EFFECTS OF CULTURAL INTENSITY, DENSITY REGIME, AND GROWING SEASON PRECIPITATION ON STAND, CROWN, AND RESOURCES USE EFFICIENCY ATTRIBUTES IN LOBLOLLY PINE STANDS FROM AGE 12 TO AGE 17 IN THE UPPER COASTAL PLAIN AND PIEDMONT OF THE SOUTHEASTERN UNITED STATES

by

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(Under the Direction of Michael Kane)

ABSTRACT

Loblolly pine culture x density installations were used to examine the effects of two cultural intensities, four initial planting densities, and their interaction on stem, stand, crown and growth efficiency attributes from age 12 through age 17 years. Plots with initial planting density of 740 trees ha^{-1} remained non-thinned, and plots with initial planting density of 1480, 2220, and 2960 trees ha^{-1} were thinned at age 12. There were few significant culture or culture x density effects. Stand and crown attribute values were generally greater under intensive than operational culture. Density regime significantly affected many stand, crown, and growth efficiency attributes. Individual trees in thinned densities for both cultures increased DBH by the same amount from age 12 to 17. Stand and crown attribute values followed patterns of growing season rainfall; stand development following thinning was delayed by two consecutive years of below average growing season rainfall during the 13th and 14th growing season. Results indicate that stand density impacted growth attributes greater than cultural intensity, and growing season precipitation levels affected stand and crown response to thinning.

INDEX WORDS: Loblolly pine, Culture, Density, Thinning, Rainfall, Piedmont, Upper Coastal Plain

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Purpose of Study

Loblolly pine is a highly valued commercial tree species widely planted for timber production in the southeastern United States. There has been much research to increase the knowledge of factors influencing loblolly pine productivity. Some studies have concentrated efforts on crown ratio and its link to thinning response which have informed current planting and thinning practices. Other research has focused on light interception attributes as potential productivity drivers for loblolly pine. Yet, there is limited research linking the response of crown attributes considered important for productivity to silvicultural practices under different combinations of density regimes and cultural intensities.

The current study is unique because it furthers our understanding of crown characteristics and their relationships with stem growth in mid-rotation loblolly pine stands for four planting density-thinning regimes in combination with two cultural intensities. This study quantifies the effects of culture and density regimes and their interaction on loblolly pine growth for five growing seasons after thinning. This research builds on that reported by Akers (2011), Akers et al. (2013) and Johnson (2013).

The results can be used to inform growth and yield model development for loblolly pine. The financial value of loblolly pine is determined by volume, with larger trees having higher value. A better understanding of volume growth in response to density regimes and cultural intensity will improve silvicultural prescription in loblolly pine plantations.

Thesis Structure

The remainder of this chapter consists of a literature review of research on loblolly pine. Research on stand, crown, and resource use efficiency in thinned stands using a mixed model analysis and linear regression approach is presented in Chapter 2. Relationships between growing season rainfall on stand and crown growth attributes using a mixed model with repeated measures are presented in Chapter 3. Main conclusions are presented in Chapter 4.

Literature Review

Importance of Loblolly Pine

Globally, plantation forests produce 50% of the wood supply yet represent 4% of all forest (Miller et al., 2009). Pine plantations cover approximately 12.9 million hectares in the U.S. South (Wear and Greis, 2002) which is more than double the 5.5 million hectares reported in 1982. Eighty percent of pines planted in the Southeast are loblolly pine (Kellison and Gingrich, 1983). Loblolly pine is the leading timber species in the United States (Schultz, 1997) and dominates on 45% of commercial forest land in the U.S. South (Schultz, 1999). High intensity culture has increased production by as much as 65% over standard site preparation and planting and 100% over natural regeneration (Wear and Greis, 2002).

Nutrient Additions

Fertilization of forest land in the southeastern United States increased from 10,000 to 81,000 hectares yr^{-1} from 1969 to 1991 and 6.5 million hectares were fertilized from 1969 to 2004 (Albaugh et al. 2007). Nutrient additions including nitrogen (N) and phosphorous (P) in loblolly pine plantations can produce substantial volume gains on a wide variety of sites (Fox et al. 2007).

Nitrogen fertilization results in significant loblolly height and diameter at breast height (DBH) growth responses (Amateis et al., 2000; Hynynen et al., 1998). In mid-rotation stands in a regional study, N fertilization significantly increased height and DBH growth with increasing N levels up to 336 kg ha^{-1} (Hynynen et al., 1998). In the same study, the response to P fertilization of rates up to 28 kg P ha^{-1} was only significant when applied with N (Hynynen al., 1998).

Fertilization significantly increased DBH, height, basal area, annual volume increment, and peak leaf area index (LAI) for four years in a study established in an 8-year-old loblolly pine stand as a result of increased foliage production due to increased site resources (Albaugh et al., 1998). Zhang et al. (1997) found an increase of 60% in annual stem increment due to N fertilization on a Piedmont site. This increase in stem growth is attributed to N additions significantly increasing shoot elongation in the upper and mid-crown, needle length, retention time of previous year fascicles, and leaf area production. Nitrogen deficiencies resulted in a reduction in foliage production rather than reduced foliar N concentration (Zhang et al., 1997).

Nutrient additions and/or interspecific competition control can greatly increase stand volume. Swindel et al. (1988) concluded that the effects of fertilization and weed control on 4-year-old loblolly and slash pine trees in the Lower Coastal Plain were additive, capable of producing a tenfold increase in stand volume. Jokela et al. (2000) determined that on a wide variety of site types (CRIFF A-E), for both loblolly and slash pine, the effects of fertilization and weed control were additive on the effects of height, DBH and stand volume by age 5 and these effects were still apparent at age 8. Gough et al. (2004b) found that nutrient additions had a relatively short-term effect on foliar N concentration in 2-year-old loblolly pine seedlings growing infertile, sandy soil, but had a lasting impact on LAI, diameter and height growth. Haywood and Tiarks (1990) showed that in the Upper Coastal Plain, the results of sustained competition control and fertilization were additive for loblolly pine. Total volume per acre at age 11 was increased by 56 m^3 ha^{-1} and mean diameter was increased by 1 cm.

Leaf area development is generally inhibited by low nutrient availability (Fox et al., 2007; King et al., 1999; Tyree et al., 2009). Nutrient additions produce elevated levels of leaf area which are responsible for stem growth due to increased photosynthetic surface area (Gough et al., 2004a) and results in increased C fixation (Tyree et al., 2009).

Competition Control

In recent years, forest managers have used herbicides for competition control on nearly 1 million ha. of pine plantations in the U.S. South (McCullough et al., 2005). Fox et al. (2007) suggest that competing vegetation should be controlled to maintain high levels of resource availability. Considerable gains in loblolly pine growth can be attributed to competition control (Martin and Shiver, 2002). Reduction or elimination of competing vegetation has been shown to have significant positive impact on height, DBH, and volume growth in loblolly pine plantations (Miller et al. 1991; Zhao et al., 2009; Zutter et al., 1986). Control of competing vegetation early in stand development has a lasting impact on stand growth rates (Zhao et al., 2009). Stand development is impacted for up to 15 years after early control of competiting vegetation (Miller et al., 2003). In the Upper Coastal Plain, control of woody and herbaceous vegetation increased height 16 to 82%, DBH 43 to 323%, and total aboveground biomass 94% to 1800% in loblolly pine seedlings during the first growing season in the field. (Zutter et al., 1986). Miller et al. (1991) found a linear relationship between pine volume reduction at age 5 and the amount of woody competition basal area. Competition control significantly increased loblolly pine average

DBH and total volume up to 14% and 45%, respectively, at age 12 in the Coastal Plain and Piedmont regions (Martin and Shiver, 2002). Fortson et al. (1996) reported significant gains in basal area (10.6%) and volume growth in mid-rotation stands of loblolly pine in the Piedmont and Coastal Plain eight years following competition control. Response was the greatest on bottom-slope locations, but was still significant on mid- and top-slope locations.

Loblolly pine canopy development was accelerated by complete control of competition during the age 1 to 15 in a Southeast regional study (Miller et al., 2006). Merchantable volume increased on average by 66% over the control at age 15. By age 15, fascicle mass and foliar nutrient concentrations did not vary by treatment. Increased interspecific competition control may have influenced total foliage production and thus lead to greater stem growth, but this relationship could not be assessed as foliage production was not reported in this study.

Initial Planting Density

It is well documented that stand level growth increases with increasing stand density in young stands (Barron-Gafford et al., 2003; Will et al., 2005), however this increase in growth is not proportional to stand density (Will et al., 2005). Will et al. (2001) reported a curvilinear relationship between growth rates and stand density caused by lower marginal growth increases at higher densities; growth rates of 9.0, 19.1, and 24.4 m^3 ha^{-1} yr^{-1} were reported for 3-year-old loblolly pine stands planted at 740, 2220, and 3700 trees ha^{-1}, respectively. Even though higher planting densities result in greater volume production, lower densities result in a shift toward larger size trees (Bailey, 1986; Cardoso et al., 2013). Bailey (1986) reported that total yield and percent sawtimber volume at harvest are highly related to planting density.

There are survival and average tree DBH tradeoffs between high and low densities. Loblolly pine survival and average tree DBH decrease with increasing planting density (Will et al., 2010). In a study by Zhao et al. (2011), increasing loblolly pine planting density from 741 to 4,448 trees ha^{-1} decreased average DBH, average height, dominate height and survival, but increased stand basal area and volume at age 12 though none of these differences were significant at densities greater than 2,224 trees ha^{-1}.

Sharma et al. (2002) reported that moderate rectanguarity of planting is not important, but density is, with DBH affected the greatest and height the least. Site index, age, and growing space per tree are the greatest predictors of stand development patterns as indicated by crown attributes such as crown ratio, crown length, and crown width.

Stem volume growth rate (m^3 ha^{-1}yr^{-1}) is inversely related to stand density at young ages (Will et al., 2001). The rate of stand growth is correlated to the amount of radiation intercepted by the crown. Volume growth was limited by some factor(s) as density increases. As stand density increases, the amount of radiation intercepted per unit leaf area most likely decreased due to self-shading causing canopy photosynthetic rates to reach a maximum.

Akers, et al. (2013) reported that stand and crown attributes of 13-year-old loblolly pine trees in the Upper Coastal Plain and Piedmont were greatly affected by planting density with a decrease in average individual tree size and increase in volume per hectare at higher densities. Also, higher planting densities produced higher LAI’s, more foliar biomass, and increased intercepted photosynthetically active radiation (IPAR).

Thinning

Thinning of 8-year-old loblolly pine trees was shown to increase DBH growth by 51% and average crown diameter growth by 500% (from 12 to 61 cm.), compared to non-thinned stands, two years after thinning (Ginn et al., 1991). These differences in growth were attributed to greater photosynthetic surface area that developed in the lower crowns of the thinned trees as compared to the lower crown of the control (Ginn et al., 1991), likely as a result of increased light interception by the lower crown (Gough et al., 2004a). The same study also reported that thinning had no effect on height growth (Ginn et al., 1991). Peterson et al. (1997) found that these same post-thin trees expanded their crowns for up to six years after thinning, maintained higher live crown ratios, produced nearly twice the litter fall, and increased bole diameter compared to control, non-thinnd trees. Zhang et al. (1997) found that in a non-thinned stand, the lower 1/3 of the crown produced and maintained lower leaf area than the upper crown as compared to thinned stands.

Kellison and Gingrich (1983) report that thinning of high density pine stands is optimal at ages 10-14 and should reduce stand density to about 870 tph with a goal of leaving 60 percent live crown and an 18 ft log free of live branches.

In a study by Sword Sayer et al. (2004) on a nutrient deficient site in the Western Gulf Coastal Plain, thinning and fertiliztion treatments at ages 7 and 14 resulted in a greater percentage of stems in larger DBH classes. However, thinned plots produced 69% of the gross stem mass observed in the non-thinned plots. In thinned plots at age 17, live crown length increased by 85% and the percentage of biomass allocated to foliage increased as a result of thinning even though peak LAI was reduced from 5.1 to 3.4 $m^2 m^{-2}$. Hennessey et al. (2004) found similar responseses to thinning. Stands thinned to 8 and 12.5 $m^2 ha^{-1}$ at age 9 resulted in 50% greater crown length at age 24 compared to non-thinned stands. By age 24, thinned stands produced 90% of the gross cumulative stem biomass compared to non-thinned stands even though 84-86% of the surviving trees were removed during the age 9 thinning.

Ecophysiology Responses to Silviculture Practices

<u>Foliar Biomass</u>

Barron-Gafford et al. (2003) suggested that, in young loblolly and slash pine stands under intensive management in the Lower Coastal Plain, stand level growth is best correlated to the amount of foliage present, as opposed to its nutrient content. Foliar biomass explained 76% of the variation in stem biomass growth across planting densities from 740 to 3700 tree ha^{-1} while N-concentration and N-content explained 57 and 59%, respectively. Fertilization and competition control increased foliar biomass by 73% and 22%, respectively, in 13-year-old loblolly pine (Will et al., 2006).

<u>LAI</u>

LAI is a measure of the amount of leaf area per unit ground area and is positively correlated to light interception (Fox et al., 2007). LAI is a factor of stand development and site quality and can be increased with fertilization and weed control treatments (Gonzalez-Benecke et al., 2012). Gough et al. (2004a) suggest that nutrient additions facilitate leaf area growth and that LAI is responsible for primary productivity. Similar results were reported by Vose and Allen (1988). King et al., (1999) also showed that resource availability has a strong impact on LAI. Vose and Allen (1988) found that in 9-12 year old lobloly pine stands with varying levels of stocking and treated with varying amounts of N and P, LAI explained 75% of the variation in productvity while Albaugh et al. (1998) reported that 93% of the variation in stem volume growth was accounted for by peak LAI estimates in 8 to 12-year-old loblolly pine stands with complete competition control, nutrient additions, and irrigation.

SLA

Specific leaf area (SLA) is the ratio of leaf surface area to dry weight. For loblolly pine it is defined as the green surface area of a fascicle divided by its dry weight, generally measured in $cm^2\ g^{-1}$ (Shelton and Switzer, 1984). SLA significantly increased with planting density in a three year-old loblolly pine stand (Will et al., 2001). Fertilization resulted in decreased SLA in loblolly pine seedlings grown in a greenhouse (Tyree et al., 2009). SLA is greater in more light limited conditions (Chmura and Tjoelker, 2008). Colbert et al. (1990) reported that in 3 to 4-year-old loblolly pine in the Lower Coastal Plain, SLA was not affectd by fertilization or weed conrtol. However, Zutter et al. (1986) reported that SLA of loblolly pine seedlings in the Upper Coastal Plain was significantly lower in stands with complete competition control.

IPAR

Intercepted photosynthetically active radiation (IPAR) represents the amount of energy captured by the foliage in a stand (Will et al., 2005). IPAR is thought to be a better measure of stem biomass growth than LAI since it is a direct measure of energy intercepted by the canopy, whereas LAI represents surface area and does not account for foliage position or self-shading (Allen et al., 2005). Several studies have shown annual volume growth to be linearly related to IPAR (Allen et al., 2005; Will et al., 2001; Will et al., 2005). Will et al. (2001) found a linear relationship between stem volume growth and canopy intercepted radiation with up to 70% of the variation in stem volume growth attributed to canopy radiation in three-year-old loblolly and slash pine stands planted at 740 to 3700 trees ha^{-1} in the Lower Coastal Plain. Allen et al. (2005) reported 78% of the variation in stem biomass growth attributed to IPAR in 6-year-old loblolly pine on an upland site in the Lower Coastal Plain. Even with variation in species, soil, environment, stem growth is related to intercepted radiation (Allen et al. 2005).

Foliar Nutrient Concentration and Content

Albaugh et al. (1998) reported age 8 foliar N concentrations of 0.95 % and 1.29% for non-fertilized and fertilized loblolly pine stands, respectively, in the Upper Coastal Plain. Slightly higher values of 1-1.2% and 1.2-1.4%, respectively, were reported by (Gough et al., 2004a) on the same site at age 14. Greater foliar N concentrations in fertilized stands were also reported by Will et al. (2006).

Foliar N concentration tends to decrease with increasing planting density, while total foliar biomass production increases with stand density (Barron-Gafford et al., 2003; Will et al., 2001; Will et al., 2005). Foliar N content increased with increasing density from 740 to 3700 trees ha^{-1} due to increases in foliar biomass in 4-year-old loblolly and slash pine in the Lower Coastal Plain (Barron-Gafford et al., 2003). However, these increases were not linear across densities indicating that resources may limit stand growth at higher densities. In a study by Will et al. (2005), canopy N content values range from 67 to 115 kg ha^{-1} for densities from 740 to 2960 trees ha^{-1}, respectively. Increases were attributed to increased foliage at higher densities since N-concentration either decreased or was unaffected at increasing densities.

Canopy N-content explained 55-59% of the variation in stem-wood production in 4-year-old stands (Barron-Gafford et al., 2003; Will et al., 2005). Barron-Gafford et al. (2003) also found that foliar biomass was a better predictor of stem biomass growth than N concentration or content.

Rainfall and Irrigation

Studies have shown that precipitation amounts have varying impacts on loblolly pine growth. In general, photosynthetic rates are decreased under drought conditions (Murthy et al.

1996). However, the degree of photosynthetic rate decrease under drought may be affected by nutrient availability.

Ewers et al (1999) suggest that response to fertilizaiton could be correlated to the amount of precipitation. Tang et al. (2004) found that in loblolly pine, reduced rainfall (and % soil water content) resulted in lower photosynthesis, transpiration, stomatal conductance and also reduced foliage production and whole-crown photosynthesis response to fertilization. Fertilization increased carbon uptake through enhanced foliage production, but nutrient uptake was limited by water availability. However, Samuelson et al. (2014) found that response to fertilization was independent of rainfall reductions, suggesting that nutrient availability rather than water availability is the primary productivity driver through increases in leaf area and light capture.

Allen et al. (2005) found that on a dry, upland site in the Lower Coastal Plain, irrigation had little effect on stem growth, IPAR or LAI over the control through age six for loblolly pine. However when combined with N fertilization, these attributes were significantly greater than with irrigation treatment alone, indicating that water availability impacts the photosynthetic process and foliage production through reduced nutrient uptake. Campoe et al. (2013) reported findings from the Southeast Tree Research and Education Site (SETRES) that irrigation beginning at age 8 had little effect on aboveground biomass production unless combined with fertilization during the 8^{th} and 9^{th} growing seasons. Irrigation only trees had similar leaf area tree^{-1} as the control while fertilization alone and irrigation+fertilization regimes produced siginificantly greater leaf area tree^{-1}. On the same site, Albaugh et al. (1998) reported similar findings in 8 to 13-year-old stands. Irrigation slightly, but not significantly, affected LAI and only significantly affected DBH, volume, and height growth during droughty years while fertilization significantly increased growth each year.

During the growing season, loblolly pine contains needles from the current as well as previous growing season (Zhang et al., 1997). In the spring, photosynthesis (P_n) from mature foliage is necessary to produce the first and subsequent flushes of the current growing season (Dickson 1987). A period of sub-optimal rainfall could have carry over effects for two years on crown and stem production (Tang et al. 2004).

Density Regime x Culture Intensity

Several studies have examined the effects of culture, density and their interaction on loblolly pine stand development. Zhao et al. (2011) reported that the effects of initial planting density and culture on stand attributes are additive in non-thinned 12-year-old loblolly pine stands in the Lower Coastal Plain of the Southeast. Intensive culture resulted in increased DBH, height, volume and basal area over operational culture. Higher initial planting density resulted in decreased DBH, height, and survival but increased basal area and volume. Similar results were reported by Akers et al. (2013) in the Upper Coastal Plain and Piedmont.

Work by Akers (2001) and Johnson (2013) on a loblolly pine cultural x density study in the Upper Coastal Plain and Piedmont during the 13th – 15th growing seasons found that stand density rather than cultural intensity had the biggest impact on stand, stem, and crown attributes. Akers et al. (2011) reported that stem and stand attributes in non-thinned stands were significantly affected by planting density and not cultural intensity at ages 12 and 13 and during the 13th growing season. Johnson (2013) reported similar findings for the 14th and 15th growing seasons. In installations thinned at age 12, crown attributes remained stable while values of stand attributes of thinned plots increased at a rate similar to their non-thinned, low planting density counterpart during the first three years after thinning. There were no significant effects of culture or culture x density. Growth efficiency was generally higher under operational than intensive culture. These results suggest that when nutrient availability is adequate, light limitations rather than soil resources influence loblolly pine growth during the ages examined in this study (Akers, 2011; Akers et al., 2013; Johnson, 2013).

These studies provide information on loblolly pine stand and crown development. The current study will build on previous research to better the understanding of productivity drivers in mid-rotation loblolly pine stands. Research in this study will build on that of Akers (2011) and Johnson (2013) by examining stand and crown development for five years post-thinning and relating development to growing season rainfall amounts.

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CHAPTER 2[1]

EFFECTS OF CULTURAL INTENSITY AND DENSITY REGIME ON STEM, STAND, CROWN, AND GROWTH EFFICIENCY ATTRIBUTES IN THINNED LOBLOLLY PINE STANDS IN THE UPPER COASTAL PLAIN AND PIEDMONT OF THE SOUTHEASTERN UNITED STATES

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Abstract

Three loblolly pine culture x density installations were used to analyze the effects of density regime and cultural intensity on stem, stand, crown and growth efficiency attributes in thinned stands. Each installation consisted of four initial planting densities (740, 1480, 2220 and 2960 trees ha^{-1}) and two cultural intensities (operational and intensive) arranged in a split plot design. At age 12, 1480, 2220, and 2960 trees ha^{-1} plots were thinned to the current trees ha^{-1} in the corresponding 740 tree ha^{-1} for that culture x installation. Stand and stem attributes were measured annually from age 12 to 17 and crown attributes were measured annually from the 13th to 17th growing season. Density regime effects were generally significant while cultural intensity and culture x density effects were generally not significant. Average DBH, volume per hectare and basal area per hectare were significantly lower in thinned densities for five years after thinning. Average stem height was unaffected by density after thinning. Stand volume and basal per hectare immediately after thinning decreased with increasing planting density. High volume current annual increment (20 – 30 m^3/ha/year) was observed in thinned stands with both cultural regimes. Stand, stem and crown values were generally greater for intensive than operational culture though differences between cultures were not statistically significant. There were significant, positive, linear, though not strong, relationships between crown attributes of foliar biomass, leaf area index (LAI), canopy nitrogen (N) content and intercepted photosynthetically active radiation (IPAR) and volume current annual increment (CAI). The thinned stands with both cultural regimes exhibited high levels of volume CAI in the presence of very adequate nutrient availability and non-limiting densities. After five growing seasons post thinning, foliar biomass, LAI, canopy N content and IPAR in thinned densities have recovered to similar values as those in non-thinned densities. Even though gross volume current annual increment of thinned

stands was similar to that of low planting density, non-thinned stands, the effects of initial planting density and the thinning implemented reduced stem and stand values through five years after thinning.

Introduction

Globally, plantations forests produce 50% of the wood supply yet they represent 4% of all forests (Miller et al., 2009). Loblolly pine is an important commercial species as it covers 13.4 million ha. (45%) of commercial forest in the southeastern United States (Schultz, 1999). Intensive management practices can increase productivity as much as 65% over standard site preparation and planting (Wear & Greis, 2002). Silvicultural methods that enhance canopy development influence pine productivity through increased light interception (Della-Tea and Jokela, 1991). Increases in stand productivity can be attained through fertilization, competition control and combinations of the treatments through increases in water, nutrient, and light availability (Fox et al., 2007a; Jokela et al., 2000; Zutter et al., 1986). Planting density and thinning treatments can influence stand level and individual tree growth dynamics (Bailey, 1986; Cardoso et al., 2013; Ginn et al., 1991; Zhao et al., 2011).

Density management is an important component of stem and stand-level growth patterns. Initial planting density can have rotation length implications on stem and stand characteristics, stand development, and productivity (Bailey, 1986; Baldwin et al., 2000). Average diameter at breast height (DBH) decreases while basal area per unit area increases with increasing planting density (Carlson et al., 2009; Zhao et al., 2011). Thinning increases individual tree growth in part by increasing photosynthesis in the lower crowns as a result of light availability (Ginn et al., 1991). Baldwin et al. (2000) reported that mean diameter at age 38 was significantly greater with increased thinning intensity. Wider spacing increases crown length and mid-rotation thinning has a prominent impact on increasing crown length by increasing light availability to residual trees (Baldwin et al., 2000; Sword Sayer et al., 2004). Thinning may have a significant effect on biomass allocation. Thinned stands allocate a greater percentage of biomass to foliage than non-thinned stands (Sword Sayer et al., 2004).

Management practices that increase soil nutrient availability (e.g. fertilization and competition control) have the ability to alter stand development and increase carrying capacity (Martin and Jokela, 2004). Critical foliar nitrogen (N) concentration for loblolly pine is 1.2%, below which growth is limited (Albaugh et al., 2010). Several studies have shown that resource availability has a strong impact on leaf area (King et al., 1999; Tyree et al., 2009). Nitrogen fertilization increases leaf area production (Zhang et al., 1997) as a result of greater photosynthetic capacity (Gough et al., 2004). Fertilization and weed control can greatly increase stand volume by age 4; the effects of these treatments are additive on some sites (Swindel et al., 1988). Herbaceous competition control during the first growing season has a marked effect on pine growth and, on some sites, may be important for initial survival (Shiver and Martin, 2002; Zutter et al., 1986).A combination of herbaceous and woody control can have additive effects on volume growth 15 years (Miller et al., 2006).

Recent research has examined the role of leaf area index (LAI) and intercepted photosynthetically active radiation (IPAR) in productivity of loblolly pine plantations. LAI represents photosynthetic surface area and is an important factor in loblolly pine productivity with productivity increasing with increasing leaf area (Fox et al., 2007a; Sword Sayer et al., 2004; Will et al., 2005). Some studies report a linear relationship between LAI and current annual volume increment (CAI) (Jokela and Martin, 2000; Albaugh et al., 1998; Will et al.,

2005) while others describe the relationship as asymptotic (Sword Sayer et al., 2004; Jokela et al., 2004). Fox et al. (2007a) notes that in fully stocked loblolly pine stands with a basal area greater than 23 m^2 ha^{-1} LAI should be at least 3.5; lesser values often indicate a nutrient deficiency. IPAR is a measure of photosynthetic energy capture and has been shown to be linearly related to annual growth in young loblolly pine plantations (Will et al., 2001; Will et al., 2005). Della-Tea and Jokela (1991) reported a linear relationship between LAI and IPAR.

Will et al. (2001) reported that foliar N concentration decreased with increasing density at age 3 in the Lower Coastal Plain. Will et al. (2005) reported a similar density effect at age 3 on foliar N concentration in current year foliage but not in previous year foliage in the Upper Coastal Plain and Piedmont. Specific leaf area (SLA), the ratio of leaf surface area to dry weight, was reported to be not affected by cultural intensity in young loblolly pine plantations in the Lower Coastal Plain (Colbert et al., 1990), however SLA was found to increase with increasing planting density in 3-year-old stands in the Upper Coastal Plain and Piedmont (Will et al., 2001).

Zhao et al. (2011) reported that the effects of initial planting density and culture on stand attributes are additive in non-thinned 12-year-old loblolly pine in the Lower Coastal Plain of the Southeast. Intensive culture resulted in increased DBH and height, and volume and basal area per hectare compared to operational culture. Higher initial planting density resulted in decreased DBH, height, and survival but increased basal area and volume per hectare. Similar results were reported by Akers et al. (2013) in the Upper Coastal Plain and Piedmont. Samuelson et al. (2004) also reported that intensive practices accelerated stand development through increased DBH and current annual volume increment.

Recent research by Akers (2011), Akers et al. (2013) and Johnson (2013) showed that density management has a greater effect than cultural treatment on individual tree, stand, and crown attributes when nutrient resources are sufficient in thinned and non-thinned loblolly pine plantations. Thinning was performed at age 12 in stands planted at 1480, 2220, and 2960 trees ha^{-1} to reduce stands to the current trees ha^{-1} on their 740 ha^{-1} initial planting density, non-thinned counterpart. Akers (2011) concluded that at age 12 and 13 years, culture did not have a significant effect on stand and crown attributes, however there was a significant difference among different densities. Johnson (2013) concluded that culture and culture x density effects were generally not significant on stand and crown attributes because operational culture in that study provided a high amount of nutrients. Planting density showed an inverse relationship with mean DBH, height and live crown length, whereas basal area and volume per hectare increased with increasing planting density. There was a weak correlation between current annual volume growth and crown attributes (foliar biomass, LAI, and IPAR) in non-thinned stands. Correlations were more evident under operational than intensive culture with the exception of N use efficiency (NUE), a measure of the amount of stem volume growth per unit of canopy N content. Johnson (2013) also concluded that age 12 DBH and basal area per hectare were better predictors of periodic tree DBH increment than initial planting density or cultural intensity. Planting density-thinning treatment had a significant effect on most stand, stem, and crown attributes during the 14^{th} and 15^{th} growing season. Values of stem, stand, and crown attributes general decreased with increasing initial planting density.

While there has been much research on the effects of cultural intensity and planting density on the effects of stand level growth, there is a lack of knowledge about how a range of planting densities and cultural intensities affect stand development following thinning or how crown attributes at time of thinning affect periodic growth. The objective of this study is to identify factors affecting productivity in post-thin loblolly pine plantations so as to help forest managers make more sound management decisions. This research builds on that of Akers (2011), Akers et al. (2013) and Johnson (2013) by extending their research in thinned study installations from the years they reported to five years post-thinning.

Hypotheses

a. Culture and density regime will have significant additive effects on mean DBH, total stem height, total standing volume ha^{-1}, basal area ha^{-1}, current trees ha^{-1}, and current annual volume increment. Intensive culture will increase mean DBH, total stem height, standing volume ha^{-1}, and basal area ha^{-1}, current trees ha^{-1} and current annual volume increment. DBH, stand volume ha^{-1}, and basal area ha^{-1} will be greatest at low, non-thinned, planting densities and least at higher, thinned densities.

b. Culture and density regime will have significant additive effects on live crown length, crown ratio, SLA, canopy N content, foliar biomass, LAI, and IPAR. Intensive culture will increase values of all attributes. Live crown length, crown ratio, SLA, canopy N content, foliar biomass, LAI, and IPAR will be lowest in higher initial planting densities prior to thinning and will increase with time from thinning in thinned stands and decrease in non-thinned stands.

c. Culture and density regime will have significant additive effects on growth efficiency measures. Intensive culture will decrease growth efficiency attributes. Thinned densities will have greater growth efficiency than non-thinned densities.

d. There will be significant, positive, linear relationships between crown attributes and gross volume CAI with CAI increasing with greater foliar biomass, LAI, foliar N content, and IPAR

Methods

Study Site Description

This study utilized three loblolly pine installations in the Upper Coastal Plain and Piedmont of Georgia and Alabama (Table 2.1). These sites, managed by the Plantation Management Research Cooperative (PMRC) at the University of Georgia, are part of the South Atlantic and Gulf Slope (SAGS) Culture Density study.

Each installation was arranged in a split-plot design containing four planting densities (740, 1480, 2220, 2960 trees ha^{-1}) and two cultural intensities (operational and intensive). There was only one replication per installation. The two cultural intensities were considered the main plots and the four planting densities were the sub-plots. The operational treatment consisted of early competition control and periodic fertilization. The intensive treatment consisted of sustained competition control and more frequent fertilization. Treatment details are presented in Table 2.2. Each installation was planted in the 1997/1998 dormant season with half-sib, loblolly pine seedlings. Seedlings were double planted then reduced to one surviving sapling after the first growing season to ensure adequate survival. Gross plot size varied based on planting density and each plot contained a measurement plot surrounded by a buffer approximately 8 m. wide (Table 2.3). At each installation, the 1480, 2220, and 2960 trees ha^{-1} plots were thinned at age 12 to match the current trees ha^{-1} on the 740 trees ha^{-1} x culture plot for that installation using third row removal in combination with a low thinning in leave rows to attain the appropriate density. Cut stems and crowns were left in the plot.

Stand Measurements

DBH was measured on all trees in the measurement plot during the dormant season at ages 10, 12, 13, 14, 15, 16 and 17. Total height and height to live crown were measured on every other tree in the measurement plot during the dormant season at ages 12, 13, 14, 15, 16 and 17. Heights of trees not measured were estimated for these attributes using heights from measured trees and the linear regression equation $\ln(\text{height})=\beta 0 + \beta 1\ DBH^{-1}$ for each plot and measurement period. Live crown length (LCL) was determined for trees with know heights using the equation LCL=total height – height to live crown. Net current annual increment (CAI) was determined by subtracting the total current standing volume per hectare of live trees from the previous age standing volume per hectare of live trees. Gross current annual increment (CAI) was calculated by subtracting the total standing volume of live trees at age (a) from the subsequent year, age (a+1), standing volume of live trees then adding volume lost to mortality during the same time period. Stand density index (SDI) was calculated as $SDI= TPH*(QDM/25.4)^{1.605}$, where TPH is trees per hectare and QDM is quadratic mean diameter in centimeters.

Crown Measurements

Foliar biomass was estimated for the 13^{th}-17^{th} growing seasons using eight circular leaf litter traps systematically placed in each measurement plot. Trap size measured 0.46 m^2. Litter was collected and combined for each plot by growing season, dried at 60^{O} C to a constant weight, then weighed. Litter falling in traps from April of the current year to March of the subsequent year was considered as an annual growing season litter fall. A growing season foliar biomass was calculated by adding that growing season litter fall and the subsequent year litter fall weights as loblolly pine retains two cohorts of foliage (Zhang et al. 1997). The litter fall biomass weights collected during the 17^{th} growing season were doubled to estimate 17^{th} growing season foliar biomass on a plot.

Foliar biomass litter collections at Installation 3, plots 1,480 and 2,220 trees ha^{-1} intensive culture, were abnormally low during the 17^{th} growing season. Values were 5,304 and 4,630 kg ha^{-1}, respectively, for these plots while the same density x culture plots at other installations was greater than 10, 000 kg ha^{-1}. There was no evidence of high mortality or disturbance on these plots. Since values of foliar biomass are added to the previous year estimates, these low values also affected the values from the 16^{th} growing season. It was decided to omit the 17^{th} growing season foliar biomass estimates at Installation 3 for the 1,480 and 2,220 trees ha^{-1} intensive culture plots and double the 16^{th} growing season estimates on the same plots. All calculations for 17^{th} growing season foliar biomass, LAI, and canopy N content in 1,480 and 2,220 trees ha^{-1} intensive culture plots only use two installations.

Live needle samples were collected to measure SLA and foliar nutrient concentration. At age 12, 14, and 16 dormant seasons, live needle samples were collected from the upper portion of the middle third of the crown on five dominate or co-dominate trees in each plot. One branch was removed and five to ten needles from each flush were collected and placed in a plastic bag for storage. Needles from a given plot were combined. All needles were refrigerated until they could be measured for specific leaf area (SLA) and processed for nutrient concentrations. A sub-sample of fifteen needles was used to measure all-sided SLA as described by Fites and Teskey (1988) calculated as the surface area of green fascicle (cm^2) per oven-dried mass (g); the remaining needles were dried at 60^{O} C and analyzed for N concentration. Peak, stand level, all-sided LAI was calculated by multiplying the mass of estimated foliar biomass by SLA for each plot. Peak projected LAI (leaf area index) was estimated by dividing all-sided LAI by 3.14. Canopy N content was calculated by multiplying foliar biomass estimates per ha by needle N concentrations. Since live needles were not collected each year, plot-level average values of SLA and foliar N concentrations were used in calculating LAI and canopy N content for the 13th and 15th growing season. The SLA and N concentration values for the 16th growing season were used to calculate 17th growing season LAI and canopy N content.

Intercepted photosynthetically active radiation (IPAR) was measured for each plot using the SunScan Canopy Analysis System (Delta-T Devices Ltd. Cambridge, UK). Measurements were taken on cloud free days around solar noon in July or August to capture maximum sun angle and peak leaf area. Approximately 200 individual IPAR measurements were taken per plot beneath the canopy along four transects parallel to tree rows and five transects perpendicular to tree rows. All attempts were made to avoid measurements interfered with by hardwood and vine competition.

Efficiency Measurements

Growth efficiency (GE) was calculated for the 13th-17th growing seasons as the ratio of gross CAI per year (m^3) and the following crown attributes: LAI (GE_{LAI}), foliar biomass (GE_{FOLBIO}), canopy N content (NUE), and IPAR (GE_{IPAR}).

Statistical Analysis

This study utilized a split-plot design with culture as the main plot and density regime as sub-plots. Installation and installation x culture were treated as random effects while density and culture were treated as fixed effects. The main effect of culture, density and their interaction on stand (mean DBH, height, trees ha^{-1}, basal area ha^{-1}, volume ha^{-1}, CAI in volume), crown (foliar biomass, LAI, canopy N content, IPAR), and growth efficiency (GE_{LAI}, GE_{FOLBIO}, NUE and GE_{IPAR}) attributes were analyzed in an ANOVA with a mixed-effects model approach in SAS (version 9.3 SAS Institute, Cary, NC). Data transformation was performed on IPAR by taking the arcsine of the square root of each measurement. Least squared means comparison using Fishers LSD test was used to compare treatment means.

Individual stem diameter growth was analyzed using linear regression to determine the effect of age 12 DBH, density regime and culture on individual stem diameter growth. A model was developed for both cultures and all density regimes; slopes and intercepts for the different densities were analyzed using dummy variables.

Results

Stand Attributes

Density effects were significant for all stand attributes, with the exception of total height, at some point during the study (Table 2.4). At age 17 all stand attributes examined, except mean height, were significantly affected by density. Mean DBH, volume ha^{-1}, basal area ha^{-1} and SDI were generally greatest on 740 tree ha^{-1} non-thinned plots and least on 2,960 tree ha^{-1} thinned plots throughout the post-thinning period (Table 2.5). At ages 13 through 17, there were no significant effects of culture or culture x density detected for any stand attribute measured (Table 2.4). Although not statistically different, mean values for all stand attributes were generally greater under intensive culture and total height generally decreased with increasing planting density (Table 2.5).

The effects of age 12 thinning on total volume ha^{-1}, basal area hectare $^{-1}$, SDI, and average DBH are evident in Figure 2.1 and Figure 2.2, respectively. Prior to thinning, stand attribute values generally increased and average DBH decreased with increasing planting density. Pre-thinning averages for total volume ranged from 179 m^3 to 262 m^3 and 232 m^3 to 315 m^3 for 740 trees ha^{-1} and 2960 trees ha^{-1} for the operational and intensive treatment, respectively. However, after thinning the trend for total volume, basal area, and SDI reversed following a pattern of 740 trees ha^{-1} non-thinned > 1480 trees ha^{-1} thinned > 2220 trees ha^{-1} thinned > 2960 trees ha^{-1} thinned. Average DBH increased with decreased planting density post thinning.

Post-thinning stand values of total volume outside bark (Figure 2.1), and basal area (Figure 2.2) increased at similar rates to that of non-thinned stands for the respective cultural intensities. In the operational treatment, the 2220 and 2960 trees ha^{-1} densities share similar values post-thin through age 15 while the other densities show clear separation for the five growing seasons after thinning. Beginning in the 16th growing season, the 2220 trees ha^{-1} began to show accelerated development compared to the 2960 trees ha^{-1} planting density.

Crown Attributes

Density effects were significant for all crown attributes at some point during this study (Table 2.4). Culture and culture x density were not significant for any crown attribute.

Live crown length (LCL) and crown ratio significantly decreased with increasing planting density with the exception of the 15th growing season (Table 2.4 and Table 2.6). Post thin average SLA was unaffected by culture or density (Table 2.4) though it varied with age (Table 2.6). Plot level SLA values ranged from 9.9 to 12.4 at age 12, 7.9 to 10.4 at age 14, and 11.5 to 14 at age 16. Foliar N concentration was not affected by cultural treatment (Table 2.4) even though the intensive culture received greater N fertilization rates. Foliar N values were similar for age 14 and 16.

All canopy level crown attributes (foliar biomass, canopy N content, LAI, and IPAR) were significantly affected by density regime from the 13th to the 15 growing season (Table 2.4).

Values of these attributes were greater at lower initial planting densities (Table 2.6). Density regime was also a significant effect for 16th growing season IPAR. Canopy N content was significantly affected by culture during the 13th growing season and was the only crown attribute significantly affected by culture during the study period (Table 2.4). Thirteenth growing season canopy N content averaged 145 kg ha^{-1} for intensive culture as compared with 111 kg ha^{-1} operational culture (Table 2.6).

Average foliar biomass was generally stable on non-thinned stands under both cultures throughout the study (Figure 2.3). In contrast, foliar biomass amounts on thinned stands increased markedly from the time of thinning to the end of the study. During the 13th growing season, the effect of thinning is evident by large differences between thinned and non-thinned stands. This difference remained during the 14th growing season, but began to decrease during the 15th growing season. Separation between thinned and non-thinned stands remained consistent from the 15th through 17th growing season.

Temporal patterns in mean LAI followed a comparable trend to foliar biomass (Figure 2.3). Values were generally lower during the 13th and 14th growing seasons then increased thereafter. However, the difference in LAI values between thinned and non-thinned stands remained similar throughout the study.

Resource-use Efficiency

Culture significantly affected GE_{FOLBIO}, GE_{LAI}, NUE during the 13th growing season and density significantly affected the same attributes during the 17th growing season (Table 2.4). Average growth efficiency was greater under operational culture than intensive culture during the 13th growing season, after which no significant differences were detected (Table 2.7). During the 17th growing season, density regime significantly affected GE_{FOLBIO}, GE_{LAI} and NUE.

Average growth efficiency was generally greater in thinned densities than the 740 trees ha^{-1} non-thinned densities. The only significant interaction found was for NUE during the 13^{th} growing season. There were large variations in GE measures. Individual plot level GE ranged from 0.61 to 5.8, 1.8 to 19.6, 0.04 to 0.34, and 0.11 to 0.64 for GE_{FOLBIO}, GE_{LAI}, NUE, and GE_{IPAR}, respectively.

There is evidence to support our fourth hypothesis that crown attributes have a significant effect on gross current annual volume increment. All slopes describing the relationship between crown attributes (foliar biomass, LAI, canopy N content, and IPAR) and gross volume CAI were positive and significantly different from zero (Figure 2.4 and Figure 2.5). Relationships between CAI and crown attributes were weak to moderate but always positive. The amount of variation in CAI explained by any single crown attribute was greater for intensive than operational culture. The coefficient of determination (r^2) ranged from 0.17 to 0.25 for operational culture and 0.19 to 0.31 for intensive culture. Among relationships examined, that between LAI and gross CAI was the strongest under both cultures (Figure 2.4). Slopes between operational and intensive cultures were not statistically different at α= 0.05 for any of the relationships. However, at α=0.1, slopes were statistically different between intensive and operational culture for the CAI and LAI relationship and the CAI and IPAR relationship.

Individual Installation Examination

A closer examination of stand and crown attributes revealed differences among sites in response to density and culture. Gross volume CAI generally increases from age 13 to 17 on Installations 3 and 12 but not Installation 11 (Figure 2.6). Differences in gross volume CAI between cultures were apparent at Installation 12 but not at the other installations (Figure 2.6). At Installation 12, during the 13^{th} growing season, the 2960 trees ha^{-1} intensive culture plot had the lowest CAI and the operational culture has a moderate CAI. By the 17th growing season, the operational culture plot still had a moderate CAI; however, the intensive culture plot had the greatest CAI.

Response of LAI to cultural treatment was also variable among sites (Figure 2.7). At Installation 3, LAI was consistently about 50% higher under intensive culture than operational culture for all densities with the exception of the 2960 tree ha^{-1} density during the 16th and 7th growing season. However, at Installation 12, there was no apparent increase in LAI during this study period due to intensive culture. At Installation 11, response to intensive culture was marked for the 2220 and 2960 trees ha^{-1} density regimes, minimal for the 1480 tree ha^{-1} density regime, and after the 15th growing season, response was negative for the 740 trees ha^{-1} planting density.

The ability to predict gross volume CAI based on an individual crown attribute was stronger for some installation x culture combinations than others (Table 2.8). The r^2 for the relationship between CAI and crown attributes ranged from 0.01 for canopy N content with intensive culture on Installation 3 to 0.55 for LAI with intensive culture on Installation 12. The relationship between CAI and crown attributes was significant (slope>0; $p<0.05$) for about half of the installations by crown attribute combinations for either intensive or operational culture. The relationships were strongest and most consistent on Installation 12 and weakest and least consistent on Installation 3 with intensive culture and Installation 11 with operational culture.

Individual Tree-Level DBH Growth

The full model was significant ($p<0.01$), indicating that across the range of cultural intensities and density regimes in this study, age 12 DBH had a significant effect on DBH growth from age 12 to 17 (Table 2.9 and Figure 2.8). The effect of culture on the model was not significant for slope or intercept (p=.45 and p=.46). Thus, a density model was used to determine the effects of initial DBH and density regime on DBH growth.

Further analysis of intensive culture showed significant, positive slopes for each of the densities ($p<0.01$), but the intercept was not significantly different from zero. Slopes for the thinned densities were not significantly different from each other, but they were greater than the non-thinned density. Under operational culture, slopes were significant and positive, but slopes for 740 non-thinned and 2960 thinned tree ha^{-1} densities were not statistically different, and less than the slopes for the other densities examined. For both cultures, DBH increment for the 740 tree ha^{-1} non-thinned density was distinctly less than that on the thinned densities.

Discussion

Stand Attributes

Our first hypothesis that culture and density would have significant additive effects on stand attributes was partially supported. In this study, growth attributes were examined at two levels of culture, operational and intensive. It is important to note that the operational culture provided significant silvicultural inputs, comparable to an intensive operational regime in the Southeast (Fox et al., 2007b). Since age 7, the intensive culture provided twice the fertilization in combination with sustained weed control compared to the operational culture. Yet, stem, crown, and growth efficiency attributes were only marginally affected. At no point during the study period were stand attributes significantly increased under intensive culture (Table 2.4 and Table 2.5).

There were three levels of stand development observed in this study evident through patterns of DBH (cm), standing volume (m^3 ha^{-1}), basal area (m^2 ha^{-1}) and SDI (Table 2.5, Figure 2.1, Figure 2.2). The 740 tree ha^{-1} non-thinned density, the 1480 tree ha^{-1} thinned density, and the

2220 and 2960 tree ha^{-1} thinned densities followed different trends. Values at age 13, 14 and 15 were 740 > 1480 > 2220 = 2960 trees ha^{-1}. At age 16th and 17th values were 740 > 1480 ≥ 2220 ≥ 2960 trees ha^{-1}. During the same five year period, gross volume CAI was initially greater for the 740 trees ha^{-1} non-thinned densities but by the 17th growing season, gross volume CAI was greatest for the thinned density stands.

Prior to thinning at age 12, average total volume outside bark and basal area were distinctly greater in higher planting density stands (Figure 2.1). Post thinning, this trend was reversed with the lower planting densities having greater volume and basal area ha^{-1} than greater planting densities. Thinned stands had not reached the current stand values of their non-thinned counterpart five years after thinning. Volume ha^{-1}, basal area ha^{-1}, and SDI were significantly less in thinned than non-thinned stands due to lower average stem diameter even though there are more stems per hectare in the higher density plots at the end of this study period (Table 2.5). Hennessey et al. (2004) reported that stands thinned at age 12 had not reached the basal area ha^{-1} of their non-thinned counterpart by age 25.

During the first two growing seasons after thinning, gross volume CAI was consistently less in thinned stands than non-thinned stands (Table 2.5). By the 15th and 16th growing season, differences were less apparent. During the 17th growing season, gross volume CAI was greater in thinned than non-thinned stands. Hennessey et al. (2004) and Sword Sayer et al. (2004) reported consistently lower values of CAI in thinned than non-thinned stands. However, their thinning treatments originated at similar densities to the non-thinned control and were thinned to densities less than the non-thinned control.

Gross CAI values were lowest during the 13th growing season on the 2220 and 2960 tree ha^{-1} intensive culture plots at installation 12 (Figure 2.6). By the 17th growing season, these plots were among the highest producers in the study. The low growth rates during the 13th growing season are the result of a legacy effect from pre-thinning stand conditions. Installation 12 has the highest site index of the three sites studied. The high cultural inputs and planting density resulted in overstocked conditions leading to suppressed canopies in residual trees at the time of thinning. Once the trees were released from intraspecific competition, crowns of residual trees recovered to supply high growth rates. After the first year lag, these stands grew at 20 to 40 m^3 ha^{-1} yr^{-1}.

Crown Attributes

Our second hypothesis that culture and density would have a significant additive effect on crown attributes was partially supported. The effect of sustained cultural inputs is indicated in the foliar N concentration values. From age 12 to 16, foliar nitrogen concentrations ranged from 1.2-2.0 % , well above the critical level of 1.1% for loblolly pine (Allen 1987) suggesting that N limitations did not impact growth during this study period. The general decrease in the magnitude of differences in crown attribute values among density regimes and lack of statistical significance by age 17 indicate that the crowns in thinned stands have reached closure and occupy similar area as the non-thinned density crowns (Table 2.4 and Table 2.6). Foliar biomass ranged from 4 to 15 Mg ha^{-1} which is similar to values reported by Jokela and Martin (2000) of 10.5 Mg ha^{-1} of foliar biomass in 13-year-old loblolly pine stands. Will et al. (2005) reported canopy N content of 67 to 114.7 kg ha^{-1} in 4-year-old loblolly pine stands for planting densities from 740 to 2960 trees ha^{-1}. In this study canopy N content ranged from 56 to 213 kg ha^{-1}. Tang et al., (2004) reported that fertilization produced ~20% more foliage in 18-year-old loblolly pine stands compared to the control. Differences between cultures in this study during the 13th to 15th growing season were similar to those reported by Tang (2004) but diminished thereafter.

IPAR values increased markedly in thinned stands during the course of this study indicating crown closure in thinned stands (Table 2.6). For example, mean IPAR for the 2960 trees ha^{-1} thinned density increased from 57% to 73%.

Mean foliar biomass values in non-thinned stands remained relatively constant and were constantly greater than in thinned stands. Values in thinned stands generally increased each growing season from time of thinning. Patterns of increasing and decreasing LAI were similar for each planting regime and cultural intensity. This pattern of increasing and decreasing LAI was also observed by Hennessey et al. (2004).

Resource-use Efficiency

Results partially support the hypothesis that culture and density have significant additive effects on growth efficiency measures. The only significant interaction between culture and density regime was on NUE during the 13th growing season.

Previous studies have described crown attributes associated with light interception as highly correlated with annual stem wood production. In this study we did not see strong relationships, however all relationship with both cultural intensities were significant and positive supporting our fourth hypothesis that crown attributes have a significant effect on gross current annual volume increment. The amount of variation in volume CAI by cultural regime across installations explained by linear models ranged from 0.17 to 0.31. Della-Tea & Jokela (1991) reported a strong relationship between dry matter production and IPAR for slash and loblolly pine (r^2 = 0.94 and 0.90, respectively) at age 6 in the Lower Coastal Plain. In a four year study from age 8 to 12 on loblolly pine with irrigation and fertilization treatments, Albaugh et al.(1998) reported a strong relationship (r^2=0.95) between peak LAI and stemwood produciton. Will et al. (2005) also reported a strong correlation with IPAR, LAI and canopy N content and current annual increment across a range of planting densities from 740 to 4440 trees ha^{-1} in age 4 loblolly pine plantations in the Piedmont and Upper Coastal Plain. A major difference between the mentioned studies and this one is the thinning treatment. The mid-rotation thinning may have introduced a large variation in the ability of stands to utilize site resources. Also, the cited studies range in age from 4 to 12 years old, whereas this study reports on the 13^{th} to 17^{th} growing season productivity. Another source of variation in this study is the use of multiple locations across two physiographic regions.

Individual Tree-Level DBH Growth

For both operational and intensive culture, age 12 to 17 DBH increment for a given age 12 DBH class was lowest in 740 tree ha^{-1}, non-thinned stands (Figure 2.8). These stands maintained the highest basal area ha^{-1} and SDI throughout the study period which limited DBH growth. Individual trees in thinned stands grew in less limiting density conditions and crowns were able to better utilize leaf area in the lower crown to capture light (Ginn 1991). In non-thinned stands, crowns were only able to capture light in the upper crown.

Individual DBH growth during the study period was influenced by age 12 DBH and growing space (as compared to density regime) and not by cultural intensity. These results agree with those of Akers (2011) and Johnson (2013) who examined individual tree characteristics on the same installations at earlier ages. Akers (2011) found that trees of a given DBH had similar crown characteristics no matter the prior silviculture treatment (density or culture). Johnson (2013) reported that DBH growth from age 12 to age 15 for a tree of a given DBH was the same for intensive or operational culture.

Conclusions

Stand and crown attributes were not significantly different between the two cultural intensities, though they were generally greater with intensive culture, but differed among planting densities. Stand and crown attributes generally increased with decreasing initial planting density. Mean standing volume, basal area, and DBH in thinned stands parallels that of non-thinned stands through five years after thinning. There was a general increase in gross CAI for all densities and both cultures with increasing CAI with time from thinning. Beginning two years after thinning, mean CAI in thinned stands was equal to or greater than that in non-thinned stands. Growth efficiency attributes were not consistently affected by culture or density regime although GE_{FOLBIO}, GE_{LAI}, and NUE were greater for operational than intensive culture during the 13th growing season and were less for non-thinned than thinned stands during the 17th growing season. NUE was lowest on non-thinned stands for three of the five years. Even though not strong, there were significant, positive, linear relationship between crown attributes and volume CAI. Trees with larger DBH at age 12 and growing under non-limiting densities exhibited relatively large 5 year periodic DBH increment. High growth rates under both cultures were sustained due to high nutrient availability and non-limiting densities.

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Tables and Figures

Table 2.1. Location, soil, physiographic province, and loblolly pine site index of three PMRC culture x density installations.

Installation	Location	Coordinates	Soil Series	Soil Taxonomy	Soil Description	Physiographic Region
3	Escambia Co., AL	-87.3154, 31.1954	Freemanville	Fine, kaolinitic, thermic plinthic kandiudults	Fine, sandy loam	Upper Coastal Palain
11	Greene Co., GA	-83.0278, 33.6235	Cecil	Fine, kaolinitic, thermic typic kanhapludults	Sandy loam	Piemont
12	Barbour Co., AL	-85.6735, 31.7467	Orangeburg	Fine-loamy, kaolinitic, thermic kandiudult	Loamy sand	Upper Coastal Palain

*Soils information from the USDA- NRCS Soil Survey; Adapted from Johnson et al. (2013)

Table 2.2. Details of cultural activities implemented in culture x density study plots.

Treatment	Growing Season	**Operational Culture**	**Intensive Culture**
Site preparation		Broadcast Chemical and Mechnical	Broadcast Chemical and Mechnical
Fertilization	At Planting	560 kg ha^{-1} 10-10-10	560 kg ha^{-1} 10-10-10
	2nd		673 kg ha^{-1} 10-10-10 + 131 kg ha^{-1} NH_4NO_3 + micronutrients
	4th		131 kg ha^{-1} NH_4NO_3
	6th		336 kg ha^{-1} NH_4NO_3
	8th	224 kg ha^{-1} N + 28 kg ha^{-1} P	
	10th		224 kg ha^{-1} N + 28 kg ha^{-1} P
	12th	224 kg ha^{-1} N + 28 kg ha^{-1} P	224 kg ha^{-1} N + 28 kg ha^{-1} P
	14th		224 kg ha^{-1} N + 28 kg ha^{-1} P
	16th	224 kg ha^{-1} N + 28 kg ha^{-1} P	224 kg ha^{-1} N + 28 kg ha^{-1} P
Interspecific competition control	1st	280 g ha^{-1} sulfometuron-methyl, banded + glyphosate and triclopyr direct spraying	280 g ha^{-1} sulfometuron-methyl, broadcast + glyphosate and triclopyr direct spraying
	2nd - 17th		841 g ha^{-1} imazapyr broadcast Glyphosate and triclopyr direct application

Table 2.3. Measurement and gross plot size by initial planting density at PMRC loblolly pine culture x density installations.

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

Table 2.4. P-values for the effects of culture, density and their interaction on mean stand, crown, and efficiency attributes in three thinned loblolly pine culture x density installations for the age 12 to 17 period.

	Age 12 Pre-thin			Age 12 Post-thin			Age 13 and 13th Growing Season			Age 14 and 14th Growing Season			Age 15 and 15th Growing Season			Age 16 and 16th Growing Season			Age 17 and 17th Growing Season		
	Culture	Density	Interaction	Culture	Density	Interaction	Culture	Density	Interaction	Culture	Density	Interaction	Culture	Density	Interaction	Culture	Density	Interaction	Culture	Density	Interaction
Stand Attributes																					
DBH (cm)	0.1195	**<0.0001** *	0.3060	0.1066	**<0.0001**	0.2562	0.1277	**<0.0001**	0.3477	0.1466	**<0.0001**	0.3808	0.1240	**<0.0001**	0.5263	0.1216	**<0.0001**	0.5792	0.1216	**<0.0001**	0.5792
Height (m)	0.2083	**0.0291**	0.3629	0.2243	0.5930	0.2351	0.4477	0.5596	0.7748	0.3886	0.3695	0.5261	0.3741	0.3154	0.2639	0.3610	0.1338	0.2336	0.6054	0.2162	0.4864
Volume ha^{-1} (m^3)	0.1443	**0.0003**	0.7878	0.1277	**<0.0001**	0.2886	0.1998	**<0.0001**	0.3573	0.2000	**<0.0001**	0.5621	0.1824	**<0.0001**	0.7811	0.1953	**<0.0001**	0.7413	0.2803	**0.0001**	0.9276
Basal Area ha^{-1} (m^2)	0.1268	**0.0001**	0.8161	0.1114	**<0.0001**	0.1042	0.1258	**<0.0001**	0.2232	0.1433	**<0.0001**	0.5241	0.1273	**<0.0001**	0.6227	0.1431	**<0.0001**	0.7971	0.1877	**<0.0001**	0.9715
Stand Density Index (SDI)	0.1444	**<0.0001**	0.9063	0.1202	**<0.0001**	0.1490	0.1402	**<0.0001**	0.3182	0.1521	**<0.0001**	0.7014	0.1369	**<0.0001**	0.7926	0.1536	**<0.0001**	0.8592	0.2047	**<0.0001**	0.9212
Current TPH	0.3986	**<0.0001**	0.8996	0.7610	**0.0469**	0.5537	0.7023	**0.0389**	0.8938	0.3315	0.3317	0.6842	0.3266	0.2196	0.7295	0.3581	**0.0094**	0.3903	0.4323	**0.0051**	0.1293
Gross CAI (m^3)	-	-	-	-	-	-	0.4271	**0.0002**	0.3188	0.1929	**0.0055**	0.5615	0.1917	0.5225	0.1643	0.3370	0.0961	0.6477	0.2611	**0.0468**	0.3384
Net CAI (m^3)	-	-	-	-	-	-	0.3077	**0.0002**	0.3720	0.1816	0.9149	0.8455	0.3239	0.4117	0.5504	0.4291	0.5022	0.9017	0.2611	**0.0468**	0.3304
Crown Attributes																					
Live Crown Length	0.3199	**<0.0001**	0.9602	0.4284	**0.0109**	0.9585	0.5250	**0.0007**	0.8916	0.8100	**0.0003**	0.9993	0.2294	0.0541	0.3806	0.6081	**0.0104**	0.4745	0.0973	**0.0010**	0.1590
Crown Ratio	0.4190	**0.0006**	0.9444	0.4950	**0.0070**	0.9717	0.1284	**0.0001**	0.7617	0.2226	**0.0002**	0.8344	0.9683	0.1382	0.1952	0.0715	**0.0111**	0.6114	0.1305	**0.0007**	**0.0150**
SLA	0.3778	**0.0379**	0.3766	-	-	-	-	-	-	0.2788	0.4355	0.3681	-	-	-	0.5244	0.3428	0.8010	-	-	-
Foliar N Concentration	0.0948	0.1765	0.1141	-	-	-	-	-	-	0.3394	**<0.0001**	0.1749	-	-	-	0.6079	0.0554	0.5930	-	-	-
Foliar Biomass	-	-	-	-	-	-	0.1047	**<0.0001**	0.7230	0.1226	**<0.0001**	0.8015	0.1989	**0.0178**	0.8011	0.2506	0.1094	0.9159	0.0644	0.0892	0.9945
Canopy N Content	-	-	-	-	-	-	0.0522	**<0.0001**	0.0971	0.1430	**<0.0001**	0.5496	0.1696	**0.0038**	0.9803	0.1410	0.1360	0.4387	0.7044	0.0840	0.7649
LAI	-	-	-	-	-	-	0.0897	**<0.0001**	0.6380	0.1405	**<0.0001**	0.6377	0.1946	**0.0151**	0.9985	0.2434	0.0740	0.9401	0.5622	**0.0362**	0.9530
IPAR	-	-	-	-	-	-	0.6816	**<0.0001**	0.6115	0.2194	**<0.0001**	0.0904	0.1317	**0.0008**	0.1252	0.3973	**0.0023**	0.2802	0.5495	0.2520	0.8994
Effeciency Attributes																					
GE$_{FOLBIO}$	-	-	-	-	-	-	**0.0281**	0.0564	0.0981	0.3211	0.4270	0.3510	0.5983	0.2622	0.6087	0.7298	0.9544	0.4608	0.8876	**0.0367**	0.5723
GE$_{LAI}$	-	-	-	-	-	-	**0.0237**	0.0585	0.1241	0.2350	0.5319	0.6295	0.5615	0.2529	0.7397	0.6505	0.9249	0.5451	0.9598	**0.0198**	0.6934
NUE	-	-	-	-	-	-	**0.0272**	**0.0043**	**0.0367**	0.4371	**0.0035**	0.6695	0.6599	0.1737	0.5656	0.9605	0.7009	0.2991	0.7305	**0.0366**	0.3415
GE$_{IPAR}$	-	-	-	-	-	-	0.1918	0.2003	0.1793	0.4189	0.5501	0.2408	0.2719	0.3958	0.1749	0.4109	0.3866	0.9126	0.5142	0.5142	0.5247

*Values in bold indicate significant effects at α=0.05

Table 2.5. Mean stand attributes by culture and density on three PMRC loblolly pine culture x density installations for the age 12 to 17 period. Means in the same age/treatment combination with the same letter are not significantly different. Planting densities of 1480, 2220, and 2960 trees ha^{-1} were thinned at age 12.

		DBH (cm)	Total Stem Height (m)	Total Standing Stem Volume (m^3 ha^{-1})	Basal Area (m^2 ha^{-1})	Stand Density Index	Current TPH (trees ha^{-1})	Gross Current Annual Increment (m^3 ha^{-1} yr^{-1})	Net Current Annual Increment (m^3 ha^{-1} yr^{-1})
					Age 12 Pre-thin				
Culture	Operational	17.2 a	14.1 a	232.7 a	34.0 a	790 a	1597 a	-	-
	Intensive	19.0 a	15.4 a	281.1 a	38.8 a	869 a	1525 a	-	-
Planting	740 (non-thinned)	**23.0 a**	**15.1 a**	**205.4 a**	**29.9 a**	**610 a**	**700 a**	-	-
Density-	1480 (non-thinned)	**18.6 b**	**15.1 a**	**261.9 b**	**36.8 b**	**817 b**	**1318 b**	-	-
thinning	2220 (non-thinned)	**16.0 c**	**14.7 ab**	**271.4 b**	**38.0 bc**	**805 b**	**1838 c**	-	-
	2960 (non-thinned)	**14.5 d**	**14.1 b**	**288.8 b**	**41.0 c**	**1003 c**	**2389 d**	-	-
					Age 12 Post-thin				
Culture	Operational	18.4 a	14.7 a	132.4 a	19.1 a	425 a	692 a	-	-
	Intensive	20.0 a	15.8 a	164.9 a	22.7 a	489 a	698 a	-	-
Planting	740 (non-thinned)	**23.0 a**	15.1 a	**205.4 a**	**29.9 a**	**610 a**	**700 a**	-	-
Density-	1480 (thinned)	**19.4 b**	15.3 a	**148.5 b**	**20.8 b**	**447 b**	**691 b**	-	-
thinning	2220 (thinned)	**17.7 c**	15.4 a	**125.5 c**	**17.2 c**	**405 c**	**693 b**	-	-
	2960 (thinned)	**16.8 c**	15.2 a	**114.3 c**	**15.8 c**	**368 d**	**696 ab**	-	-
					Age 13 and 13th Growing Season				
Culture	Operational	19.2 a	15.8 a	153.1 a	20.8 a	452 a	686 a	21.3 a	17.6 a
	Intensive	20.8 a	16.5 a	183.0 a	24.4 a	513 a	695 a	18.7 a	14.1 a
Planting	740 (non-thinned)	**23.6 a**	16.1 a	**229.0 a**	**31.5 a**	**637 a**	**699 a**	**25.1 a**	**23.6 a**
Density-	1480 (thinned)	**20.3 b**	16.3 a	**169.3 b**	**22.3 b**	**484 b**	**678 b**	**22.3 a**	**18.4 b**
thinning	2220 (thinned)	**18.5 c**	16.2 a	**142.1 c**	**18.7 c**	**417 c**	**686 ab**	**17.2 b**	**8.3 c**
	2960 (thinned)	**17.6 d**	15.9 a	**131.7 c**	**17.4 c**	**397 c**	**701 a**	**15.3 b**	**13.0 c**
					Age 14 and 14th Growing Season				
Culture	Operational	20.2 a	16.4 a	165.6 a	21.8 a	464 a	656.6 a	19.7 a	12.5 a
	Intensive	21.7 a	17.4 a	203.3 a	26.0 a	541 a	687.3 a	23.7 a	20.3 a
Planting	740 (non-thinned)	**24.6 a**	17.0 a	**246.9 a**	**32.7 a**	**649 a**	673.6 a	**27.5 a**	17.9 a
Density-	1480 (thinned)	**21.1 b**	17.0 a	**184.7 b**	**23.6 b**	**499 b**	654.6 a	**21.2 b**	15.5 a
thinning	2220 (thinned)	**19.4 c**	16.9 a	**157.2 c**	**20.1 c**	**439 c**	669.0 a	**19.1 b**	15.2 a
	2960 (thinned)	**18.6 c**	16.6 a	**149.0 c**	**19.2 c**	**427 c**	690.7 a	**19.1 b**	17.3 a
					Age 15 and 15th Growing Season				
Culture	Operational	21.0 a	17.3 a	184.8 a	23.3 a	491 a	655.0 a	21.0 a	16.9 a
	Intensive	22.5 a	18.1 a	224.1 a	27.7 a	570 a	684.2 a	25.0 a	21.7 a
Planting	740 (non-thinned)	**25.1 a**	18.0 a	**268.4 a**	**33.8 a**	**667 a**	670.4 ab	21.5 a	19.3 a
Density-	1480 (thinned)	**22.1 b**	17.7 a	**204.2 b**	**25.4 b**	**528 b**	648.3 a	22.3 a	22.3 a
thinning	2220 (thinned)	**20.2 c**	17.7 a	**177.1 c**	**21.8 c**	**469 c**	669.0 ab	25.7 a	14.0 a
	2960 (thinned)	**19.4 c**	17.3 a	**168.1 c**	**21.0 c**	**459 c**	690.7 a	22.6 a	21.7 a
					Age 16 and 16th Growing Season				
Culture	Operational	22.1 a	18.4 a	220.2 a	25.6 a	531 a	654.5 a	30.1 a	29.4 a
	Intensive	23.5 a	19.3 a	265.9 a	30.0 a	605 a	682.3 a	34.4 a	32.9 a
Planting	740 (non-thinned)	**26.0 a**	19.3 a	**310.6 a**	**35.2 a**	**684 a**	**648.2 a**	38.1 a	34.2 a
Density-	1480 (thinned)	**23.1 b**	18.8 ab	**238.7 b**	**27.4 b**	**558 b**	**637.4 a**	31.0 ab	31.0 a
thinning	2220 (thinned)	**21.3 c**	18.8 ab	**220.3 bc**	**25.1 bc**	**531 bc**	**695.7 b**	30.9 ab	30.9 a
	2960 (thinned)	**20.6 c**	18.4 b	**202.5 c**	**23.5 c**	**501 c**	**692.3 b**	29.2 b	28.6 a
					Age 17 and 17th Growing Season				
Culture	Operational	23.0 a	19.5 a	249.4 a	27.7 a	563 a	649.5 a	30.6 a	30.6 a
	Intensive	24.2 a	20.0 a	288.9 a	31.7 a	632 a	676.9 a	25.8 a	25.8 a
Planting	740 (non-thinned)	**26.7 a**	20.1 a	**330.6 a**	**36.3 a**	**699 a**	**638.9 a**	**24.6 a**	**24.6 a**
Density-	1480 (thinned)	**24.0 b**	19.8 ab	**268.7 b**	**29.5 b**	**590 b**	**634.2 a**	**31.1 b**	**31.1 b**
thinning	2220 (thinned)	**22.2 c**	19.7 ab	**247.5 bc**	**27.2 bc**	**565 bc**	**695.7 b**	**27.4 ab**	**27.4 ab**
	2960 (thinned)	**21.5 c**	19.3 b	**229.7 c**	**25.6 c**	**536 c**	**684.0 b**	**29.7 b**	**29.7 b**

*Values in bold indicate significant effects at α=0.05

Table 2.6. Mean crown attributes by culture and density on three PMRC loblolly pine culture x density installations for the age 12 to age 17 period. Means in the same age/treatment combination with the same letter are not significantly different. Planting densities of 1480, 2220, and 2960 trees ha^{-1} were thinned at age 12.

		DBH (cm)	Total Stem Height (m)	Total Standing Stem Volume (m^3 ha^{-1})	Basal Area (m^2 ha^{-1})	Stand Density Index (metric units)	Current TPH (trees ha^{-1})	Gross Current Annual Increment (m^3 ha^{-1} yr^{-1})	Net Current Annual Increment (m^3 ha^{-1} yr^{-1})
					Age 12 Pre-thin				
Culture	Operational	17.2 a	14.1 a	232.7 a	34.0 a	790 a	1597 a	-	-
	Intensive	19.0 a	15.4 a	281.1 a	38.8 a	869 a	1525 a	-	-
Planting	740 (non-thinned)	**23.0 a**	**15.1 a**	**205.4 a**	**29.9 a**	**610 a**	**700 a**	-	-
Density-	1480 (non-thinned)	**18.6 b**	**15.1 a**	**261.9 b**	**36.8 b**	**817 b**	**1318 b**	-	-
thinning	2220 (non-thinned)	**16.0 c**	**14.7 ab**	**271.4 b**	**38.0 bc**	**805 b**	**1838 c**	-	-
	2960 (non-thinned)	**14.5 d**	**14.1 b**	**288.8 b**	**41.0 c**	**1003 c**	**2389 d**	-	-
					Age 12 Post-thin				
Culture	Operational	18.4 a	14.7 a	132.4 a	19.1 a	425 a	692 a	-	-
	Intensive	20.0 a	15.8 a	164.9 a	22.7 a	489 a	698 a	-	-
Planting	740 (non-thinned)	**23.0 a**	15.1 a	**205.4 a**	**29.9 a**	**610 a**	**700 a**	-	-
Density-	1480 (thinned)	**19.4 b**	15.3 a	**148.5 b**	**20.8 b**	**447 b**	**691 b**	-	-
thinning	2220 (thinned)	**17.7 c**	15.4 a	**125.5 c**	**17.2 c**	**405 c**	**693 b**	-	-
	2960 (thinned)	**16.8 c**	15.2 a	**114.3 c**	**15.8 c**	**368 d**	**696 ab**	-	-
					Age 13 and 13th Growing Season				
Culture	Operational	19.2 a	15.8 a	153.1 a	20.8 a	452 a	686 a	21.3 a	17.6 a
	Intensive	20.8 a	16.5 a	183.0 a	24.4 a	513 a	695 a	18.7 a	14.1 a
Planting	740 (non-thinned)	**23.6 a**	16.1 a	**229.0 a**	**31.5 a**	**637 a**	**699 a**	**25.1 a**	**23.6 a**
Density-	1480 (thinned)	**20.3 b**	16.3 a	**169.3 b**	**22.3 b**	**484 b**	**678 b**	**22.3 a**	**18.4 b**
thinning	2220 (thinned)	**18.5 c**	16.2 a	**142.1 c**	**18.7 c**	**417 c**	**686 ab**	**17.2 b**	**8.3 c**
	2960 (thinned)	**17.6 d**	15.9 a	**131.7 c**	**17.4 c**	**397 c**	**701 a**	**15.3 b**	**13.0 c**
					Age 14 and 14th Growing Season				
Culture	Operational	20.2 a	16.4 a	165.6 a	21.8 a	464 a	656.6 a	19.7 a	12.5 a
	Intensive	21.7 a	17.4 a	203.3 a	26.0 a	541 a	687.3 a	23.7 a	20.3 a
Planting	740 (non-thinned)	**24.6 a**	17.0 a	**246.9 a**	**32.7 a**	**649 a**	673.6 a	**27.5 a**	17.9 a
Density-	1480 (thinned)	**21.1 b**	17.0 a	**184.7 b**	**23.6 b**	**499 b**	654.6 a	**21.2 b**	15.5 a
thinning	2220 (thinned)	**19.4 c**	16.9 a	**157.2 c**	**20.1 c**	**439 c**	669.0 a	**19.1 b**	15.2 a
	2960 (thinned)	**18.6 c**	16.6 a	**149.0 c**	**19.2 c**	**427 c**	690.7 a	**19.1 b**	17.3 a
					Age 15 and 15th Growing Season				
Culture	Operational	21.0 a	17.3 a	184.8 a	23.3 a	491 a	655.0 a	21.0 a	16.9 a
	Intensive	22.5 a	18.1 a	224.1 a	27.7 a	570 a	684.2 a	25.0 a	21.7 a
Planting	740 (non-thinned)	**25.1 a**	18.0 a	**268.4 a**	**33.8 a**	**667 a**	670.4 ab	21.5 a	19.3 a
Density-	1480 (thinned)	**22.1 b**	17.7 a	**204.2 b**	**25.4 b**	**528 b**	648.3 a	22.3 a	22.3 a
thinning	2220 (thinned)	**20.2 c**	17.7 a	**177.1 c**	**21.8 c**	**469 c**	669.0 ab	25.7 a	14.0 a
	2960 (thinned)	**19.4 c**	17.3 a	**168.1 c**	**21.0 c**	**459 c**	690.7 a	22.6 a	21.7 a
					Age 16 and 16th Growing Season				
Culture	Operational	22.1 a	18.4 a	220.2 a	25.6 a	531 a	654.5 a	30.1 a	29.4 a
	Intensive	23.5 a	19.3 a	265.9 a	30.0 a	605 a	682.3 a	34.4 a	32.9 a
Planting	740 (non-thinned)	**26.0 a**	19.3 a	**310.6 a**	**35.2 a**	**684 a**	**648.2 a**	38.1 a	34.2 a
Density-	1480 (thinned)	**23.1 b**	18.8 ab	**238.7 b**	**27.4 b**	**558 b**	**637.4 a**	31.0 ab	31.0 a
thinning	2220 (thinned)	**21.3 c**	18.8 ab	**220.3 bc**	**25.1 bc**	**531 bc**	**695.7 b**	30.9 ab	30.9 a
	2960 (thinned)	**20.6 c**	18.4 b	**202.5 c**	**23.5 c**	**501 c**	**692.3 b**	29.2 b	28.6 a
					Age 17 and 17th Growing Season				
Culture	Operational	23.0 a	19.5 a	249.4 a	27.7 a	563 a	649.5 a	30.6 a	30.6 a
	Intensive	24.2 a	20.0 a	288.9 a	31.7 a	632 a	676.9 a	25.8 a	25.8 a
Planting	740 (non-thinned)	**26.7 a**	20.1 a	**330.6 a**	**36.3 a**	**699 a**	**638.9 a**	**24.6 a**	**24.6 a**
Density-	1480 (thinned)	**24.0 b**	19.8 ab	**268.7 b**	**29.5 b**	**590 b**	**634.2 a**	**31.1 b**	**31.1 b**
thinning	2220 (thinned)	**22.2 c**	19.7 ab	**247.5 bc**	**27.2 bc**	**565 bc**	**695.7 b**	**27.4 ab**	**27.4 ab**
	2960 (thinned)	**21.5 c**	19.3 b	**229.7 c**	**25.6 c**	**536 c**	**684.0 b**	**29.7 b**	**29.7 b**

*Values in bold indicate significant effects at α=0.05

Table 2.7. Mean growth efficiency attributes by culture and density on three PMRC loblolly pine culture x density installations during the 13th to 17th growing season. Means in the same age/treatment combination with the same letter are not significantly different. Planting densities of 1480, 2220, and 2960 trees ha^{-1} were thinned at age 12.

		GE_{Folbio} (m^3 tonne^{-1})	GE_{LAI} (m^3 LAI^{-1})	NUE (m^3 kg^{-1})	GE_{IPAR} (m^3 %IPAR^{-1})
			13th Growing Season		
Culture	Operational	**2.9 a**	**9.2 a**	**.20 a**	.32 a
	Intensive	**2.0 b**	**6.1 b**	**.13 b**	.26 a
Planting Density-thinning	740 (non-thinned)	2.1 a	6.9 a	**.14 a**	.28 a
	1480 (thinned)	2.8 b	8.9 b	**.20 b**	.32 a
	2220 (thinned)	2.3 a	7.5 ab	**.15 ac**	.31 a
	2960 (thinned)	2.4 ab	7.3 a	**.17 bc**	.26 a
			14th Growing Season		
Culture	Operational	3.0 a	11.0 a	.19 a	.39 a
	Intensive	2.7 a	9.4 a	.18 a	.34 a
Planting Density-thinning	740 (non-thinned)	2.5 a	9.0 a	**.15 a**	.33 a
	1480 (thinned)	3.0 a	10.9 a	**.22 b**	.36 a
	2220 (thinned)	2.7 a	10.3 a	**.16 a**	.37 a
	2960 (thinned)	3.0 a	10.5 a	**.22 b**	.39 a
			15th Growing Season		
Culture	Operational	2.8 a	8.2 a	.18 a	.27 a
	Intensive	2.5 a	7.2 a	.16 a	.31 a
Planting Density-thinning	740 (non-thinned)	2.1 a	5.9 a	.13 a	.27 a
	1480 (thinned)	2.7 a	8.2 a	.18 a	.32 a
	2220 (thinned)	3.0 a	9.0 a	.19 a	.31 a
	2960 (thinned)	2.7 a	7.7 a	.18 a	.28 a
			16th Growing Season		
Culture	Operational	3.4 a	8.6 a	.22 a	.38 a
	Intensive	3.4 a	8.1 a	.22 a	.43 a
Planting Density-thinning	740 (non-thinned)	3.4 a	8.2 a	.23 a	.44 a
	1480 (thinned)	3.4 a	8.8 a	.22 a	.39 a
	2220 (thinned)	3.4 a	8.3 a	.23 a	.42 a
	2960 (thinned)	3.2 a	8.0 a	.21 a	.37 a
			17th Growing Season		
Culture	Operational	2.6 a	6.6 a	.17 a	.36 a
	Intensive	2.7 a	6.7 a	.18 a	.40 a
Planting Density-thinning	740 (non-thinned)	**1.9 a**	**4.7 a**	**.13 a**	.30 a
	1480 (thinned)	**3.2 b**	**8.6 b**	**.21 b**	.42 b
	2220 (thinned)	**2.5 a**	**6.2 ab**	**.17 ab**	.38 ab
	2960 (thinned)	**3.0 b**	**7.3 b**	**.19 b**	.41 b

*Values in bold indicate significant effects at α=0.05

Table 2.8. Linear regression equations and r^2 values for the relationship between four crown attributes and gross current annual increment during the age 12 to age 17 period by loblolly pine culture x density installations.

	Intensive Culture					
	Installation 3		Installation 11		Installation 12	
Foliar Biomass	y=0.0009025(x) + 17.13	r^2=0.11	y= 0.00173(x) + 7.25	r^2=0.17	y= 0.00483(x)** - 20.50	r^2=0.45
LAI	y=0.084518(x) + 23.55	r^2=0.03	y= 3.79974(x)** + 11.13	r^2=0.32	y= 8.39692(x)** -2.23	r^2=0.55
Canopy N Content	y=0.001330(x) + 24.56	r^2=0.01	y=0.09516(x)* + 10.36	r^2=0.18	y=0.19469(x)** - 3.08	r^2=0.37
IPAR	y=0.28755(x)* + 4.75	r^2=0.24	y=0.16045(x) + 12.89	r^2=0.07	y=.28246(x)* + 2.87	r^2=0.20
	Operational Culture					
	Installation 3		Installation 11		Installation 12	
Foliar Biomass	y=0.00136(x)* + 13.30	r^2=0.21	y=0.00102(x) + 14.62	r^2=0.11	y= 0.00121(x) + 12.74	r^2=0.18
LAI	y=3.77683(x)**+13.79	r^2=0.30	y=2.19528(x)+ 17.01	r^2=0.11	y=2.93782(x)** + 14.09	r^2=0.38
Canopy N Content	y=0.10316(x)** + 11.57	r^2=0.31	y=0.05419(x)+ 16.55	r^2=0.07	y=0.06003(x) + 15.49	r^2=0.13
IPAR	y= 0.16934(x)* + 11.43	r^2=0.22	y=.1740(x) + 11.70	r^2=0.16	y= 0.61382(x)** -18.23	r^2=0.40

* slope significant at p≤ .05

** slope significant at p≤ .01

Table 2.9. Linear growth parameters by cultural and density treatment for individual tree diameter growth analysis from age 12 to 17 on three PMRC culture x density installations. Planting densities of 1480, 2220, and 2960 trees ha-1 were thinned at age 12.

Culture and Density	Intercept		Slope	
Intensive Culture				
740 non-thinned	-0.1438	a	0.1405	a
1480 thinned	-0.3772	a	0.2411	b
2220 thinned	-0.7139	a	0.2759	b
2960 thinned	0.0052	a	0.2673	b
Operational Culture				
740 non-thinned	1.3279	a	0.1178	a
1480 thinned	-0.2826	a	0.2717	b
2220 thinned	-0.1424	a	0.2833	b
2960 thinned	3.6739	a	0.0746	a

*Different letters in the same column for each culture indicate significant differences

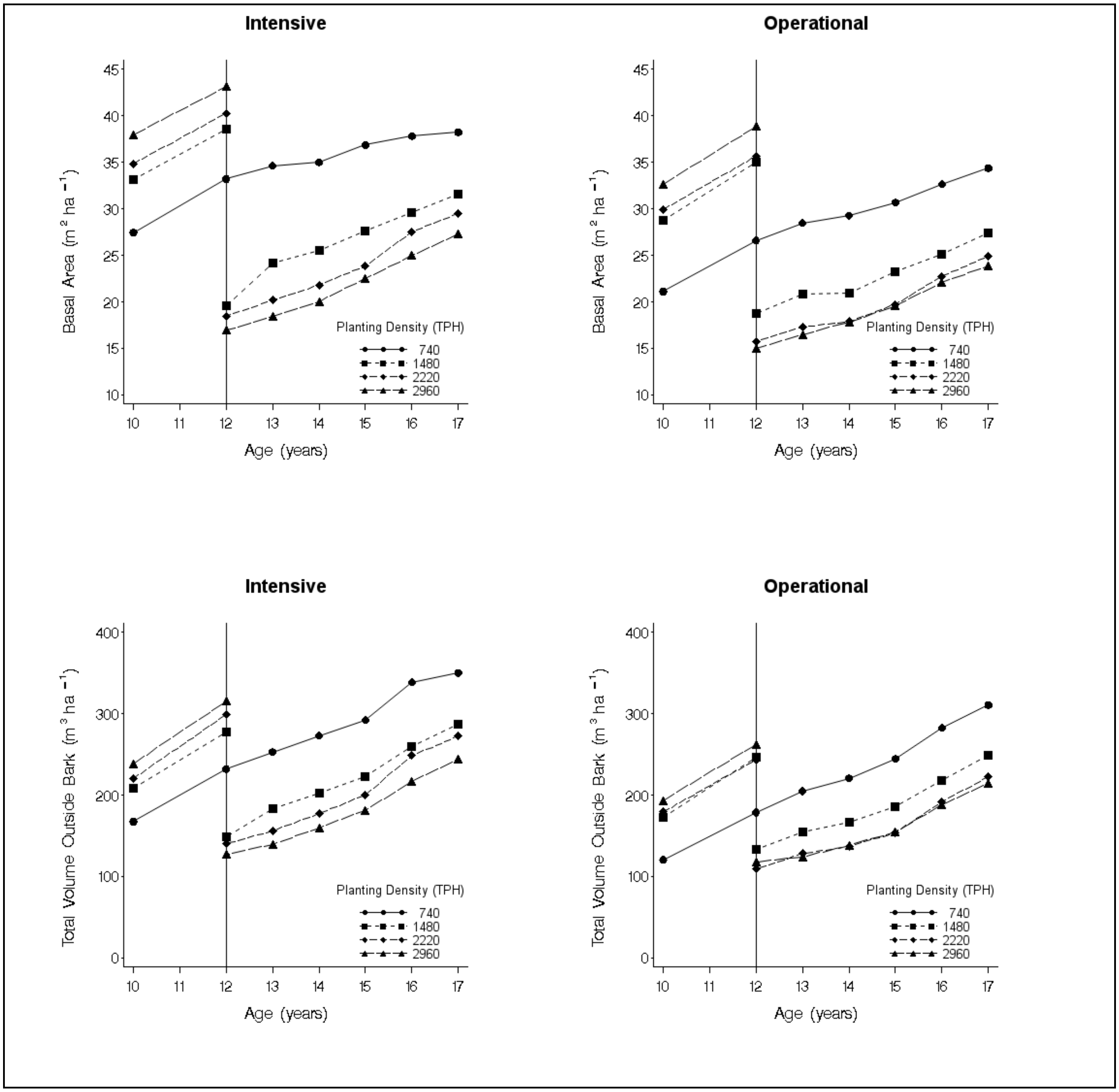

Figure 2.1. Pre- and post-thin mean values of basal area and total volume per hectare by cultural intensity and density regime of three PMRC culture x density installations. Planting densities of 1480, 2220, and 2960 trees ha^{-1} were thinned at age 12.

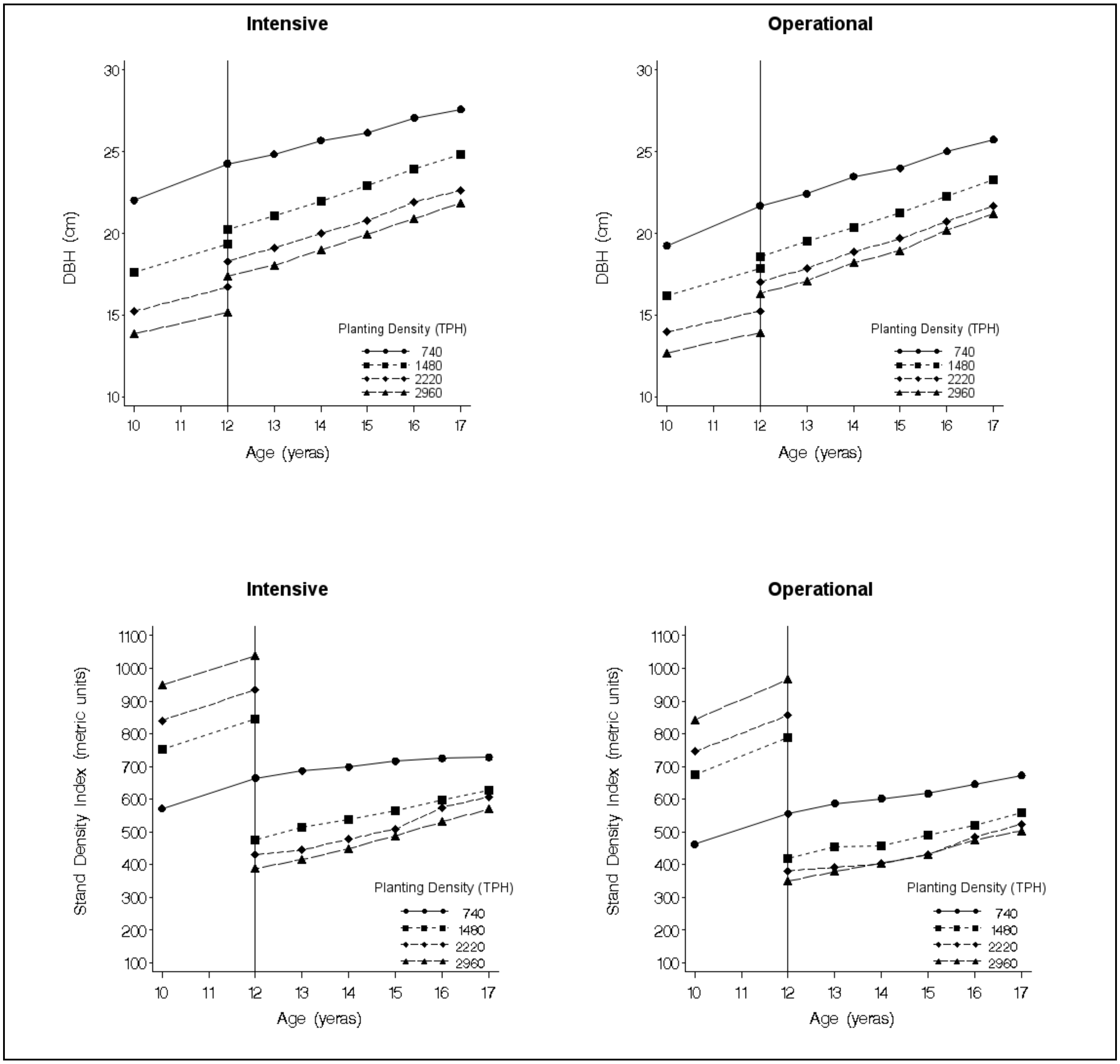

Figure 2.2. Pre- and post-thin mean DBH and stand density index by cultural intensity and density regime of three PMRC culture x density installations. Planting densities of 1480, 2220, and 2960 trees ha^{-1} were thinned at age 12.

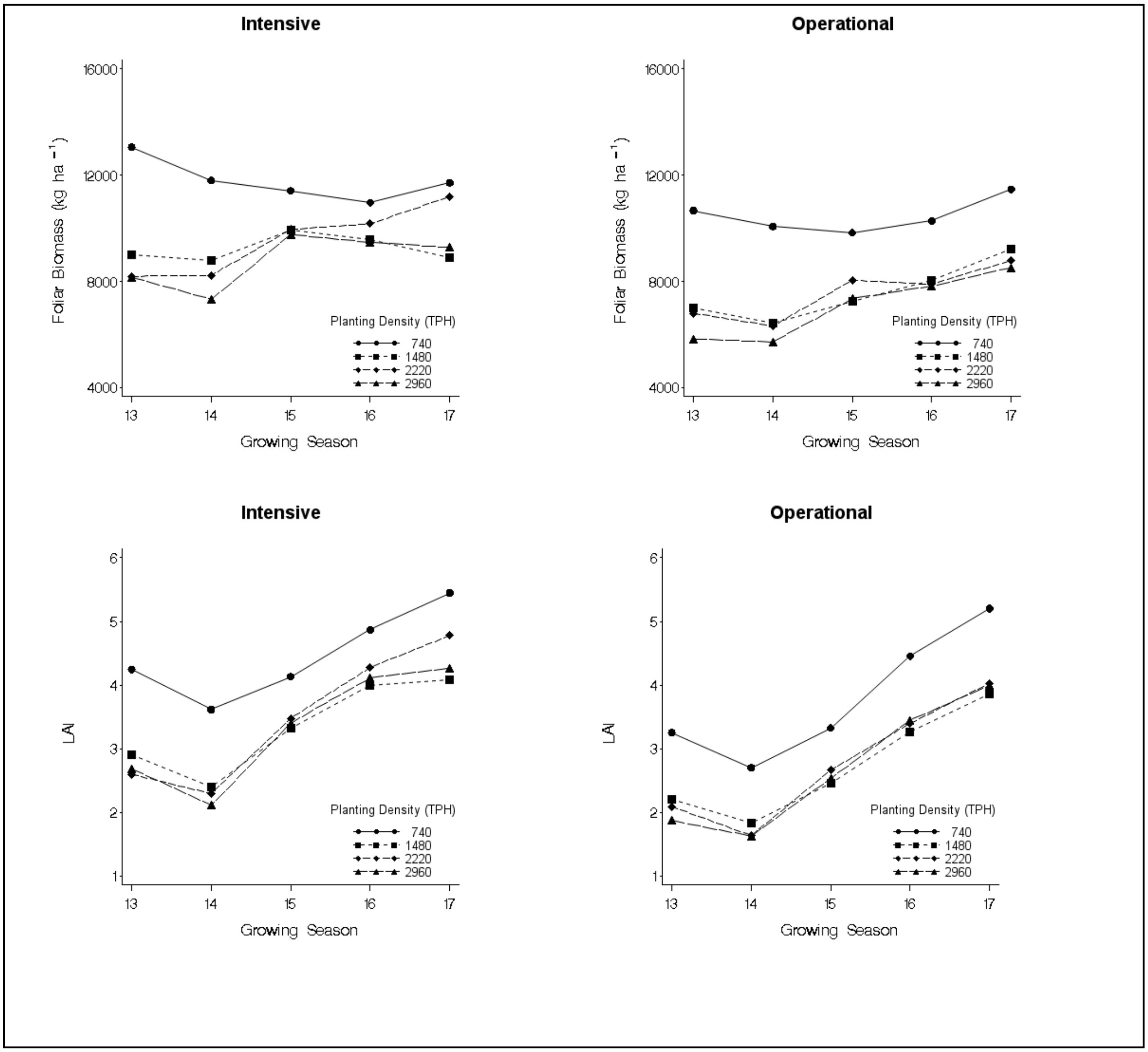

Figure 2.3. Average foliar biomass and LAI by cultural intensity and density regime from age 12 to age 17 across three culture x density installations. Planting densities of 1480, 2220, and 2960 trees ha $^{-1}$ were thinned at age 12.

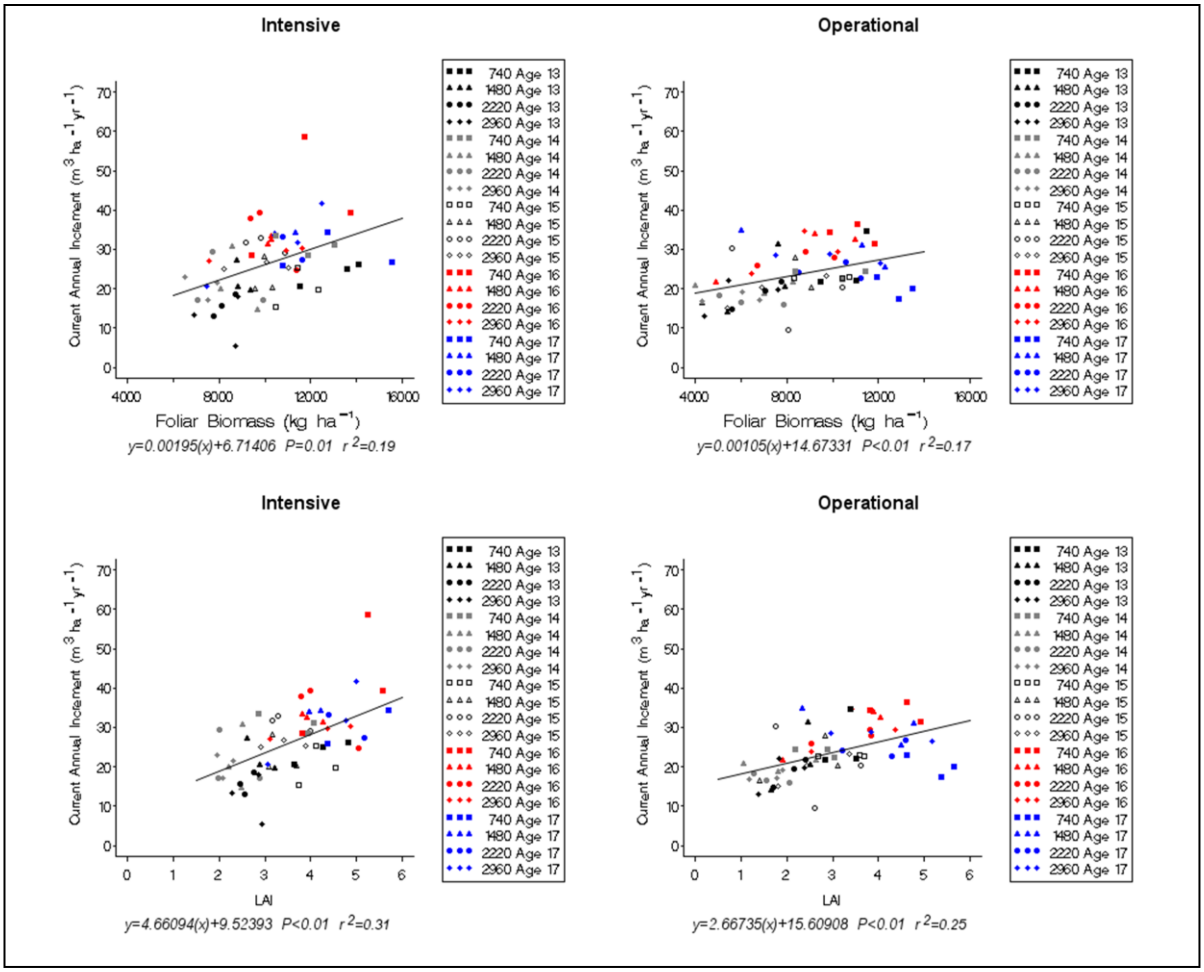

Figure 2.4. Gross volume CAI per unit of foliar biomass and LAI by cultural intensity during the 13th to 17th growing seasons on three PMRC culture x density installations. Slopes between intensive and operational culture were significantly different for LAI (α=0.10). Planting densities of 1480, 2220, and 2960 trees ha^{-1} were thinned at age 12.

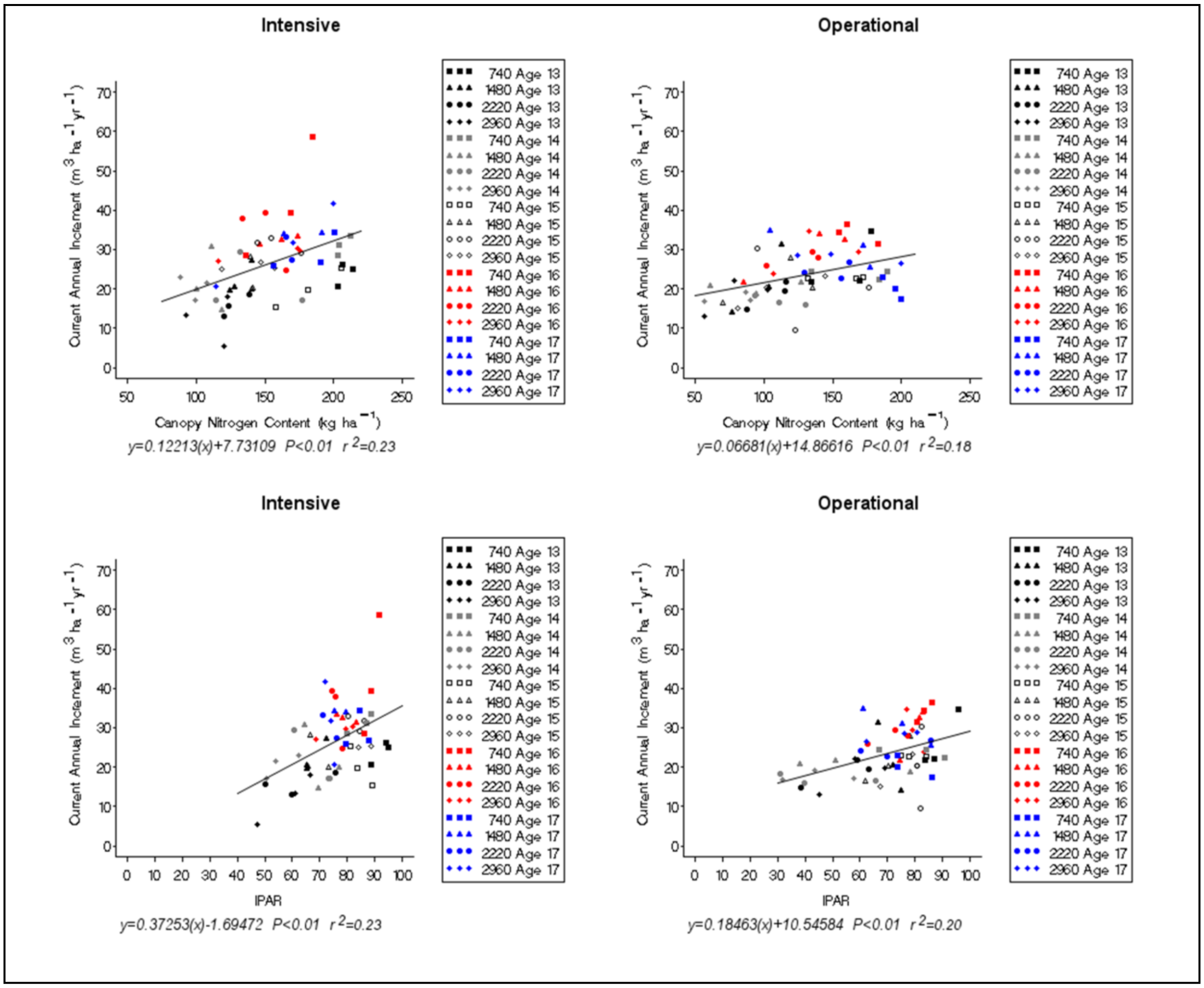

Figure 2.5. Gross volume CAI per unit of canopy nitrogen content and IPAR by cultural intensity during the 13th to 17th growing seasons on three PMRC culture x density installations. Slopes between intensive and operational culture were significantly different for IPAR (α=0.10). Planting densities of 1480, 2220, and 2960 trees ha^{-1} were thinned at age 12.

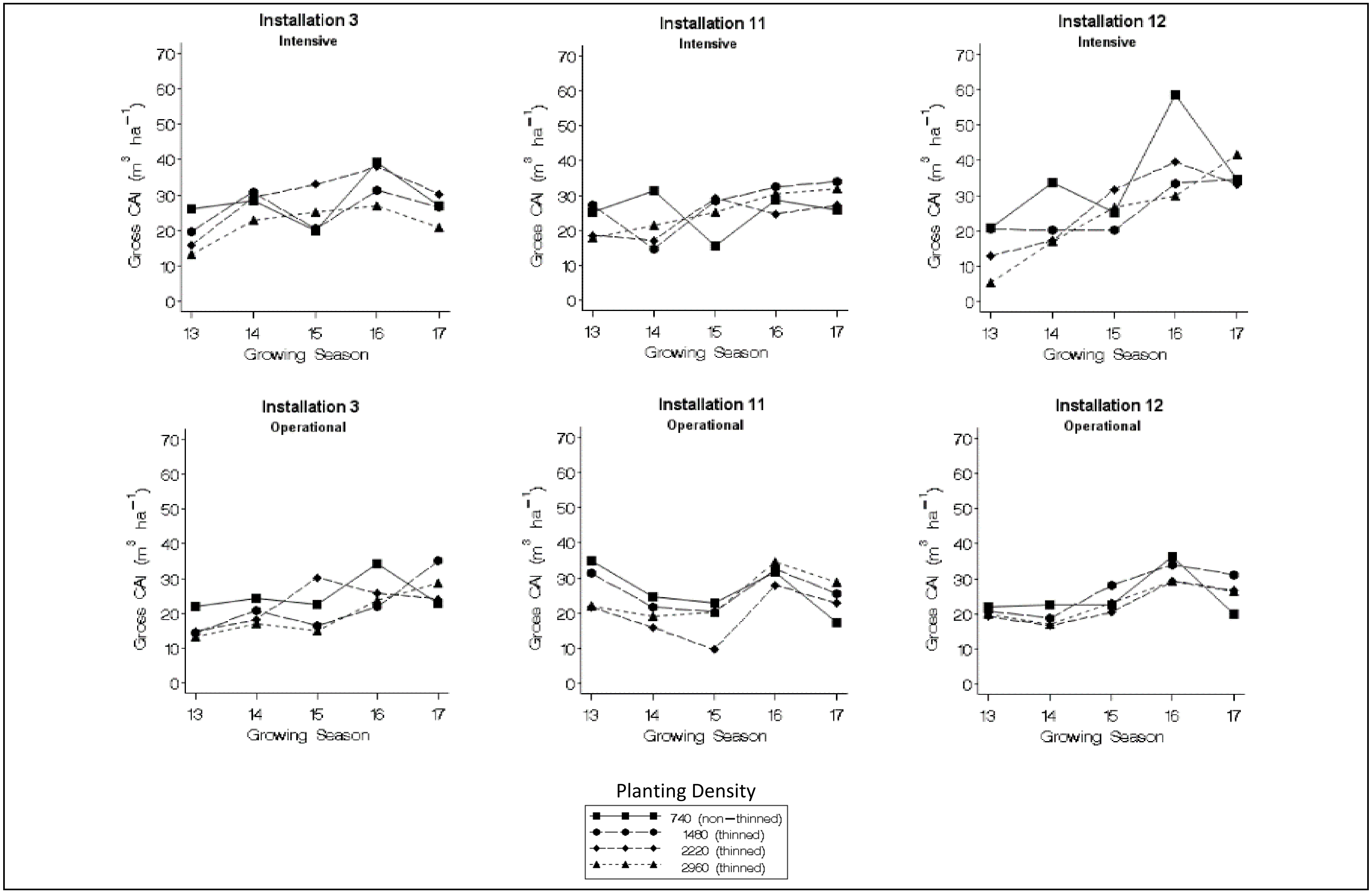

Figure 2.6. Gross volume CAI by growing season from age 12 to age 17 by cultural intensity and density regime combination by installation at the three culture x density installations. Each point represents a measurement value at the plot level. Planting densities of 1480, 2220, and 2960, trees ha^{-1} were thinned at age 12.

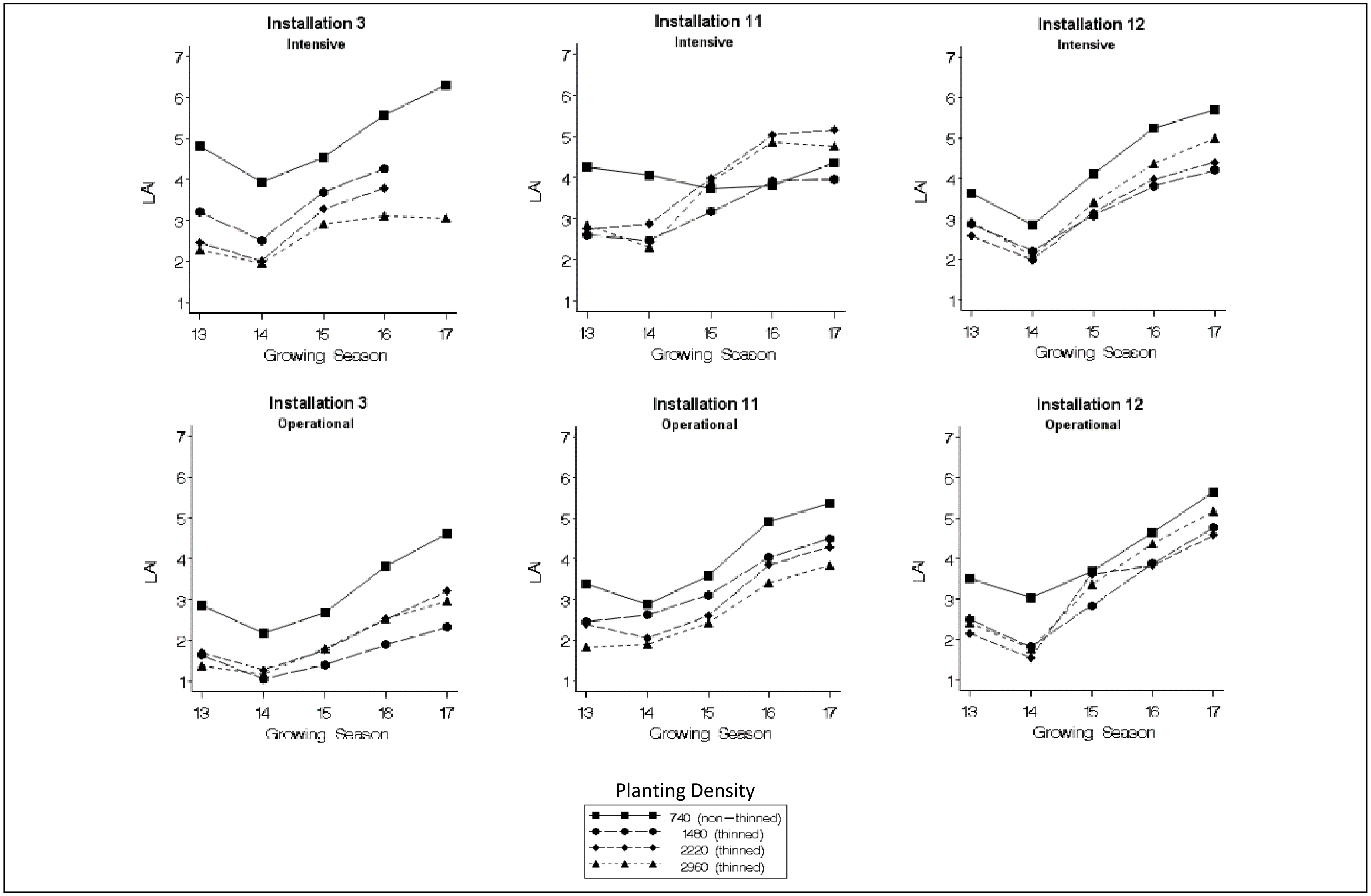

Figure 2.7. Peak projected LAI by growing season from age 12 to age 17 by cultural intensity and density regime combination by installation at three culture x density installations. Each point represents a measurement value at the plot level. Installation 3 data for LAI during the 16th and 17th growing season on the 1480 and 2220 trees ha^{-1} plots for intensive culture was unavailable. Planting densities of 1480, 2220, and 2960 trees ha^{-1} were thinned at age 12.

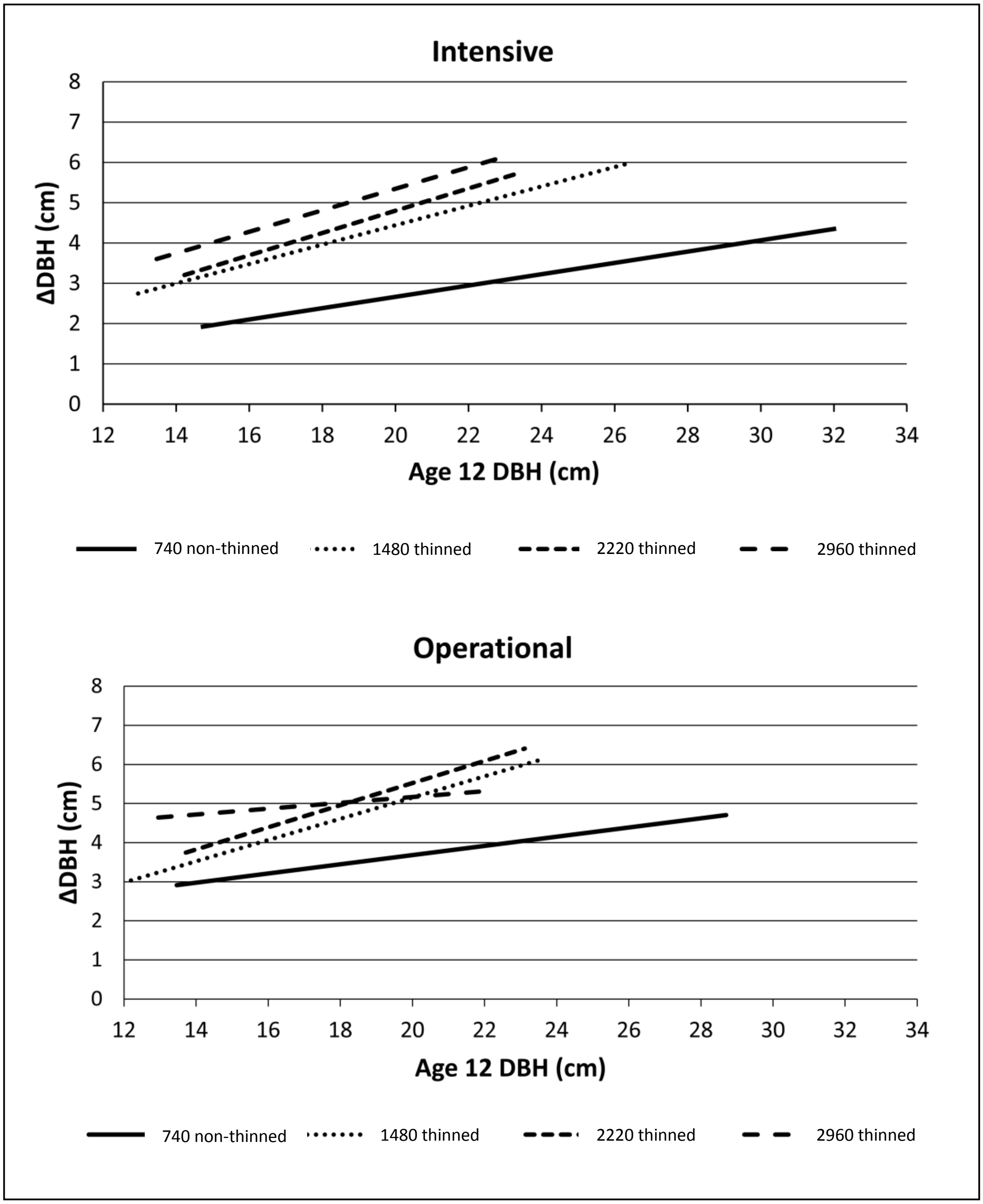

Figure 2.8. Linear trend lines in DBH increment from age 12 to 17 with age 12 DBH by by culture and density regime across the culture x density installations. Planting densities of 1480, 2220, and 2960 trees ha^{-1} were thinned at age 12.

CHAPTER 3[1]

STAND AND CROWN ATTRIBUTE RELATIONSHIPS WITH GROWING SEASON RAINFALL IN MIDROTATION LOBLOLLY PINE PLANTATIONS IN THE UPPER COASTAL PLAIN AND PIEDMONT OF THE SOUTHEASTERN UNITED STATES

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Abstract

Three loblolly pine culture x density installations were used to examine the relationship of density regime, cultural intensity and growing season precipitation on stand, crown and growth efficiency attributes in mid-rotation stands. Each installations consisted of four initial planting densities (740, 1480, 2220 and 2960 trees ha^{-1}) and two cultural intensities (operational and intensive) arranged in a split plot design. Thinning was performed at age 12 in the 1480, 2220, and 2960 trees ha^{-1} plots to the current trees ha^{-1} in the corresponding 740 tree ha^{-1} plot for that culture and installation. Growing season precipitation was measured annually at a local weather station from March 1st to October 31st. Stand and stem attributes were measured annually from age 12 to 17 and crown attributes were measured annually during the 13 to 17th growing season. A model was developed to determine the significance of age, culture, density regime and current and previous growing season rainfall on stand, crown, and growth efficiency attributes. Current growing season rainfall effect was significant for gross volume current annual increment (CAI), foliar biomass, and growth efficiency attributes. Previous growing season rainfall effect was significant for all attributes except leaf area index (LAI). Mean CAI, foliar biomass and LAI were generally lowest during the periods of low growing season precipitation. Average CAI values were 20 and 28 m^3 ha^{-1} yr^{-1}, respectively, and LAI values were 2.7 and 4.4, respectively, during periods of below and near or above long term precipitation averages, respectively. Gross volume CAI, foliar biomass and LAI had significant, positive, linear relationships with current growing season precipitation. Quadratic trends were only significant under operational culture for CAI with current and previous growing season rainfall and for foliar biomass, LAI and growth efficiency (foliar biomass, LAI, and canopy nitrogen) with current growing season rainfall. Results suggest the importance of growing season precipitation

as a factor for stand and crown maintenance and development in mid-rotation loblolly pine stands.

Introduction

Loblolly pine covers 13.4 million ha. of commercial forest and in the Southeast (Schultz, 1999). Planting density and thinning treatments can influence stand level and individual tree growth dynamics (Bailey, 1986; Cardoso et al., 2013; Ginn et al., 1991; Zhao et al., 2011). Increases in stand productivity can be attained through fertilization, competition control and combinations of the treatments through increases in water, nutrient, and light availability (Fox et al., 2007; Jokela et al., 2000; Zutter et al., 1986). The mechanisms that are responsible for greater production are less understood but are believed to be attributed to improved canopy conditions.

It is suggested that canopy development as influenced by silvicultural inputs has a major input on productivity. There is evidence that canopy light interception is the main driver in stem and stand development (Campoe et al., 2013; Colbert et al., 1990). Della-Tea and Jokela (1991) reported that leaf area index (LAI) and the amount of intercepted radiation for slash and loblolly pine was increased with fertilization and weed control. Intercepted radiation was well correlated with aboveground dry matter production.

Water additions through irrigation have been demonstrated to have minimal to moderate impacts on hydraulic, stem, stand or crown attributes on sites with a range of water holding capacities (Albaugh et al., 1998; Allen et al., 2005; Campoe et al., 2013; Samuelson et al., 2008). Generally, a response to irrigation is only seen in drought conditions, and irrigation may increase the response to fertilization (Albaugh et al., 1998; Samuelson et al., 2008). Increased growth is attributed to increased light interception, mostly through higher amounts of leaf area, and greater light use efficiency (Albaugh et al., 1998).

Other studies have examined water relations by imposing water reduction treatments. Samuelson et al. (2014) reported that a 30% throughfall reduction implemented in a 7-year-old loblolly pine plantation studied over two years in the Georgia Piedmont decreased leaf physiological function and stand growth during a year with below average precipitation. The following year, with greater precipitation and no drought conditions, only leaf water potential was decreased while stem and stand growth were unaffected. No interactions between throughfall reduction and fertilization were detected. Tang et al. (2004) also reported a leaf-level response to precipitation amounts. A 100% throughfall exclusion for one growing season in an 18-year-old loblolly pine plantation resulted in significantly reduced needle-level photosynthesis, transpiration, stomatal conductance, and pre-dawn xylem pressure potential. There was no statistical interaction at $\alpha=0.05$ but the annual foliage mass and daily whole crown photosynthesis response to fertilization was reduced with throughfall exclusion. Hennessey et al. (2004) noted that in a thinned loblolly pine stand in Oklahoma, LAI was reduced by 1.5-1.7 units during extended drought periods from age 10 to 12 and 19 to 21 years.

Thinning increases tree level growth through increased light availability (Ginn et al., 1991). However, Teskey et al. (1987) suggest that the effects of thinning on tree water relations may be complex due to altered above ground growing conditions. Even though individuals have greater water availability, they are also subject to higher transpiration water loss due to increased photosynthesis in the lower crown and increased air turbulence.

The objective of this study was to identify the apparent effects of growing season precipitation on midrotation loblolly pine plantation productivity and crown attributes under different culture inputs and density management regimes.

Hypotheses

a. Growing season precipitation will have a significant effect on gross current annual increment and the effect will be independent of culture or density.
b. Growing season precipitation will have a significant effect on crown attributes and effects will be independent of culture or density.
c. Growing season precipitation will have a significant effect on growth efficiency and effects will be independent of culture or density.

Methods

Study Site Description

This study utilized three loblolly pine installations on well drained soils in the Upper Coastal Plain and Piedmont of Georgia and Alabama (Table 3.1). These sites, managed by the Plantation Management Research Cooperative (PMRC) at the University of Georgia, are part of the South Atlantic and Gulf Slope (SAGS) Culture Density study. Each installation was arranged in a split-plot design containing four planting densities and two cultural intensities. Planting densities were 740, 1480, 2220, and 2960 trees ha $^{-1}$; the two cultural intensities were ‘intensive’ and ‘operational’ (Table 3.2). The operational treatment consisted of early competition control and periodic fertilization. The intensive treatment consisted of sustained competition control and more frequent fertilization. Each installation was planted during the 1998/1999 dormant season with half-sib, loblolly pine seedlings. Seedlings were double planted then reduced to one surviving sapling after the first growing season to ensure adequate survival. Gross plot size varied based on planting density and each treatment plot contained an interior measurement plot surrounded by a buffer approximately 8 m. wide (Table 3.3). At each installation, the 1,480, 2220, and 2,960 trees ha^{-1} plots were thinned at age 12 to the current trees ha^{-1} on the 740 trees ha^{-1} x culture plot counterpart at that installation using third row removal in combination with a low thinning in leave rows to attain the appropriate density. Cut stems and crowns were left in the plot.

Rainfall

Total growing season rainfall amounts were determined for each installation using reports from Weather Underground (Weather Underground). The growing season for each year was defined as March 1st to October 31st. Rainfall data during the 13th through 17th growing seasons was obtained from a local weather station(s) near each installation. Since the precipitation recordings were not taken at the study site, when recording sites were greater than 32 kilometers from the study site, rainfall amounts were averaged from two different weather stations (Table 3.1).

Stand and Crown Measurements

Diameter at breast height (DBH) was measured on all trees in the measurement plot during the dormant season at ages 10, 12, 13, 14, 15, 16 and 17. Total height and height to live crown were measured on every other tree in the measurement plot during the dormant season at ages 12, 13, 14, 15, 16 and 17. Heights of trees not measured for these attributes were estimated using heights from measured trees and the linear regression equation $\ln(\text{height})=\beta 0 + \beta 1\ DBH^{-1}$ for each plot and measurement period. Live crown length (LCL) was determined for trees with known heights using the equation LCL=total height – height to live crown. Gross current annual increment (CAI) was calculated by subtracting the total current standing volume per hectare of live trees at age (a) from the subsequent year standing volume of live trees per hectare, age (a+1), then adding volume lost to mortality during the same time period.

Circular leaf litter traps were placed in each plot to collect litter fall from the 13th-17th growing seasons. Seven traps were systematically placed in each plot. Traps size measured 0.46 m^2. Litter was collected and combined for each plot x growing season and taken back to the lab where it was dried at 60^{O} C to a constant weight. Since loblolly pine retains two cohorts of foliage, a growing season foliar biomass was calculated by adding that years litter fall and that of the subsequent year litter fall weights. Estimates were updated after each growing season using current growing season foliage collection. Litter collection from the 17th growing season was doubled to estimate growing season foliar biomass.

Foliar biomass litter collections at Installation 3, plots 1,480 and 2,220 trees ha^{-1} intensive culture, were abnormally low during the 17th growing season. Values were 5,304 and 4,630 kg ha^{-1}, respectively, for these plots while the same density x culture plots at other installations was greater than 10, 000 kg ha^{-1}. There was no evidence of high mortality or disturbance on these plots. Since values of foliar biomass are added to the previous year estimates, these low values also affected the values from the 16th growing season. It was decided to omit the 17th growing season foliar biomass estimates at Installation 3 for the 1,480 and 2,200 trees ha^{-1} intensive culture plots and double the 16th growing season estimates on the same plots. All calculations for 17th growing season foliar biomass, LAI, and canopy nitrogen content in 1,480 and 2,220 trees ha^{-1} intensive culture plots only use two installations.

During the age 12, 14, and 16 dormant seasons, live needle samples were collected from the upper portion of the middle third of the crown on five dominate or co dominate trees in each plot. One branch was removed and five to ten fascicles from each flush were collected and placed in a plastic bag for storage. Needles for a given plot were combined. All needles were refrigerated until they could be measured for specific leaf area (SLA) and nutrient concentrations. A sub sample of fifteen needles was used to measure all-sided SLA as described by Fites and Teskey (1988) calculated as the surface area of green fascicle (cm^2) per oven-dried mass (g); the remaining needles were dried at 60^{O} C and analyzed for nitrogen concentration. Peak, stand level, all-sided LAI was calculated by multiplying the mass of estimated foliar biomass by SLA for each plot. Peak projected LAI (leaf area index) was estimated by dividing all-sided LAI by 3.14. Measurements from estimated foliar biomass were combined with nitrogen (N) concentrations to estimate and canopy N content. Since live needles were not collected each year, plot-level average values of SLA and foliar N concentrations were used in calculating LAI and canopy N content for the 13^{th} and 15^{th} growing season. The SLA and N concentration values for the 16^{th} growing season were used to calculate 17^{th} growing season LAI and canopy N content.

Intercepted photosynthetically active radiation (IPAR) was measured for each plot using the SunScan Canopy Analysis System (Delta-T Devices Ltd. Cambridge, UK). Measurements were taken around solar noon in July or August of each growing season to capture maximum sun angle and peak leaf area. Approximately 200 individual IPAR measurements were taken beneath the canopy along four transects parallel to tree rows and five transects perpendicular to tree rows (Akers et al., 2013). All attempts were made to avoid measurements that were interfered with by vine or hardwood competition.

Efficiency Measurements

Growth efficiency calculations measurements were made for the 13^{th}-17^{th} growing season to determine the amount of stem volume growth per unit of crown measure. Growth efficiency measurements were calculated as a ratio of gross CAI per year (m^3) and the following crown attributes: foliar biomass (GE_{FOLBIO}), LAI (GE_{LAI}), canopy N content (NUE), IPAR (GE_{IPAR}).

Statistical Analysis

The study design was a split plot with culture as the main plot and planting density as subplots. Installations were treated as random factors since each installation is a sample of all possible locations. The interaction of installation x culture was also treated as a random factor. Analysis of variance using a mixed effects model was used to determine the significance of current and previous growing season rainfall on stand and crown attributes. Since measurements were made on the same three installations over a five year period, the resulting model is a mixed effects model with repeated measures. The model was used to determine the effects of rainfall on stand (gross CAI), crown (foliar biomass, LAI, canopy nitrogen, and IPAR) and growth efficiency attributes (GE_{LAI} , GE_{FOLBIO},NUE, GE_{IPAR}). Rainfall amounts were treated as continuous variables.

Results

Rainfall

Growing season rainfall varied by site and year but averaged 81 cm across all sites during the five-year period (Figure 3.1). The 30-year average growing season rainfall across the three sites was 91 cm (1981-2010). Growing season rainfall was markedly below the 30-year average during the first two years after thinning (13th and 14^{th} growing season) and closer to the long-term average during the 12^{th}, 15, 16^{th}, and 17^{th} growing seasons. Over the 5-year assessment period, rainfall was generally greater on Installation 3, intermediate on Installation 12, and least at Installation 11.

Stand Attributes

Mean gross CAI and precipitation are presented for each density regime over the 5-year period for intensive and operational culture in Figure 3.2. Gross CAI tended to be greater later than earlier in the evaluation period. Average growing season rainfall and gross CAI values were generally lowest during the 13th and 14th growing season. Gross CAI generally increased when growing season rainfall levels increased.

Previous year as well as current year growing season precipitation effects on gross CAI were significant (Table 3.4). Gross CAI, with both intensive and operational cultures, was significantly and linearly related to current growing season rainfall (Figure 3.3). Under operational culture, there were significant quadratic relationships between both current and previous growing season rainfall amounts and gross CAI (Figure 3.4). These quadratic relationships had r^2 values of 0.18 and 0.20 with current and previous growing season rainfall respectively, and were stronger than the linear trend ($r^2 < 0.1$). Maximum CAI on operational culture plots was associated with growing season rainfall in the 80 to 100 cm range.

The interaction for gross CAI with previous and current growing season rainfall was significant (Table 3.4). Greater CAI occurred with relatively high rainfall during both the previous and current growing season (Figure 3.2). During the 16th and 17th growing season when both previous and current growing season rainfall were above average, CAI values were 28 and 33 m^3 ha^{-1} yr^{-1}, respectively. In contrast, CAI was lower when either the previous or current year growing season rainfall or both were relatively low. Average CAI during the 13th, 14th, and 15th

growing seasons, when there was less than two consecutive growing seasons of high rainfall, was 20, 22, and 23 m^3 ha^{-1} yr^{-1}.

The interaction for gross CAI with current year growing season rainfall and both age and culture were significant. The current growing season rainfall with age interaction for CAI may be associated with the previous and current growing season rainfall interaction mentioned above. The current growing season rainfall and culture interaction reflects the different development patterns for the 2220 and 2960 trees ha^{-1} planting density-thinned plots; these density regimes exhibited relatively stable CAI during the relatively dry 13th and 14th and wet 15th growing season on the operational culture plots as compared to increasing CAI on the intensive plots (Figure 3.2).

Crown Attributes

Average foliar biomass levels were generally lowest during the 13th and 14th growing season which corresponded to the lowest average rainfall amounts (Figure 3.5). Values throughout the study period were greater for intensive than operational culture. When rainfall amounts returned to near long-term average amounts during the 15th growing season, values of foliar biomass began to increase.

Effects of current and previous growing season rainfall and their interaction were significant on foliar biomass (Table 3.4). Current and previous growing season rainfall showed weak or not significant linear correlations with foliar biomass (Figure 3.6). The linear relationship between foliar biomass and current growing season rainfall under operational culture was not significant, but there was a significant quadratic relationship (Figure 3.7). Foliar biomass increased as growing season rainfall increased from 50 to 90 cm; greater amounts of rainfall were associated with reduced foliar biomass.

The significance of the interaction indicates that the effects of previous and current growing season rainfall on foliar biomass were more than additive. Mean values of foliar biomass were the least (8,000 kg ha^{-1}) during the 14^{th} growing season when both previous and current growing season rainfall were below average. During the 13^{th} and 15^{th} growing seasons when either previous or current growing season rainfall was near or above average and the other was below average, mean values of foliar biomass was 8,500 and 9,100 kg ha^{-1}, respectively. Foliar biomass amounts tended to be the greatest when there were consecutive growing seasons of near or above average rainfall during the 16^{th} and 17^{th} growing season,. Mean values were 9,700 and 11,000 kg ha^{-1}, respectively.

The interaction for foliar biomass with current growing season rainfall and both age and culture were significant. The current growing season rainfall and age interaction may be associated with the previous and current growing season interaction mentioned above. The current growing season rainfall and culture interaction reflects a tendency for declines for intensive culture and increases for operational culture in foliar biomass during the 15^{th} through 17^{th} growing season.

SLA was significantly affected by age, density regime, and current growing season rainfall (Table 3.4). Average SLA was markedly lower (<10 m^2 kg^{-1}) for all density regime and cultures combinations at age 14 which corresponded with a 2-year period of below average growing season rainfall (Figure 3.8). After two years of above average rainfall, mean SLA values at age 16 increased to greater than 12 m^2 kg^{-1}.

Mean LAI declined from the 13^{th} to 14^{th} growing season and increased markedly during the remainder of the study period (Figure 3.9). LAI was not significantly affected by current or previous growing season rainfall or their interaction (Table 3.4). Current growing season rainfall showed a significant, positive linear relationship with LAI while the relationship with previous growing season rainfall was not significant (Figure 3.10). The linear relationship between LAI and current growing season rainfall was the strongest observed between any crown attribute and growing season rainfall (r^2 = 0.21 and 0.11 for intensive and operational culture, respectively). Under operational culture, LAI values appeared to follow a quadratic trend with current growing season rainfall (r^2=0.34) (Figure 3.7). Values of LAI increased as growing season rainfall increased from 50 to 90 cm; reduced LAI occurred with greater amounts of rainfall.

There were marked differences in canopy N content and IPAR patterns between the 740 tree ha^{-1} non-thinned planting density and the other density regimes (Figure 3.12 and Figure 3.13). The 740 trees ha^{-1} density regime started with high canopy N content and IPAR values and showed decline with time except for canopy N content with operational culture. Thinned density regimes increased canopy N content and IPAR with time from thinning. Previous growing season rainfall and the interaction of age and current growing season rainfall significantly affected canopy N content and IPAR (Table 3.4). Canopy N content and IPAR on thinned densities tended to be greater during the later portion of the assessment period which corresponded to higher rainfall in both the previous and current growing seasons.

Resource-use Efficiency

GE_{FOLBIO} and GE_{LAI} patterns with respect to density ranking were similar for each culture (Figure 3.14 and Figure 3.15). With operational culture, thinned densities consistently maintained a higher efficiency than the non-thinned density regime for GE_{FOLBIO}, GE_{LAI}, and NUE. With intensive culture thinned densities tended to have their lowest GE during the 13th growing season which corresponded with a high previous and low current growing season rainfall and the growing season after thinning.

GE_{FOLBIO} was significantly affected by current and previous growing season rainfall and their interaction (Table 3.4). Mean GE_{FOLBIO} tended to increase from the 13th to the 14th growing season, a period of below average growing season rainfall (Figure 3.14). GE_{FOLBIO} was greatest for each culture x density regime during the 16th growing season when there were two consecutive growing seasons with above average rainfall (Figure 3.14). GE_{FOLBIO} for intensive culture 740, 2220, and 2960 trees ha^{-1} density regimes had relatively low growth efficiency during the 13th growing season the following a wet –dry sequence but increased markedly to the highest values for the 14th growing season. GE_{FOLBIO} for operational culture was relatively stable during the 13th to 15th growing season then increased markedly during the 16th growing season. GE_{FOLBIO} consistently increased for each density regime and cultural intensity during the 16th growing season and decreased during the 17th growing season.

There was also a significant three-way interaction for GE_{FOLBIO} with current growing season rainfall, density regime and culture (Table 3.4).

During the 13th to 15th growing season period, GE_{FOLBIO} on the 740 trees ha^{-1} non-thinned intensive plots increased as compared with stable GE_{FOLBIO} on operational non-thinned densities. In contrast, during the same time period the GE_{FOLBIO} on the 2,220 and 2,960 tree ha^{-1}thinned stands increased markedly with intensive culture and was relatively stable with operational culture.

Current and previous growing season rainfall effects and their interaction on GE_{LAI} were significant (Table 3.4). GE_{LAI} was especially low with intensive culture during the 13th growing season compared to moderately high efficiency levels for operational culture (Figure 3.15). GE_{LAI} with operational culture increased during the 14th growing season when growing season rainfall was the least then tended to decline thereafter when growing season rainfall was moderate to high. GE_{LAI} for each of the thinned densities was greater with operational culture than intensive culture during the 13^{th} and 14^{th} growing season. GE_{LAI} with each culture was greatest when there were two consecutive growing seasons of below average rainfall. During the 15^{th}-17^{th} growing seasons GE_{LAI} for thinned densities was similar between cultures.

Current and previous growing season rainfall effects and their interaction on NUE were significant (Table 3.4). With intensive culture, NUE tended to be relatively high when there were two consecutive growing seasons with above average growing season rainfall (Figure 3.16). NUE was similar for the different cultures (0.15-0.25) for most of the assessment period except during the 13^{th} growing season when intensive culture NUE was markedly lower. NUE declined from the 16^{th} to 17^{th} growing season for most culture density combinations.

There was also a significant three-way interaction for NUE with current growing season rainfall, density regime and culture (Table 3.4). From the 14^{th} and 15^{th} growing season when there was an increase in growing season rainfall, NUE for the intensive culture 740 trees ha^{-1} non-thinned plots decreased while the 2220 trees ha^{-1} thinned plots increased. During the same time period the operational culture 740 trees ha^{-1} non-thinned plots and 1480 trees ha^{-1} thinned plots remained stable.

Current and previous growing season rainfall effects and their interaction GE_{IPAR} were significant (Table 3.4). GE_{IPAR} in thinned stands generally increased from the 13^{th} to 17^{th} growing seasons and, with intensive culture, was highest when there were two consecutive growing seasons with near long-term average rainfall (Figure 3.17). High levels of current growing season rainfall during the 15^{th} and 16^{th} growing seasons were associated with higher GE_{IPAR} values for intensive than operational culture.

Linear relationships between growing season rainfall and GE_{FOLBIO}, GE_{LAI}, NUE, and GE_{IPAR} were not significant under operational or intensive culture (Figure 3.18, Figure 3.19, Figure 3.20 and Figure 3.21, respectively). However, under operational culture, some relationships were significantly quadratic. Values of GE_{FOLBIO}, GE_{LAI}, and NUE decreased with increasing rainfall up to ~80 cm of growing season precipitation and then increased.

Discussion

In this study growing season precipitation is reported. Growing season precipitation may not directly reflect the amount of soil water available to the trees. Plant available water is influenced by soil physical properties, specifically textural class and rooting depth. The three sites had soil texture classes (Table 3.1) ranging from loamy sand to fine sandy loam, and may have different levels of plant available water. It is important to recognize that this factor may have a greater impact on loblolly pine growth than the actual amount of precipitation.

During the study period, thinned stands were responding to thinning treatment in addition to growing season rainfall amounts. Apparent trends with rainfall may be also associated with stand development after thinning. Thinning response may be delayed or accelerated depending on amount and time from thinning of growing season precipitation. Thinning increases individual tree water availability, but increased light interception by the lower crown increases transpiration (Teskey et al., 1987). Non-thinned stands are independent of the thinning effect and may respond to varying levels of growing season precipitation differently than that of recently thinned stands due to higher stand density and intraspecific crown competition slowing stand growth.

Stand Attributes

The results partially support the first hypothesis regarding the significant effects of growing season precipitation on gross current annual increment. Gross CAI was significantly affected by previous and current growing season rainfall amounts and their interaction. The interaction of rainfall and density was not significant while the interaction of rainfall and cultural intensity was significant. This indicates that the effects of current growing season rainfall amount is the same across all densities and is different under the different cultures. The interaction with cultural intensity where CAI was stable for operational cultural but increasing for intensive culture during the 13th -15th growing season period is expected since the two cultures provide different levels of soil resources whereas all density regimes provide adequate growing space per tree and are growing in non-density limiting conditions. These results contrast with results reported by Samuelson et al. (2014) of a lack of interaction between throughfall reduction and fertilization treatment during two consecutive years in which a drought was detected in the first year. A lack of interaction between irrigation and fertilization treament on above ground biomass was also reported by Samuelson et al. (2008) in a 4-year-old loblolly pine.

Crown Attributes

The second hypothesis tested that crown attributes would be affected by rainfall and the effect would be independent of management was partially supported. All crown attributes except LAI were impacted by previous and/or current growing season rainfall (Table 3.4). The only crown attribute that was significantly affected by the interaction of rainfall and culture was foliar biomass production. In a study by Samuelson et al. (2014), a 30% throughfall exclusion treatment and fertilization treatment produced somewhat similar contrasting resource conditions to those in this study (varying precipitation and two different cultures). They reported that the fertilization effect on crown and physiological attributes was independent of throughfall reduction treatment. The general lack of strong linear relationships between growing season rainfall amounts and gross volume CAI (Figure 3.3), foliar biomass (Figure 3.6) and LAI (Figure 3.10) indicates that factors other than growing season rainfall also strongly affected these stand and crown attributes.

The amount of foliar biomass produced is a function of current and previous year growing season rainfall and their interaction. Effects of current growing season rainfall are different for a given amount of previous growing season rainfall. Values of mean foliar biomass were lowest during growing seasons when there were below average previous and/or current year growing season rainfall. Mean foliar biomass was highest when there were two or more consecutive growing seasons with above average rainfall. Foliar biomass is impacted more by consecutive growing seasons of adequate rainfall than by one growing season of adequate rainfall.

The significant interaction of current season rainfall and cultural intensity on foliar biomass indicates that the effects were not additive. That is, the two management intensities examined responded differently to a given level of current growing season rainfall. With operational culture, rainfall amounts above the 30-year average resulted in increased foliar biomass amounts for each of the thinned densities. With intensive culture, foliar biomass amounts declined from the 15th to 16th growing season even though rainfall amounts during the 16th growing season were above average. This result is consistent with that of Tang et al. (2004) who reported that nutrient additons, throughfall exclusion and their interaction significantly affected foliage biomass production ($p<0.1$). They found that the interactions between water availability and nutrient additions were more than additive. In the normal throughfall treatment, fertilization produced 26% more foliage compared to normal throughfall-nonfertilized. In the throughfall exclusion treatment, fertilization only increased foliage production by 15%.

LAI was not significantly affected by previous or current growing season rainfall or the interaction of current growing season rainfall with cultural intensity or density (Table 3.4). Albaugh et al. (1998) similarly reported no significant effect of irrigation or irrigation x fertilization on peak LAI in 8 to 11 year old loblolly pine stands. However, Samuelson et al. (2008) reported a significant fertilization x irrigation interaction on LAI indicating that the effect of fertilization on LAI was dependent on irrigation levels and the effects of fertilization and irrigation are less than additive. The study by Samuelson was conducted in 4-year-old loblolly pine. These results combined with the current study suggest that the interaction between water relations and nutrient availability on LAI in loblolly pine may diminish with age.

Even though the model did not indicate a significant effect, average LAI was lowest across both cultures and all densities during the two growing seasons with the lowest rainfall (Figure 3.9). When rainfall amounts returned to near the long term average during and after the 15th growing season, LAI levels steadily increased. These results are consistant with findings from Hennessey et al. (2004) on a long-term loblolly pine thinning study in eastern Oklahoma who noted that LAI is sensitive to drought conditions. They reported a 1.5 to 1.7 unit decrease in LAI during two drought periods which occurred at age 12 and age 19. In the present study, it is unkown what LAI levels were prior to the low rainfall condition during the 13th growing season, but decreases in LAI from the 13th (first dry growing season) to the 14th (second dry growing season) growing season ranged from 0.5 to 0.9 units (Figure 3.9). In both the Hennessey et al. (2004) and current studies, LAI did not reach maximum values the year after the drought period. LAI continued to increase during several years with sufficient rainfall.

Specific leaf area was only measured at age 12, 14, and 16. SLA at age 13, 15 and 17 were estimated using the measured plot-level values. Even though the model indicated density regime as a significant effect on SLA, there is no apparent trend consistant across age. Culture was not significant indicating that the increased soil resources in the intensive regime did not impact SLA. Leaf morphology appears to be strongly impacted by available water and less by growing space or soil resource. Values of SLA in this study are consistant with Shelton (1984) who reported mean SLA values of 8.9 to 14.4 $m^2\,kg^{-1}$ for loblolly pine fascicles of various ages in different aged stands. Contrary to this study, Zutter (1986) reported greater mean SLA values of 12.7 to 18.6 $m^2\,kg^{-1}$ in 2-year-old loblolly pine seedlings.

Resource-use Efficiency

The results indicate that current and previous growing season rainfall significantly affected GE signifying that the ability of mid-rotation loblolly pine stands to accrue stem volume per unit of foliar biomass, LAI, canopy N content and IPAR is affected by growing season precipitation (Table 3.4).

High growth efficiency did not always correspond to high growth. GE_{LAI} in stands with operational culture was highest during the 14th growing season (Figure 3.15). However, these stands had their lowest LAI and productivity during the 14th growing season.

Crown attribute values were consistently higher in non-thinned than thinned densities. However, this did not always translate to higher growth rates in non-thinned stands in part because growth efficiency tended to be greater in thinned stands. For example, growth efficiency on operational culture stands was less on thinned than non-thinned stands during the 14th growing season when previous growing season rainfall was low and current growing season rainfall was high.

Patterns of GE_{FOLBIO}, NUE and GE_{IPAR} for thinned and non-thinned densities with intensive culture followed same pattern as CAI (Figure 3.2, Figure 3.14, Figure 3.16 and Figure 3.17). Growth efficiency and CAI in thinned stands generally increased from the 13th to 16th growing season then remained constant during the 17th growing season. This pattern suggests that the respective crown attributes in these intensive culture stands are less influential in stand productivity than growth efficiency.

For operational culture, thinned stands maintained a greater GE_{FOLBIO}. GE_{LAI}, and NUE than non-thinned stands. The respective crown attribute values were consistently and markedly higher in non-thinned stands than thinned stands while gross CAI in non-thinned stands was only marginally greater or less than that in thinned stands.

GE_{LAI} in thinned stands with intensive culture was consistent for the 14th to 17th growing seasons even though gross CAI and LAI were continually changing. This suggest that in these stands growth efficiency is relatively stable and stand level growth is directly related to LAI. Even though LAI decreased from the 13th to the 14th growing season following patterns of decreased growing season rainfall (Figure 3.9), gross CAI was maintained or increased for all culture density combinations as a result of increased growth efficiency.

The lack of significant linear trends between growth efficiency attributes and current or previous growing season rainfall indicates that volume CAI per unit of foliar biomass, LAI, canopy N content or IPAR during a given growing season is not strongly correlated to growing season rainfall. Other studies have reported correlations of precipitation deficits and decreased GE. Sword Sayer (2004) reported the lowest values of GE_{LAI} at ages 15 and 16 corresponded with the greatest growing season water deficits of the study period. Hennessey (2004) reported that GE_{LAI} increased after thinning from age 10 to 12 even though a growing season water deficit was present, but decreased from age 21 to age 23 across all density regimes during an extended drought.

Conclusions

The objective of this study was to identify the impacts of current and previous growing season rainfall on mid-rotation loblolly pine stand, crown and growth efficiency attributes under two different cultural intensities and four density regimes.

Growing season rainfall amount during the 13th and 14th growing seasons were less than the 30-year-average and 12th, 15th, 16th and 17th growing seasons rainfall approximated or were greater than the long-term average. Current and previous growing season rainfall effects and their interaction were significant for gross CAI, foliar biomass, and growth efficiency attributes. Gross CAI tended to be greatest for all density regime cultural intensity combinations during years in which there were two or more consecutive years with high growing season rainfall. Foliar biomass and specific leaf area were significantly affected by current growing season rainfall which lead to decreased LAI for all density regimes and cultural treatments during drier periods. Once growing season rainfall increased during the 15th growing season, LAI values increased leading to improved stand volume growth. Linear and quadratic relationships between growing season rainfall and growth efficiency were poor though model analysis indicated growing season rainfall as a significant growth efficiency factor. There were significant rainfall by cultural intensity on growth efficiency interactions suggesting that growth efficiency differs for varying levels of growing season rainfall amounts across a range of cultural intensities. Results indicate that growing season precipitation influences foliage production, needle morphology and light interception which are drivers of stand productivity.

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Tables and Figures

Table 3.1. Location, soil, physiographic province, and loblolly pine site index of three PMRC three culture x density installations.

Installation	Location	Coordinates	Soil Series	Soil Taxonomy	Soil Minerology	Physiographic Region	Precipitation Record Location	Average Growing Season Precipitation (cm)[1]	Site Index (m)[2]
3	Escambia Co., AL	-87.3154, 31.1954	Freemanville	Fine, kaolinitic, thermic plinthic kandiudults	Fine, sandy loam	Upper Coastal Palain	Evergreen and Mobile, AL	108	24.1
11	Greene Co., GA	-83.0278, 33.6235	Cecil	Fine, kaolinitic, thermic typic kanhapludults	Sandy loam	Piemont	Athens and Augusta, GA	76	25.0
12	Barbour Co., AL	-85.6735, 31.7467	Orangeburg	Fine-loamy, kaolinitic, thermic kandiudult	Loamy sand	Upper Coastal Palain	Troy, AL	88	26.2

1. 30 year average growing season precipitation, March 1st to October 31st, 1981-2010
2. Site index base age 25 on the 1480 trees ha^{-1} thinned density with operational culture
*Soils information from the USDA- NRCS Soil Survey; Adapted from Johnson et al. (2013)

Table 3.2. Details of cultural activities implemented each installation of the PMRC culture x density study.

Treatment	Growing Season	**Operational Culture**	**Intensive Culture**
Site preparation		Broadcast Chemical and Mechnical	Broadcast Chemical and Mechnical
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	
	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
	14^{th}		224 kg ha^{-1} N + 28 kg ha^{-1} P
	16^{th}	224 kg ha^{-1} N + 28 kg ha^{-1} P	224 kg ha^{-1} N + 28 kg ha^{-1} P
Interspecific competition control	1st	280 g ha^{-1} sulfometuron-methyl, banded + glyphosate and triclopyr direct spraying	280 g ha^{-1} sulfometuron-methyl, broadcast + glyphosate and triclopyr direct spraying
	2nd - 17th		841 g ha^{-1} imazapyr broadcast Glyphosate and triclopyr direct application

Table 3.3. Measurement and gross plot size by initial planting density at PMRC loblolly pine culture x density installations

Planting Density (trees ha^{-1})	Planting Spacing (m x m)	Gross Plot Size (ha)	Measurement Plot Size (ha)
740	3.66 x 3.66	0.227	0.105
1480	2.44 x 2.74	0.15	0.053
2220	2.44 x 1.83	0.125	0.046
2960	1.83 x 1.83	0.121	0.040

Table 3.4. P-values for the effects of age, culture, density, and current (A) and previous (B) growing season rainfall and their interactions on stand, crown, and growth efficiency attributes on three PMRC installations during the 13th through 17th growing seasons.

	Gross CAI	Foliar Biomass	SLA	LAI	Canopy N Content	IPAR	GE_{FOLBIO}	GE_{LAI}	NUE	GE_{IPAR}
Age	< 0.01	< 0.01	< 0.01	< 0.01	0.01	0.04	< 0.01	< 0.01	< 0.01	< 0.01
Culture	0.08	0.09	NS	NS	0.10	NS	NS	NS	NS	NS
Density	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	NS	< 0.01	< 0.01	NS
Culture*Age	< 0.01	< 0.01	NS	NS	0.03	0.01	< 0.01	< 0.01	< 0.01	< 0.01
Density*Age	< 0.01	< 0.01	NS	NS	< 0.01	< 0.01	NS	NS	NS	NS
RainfallA	< 0.01	< 0.01	0.01	NS	NS	NS	< 0.01	< 0.01	< 0.01	< 0.01
RainfallB	< 0.01	< 0.01	NS	NS	0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
Rainfall A * Rainfall B	0.02	0.02	NS	NS	NS	NS	< 0.01	< 0.01	< 0.01	0.03
Rainfall A * Age	< 0.01	< 0.01	NS	NS	0.09	0.01	< 0.01	< 0.01	< 0.01	0.02
Rainfall A * Culture	< 0.01	< 0.01	NS	NS	NS	NS	0.01	0.03	0.02	0.01
Rainfall A * Density	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
RainfallA * Density * Culture	NS	NS	NS	NS	NS	NS	<0.01	NS	< 0.01	NS

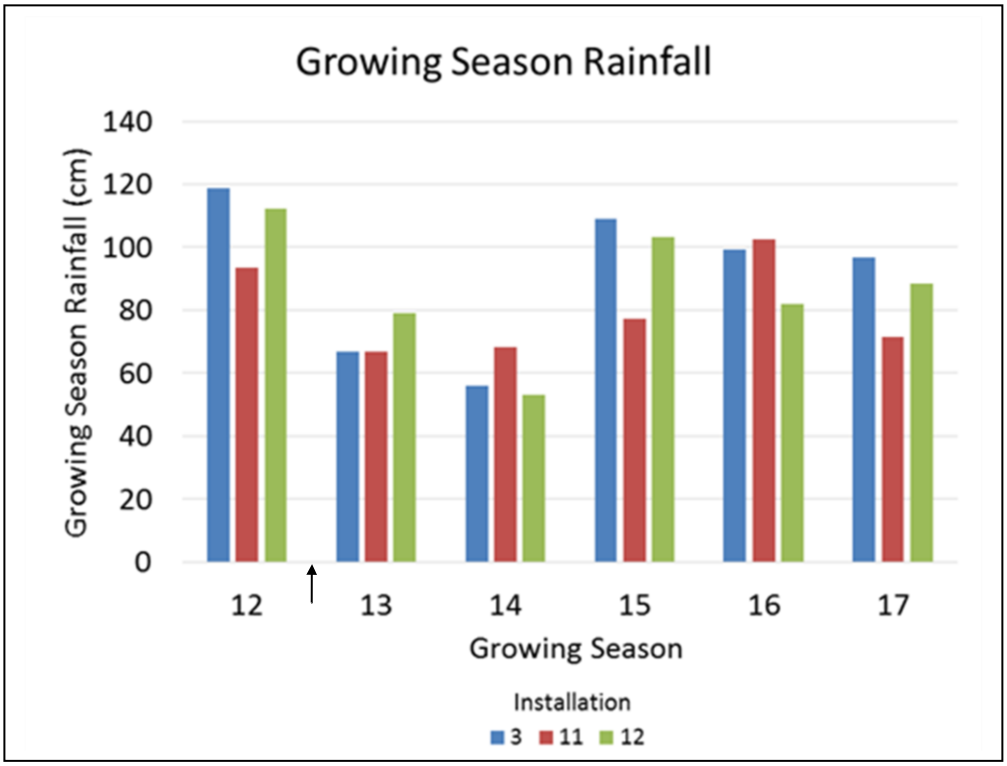

Figure 3.1. Growing season rainfall amounts by growing season and installation for three PMRC culture density installations. Growing season was defined as March 1st to October 31st. Arrow indicates time of thinning. The 30-year growing season average across all installation is 91 cm (1981-2010).

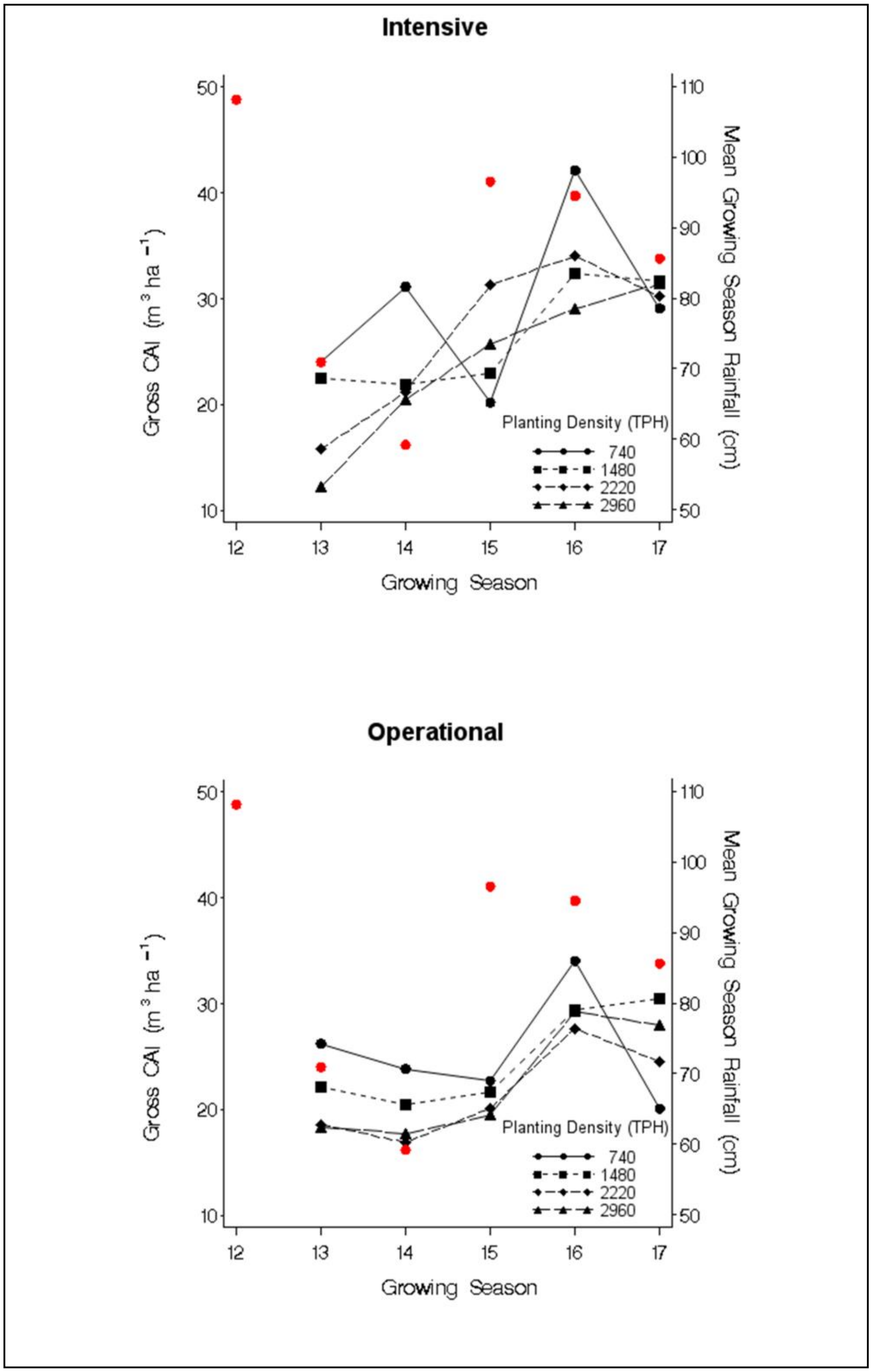

Figure 3.2. Average gross CAI of three installations by growing season and density for each culture in the PMRC culture x density study. Red dots dots indicate growing season rainfall amounts averaged over all three installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12. The 30-year average growing season rainfall amount is 91 cm.

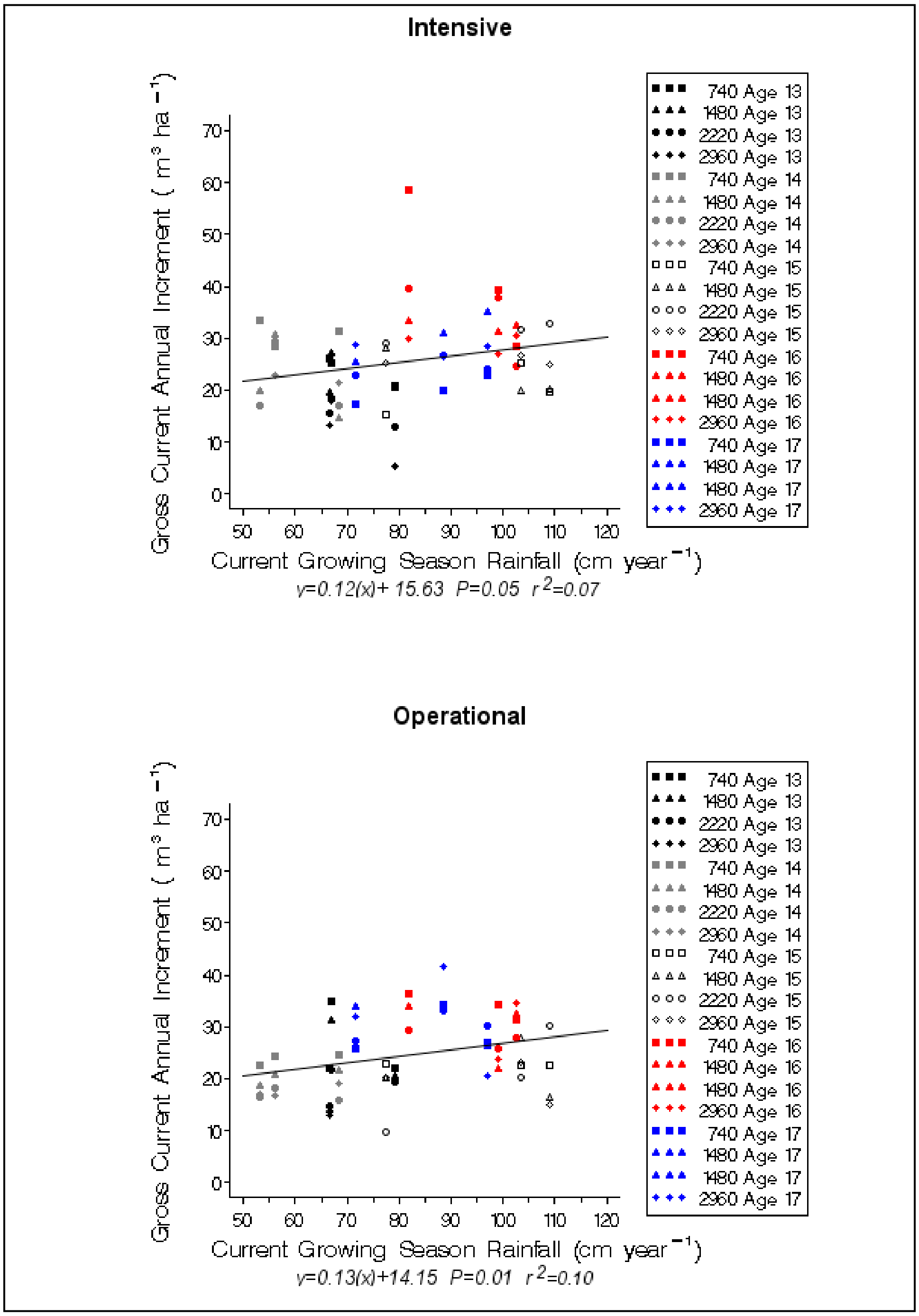

Figure 3.3. Linear relationship between gross volume current annual increment and current growing season rainfall for intensive and operational culture by density regime (trees ha^{-1}) and growing season and on three PMRC installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12.

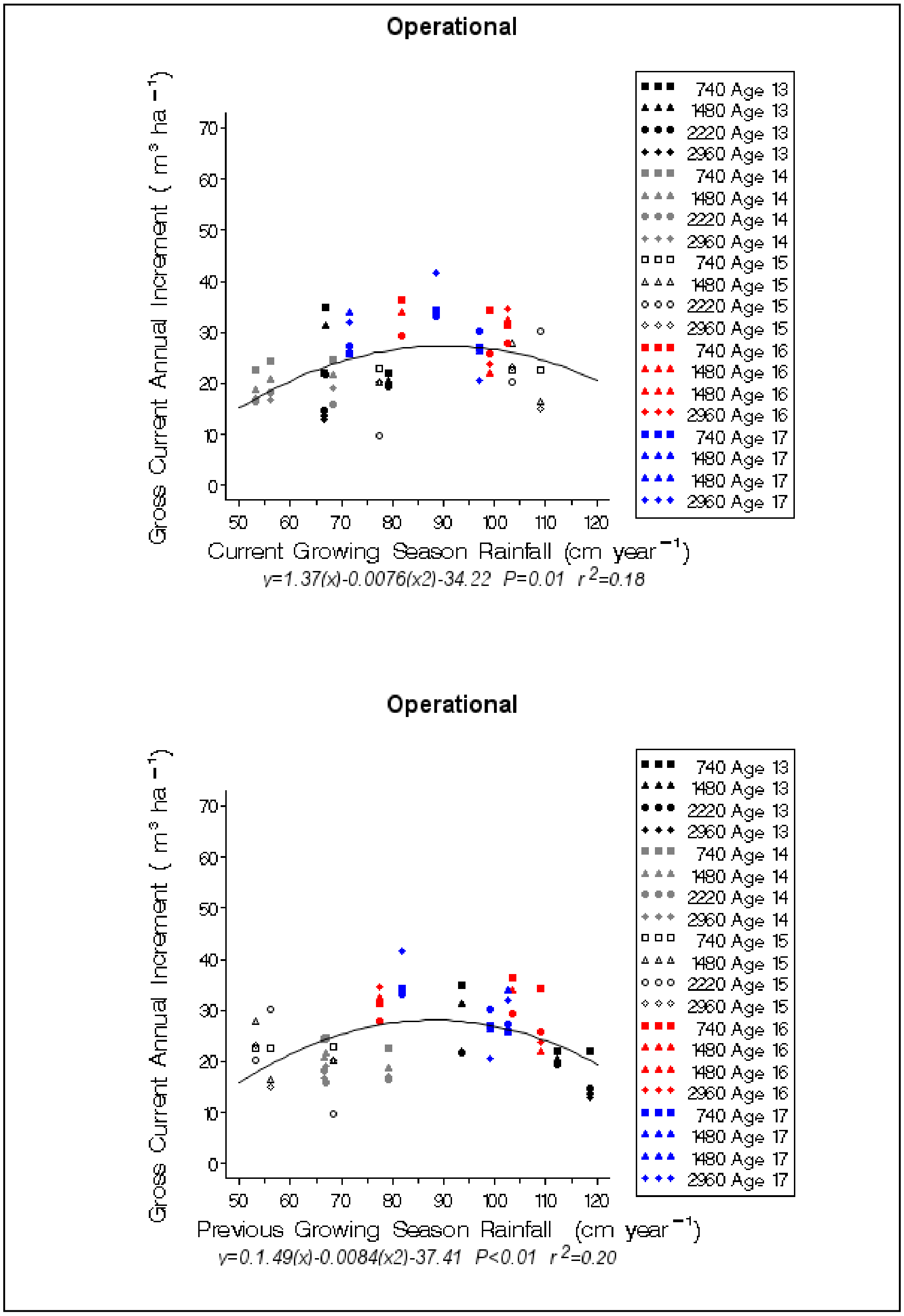

Figure 3.4. Quadratic relationship between gross current annual increment and current and previous growing season rainfall for operational culture by density regime (trees ha^{-1}) and growing season and on three PMRC installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12.

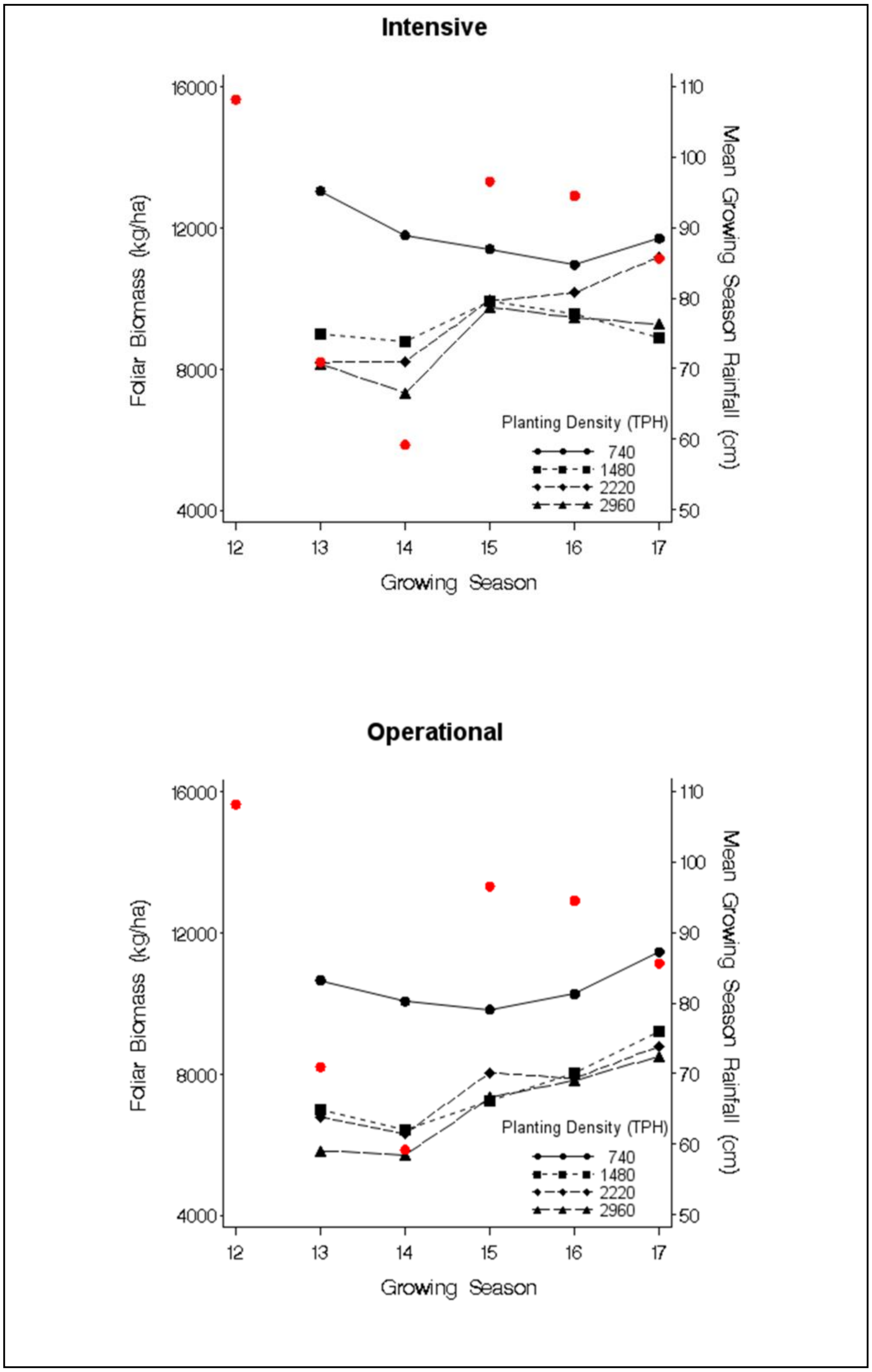

Figure 3.5. Average foliar biomass values for each culture by density and growing season for three PMRC installations. Values are means of three installations. Red dots indicate growing season rainfall amounts averaged over all three installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12.

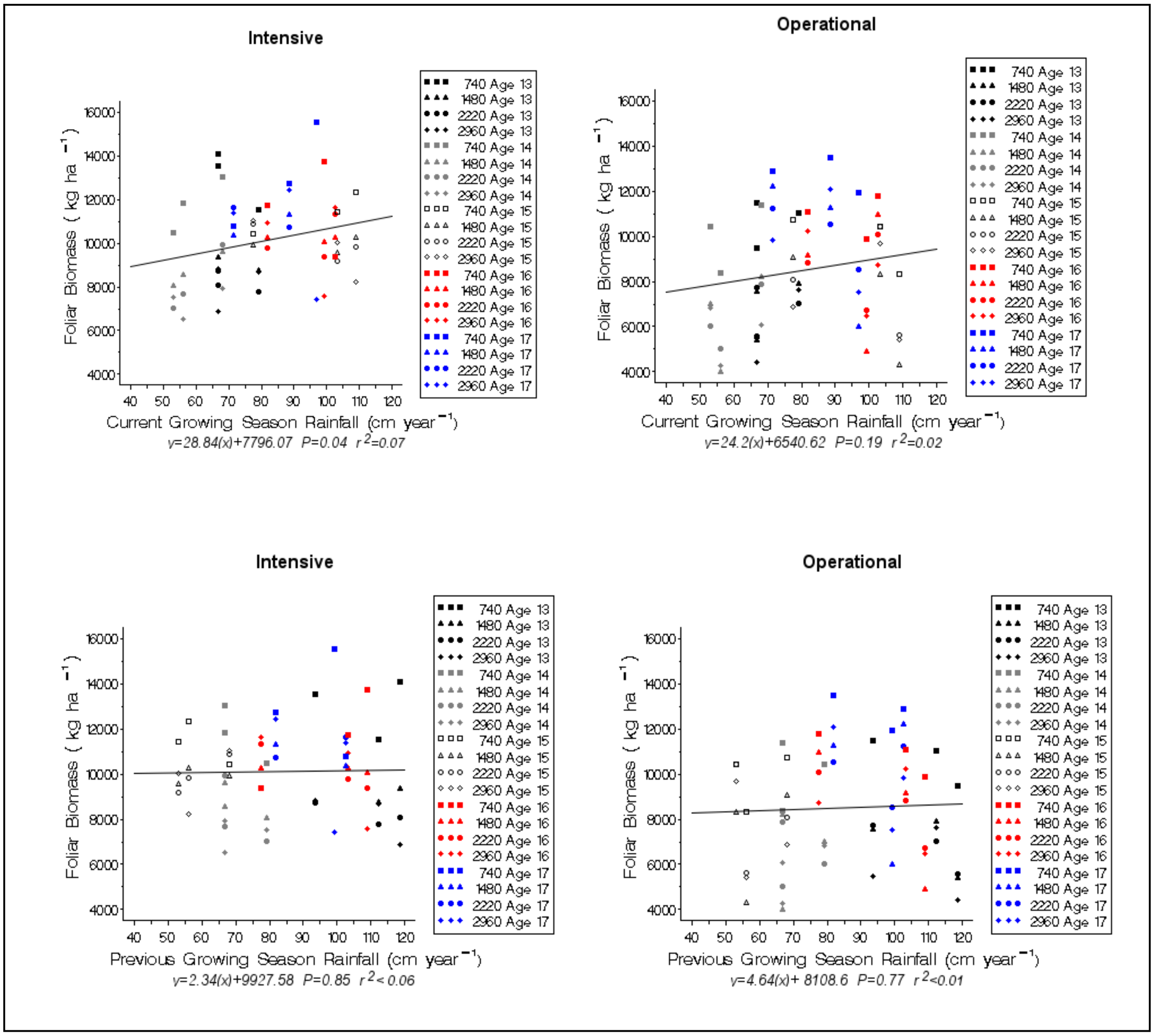

Figure 3.6. Linear relationship between estimated foliar biomass and current and previous growing season rainfall by growing season and density regime for intensive and operational culture on three PMRC installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12.

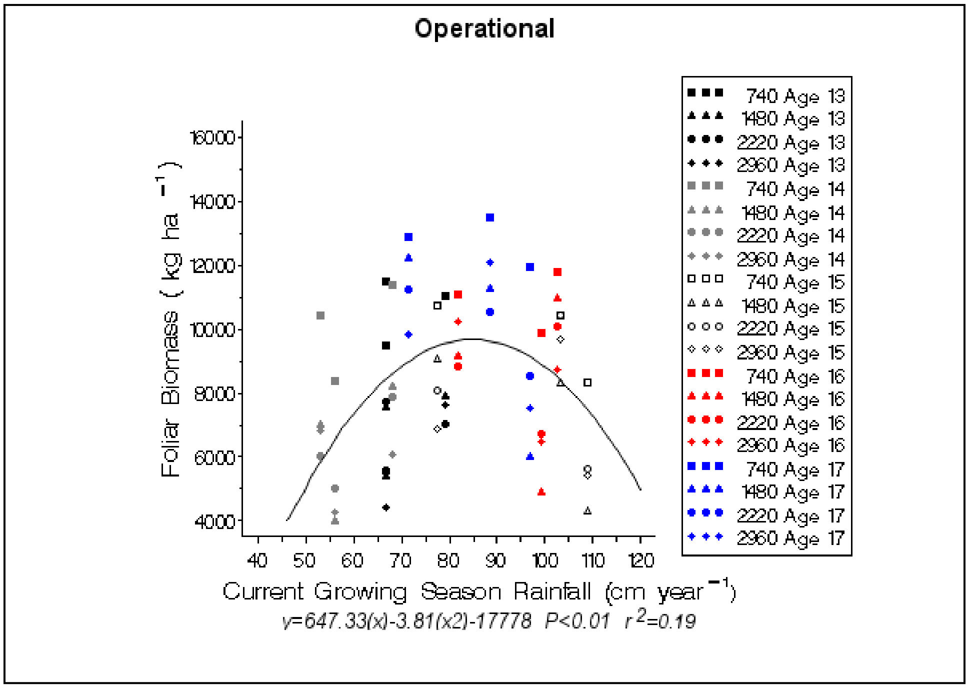

Figure 3.7. Quadratic relationship between foliar biomass and current growing season rainfall for operational culture by age and density regime (trees ha^{-1}) on three PMRC installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12.

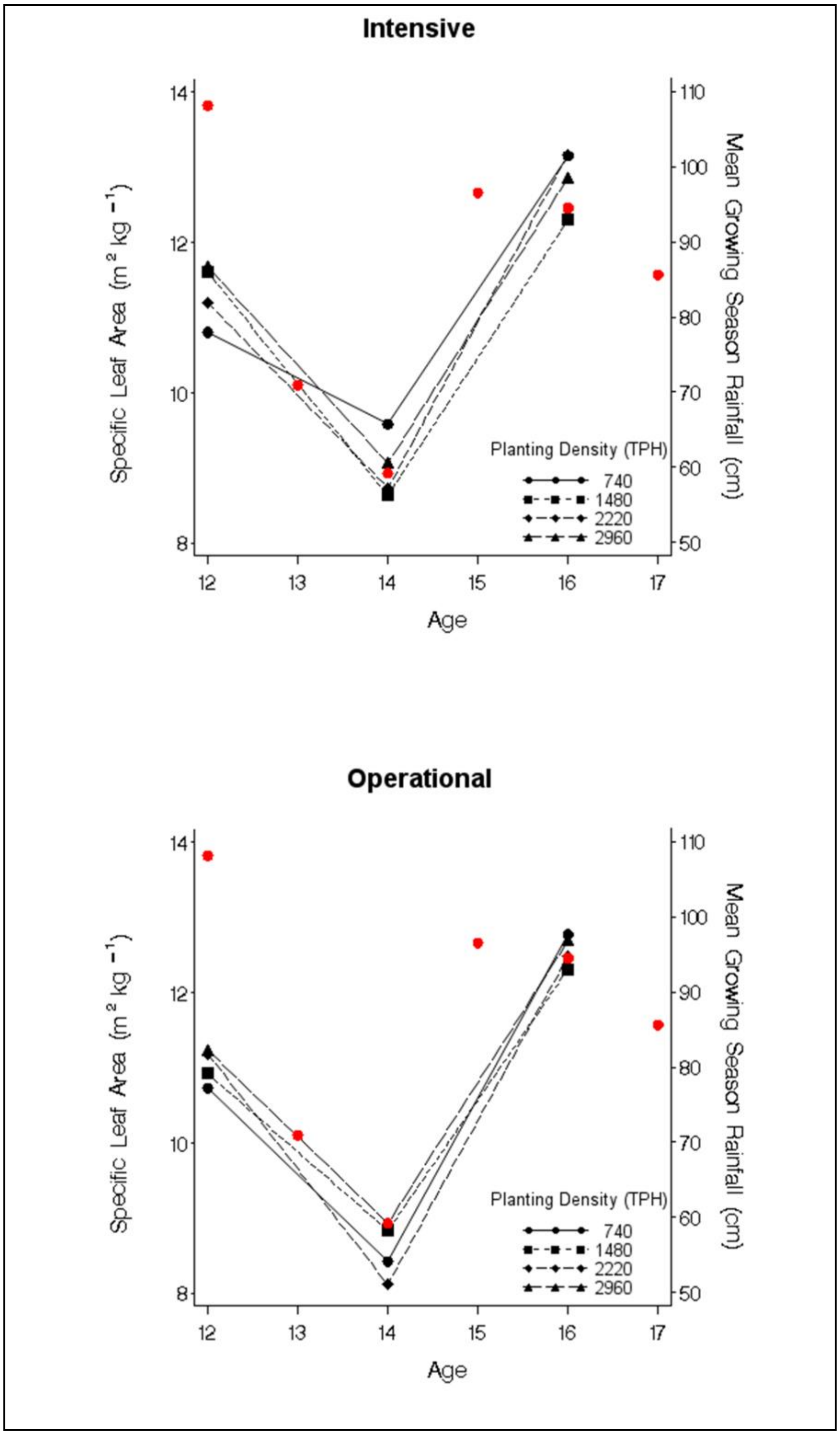

Figure 3.8. Average SLA values for each culture and age for three PMRC installations. Values are means of three installations. Red dots indicate growing season rainfall amounts over all three installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12.

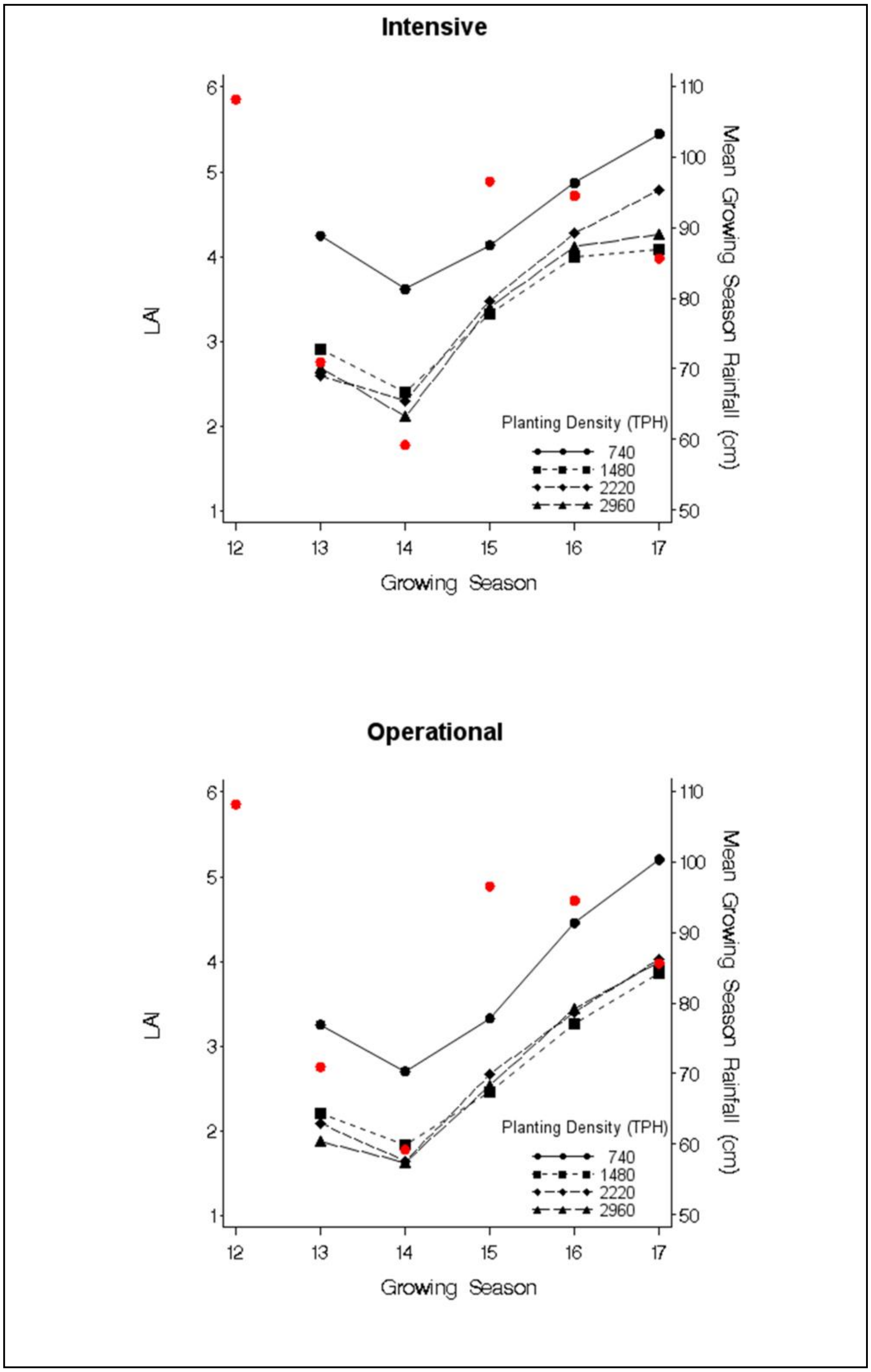

Figure 3.9. Average projected peak LAI values for each culture by density and growing season for three PMRC installations. Values are means of three installations. Red dots indicate growing season rainfall amounts averaged over all three installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12.

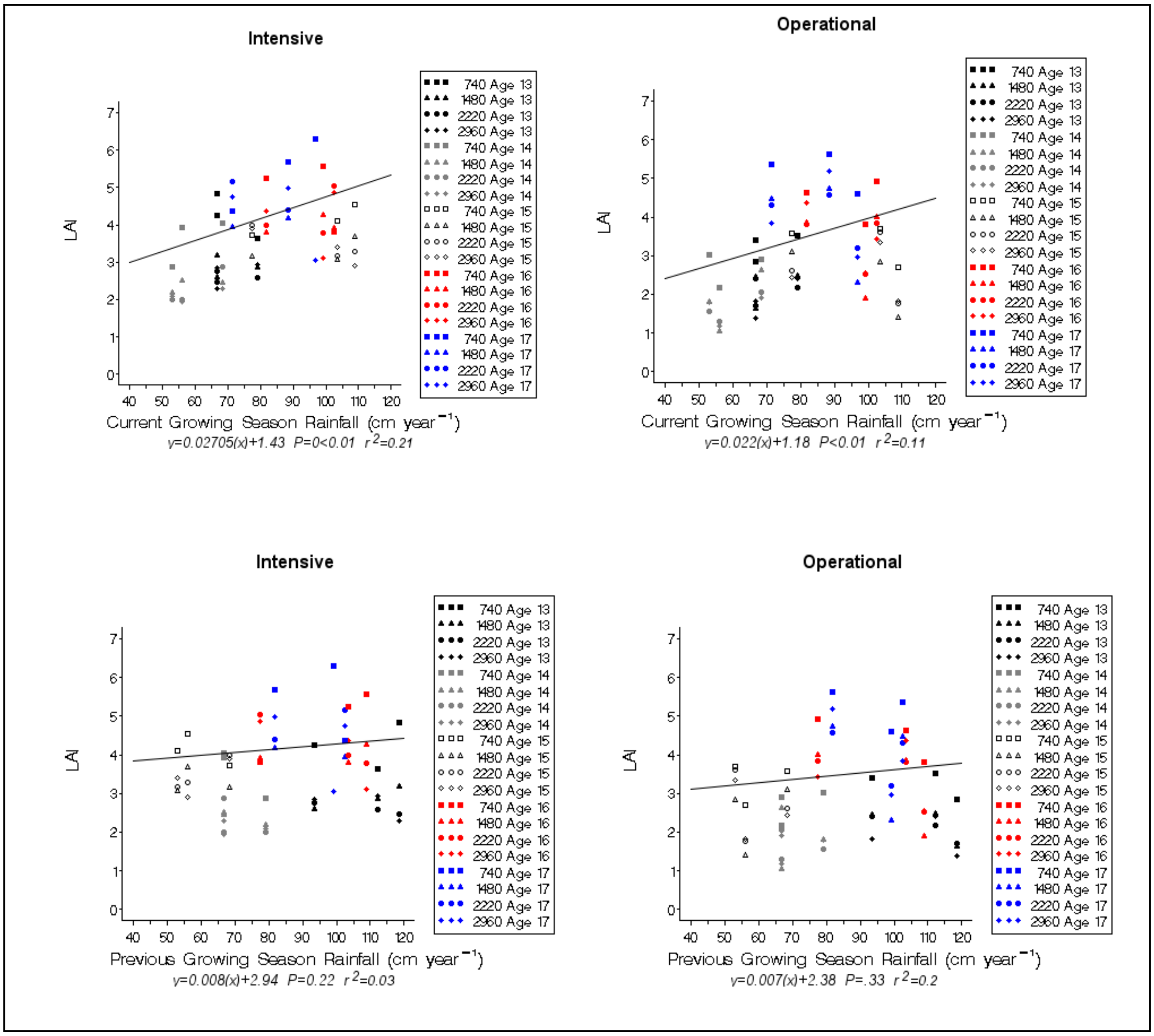

Figure 3.10. Linear relationship between peak LAI and current and previous growing season rainfall by growing season and density regime (trees ha^{-1}) for intensive and operational culture on three PMRC installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12.

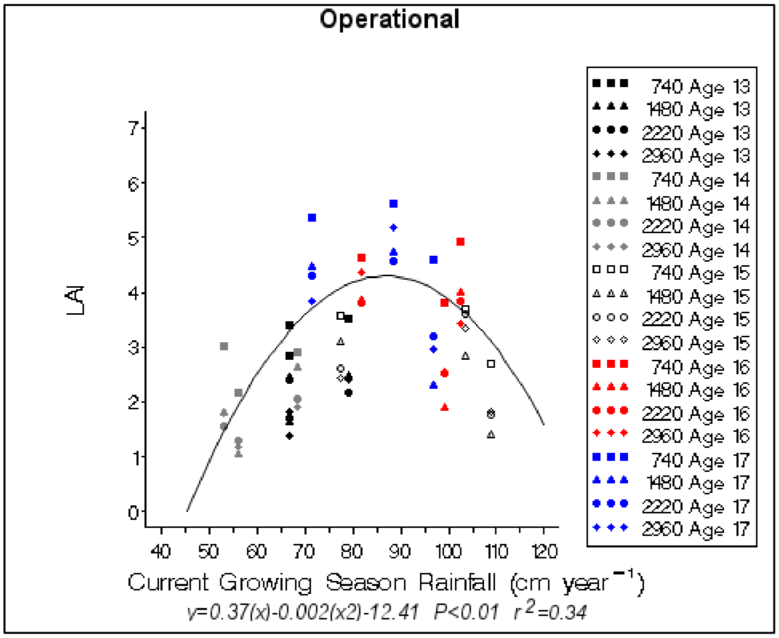

Figure 3.11 Quadratic relationship between LAI and current growing season rainfall for operational culture by age and density regime (trees ha^{-1}) on three PMRC installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12.

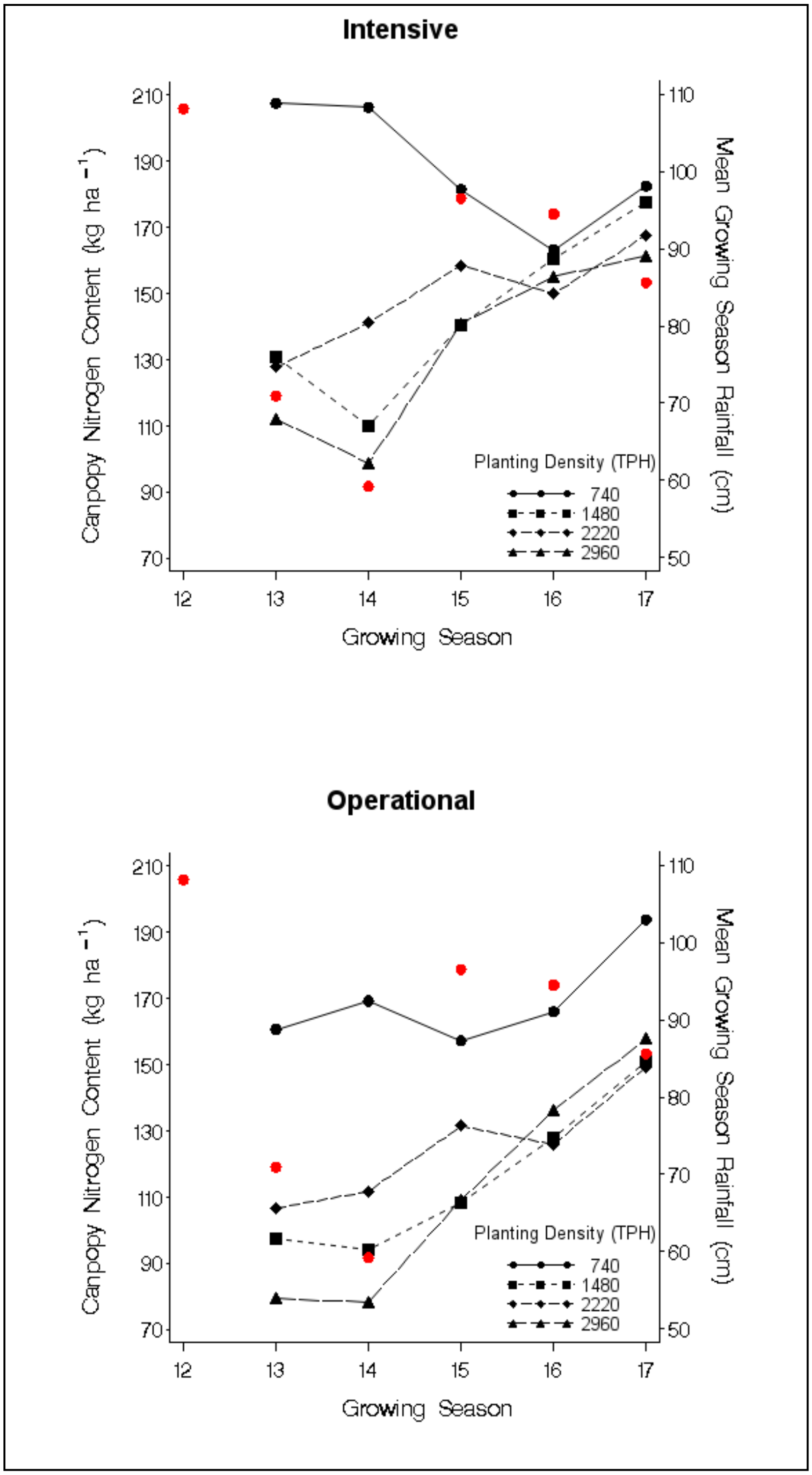

Figure 3.12. Canopy nitrogen content values for each culture and growing season for three PMRC installations. Values are means of three installations. Red dots indicate growing season rainfall amounts over all three installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12. Operational stands were fertilized at the beginning of the 12th and 14th growing seasons; intensive stands were fertilized before the 12th, 14th and 16th growing season.

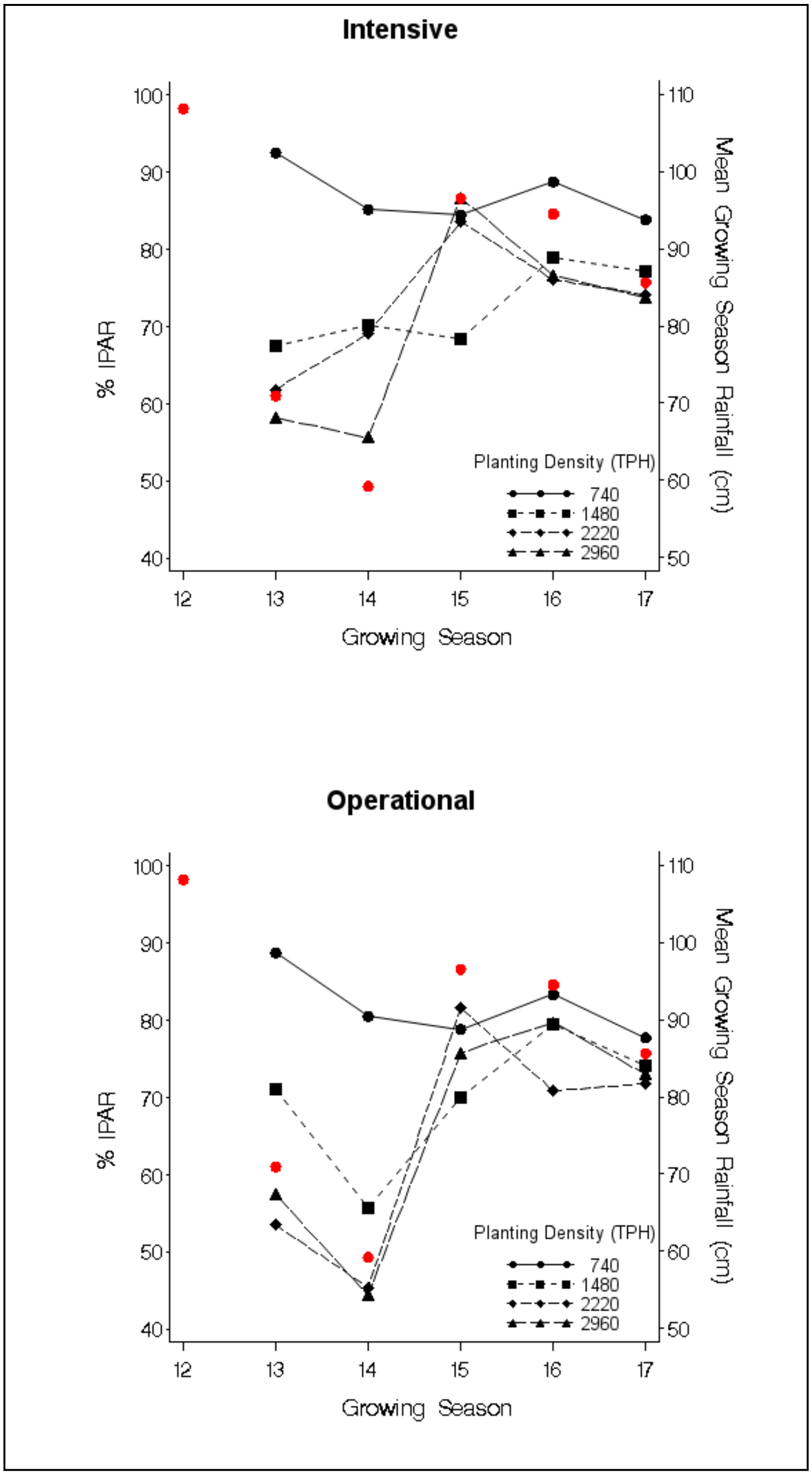

Figure 3.13. Percent IPAR values for each culture and growing season for three PMRC installations. Values are means of three installations. Red dots indicate growing season rainfall amounts over all three installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12.

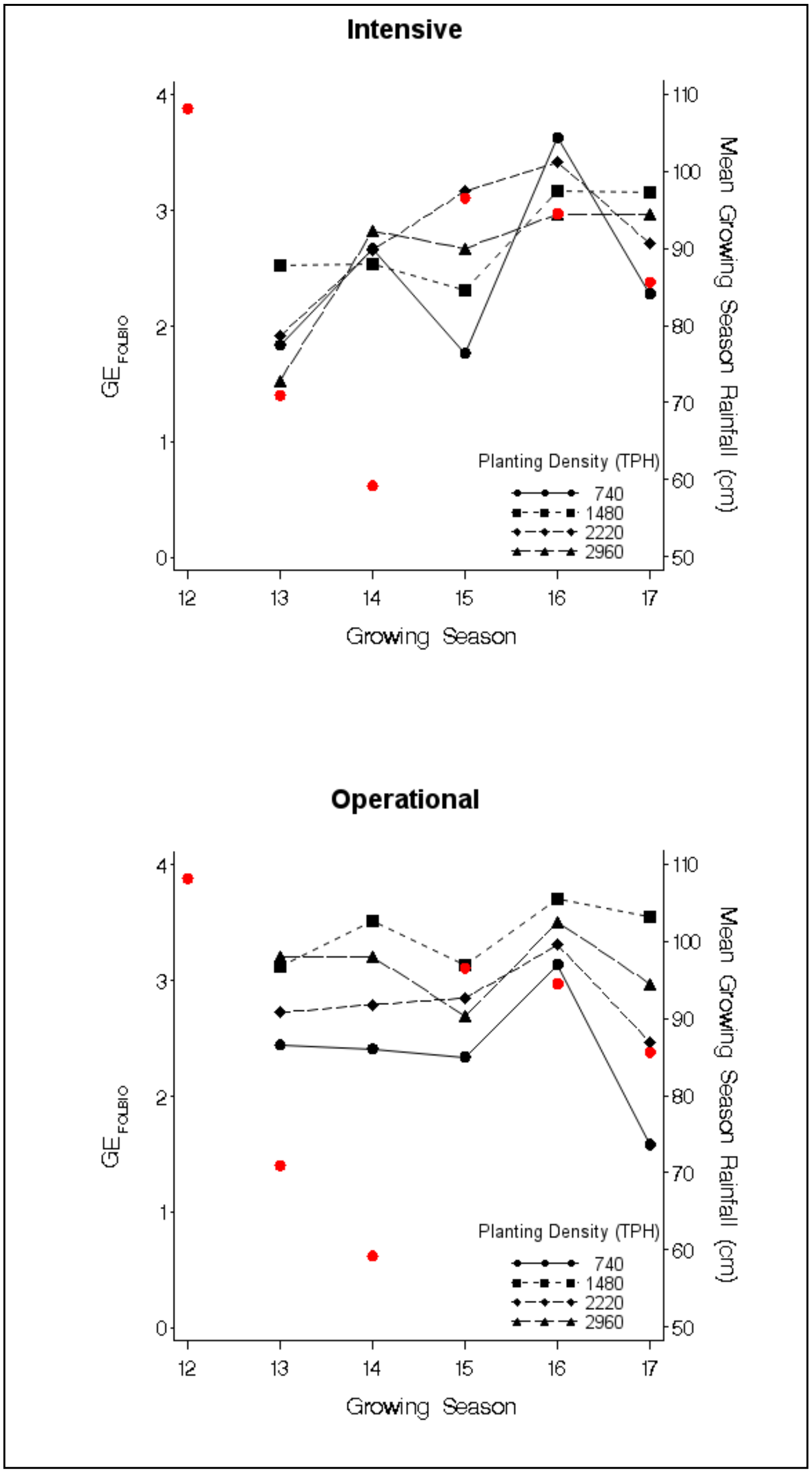

Figure 3.14. Foliar biomass growth efficiency values for each culture and growing season f or three PMRC installations. Values are means of three installations. Red dots indicate mean growing season rainfall amounts over all three installations. Planting densities of 1480, 2220, and 2960 trees ha^{-1} were thinned at age 12.

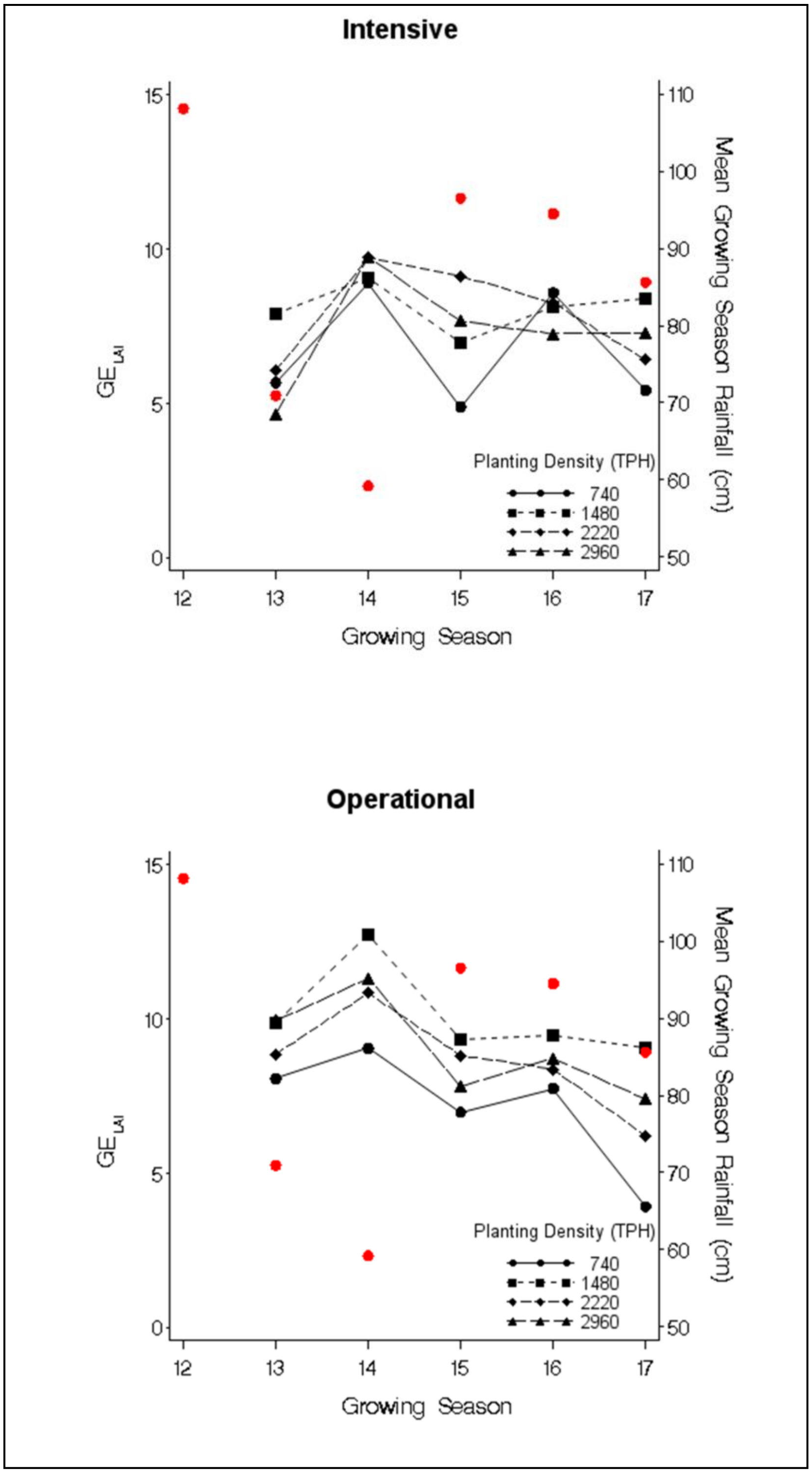

Figure 3.15. LAI growth efficiency values for each culture and growing season f or three PMRC installations. Values are means of three installations. Red dots indicate mean growing season rainfall amounts over all three installations. Planting densities of 1480, 2220, and 2960 trees ha^{-1} were thinned at age 12.

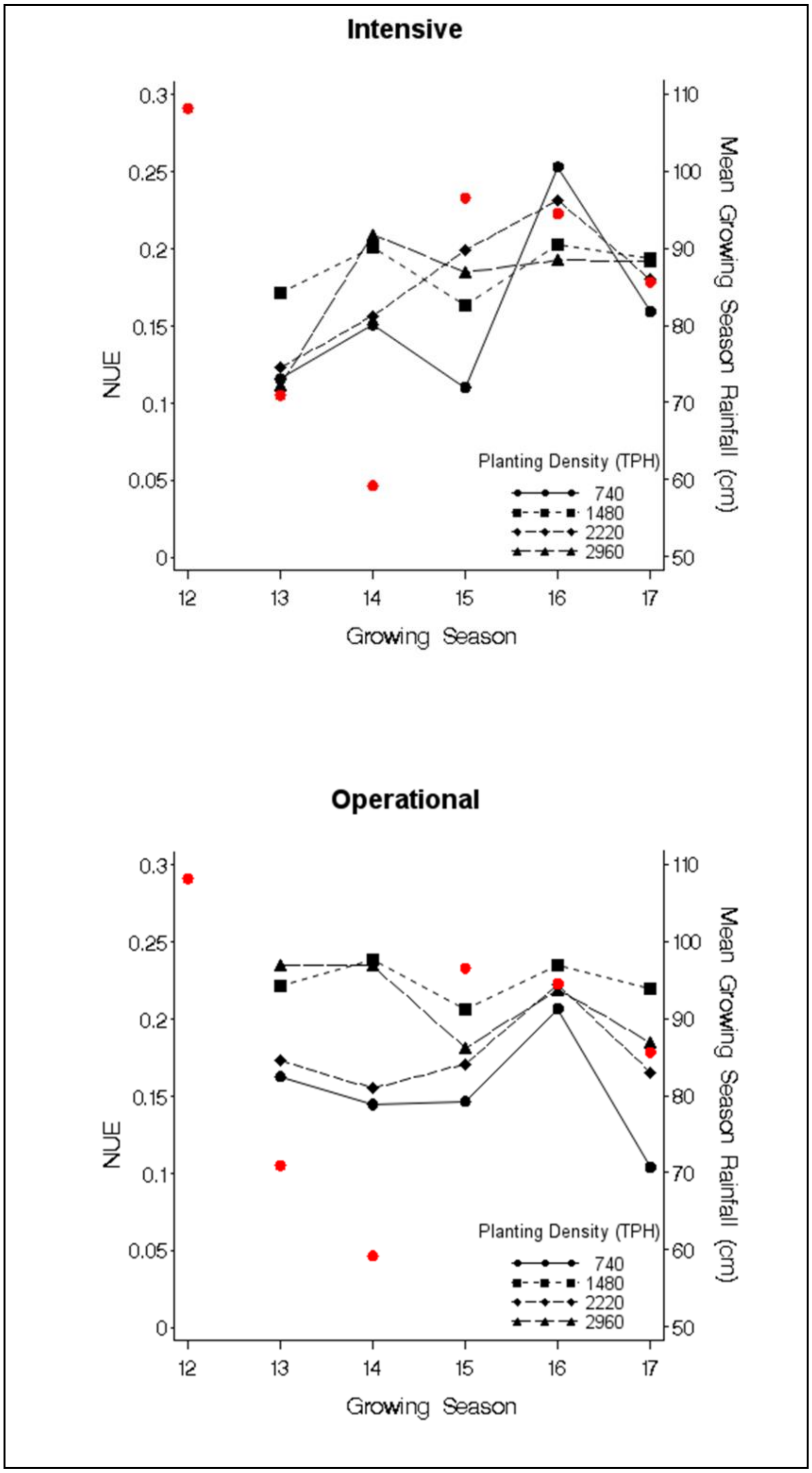

Figure 3.16. Nitrogen use efficiency values for each culture and growing season f or three PMRC installations. Values are means of three installations. Red dots indicate mean growing season rainfall amounts over all three installations. Planting densities of 1480, 2220, and 2960 trees ha^{-1} were thinned at age 12. Operational stands were fertilized at the beginning of the 12^{th} and 14^{th} growing seasons; intensive stands were fertilized before the 12^{th}, 14^{th} and 16^{th} growing season.

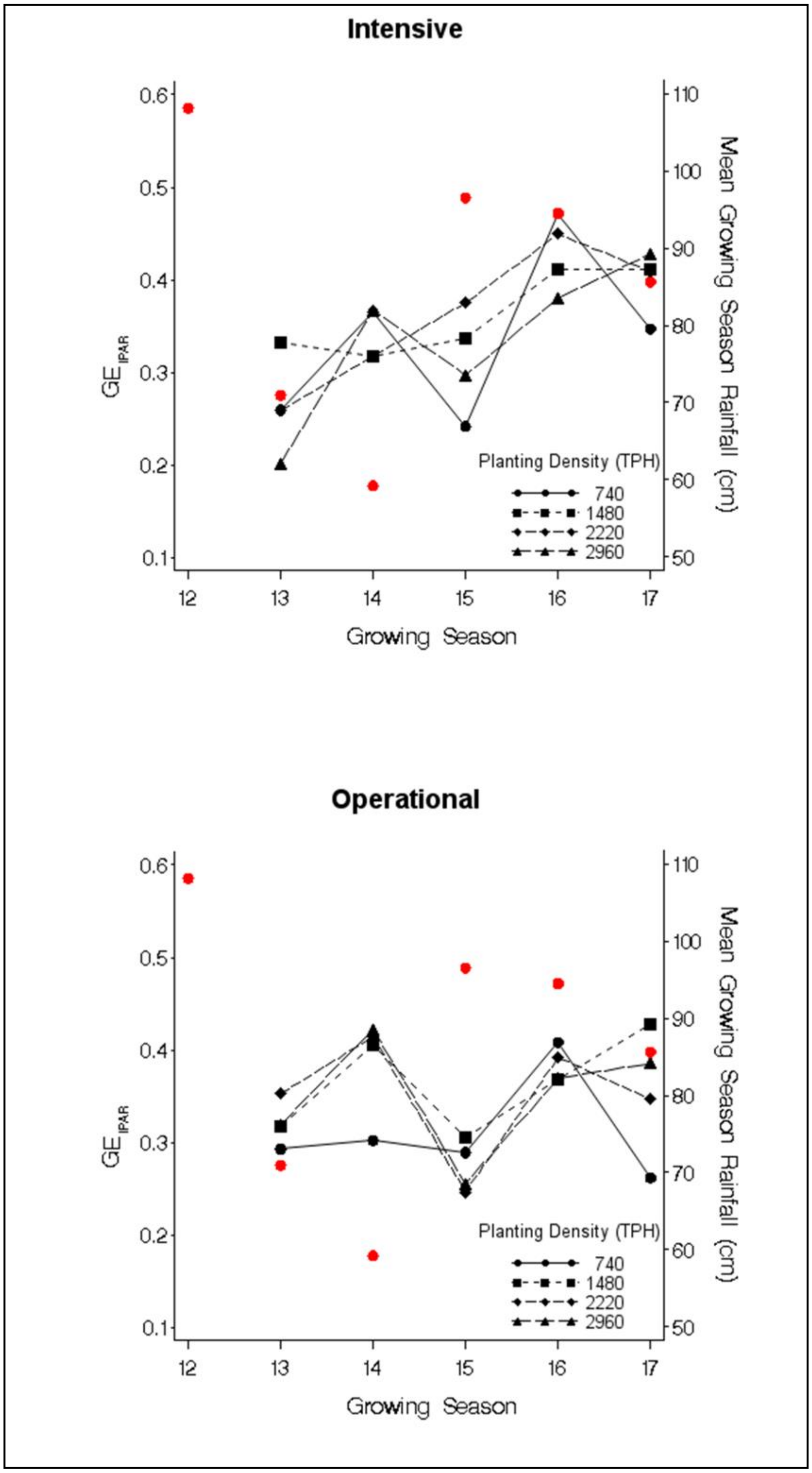

Figure 3.17. IPAR growth efficiency values for each culture and growing season f or three PMRC installations. Values are means of three installations. Red dots indicate mean growing season rainfall amounts over all three installations. Planting densities of 1480, 2220, and 2960 trees ha^{-1} were thinned at age 12.

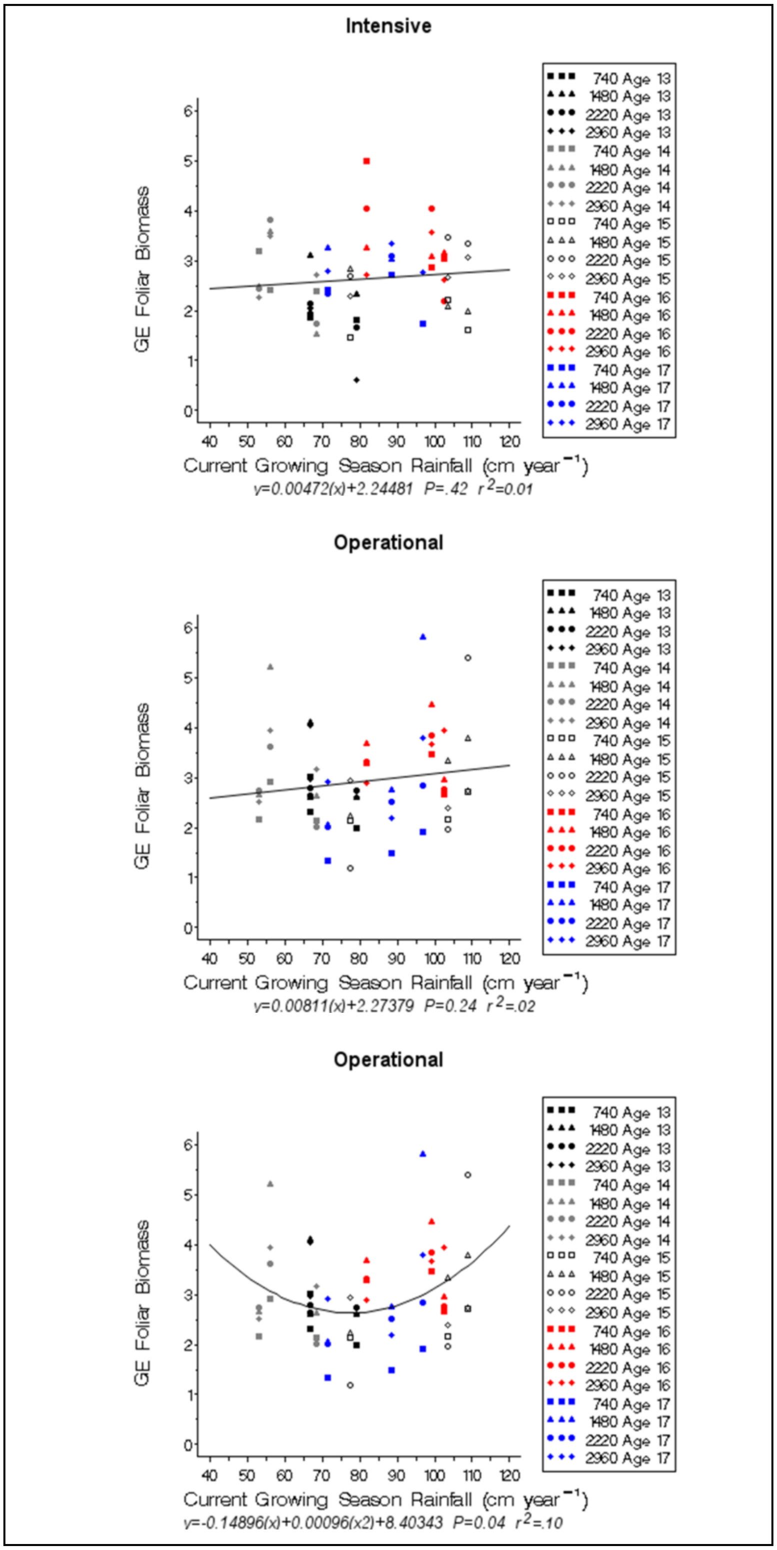

Figure 3.18. Linear and quadratic relationships between foliar biomass growth efficiency and current growing season precipitation at three PMRC culture x density study installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12.

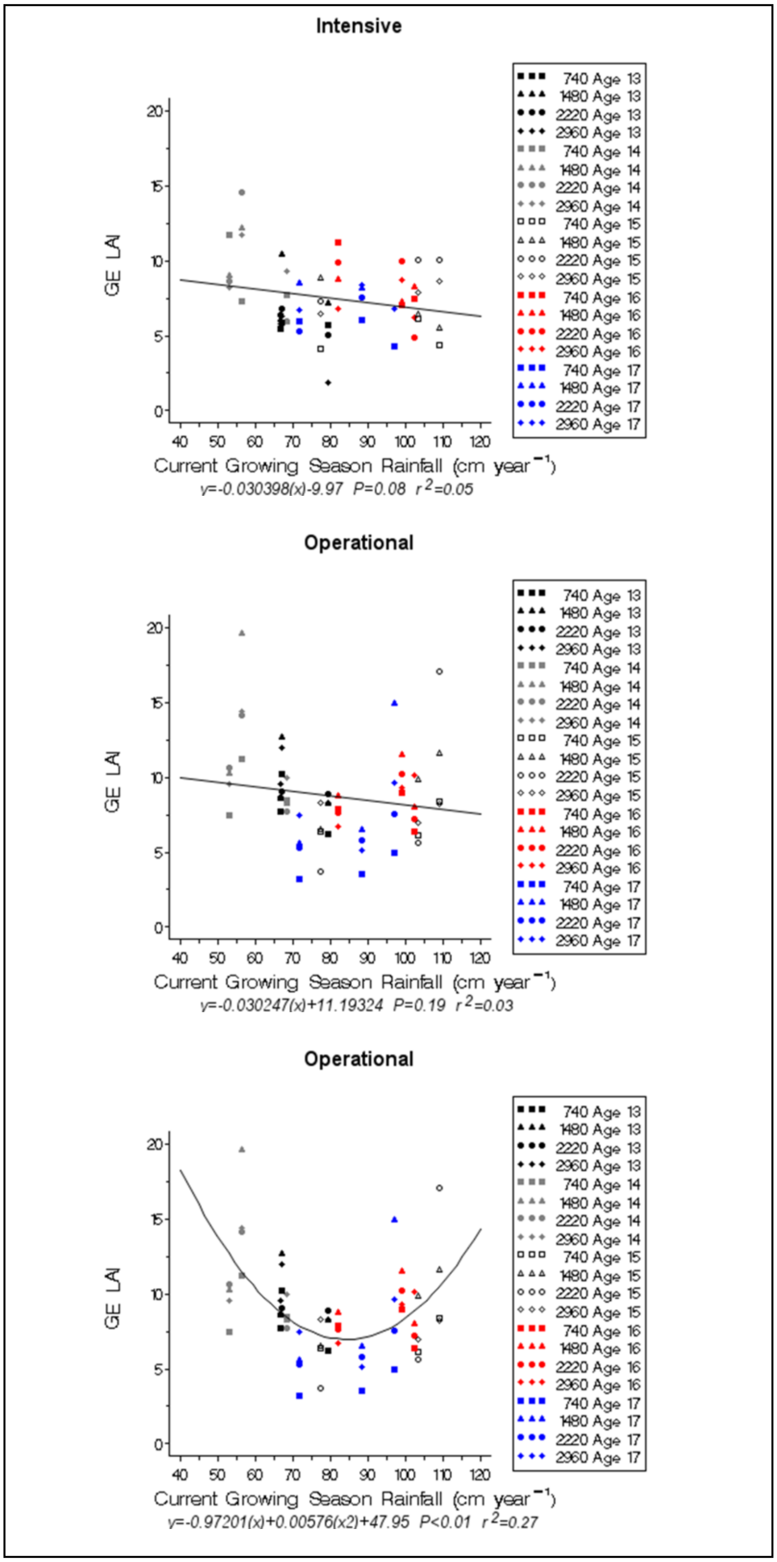

Figure 3.19. Linear and quadratic relationship between LAI growth efficiency and current growing season precipitation at three PMRC culture x density study installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12.

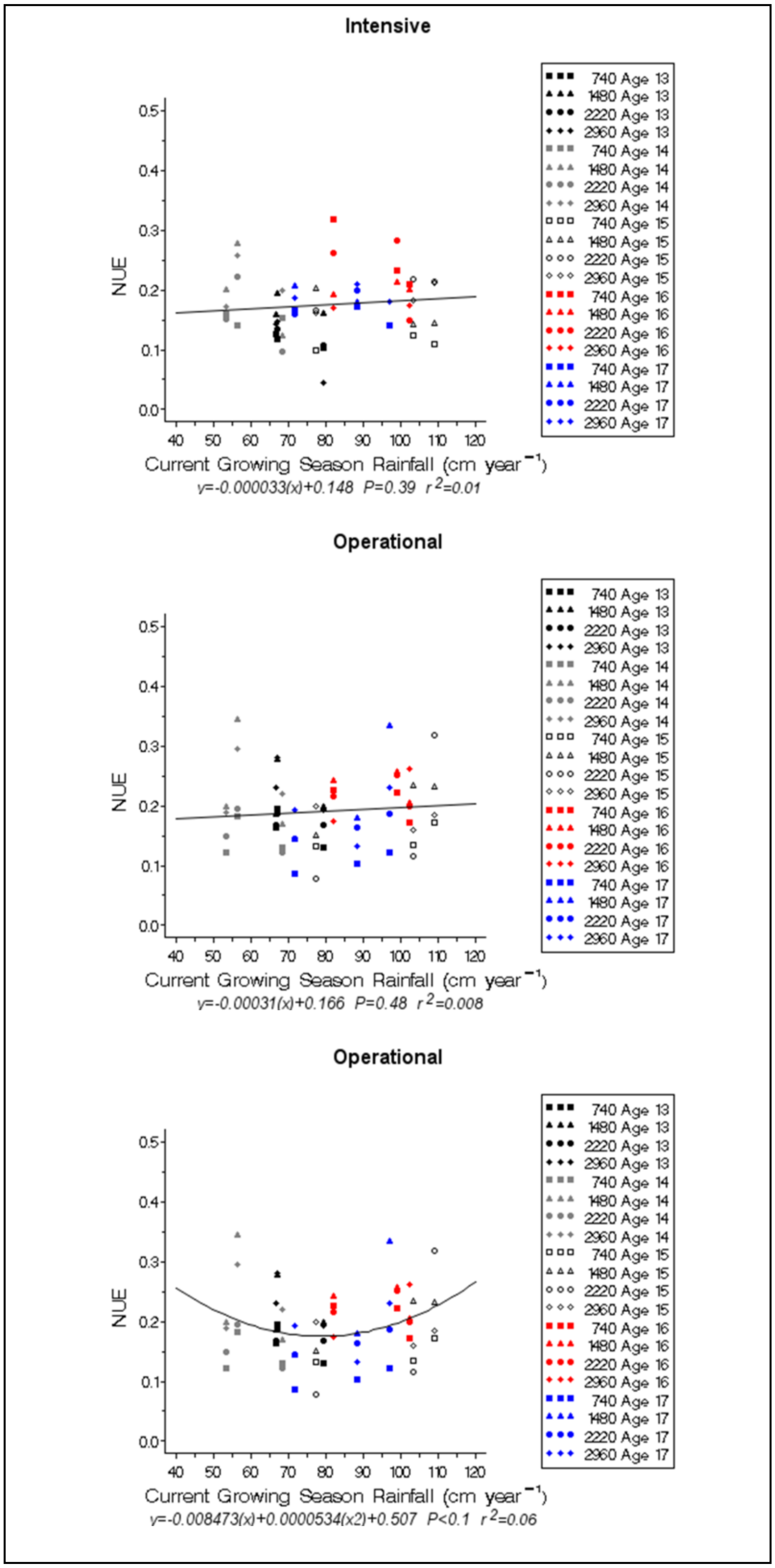

Figure 3.20. Linear and quadratic relationship between canopy nitrogen growth efficiency and current growing season precipitation at three PMRC culture x density study installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12.

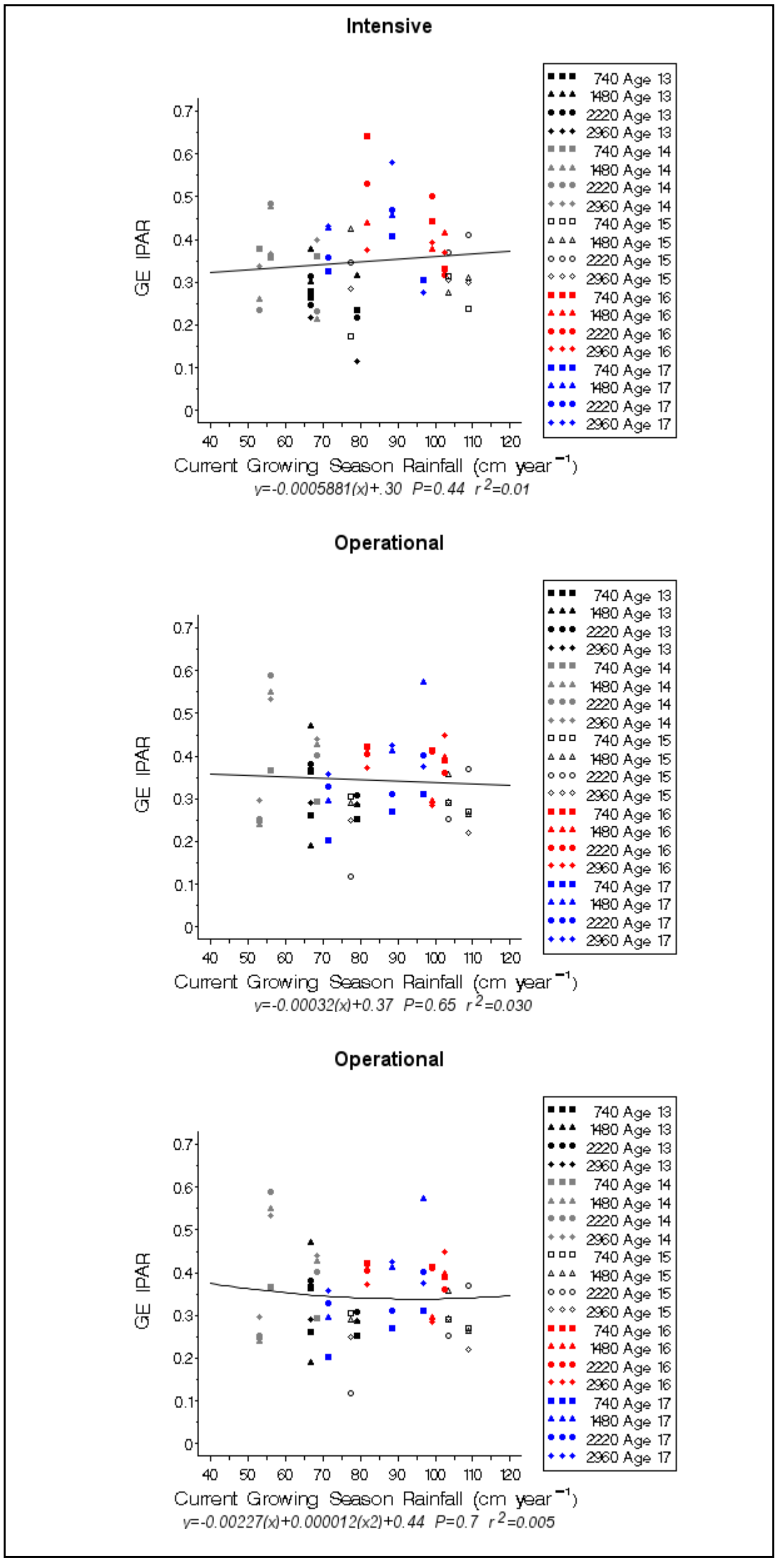

Figure 3.21. Linear and quadratic relationship between IPAR growth efficiency and current growing season precipitation at three PMRC culture x density study installations. Planting densities of 1480, 2220 and 2960 trees ha^{-1} were thinned at age 12.

CHAPTER 4

CONCLUSIONS

Throughout the study, the effects of cultural intensity on stem, stand and crown attributes were generally not statistically significant although values were generally greater with intensive culture. Intensive culture significantly decreased 13th growing season GE_{FOLBIO}, GE_{LAI}, and NUE. This trend, though not significant, remained through the 15th growing season, then began to reverse during the 16th and 17th growing seasons.

Density regime had a greater effect on stand, stem, and crown attributes than cultural intensity. Prior to thinning, values of volume (m^3) and basal area (m^2) were greatest in the higher initial planting densities. After thinning this trend reversed and remained through five years after thinning. Throughout the post-thin period, mean foliar biomass and LAI values were greater in non-thinned densities than thinned densities.

There were constant and marked differences between the thinned and non-thinned densities for foliar biomass and LAI values with both intensive and operational culture and canopy N content for operational culture. Differences between thinned and non-thinned densities for IPAR with both intensive and operational culture and canopy N content with intensive culture were marked during the first three growing seasons after thinning. Differences between density regimes were less apparent thereafter. SLA was markedly lower at age 14, which corresponded with a two year period of below average rainfall, than at age 12 or 16.

Current growing season rainfall amounts significantly affected gross CAI, foliar biomass, SLA, GE_{FOLBIO}, GE_{LAI}, NUE, and GE_{IPAR}. Previous growing season rainfall significantly affected gross CAI, foliar biomass, foliar nitrogen content, IPAR, GE_{FOLBIO}, GE_{LAI}, NUE, and GE_{IPAR}. Stand and crown attribute values were generally lowest during the 13th and 14th growing season which corresponded with below average growing season rainfall amounts. Gross CAI tended to be greatest for all density regime-culture combinations during years in which there were two or more consecutive years with growing season rainfall near or above the long-term average. Stands with operational culture exhibited highest GE during the 14th and 16th growing seasons which corresponded to two consecutive growing seasons of low and high rainfall amounts, respectively. Stands with intensive culture tended to display the highest growth efficiency during the 16th growing season with the exception of GE_{LAI}. GE_{LAI} in thinned stands with intensive culture increased from the 13th to 14th growing season then remained constant through the 17th growing season.

Findings demonstrate the effects of growing season precipitation and density regime on mid-rotation stand development when soil nutrient resources are adequate and stand density is not limiting.