation was arranged in a split-plot design, with two main plots that received one of two cultural treatments (operational or maximum) and four sub-plots that received one of four density management regimes: (1) 740 trees ha^{-1} planting density; no thinning, (2) 1480 trees ha^{-1} planting density; thinned at age 12, (3) 2220 trees ha^{-1} planting density; thinned at age 12, and (4) 2960 trees ha^{-1} planting density; thinned at age 12. All thinned plots were thinned to match the current trees ha^{-1} on the 740 trees ha^{-1} plot with the corresponding cultural treatment. The objective of the research reported here was to:

(1) determine effects of planting density, cultural intensity, and their interaction on stand and crown conditions prior to and immediately following thinning at age 12;

(2) assess effects of planting density, cultural intensity, and their interaction on 13^{th} growing season productivity, crown development, and production dynamics.

Specific hypotheses include:

At age 12 (prior to thinning):

(1a) The more intensive cultural treatment will result in significantly greater average DBH, total stem height, standing stem volume per hectare, basal area per hectare, live crown length, SLA, and foliar N concentration and significantly less average current density and crown ratio compared to the less intensive cultural treatment.

(1b) Lower planting density stands will result in significantly greater average DBH, total stem height, live crown length, crown ratio, and foliar N concentration and significantly less average

standing stem volume per hectare, basal area per hectare, current density, and specific leaf area (SLA) compared to the stands planted at the higher densities.

(1c) There will not be a significant cultural intensity x planting density interaction effect on average DBH, total stem height, standing stem volume per hectare, basal area per hectare, current density, live crown length, crown ratio, SLA, or foliar N concentration.

At age 12 and13 (post-thinning):

(2a) The more intensive cultural treatment will result in significantly greater average DBH, total stem height, standing stem volume per hectare, basal area per hectare, and live crown length and significantly less average current density and crown ratio compared to the less intensive cultural treatment.

(2b) Lower planting density stands will result in significantly greater average DBH, total stem height, standing stem volume per hectare, basal area per hectare, live crown length, and crown ratio and no significant difference in average current density compared to the stands planted at the higher densities.

(2c) There will not be a significant cultural intensity x planting density interaction on average DBH, total stem height, standing stem volume per hectare, basal area per hectare, current density, live crown length, or crown ratio.

During the 13^{th} growing season (post-thinning):

(3a) The more intensive cultural treatment will result in significantly greater average current annual increment (CAI) standing stem volume growth per hectare, foliar biomass per hectare, leaf area index (LAI), foliar N content, IPAR, $GE_{folmass}$, GE_{LAI}, and NUE and no significant difference in average IPAR efficiency compared to the less intensive cultural treatment.

(3b) Lower planting density stands will result in significantly greater average CAI standing stem volume growth per hectare, foliar biomass per hectare, LAI, foliar N content, and IPAR compared to higher planting density stands, and planting density will not have a significant effect on average $GE_{folmass}$, GE_{LAI}, NUE, or IPAR efficiency.

(3c) There will not be a significant cultural intensity x planting density interaction effect on average CAI standing stem volume per hectare, foliar biomass per hectare, LAI, foliar N content, IPAR, $GE_{folmass}$, $GE_{LAI,}$ NUE, or IPAR efficiency.

2. Methods

2.1 Study sites and treatments

This study utilized three permanent loblolly pine research installations maintained by the University of Georgia Plantation Management Research Cooperative (PMRC). Two installations were located in the Upper Coastal Plain region of Alabama, and one installation was located in the Piedmont region of Georgia (Table 4.1). The installations were planted in early 1998 with open-pollinated, bare-root loblolly pine seedlings chosen by the PMRC cooperator for that site. Although planting material may have differed among installations, only one half-sib family was planted within each installation. Each installation was arranged in a split-plot design, with two main plots that received one of two cultural treatments and four sub-plots that were planted at one of four densities. The two cultural treatments were termed "operational" and "maximum" (Table 4.2). The maximum treatment included frequent fertilization and complete sustained competition control. The operational treatment included less frequent fertilization and early competition control. The four sub-plots were planted at 740, 1480, 2220, and 2960 trees ha^{-1}. To ensure adequate first-year survival, planting locations were double-planted and reduced to a single surviving seedling after the first growing season. The combination of two cultural

treatments and four planting densities resulted in eight plots per installation, with a different randomly-assigned combination of cultural intensity and planting density for each plot. Plot size varied to accommodate the different planting densities (Table 4.3). Gross plots contained an interior measurement plot surrounded by an approximate 8 m wide buffer. The entire gross plot received the designated planting density and cultural regime. Measurements were obtained only from trees in the interior measurement plots.

A thinning was performed on selected plots from the three installations in February of 2010 when the stands were at age 12. Plots with initial planting densities of 1480, 2220, and 2960 trees ha^{-1} were thinned, while the 740 trees ha^{-1} planting density plots were not thinned. The plots targeted for thinning receiving the operational cultural treatment were thinned to match the current trees ha^{-1} exhibited in the operational plot with an initial planting density of 740 trees ha^{-1} for that particular installation. The plots targeted for thinning receiving the maximum cultural treatment were thinned to match the current trees ha^{-1} exhibited in the maximum plot with an initial planting density of 740 trees ha^{-1} for that particular installation. To carry out the thinning, every third row of trees was removed and individual tree selection was performed in the remaining rows to meet the desired density. All thinned materials were left on the plot.

2.2 Stand and crown measurements

In the measurement plots, diameter at breast height (DBH) was measured on all trees and total height and live crown length were measured on every other tree during the dormant season prior to thinning at age 12 and post-thinning at ages 12 and 13. Crown ratio was calculated as live crown length divided by total stem height. For the trees that were not measured for total height, estimates of total height were made using an equation fit for trees with both measured

total height and DBH for each plot and measurement year using the model form: ln (height) = $\beta 0 + \beta 1\ DBH^{-1}$.

Total outside-bark stem volume was estimated for all trees at ages 12 (pre- and post-thinning) and 13 using the volume equation developed by Pienaar et al. (1987). Current annual increment (CAI) of stem volume growth per hectare was estimated by subtracting total volume at age 12 (pre-thinning) from total volume at age 13. When estimating CAI on the thinned plots, removed-tree volume per hectare was included in the total volume at age 13 to ensure that CAI reflected the growth rate of the trees remaining after thinning. When estimating CAI, tree volume lost to mortality from age 12 (pre-thinning) to age 13 years old was included in the total volume at age 13 to ensure that CAI reflected the growth rate of the remaining trees. Basal area ($m^2\ ha^{-1}$) and current trees per acre were also determined at ages 12 (pre- and post-thinning) and 13.

Leaf litter traps were used to estimate plot level foliar biomass post-thinning. Circular traps (0.46 m^2) were constructed using PVC pipe as the frame, window screen as the lining, and metal wire as legs. Eight traps were randomly distributed per plot on all three installations. Litter was collected from the traps over the course of the 13^{th} year (March 2010 – March 2011) at approximately 13 week intervals. Litter was dried in a drying oven at 65° C to a constant weight and then hand-sorted to remove debris (bark, weeds, reproductive material, etc). Pine needles were weighed to estimate previous-year (2009) age-class foliar biomass for each plot; as loblolly in the southeastern U.S. typically retains needles for 1.5 years. Foliar biomass estimates were then doubled to represent peak foliar biomass (two foliar age classes) for each plot.

Needle samples were collected for all-sided specific leaf area (SLA) measurements. SLA was measured as the ratio of needle surface area (green) to needle mass (dry) using the method by Fites and Teskey (1988). Four trees were destructively sampled in each plot as part of a

concurrent biomass project in February 2010 (Subedi 2011). For each sampled tree, the crown was divided into three sections of equal length representing the lower, middle, and top portion of the crown. For each of the four sampled trees per plot, two branches were randomly selected from each crown position. At least five fascicles were removed from the middle of each of the two to four flushes of foliage present on each of the selected branches. For each crown position per plot, 15 to 30 needles were randomly chosen and measured to determine average SLA per plot. Plot-level SLA values were multiplied by plot-level foliar biomass values to estimate peak all-sided leaf area per plot. Peak all-sided leaf area was converted to peak projected leaf area by dividing by 3.14 (Grace et al. 1987).

The two randomly selected branches used for SLA samples were also used for foliar N concentration samples. At least five fascicles were removed from the middle of each of the two to four flushes of foliage present on each of the selected branches. Fascicles from the three crown positions were combined, and at least 30 fascicles were randomly chosen as foliar N concentration samples for each plot. Samples were dried and ground using a Certiprep 8000-D mixer/mill (Spex, Metuchen, NJ, USA). The dry combustion method was used for foliar N concentration analysis using a CE Elantech NA2100 (CE Elantech Inc., Lakewood, NJ, USA). Foliar nitrogen content (kg ha^{-1}) was estimated as the product of plot-level foliar nitrogen concentration and plot-level foliar biomass.

Intercepted photosynthetically active radiation (IPAR) was measured for each plot using the SunScan Canopy Analysis System (Delta-T Devices Ltd., Cambridge, UK). Solar radiation was measured under the canopy and in nearby areas receiving full sunlight to determine the proportion of IPAR for each plot. Approximately 200 individual IPAR measurements were taken beneath the canopy of each plot along 4 transects parallel to the tree rows and 5 transects

perpendicular to the tree rows. Measurements were taken around solar noon between July 23, 2010 and August 4, 2010 to capture peak leaf area and a desirable sun angle. Each installation was measured within a single day. In this study, IPAR for each treatment is reported as the percentage of total photosynthetically active radiation intercepted by the foliage.

2.3 Resource-use efficiency calculations

Efficiency calculations were used to measure stem growth (volume) per unit crown measure. Growth efficiency was measured using foliar biomass ($GE_{folmass}$) and LAI (GE_{LAI}). $GE_{folmass}$ was calculated as m^3 CAI growth per tonne of peak foliar biomass. GE_{LAI} was calculated as m^3 CAI growth per unit peak projected LAI. Nitrogen-use efficiency (NUE) was calculated as m^3 CAI growth per tonne N content. Radiation-use efficiency (RUE) could not be calculated because IPAR was only measured once during the year. Instead, IPAR efficiency was calculated as m^3 CAI per IPAR percentage.

2.4 Statistical analysis

The main effects of culture, planting density, and their interaction were analyzed using a mixed-model approach. Each of the three installations was treated as a replication. Culture and planting density served as fixed effects and installation and installation x culture served as random effects (Littell et al. 1996). ANOVA was used to assess treatment effects on average crown (live crown length, crown ratio, foliar biomass, LAI, SLA, IPAR, N concentration, and N content), average stem (DBH, height, standing volume $hectare^{-1}$, basal area $hectare^{-1}$, current density, and CAI), and average efficiency ($GE_{folmass}$, GE_{LAI}, NUE, and IPAR efficiency) attributes for each year (age 12 pre-thinning, age 12 post-thinning, or age 13) or growing season (13^{th}) they were measured. For statistical analysis purposes, data transformation was performed on IPAR by taking the arcsine of the square root of each value. Least square means comparisons

for significant treatment effects were conducted using Fisher's LSD test. All analyses were performed using the mixed-model procedure (proc mixed) in SAS (version 9.1.3 SAS Institute Inc., Cary, North Carolina) with a type-I error rate of 0.05.

3. Results

3.1 Stand and crown attributes at age 12 (pre-thinning):

Average DBH, total stem height, total standing stem volume per hectare, basal area per hectare, and current density did not significantly ($p>0.05$) differ between the two cultural treatments prior to thinning at age 12 (Tables 4.4 and 4.5). At age 12 (pre-thinning), average DBH ($p<0.0001$) and total stem height ($p=0.03$) decreased with increasing planting density, while average total standing stem volume per hectare ($p=0.0003$) and basal area per hectare ($p=0.0001$) increased as planting density increased (Tables 4.4 and 4.6). Planting density had a significant ($p<0.0001$) effect on average current density at age 12 (pre-thinning), and ranged from 700 trees ha^{-1} for the 740 trees ha^{-1} planting density to 2389 trees ha^{-1} for the 2960 trees ha^{-1} planting density (Tables 4.4 and 4.6). There was no significant effect of the interaction between culture and planting density for the average stem attributes evaluated at age 12 (pre-thinning) (Table 4.4).

Cultural intensity did not have a significant effect on average live crown length ($p=0.3$) or crown ratio ($p=0.4$) at age 12 (prior to thinning) (Tables 4.4 and 4.7), although both were significantly affected by planting density. Average live crown length ($p<0.0001$) decreased with increasing planting density at age 12 (pre-thinning) (Table 4.8). Average crown ratio ($p=0.0006$) decreased with increasing planting density, although only the 740 trees ha^{-1} planting density was significantly different than the higher planting densities at age 12 (pre-thinning). Average crown

ratio was greater than one-third for all planting densities and greater than one-half for the 740 trees ha^{-1} planting density (Table 4.8).

At age 12 (pre-thinning), average SLA ($p=0.4$) and foliar N concentration ($p=0.09$) did not significantly differ between the two cultural treatments (Tables 4.4 and 4.7). Average SLA was significantly ($p=0.04$) affected by planting density, with the lowest planting density (740 trees ha^{-1}) resulting in the lowest SLA value (10.8 m^2 kg^{-1}) and the highest planting density (2960 trees ha^{-1}) resulting in the highest SLA value (11.5 m^2 kg^{-1}) (Table 4.8). Average foliar N concentration was not significantly ($p=0.2$) affected by planting density (Table 4.4), and averages for each planting density were above 1.35 percent (Table 4.8). The interaction effect of culture and planting density was not significant for the average crown attributes evaluated at age 12 prior to thinning (Table 4.4).

3.2 Stand and crown attributes at age 12 (post-thinning)

At age 12 (post-thinning) average DBH, total stem height, total standing stem volume per hectare, basal area per hectare, and current density did not differ significantly ($p>0.05$) between the two cultural treatments (Tables 4.9 and 4.10). Following thinning, average DBH decreased significantly ($p<0.0001$) with increasing planting density, while average total stem height was not significantly ($p=0.6$) affected by planting density (Tables 4.9 and 4.11). Average total standing stem volume per hectare and basal area per hectare were significantly ($p<0.0001$) affected by planting density, and decreased with increasing planting density (Tables 4.9 and 4.11). Average current density differed by less than 10 trees ha^{-1} among the four density regimes post-thinning, although there were significant ($p=0.05$) differences in current density among planting densities (Tables 4.9 and 4.11). The 740 trees ha^{-1} planting density, non-thinned

treatment had significantly greater current density than the 1480 and 2220 trees ha^{-1}, thinned treatments.

Average post-thinning live crown length ($p=0.4$) and crown ratio ($p=0.5$) were not significantly affected by culture at age 12 (Tables 4.9 and 4.11), although both were significantly affected by planting density. Average post-thinning live crown length ($p=0.01$) and crown ratio ($p=0.0007$) at age 12 decreased with increasing planting density (Table 4.11). Average live crown length and crown ratio did not differ significantly among the plots that received thinning, i.e. the 1480, 2220, and 2960 trees ha^{-1} planting density plots. The interaction effect of culture and planting density was not significant for the average post-thinning stem and crown attributes evaluated at age 12 (Table 4.9).

3.3 Stand and crown attributes at age 13 (post-thinning)

Average DBH, total stem height, total standing stem volume per hectare, basal area per hectare, and current density did not significantly ($p>0.05$) differ between the two cultural treatments at age 13 (Tables 4.12 and 4.13). At age 13, average DBH decreased significantly ($p<0.0001$) with increasing planting density, while average total stem height was not significantly ($p=0.6$) affected by planting density (Tables 4.12 and 4.14). Average total standing stem volume per hectare and basal area per hectare were significantly ($p<0.0001$) affected by planting density, and decreased with increasing planting density at age 13 (Tables 4.12 and 4.14). Average current density was not significantly different among the different density regimes at age 13 (Table 4.14).

Cultural intensity did not have a significant ($p>0.05$) effect on average live crown length or crown ratio at age 13 (Tables 4.12 and 4.15), although both were significantly affected by planting density. Average live crown length ($p=0.0007$) and crown ratio ($p=0.0001$) decreased

with increasing planting density at age 13 (Table 4.16). Average crown ratio was greater than one-third for all planting densities and greater than one-half for the 740 trees ha^{-1} planting density. The interaction effect of culture and planting density was not significant for the average stem and crown attributes evaluated at age 13 (Table 4.12).

3.4 CAI and foliar attributes during the 13th growing season (post-thinning)

Average current annual increment (CAI) for the 13th growing season was not significantly ($p=0.4$) affected by cultural intensity, but there was a significant ($p=0.0002$) planting density effect (Table 4.12). Average CAI decreased with increasing planting density, although the 740 and 1480 trees ha^{-1} planting densities were not significantly different from each other, and the 2220 and 2960 trees ha^{-1} planting densities were not significantly different from each other (Table 4.14).

During the 13th growing season, average foliar biomass per hectare ($p=0.09$) and LAI ($p=0.1$) did not significantly differ between the two cultural treatments (Tables 4.12 and 4.15). Average foliar biomass was significantly ($p<0.0001$) affected by planting density, with the 740 trees ha^{-1} planting density resulting in significantly greater foliar biomass per hectare compared to the thinned plots (1480, 2220, and 2930 trees ha^{-1} planting densities) (Tables 4.12 and 4.16). Similarly, planting density had a significant ($p=0.0002$) effect on average LAI, with the 740 trees ha^{-1} planting density resulting in significantly greater LAI compared to the thinned plots (Table 4.16).

Both cultural intensity ($p=0.02$) and planting density ($p<0.0001$) had a significant effect on average foliar N content during the 13th growing season (Table 4.12). Average foliar N content was significantly greater under the maximum cultural regime (74 kg ha^{-1}) compared to the operational cultural regime (54 kg ha^{-1}) (Table 4.15). Average foliar N content decreased

with increasing planting density and ranged from 52 to 88 kg ha^{-1} for the 2960 and 740 trees ha^{-1} planting densities, respectively (Table 4.16).

At peak leaf area during the 13th growing season, average IPAR (percent) was not significantly ($p=0.6$) affected by cultural regime, but the effect of planting density was significant ($p<0.0001$) (Table 4.12). The 740 trees ha^{-1} planting density (non-thinned) intercepted approximately 20 percent more photosynthetically active radiation than the next lowest planting density, 1480 trees ha^{-1} (Table 4.16). Average IPAR values for the 2220 and 2960 trees ha^{-1} planting densities were not significantly different from each other, however, they were significantly less than the average IPAR value for the 1480 trees ha^{-1} planting density. The interaction effect of culture and planting density was not significant for average CAI, foliar biomass, LAI, foliar N content, or IPAR during the 13th growing season (Table 4.12).

3.5 Resource-use efficiency during the 13th growing season (post-thinning)

Average $GE_{folmass}$, NUE, and IPAR efficiency were not significantly ($p>0.05$) affected by cultural intensity or planting density during the 13th growing season (Tables 4.12, 4.17 & 4.18). Average GE_{LAI} differed significantly ($p=0.05$) by cultural regime but showed no significant ($p=0.2$) difference between planting densities during the 13th growing season (Table 4.12). Average GE_{LAI} was significantly greater for the less intensive cultural treatment, with GE_{LAI} values of 5.1 and 3.4 m^3 LAI^{-1} for the operational and maximum treatments, respectively (Table 4.17). The interaction effect of culture and planting density was not significant for the average resource-use efficiency measures evaluated during the 13th growing season (Table 4.12).

4. Discussion

4.1 Cultural intensity effect on stand and crown attributes

Stem and crown attributes were not significantly affected by cultural intensity at age 12 before thinning. Although the maximum cultural regime provided more frequent fertilization and competition control relative to the operational cultural regime, the operational treatment still provided considerable inputs (e.g. chemical competition control at planting and three fertilizer treatments). Foliar N concentration was above 1.30 percent for all cultural intensity and planting density combinations; above the critical level of 1.10 percent for loblolly pine (Allen 1987), suggesting that loblolly pine N nutrition is not deficient for either treatment. Although cultural intensity may have affected growth earlier in stand development, it is possible that stand growth rate and foliar development have peaked at age 12, allowing for convergence of stem size and live crown length among the cultural treatments. Although not statistically significant, the actual average CAI value was greater for the less intensive cultural treatment during the 13th growing season.

To help mitigate the effect of reduced stand growth rate with stand development, thinning can be used to stimulate individual remaining tree growth rate (Ginn et al. 1991; Hennessey et al. 2004; Jokela et al. 2004). One year following thinning at age 13, cultural intensity did not have a significant effect on stem size measures, live crown length and ratio, or IPAR. It is possible that the cultural regimes are too similar to elicit a significant treatment effect, however, it is also possible that one year following thinning is too soon for a significant stand and crown response to increased resources. The significant cultural effect on foliar N content during the year following thinning may indicate potential stand response to culture over time following the thinning.

4.2 Density regime effect on stand attributes

Stem attributes followed traditional density relationships at age 12 (pre-thinning). Individual tree stems were larger in the lower density stands as evidenced by greater average DBH and total stem height. At the stand level, greater standing stem volume per hectare, basal area per hectare, and trees per hectare were exhibited in the higher density stands prior to thinning at age 12. Clearly, there was a trade-off between individual tree growth and stand growth. Lower planting densities allow for increased growth rates among individual trees due to less competition among crop trees for site resources, whereas stands planted at higher densities have the ability to utilize site resources more quickly due to the greater number of stems per unit land area. At the higher density stands, however, there is a reduction in crop tree survival due to competition-induced mortality (Albaugh et al. 2006; Barron-Gafford et al. 2003; Carlson et al. 2009; Harms et al. 2000; Will et al. 2010).

After thinning, planting density trends for average DBH were not altered from the pre-thinning trends at age 12 (average DBH decreased with increasing planting density). Total height, however, was no longer significantly affected by planting density. This was most likely the result of choosing trees in the suppressed and intermediate crown classes to be removed during the thinning. At the stand level, greater standing stem volume per hectare, basal area per hectare, and CAI were exhibited in the lower planting density stands post-thinning. Because the 1480, 2220, and 2960 trees ha^{-1} planting density stands were thinned to match the age 12 trees per hectare on the 740 trees ha^{-1} planting density stands, stand growth (stem volume, basal area, CAI) was regulated by average individual tree size post-thinning.

4.3 Planting density and crown attributes

Live crown length and crown ratio showed a similar response to planting density both before and after thinning (decreasing with increasing planting density). Over time, however, this

trend may cease to be significant due to increased light availability in the thinned stands. Peterson et al. (1997) attributed increased live crown length and crown ratio in thinned loblolly pine stands to increased light availability in the lower crown. Development and maintenance of larger crowns in thinned stands has been identified as the mechanism for increased stem diameter growth in thinned stands (Peterson et al. 1997).

Specific leaf area (SLA) is another measurement of crown morphology that can vary under different light levels (Chmura and Tjoelker 2008; McCrady and Jokela 1996; Will et al. 2001). At age 12 (pre-thinning), the 2960 trees ha^{-1} planting density resulted in significantly greater average SLA compared to the 740 trees ha^{-1} planting density. Increased SLA allows for more photosynthetic surface are per unit of needle biomass (longer, thinner needles), which may help mitigate the effects of increased shading in higher density stands by enhancing foliar biomass efficiency (Meir et al. 2002; Samuelson et al. 2008; Samuelson et al. 2010; Will et al. 2001).

Average foliar biomass per hectare, LAI, foliar N content per hectare, and IPAR were significantly less in the thinned stands compared to the non-thinned 740 trees ha^{-1} planting density stands with a similar current density. The reduction in stand level foliage compared to the non-thinned treatment was due to smaller individual crown size for the trees originally grown under more competitive (higher planting density) conditions. The typical trade-off between individual tree foliar development and stand level foliar development (Albaugh et al. 2006) was altered by the thinning. Studies have shown that this altered foliar development pattern following thinning can be maintained for several years (Hennessey et al. 2004; Sword Sayer et al. 2004).

4.4 Cultural intensity and planting density effect on resource-use efficiency

Density regime did not have a significant effect on any of the resource-use efficiency measures during the 13th growing season. However, GE_{LAI} was significantly greater for the operational cultural treatment compared to the maximum cultural treatment. Measures of $GE_{folmass}$, NUE, and IPAR efficiency did not show a statistically significant response to cultural intensity, but the average actual values for each of these measures were greater for the less intensive (operational) cultural regime during the 13th growing season. This trend could be attributed to decreasing growth rate (CAI) with more intensive culture, although this decrease was not statistically significant. Less dense foliage on the stands grown under operational culture could be another explanation for increased GE_{LAI}. Although not statistically significant, average actual LAI was greater and average actual live crown length was less for the maximum cultural treatment. Less shaded conditions in the operational plots may have allowed a more efficient response to the increased light availability lower in the canopy following thinning.

Increased nutrient availability in loblolly pine stands has resulted in increased growth efficiency (Albaugh et al. 2004), decreased growth efficiency (Xiao et al. 2003b), or no significant growth efficiency response (Samuelson et al. 2008). Interestingly, studies have found that early increases in growth efficiency attributed to increased nutrient availability may disappear or become negative as the stands age (Colbert et al. 1990; Jokela and Martin 2000; Will et al. 2002). Will et al. (2002) reported that changes in growth efficiency related to fertilization may be confounded with changes in tree size because growth efficiency decreased as mean tree size increased (Will et al. 2002). This suggests that differences in growth efficiency could be related to changes in stand development, which is influenced by resource availability. A decrease in growth efficiency with increasing tree age/size has been observed in other studies as well (Jokela and Martin 2000; Martin and Jokela 2004b). This decrease in efficiency has been

attributed to increased respiration and/or increased biomass partitioning below ground relative to stem for older/larger trees (Borders et al. 2004; Will et al. 2002).

5. Conclusions

Hypotheses 1a and 2a were not supported as cultural treatment did not have a significant effect on stem and crown attributes at age 12 (pre- and post-thinning) or age 13. Lower planting density stands resulted in significantly greater DBH, total stem height, live crown length, and crown ratio and significantly less standing stem volume per hectare, basal area per hectare, current density, and specific leaf area (SLA) compared to the stands planted at the higher densities at age 12 prior to thinning, lending support to Hypothesis 1b. In contrast to Hypothesis 1b, foliar N concentration was not significantly affected by planting density at age 12 (pre-thinning). Lower planting density stands resulted in significantly greater DBH, total stem height, standing stem volume per hectare, basal area per hectare, live crown length, and crown ratio at age 12 (post-thinning) and age 13, lending support to Hypothesis 2b. At age 12 (post-thinning), current density was significantly greater for the stands planted at 740 trees ha^{-1} compared to those planted at 1480 and 2220 trees ha^{-1}, but by age 13 this trend had become insignificant. In contrast to Hypothesis 3a, cultural treatment did not have a significant effect on CAI, foliar biomass per hectare, LAI, IPAR, $GE_{folmass}$, or NUE and GE_{LAI} was greater for the stands grown under less intensive culture during the 13^{th} growing season. In agreement with Hypothesis 3a, foliar N content was significantly greater for the maximum cultural regime and IPAR efficiency was not significantly affected by culture during the 13^{th} growing season. During the 13^{th} growing season lower planting density stands resulted in significantly greater CAI, foliar biomass per hectare, LAI, foliar N content, and IPAR compared to higher planting density stands, and planting density did not have a significant effect on the resource-use efficiency measures,

supporting Hypothesis 3c. Hypotheses 1c, 2c, and 3c were supported as there were no significant cultural intensity x planting density interactions for any of the attributes previously mentioned.

The typical trade-off between individual tree foliar development and stand level foliar development for non-thinned stands was altered by the thinning, resulting in reduced individual tree crown size and reduced foliar biomass per hectare in the higher planting density stands one year following thinning. It is of great interest to monitor this trend over time, as foliar development has a strong relationship with tree and stand productivity and therefore, important implications for growth and yield modeling. At ages 12 and 13, stem and crown attributes were generally similar between the two levels of culture, but varied greatly with planting density. It appears that at this stage of stand development, light limitations due to high stocking have a greater influence on growth than soil limitations due to poor nutrition for the loblolly pine plantations evaluated in this study. Knowledge of growth limitation trends over time is important for forest management decisions regarding silvicultural prescriptions.

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Table 4.1. Site location and attributes for three PMRC culture x planting density study installations

County, State	Latitude	Longitude	Soil series*	Soil Taxonomy*	Physiographic region
Barbour Co., AL	31.7467	-85.6735	Orangeburg – Springhill	Fine-loamy, kaolinitic, thermic typic kandiudults and kanhapludults	Upper Coastal Plain
Escambia Co., AL	31.1954	-87.3154	Freemanville	Fine, kaolinitic, thermic plinthic kandiudults	Upper Coastal Plain
Greene Co., GA	33.6235	-83.0278	Cecil - Madison – Pacolet	Fine, kaolinitic, thermic typic kanhapludults	Piedmont

* Soils information provided by the USDA-NRCS Soil Survey Division

Table 4.2. Description of operational and maximum cultural treatments on the PMRC culture x planting density study

Treatment	Growing Season	Operational	Maximum
Site preparation		Chemical and mechanical	Chemical and mechanical
Fertilization	At planting	560 kg ha^{-1} 10-10-10	560 kg ha^{-1} 10-10-10
	2^{nd}		673 kg ha^{-1} 10-10-10 + 131 kg ha^{-1} NH_4NO_3 + micronutrients
	4^{th}		131 kg ha^{-1} NH_4NO_3
	6^{th}		336 kg ha^{-1} NH_4NO_3
	8^{th}	224 kg ha^{-1} N + 28 kg ha^{-1} P	224 kg ha^{-1} N + 28 kg ha^{-1} P
	10^{th}		224 kg ha^{-1} N + 28 kg ha^{-1} P
	12^{th}	224 kg ha^{-1} N + 28 kg ha^{-1} P	224 kg ha^{-1} N + 28 kg ha^{-1} P
Competition control (chemical)	1^{st}	280 g ha^{-1} sulfometuron-methyl banded application + glyphosate and tryclopyr direct spraying	280 g ha^{-1} sulfometuron-methyl broadcast application + glyphosate and tryclopyr direct spraying
	2^{nd}		841 g ha^{-1} imazapyr broadcast application
	3^{rd} through 12^{th}		Glyphosate and tryclopyr repeated direct spraying

Table 4.3. Plot size and spacing for different planting densities on the PMRC culture x planting density study

Planting Density (trees ha^{-1})	Original spacing (m x m)	Measurement plot size (ha)	Gross plot size (ha)
740	3.66 x 3.66	0.105	0.227
1480	2.44 x 2.74	0.053	0.150
2220	2.44 x 1.83	0.046	0.125
2960	1.83 x 1.83	0.040	0.121

Table 4.4. P-values for the effects of culture, planting density, and their interaction on mean stem and crown attributes on three PMRC loblolly pine installations at age 12 prior to thinning

Attribute	Source		
	Culture	Planting density	Interaction
Stem attributes			
DBH	0.1195	<0.0001	0.3060
Total stem height	0.2083	0.0291	0.3629
Total stem volume	0.1443	0.0003	0.7878
Basal area	0.1268	0.0001	0.8161
Current density	0.3986	<0.0001	0.8996
Crown attributes			
Live crown length	0.3199	<0.0001	0.9602
Crown ratio	0.4190	0.0006	0.9444
SLA	0.3778	0.0379	0.3766
Foliar N concentration	0.0948	0.1765	0.1141

Table 4.5. Mean stem attributes by culture on three PMRC loblolly pine installations at age 12 prior to thinning

Culture	DBH (cm)	Total stem height (m)	Total standing stem volume (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Current density (trees ha^{-1})
Operational	17.2 a	14.1 a	232.7 a	34.0 a	1597 a
Maximum	19.0 a	15.4 a	281.1 a	38.8 a	1525 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 4.6. Mean stem attributes by planting density on three PMRC loblolly pine installations at age 12 prior to thinning

Planting density (trees ha^{-1})	DBH (cm)	Total stem height (m)	Total standing stem volume (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Current density (trees ha^{-1})
740	23.0 a	15.1 a	205.4 a	29.9 a	700 a
1480	18.6 b	15.1 a	261.9 b	36.8 b	1318 b
2220	16.0 c	14.7 ab	271.4 b	38.0 bc	1838 c
2960	14.5 d	14.1 b	288.8 b	41.0 c	2389 d

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 4.7. Mean crown attributes by culture on three PMRC loblolly pine installations at age 12 prior to thinning

Culture	Live crown length (m)	Crown ratio (%)	SLA (m^2 kg^{-1})	Foliar N concentration (%)
Operational	6.7 a	47.0 a	11.02 a	1.34 a
Maximum	7.0 a	45.3 a	11.32 a	1.48 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 4.8. Mean crown attributes by planting density on three PMRC loblolly pine installations at age 12 prior to thinning

Planting density (trees ha^{-1})	Live crown length (m)	Crown ratio (%)	SLA (m^2 kg^{-1})	Foliar N concentration (%)
740	8.2 a	54.6 a	10.77 a	1.38 a
1480	6.9 b	45.7 b	11.27 b	1.50 a
2220	6.4 bc	43.4 b	11.19 ab	1.38 a
2960	5.8 c	40.9 b	11.46 b	1.38 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 4.9. P-values for the effects of culture, planting density, and their interaction on mean stem and crown attributes on three PMRC loblolly pine installations at age 12 post thinning

Attribute	Source		
	Culture	Planting density	Interaction
Stem attributes			
DBH	0.1066	<0.0001	0.2562
Total stem height	0.2243	0.5930	0.2351
Total stem volume	0.1277	<0.0001	0.2886
Basal area	0.1114	<0.0001	0.1042
Current density	0.7610	0.0469	0.5537
Crown attributes			
Live crown length	0.4284	0.0109	0.9585
Crown ratio	0.4950	0.0070	0.9717

Table 4.10. Mean stem and crown attributes by culture on three PMRC loblolly pine installations at age 12 post thinning

Culture	DBH (cm)	Total stem height (m)	Total standing stem volume (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Current density (trees ha^{-1})	Live crown length (m)	Crown ratio (%)
Operational	18.4 a	14.7 a	132.4 a	19.1 a	692 a	7.1 a	48.1 a
Maximum	20.0 a	15.8 a	164.9 a	22.7 a	698 a	7.3 a	46.5 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 4.11. Mean stem and crown attributes by planting density on three PMRC loblolly pine installations at age 12 post thinning

Planting density (trees ha^{-1})	DBH (cm)	Total stem height (m)	Total standing stem volume (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Current density (trees ha^{-1})	Live crown length (m)	Crown ratio (%)
740 (non-thin)	23.0 a	15.1 a	205.4 a	29.9 a	700 a	8.2 a	54.6 a
1480 (thinned)	19.4 b	15.3 a	148.5 b	20.8 b	691 b	7.0 b	46.1 b
2220 (thinned)	17.7 c	15.4 a	125.5 c	17.2 c	693 b	7.0 b	44.3 b
2960 (thinned)	16.8 c	15.2 a	115.3 c	15.8 c	696 ab	6.5 b	43.4 b

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 4.12. P-values for the effects of culture, planting density, and their interaction on mean stem, crown, and efficiency attributes on three PMRC loblolly pine installations at age 13 or during the 13th growing season

Attribute	Source		
	Culture	Planting density	Interaction
Stem attributes			
DBH	0.1277	<0.0001	0.3477
Total stem height	0.4477	0.5596	0.7748
Total stem volume	0.1998	<0.0001	0.3573
Basal area	0.1258	<0.0001	0.2232
Current density	0.7367	0.1359	0.5967
CAI	0.4271	0.0002	0.3188
Crown attributes			
Live crown length	0.5250	0.0007	0.8916
Crown ratio	0.1284	0.0001	0.7617
Foliar biomass	0.0878	<0.0001	0.3775
LAI	0.0962	0.0002	0.4628
Foliar N content	0.0197	<0.0001	0.1484
IPAR	0.6379	<0.0001	0.5789
Efficiency attributes			
$GE_{folmass}$	0.0621	0.1084	0.0903
GE_{LAI}	0.0499	0.1817	0.1527
NUE	0.0550	0.2207	0.0885
IPAR efficiency	0.1918	0.2003	0.1793

Table 4.13. Mean stem attributes by culture on three PMRC loblolly pine installations (DBH, height, volume, basal area, and current density at age 13 and current annual increment for the 13th growing season)

Culture	DBH (cm)	Total stem height (m)	Total stem volume (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Current density (trees ha^{-1})	Current annual increment (m^3 ha^{-1} $year^{-1}$)
Operational	19.2 a	15.8 a	153.1 a	20.8 a	685 a	21.3 a
Maximum	20.8 a	16.5 a	183.0 a	24.4 a	694 a	18.7 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 4.14. Mean stem attributes by planting density on three PMRC loblolly pine installations (DBH, height, volume, basal area, and current density at age 13 and current annual increment for the 13th growing season)

Planting density (trees ha^{-1})	DBH (cm)	Total stem height (m)	Total stem volume (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Current density (trees ha^{-1})	Current annual increment (m^3 ha^{-1} year^{-1})
740 (non-thin)	23.6 a	16.1 a	229.0 a	31.5 a	695 a	25.1 a
1480 (thinned)	20.3 b	16.3 a	169.3 b	22.5 b	681 a	22.3 a
2220 (thinned)	18.5 c	16.2 a	142.1 c	18.7 c	689 a	17.2 b
2960 (thinned)	17.6 d	15.9 a	131.7 c	17.4 c	696 a	15.3 b

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 4.15. Mean crown attributes by culture on three PMRC loblolly pine installations (live crown length and crown ratio at age 13 and foliar biomass, LAI, N content, and IPAR for the 13th growing season)

Culture	Live crown length (m)	Crown ratio (%)	Foliar biomass (tonnes ha^{-1})	Peak projected LAI (m^2 m^{-2})	Foliar N content (kg ha^{-1})	IPAR (%)
Operational	8.1 a	51.2 a	8.0 a	2.8 a	107.4 a	67.7 a
Maximum	7.6 a	45.6 a	10.2 a	3.7 a	148.9 b	70.0 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 4.16. Mean crown attributes by planting density on three PMRC loblolly pine installations (live crown length and crown ratio at age 13 and foliar biomass, LAI, N content, and IPAR for the 13th growing season)

Planting density (trees ha^{-1})	Live crown length (m)	Crown ratio (%)	Foliar biomass (tonnes ha^{-1})	Peak projected LAI (m^2 m^{-2})	Foliar N content (kg ha^{-1})	IPAR (%)
740 (non-thin)	8.8 a	54.4 a	12.8 a	4.4 a	176.5 a	90.6 a
1480 (thinned)	8.0 b	48.6 b	8.4 b	3.0 b	125.5 b	69.3 b
2220 (thinned)	7.4 bc	46.0 bc	7.7 b	2.8 b	107.2 c	57.7 c
2960 (thinned)	7.1 c	44.5 c	7.5 b	2.7 b	103.4 c	57.8 c

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 4.17. Mean resource-use efficiency attributes by culture on three PMRC loblolly pine installations for the 13th growing season

Culture	$GE_{folmass}$ (m^3 $tonne^{-1}$)	GE_{LAI} (m^3 LAI^{-1})	NUE (m^3 $tonne^{-1}$)	IPAR efficiency (m^3 $\%IPAR^{-1}$)
Operational	2.8 a	7.9 a	205.7 a	0.32 a
Maximum	1.9 a	5.3 b	127.2 a	0.26 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

Table 4.18. Mean resource-use efficiency attributes by planting density on three PMRC loblolly pine installations for the 13th growing season

Planting density (trees ha^{-1})	$GE_{folmass}$ (m^3 $tonne^{-1}$)	GE_{LAI} (m^3 LAI^{-1})	NUE (m^3 $tonne^{-1}$)	IPAR efficiency (m^3 $\%IPAR^{-1}$)
740 (non-thin)	2.0 a	5.9 a	146.1 a	0.28 a
1480 (thinned)	2.8 a	7.8 a	185.1 a	0.32 a
2220 (thinned)	2.3 a	6.3 a	163.7 a	0.31 a
2960 (thinned)	2.3 a	6.5 a	170.9 a	0.26 a

Means in the same column with the same letters are not significantly different (Fisher's LSD multiple comparison test; α=0.05).

CHAPTER 5

CONCLUSIONS

At age 12, cultural intensity had a minor effect on individual tree- and stand level stem and crown attributes in non-thinned loblolly pine stands. Different planting densities, however, resulted in a range of significantly different average individual tree- and stand-level stem and crown attributes in non-thinned stands at age 12. There was a trade-off between individual tree foliar development and stand-level foliar development, with higher planting density stands exhibiting less individual tree foliar biomass and greater foliar biomass per hectare compared to lower planting density stands. Because trees of a given DBH had similar crown characteristics regardless of the silvicultural treatments they received, knowledge of DBH distribution appears to be a sufficient modeling tool for non-thinned stands regardless of past cultural or planting density treatment.

At age 13 and during the 13^{th} growing season cultural intensity had a minor effect on average stand-level stem and crown attributes in both non-thinned and thinned loblolly pine stands. It appears, however, that stands may be beginning to respond to increased resource availability in the thinned stands, as average GE_{LAI} was significantly greater for stands grown under the operational treatment and average foliar N content was significantly greater for stands grown under the maximum treatment following thinning. Different planting densities resulted in a range of significantly different average stand-level stem and crown attributes in non-thinned and thinned stands at age 13 and during the 13^{th} growing season. In non-thinned stands there was a trade-off between individual tree foliar development and stand level foliar development, with

higher planting density stands exhibiting less average live crown length and greater foliar biomass per hectare compared to lower planting density stands. In the thinned stands, this trend was altered, and higher planting density stands exhibited less average live crown length and less foliar biomass per hectare compared to lower planting density stands. Resource-use efficiency was mostly unaffected by planting density, with the exception of IPAR efficiency in non-thinned stands during the 13^{th} growing season. Average IPAR efficiency was greatest in the 4440 trees ha^{-1} planting density stands. This result along with increased SLA in the higher density stands suggests that higher density stands utilize the available light source more efficiently than lower density stands.