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# Long-term trends in loblolly pine productivity and stand characteristics in response to thinning and fertilization in the West Gulf region

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**Abstract**

Two levels each of thinning and fertilization were applied to a 7-year-old loblolly pine (*Pinus taeda* L.) plantation on a nitrogen- and phosphorus-deficient West Gulf Coastal Plain site in Louisiana. Levels of thinning were no thinning, or thinning applied 7 and 14 years after stand initiation. Levels of fertilization were no fertilization or broadcast fertilization with diammonium phosphate at age 7 years plus refertilization with urea, monocalcium phosphate, and potash at age 14 years. Long-term measurements of climate, stand development and productivity, projected leaf area index, and foliar nutrition were initiated at age 11 years. We found that by age 17 years, thinning increased mean live-crown length from 4.2 to 7.8 m, and mean tree diameter from 15.0 to 21.8 cm compared to the unthinned treatment. After rethinning at age 14 years, stand basal area increased 1.2 and 19.2% between ages 15 and 17 years on the unthinned and thinned plots, respectively. Refertilization at age 14 years reestablished foliar N, P and K sufficiency, which increased leaf area index from 4.2 to 6.0 $m^2\ m^{-2}$ on the unthinned plots and from 3.2 to 3.8 $m^2\ m^{-2}$ on the thinned plots, and subsequently, increased gross stand biomass from 114 to 141 Mg $ha^{-1}$ on the unthinned plots and from 78 to 95 Mg $ha^{-1}$ on the thinned plots by age 17 years. Leaf area was an important factor controlling loblolly pine productivity. At our study site, however, competition for light and water and nutrition-limited foliage growth influenced the variability and scope of this relationship. Our results suggest that a positive and linear relationship between leaf area and loblolly pine productivity does not universally occur on loblolly pine sites.


*Keywords:* Density-related mortality; Growth efficiency; Louisiana; Nitrogen; Projected leaf area index; Phosphorus

## 1. Introduction

The United States is the world leader in the production of industrial wood products, and the majority of our Nation's timber products are supplied by the southern region (Prestemon and Abt, 2002). Loblolly pine (*Pinus taeda* L.) is the dominant timber species in the majority of commercial forests in the southern United States (Schultz, 1997). Because the national and worldwide demand for wood products has been predicted to increase, it is anticipated that the highly productive forests of the South will continue to lead our nation's timber production (Prestemon and Abt, 2002). This effort will likely be dominated by

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intensive loblolly pine management. Simultaneous increases in timber demand (Prestemon and Abt, 2002) and loss of forest land to urbanization in the South (Wear, 2002) justify intensive management of loblolly pine wherever this species is grown for timber.

To realize the full potential of intensive forest management, a better understanding of how silvicultural treatments increase natural and planted stand productivity and value is needed (Siry, 2002). Past research has shown that light interception, and by implication leaf area, control the growth of plantation loblolly pine, and intensive forest management practices that augment leaf area increase stem volume and standing aboveground biomass production (Vose and Allen, 1988; Colbert et al., 1990; Albaugh et al., 1998; Jokela and Martin, 2000; Samuelson et al., 2001). Furthermore, intensive management may increase the growth efficiency, or rate of aboveground biomass accumulation per unit of leaf area, in loblolly pine plantations (Colbert et al., 1990; Albaugh et al., 1998; Jokela and Martin, 2000).

Anticipated responses of stand production to silvicultural treatments, however, are not always realized in loblolly pine stands. For example, Borders and Bailey (2001) found that when fertilization and weed control were applied together, stand basal area and volume of 10–12-year-old loblolly pine increased at only four of six sites in Georgia. Growth efficiency responses to silvicultural treatments are also unpredictable across the loblolly pine range. For example, Albaugh et al. (1998) found that the growth efficiency of 8-year-old loblolly pine was positively affected by fertilization on a nutrient-deficient, droughty site, whereas Samuelson et al. (2001) reported no effect of fertilization on the growth efficiency of 4-year-old loblolly pine on an old-field site of moderate quality. Long-term study of the relationship between loblolly pine leaf area and aboveground productivity, and how stand conditions affect this relationship should provide insight to the physiological mechanisms that control carbon gain in this valuable species. To better understand the key physiological relationships that affect loblolly pine growth in the western region of this species' range, we present 7 years of loblolly pine aboveground productivity in response to four treatment combinations created by thinning and fertilization. Our objectives are to (1) quantify loblolly pine aboveground productivity in four stand environments and (2) combine this information with stand environment characteristics to examine the ecophysiological relationships that occurred with these growth trends.

## 2. Materials and methods

### 2.1. Site description

This study is located in Rapides Parish, in central Louisiana, USA on the Palustris Experimental Forest (31°11′N, 92°41′W). In May 1981, container-grown loblolly pine seedlings from a woods-run source were planted at 1.8 m × 1.8 m. In 1988, sixteen 0.06 ha treatment plots, 13 × 13 trees each, were established. Measurement plots were the interior seven rows of seven trees, or initially 49 trees (0.016 ha). Planted pine, hardwood trees, shrubs, grasses and herbaceous plants were the dominant vegetation when the plots were established. Hardwood trees and shrubs were mowed from the plots. Throughout the study, 2% aqueous glyphosate was applied as needed to control grass and herbaceous plants. Shortly after plot establishment in 1988, tree mortality caused by southern pine beetle (*Dendroctonus frontalis* Zimmermann) eliminated four plots from the study.

The ground surface is very gently sloping, and the soil is a moderately well-drained Beauregard silt loam (fine silty, siliceous, thermic, Plinthaquic Paleudults) that is low in natural fertility (Kerr et al., 1980) (Table 1). The humid, subtropical climate is characterized by a mean annual precipitation of 156 cm with 45% received in spring and summer and 55% received in fall and winter. Mean daily air temperature is 27.4 °C in summer and 11.4 °C in winter with an average of 250 frost-free days. Annual and monthly water balances were calculated for the 7-year period between 1992 and 1998 using latitude, monthly total precipitation, monthly mean air temperature, and plant available soil water holding capacity (Thornthwaite and Mather, 1955). Precipitation was monitored with an electronic weather station in an open field approximately 25 m from the study area. Air temperature was obtained from the LSU AgCenter's Dean Lee Research Station located approximately 37 km east of the study area. Mean plant available water holding capacity at 32 locations within the study site was determined at a soil depth of 1 m by subtracting soil

Table 1
General properties of a Beauregard silt loam soil supporting the loblolly pine plantation in central Louisiana

| | |
|---|---|
| Taxonomic family | Fine silty, siliceous, thermic Plinthaquic Paleudults |
| Site index[a] | 21.3 m |
| Texture | |
| A horizon | Silt loam |
| E horizon | Silt loam |
| B horizon | Silty clay loam |
| Depth to argillic horizon | 23 cm |
| Slope | 1–3% |
| Drainage class | Moderately well-drained |
| Plant available water[b] to 1 m | 183 mm |
| A horizon pH | 5.3 |
| A horizon organic C | 1.1% |
| A horizon available P | 1.9 mg/kg |

[a] The base age is 25 years.
[b] Plant available water is the maximum amount of soil water between 0.03 and 1.5 MPa of tension.

water content at wilting point (−1.5 MPa) from soil water content at field capacity (−0.03 MPa).

## 2.2. Experimental design

At age 7 years, two levels each of broadcast fertilization with diammonium phosphate (0; 135 kg N $ha^{-1}$ plus 150 kg P $ha^{-1}$), and precommercial row thinning (none: 2990 trees $ha^{-1}$ remaining; thinned: 749 trees $ha^{-1}$ remaining) were randomly applied in a factorial design with three replications (Haywood, 1994). At age 14 years, the fertilized plots were refertilized with a broadcast application of urea, monocalcium phosphate, and potash (200 kg N $ha^{-1}$, 50 kg P $ha^{-1}$, and 50 kg K $ha^{-1}$). Concurrent with the fertilization, previously thinned plots were thinned from below; basal area was reduced from 18.2 to 15.4 $m^2$ $ha^{-1}$. The second thinning reduced the relative density from 37 to 31% of the maximum value of Reineke's stand density index for loblolly pine (450).

Three years after retreatment, all trees on the thinned plots and the tallest 25% of trees on the unthinned plots were designated as dominant or codominant, and from these trees the apparent site indices of the four treatments were determined using the equations of Baldwin and Feduccia (1987). Apparent site indices at age 16 years were 21.3 and 22.9 m for the unthinned–unfertilized and unthinned–fertilized plots, respectively. For the thinned–unfertilized and thinned–fertilized plots, the apparent site indices were 19.2 and 21.0 m, respectively.

## 2.3. Measurements and calculations

### 2.3.1. Growth

Survival and diameter at breast height (dbh, 1.37 m) of all measurement trees were recorded after thinning in 1989 and from 1992 to 1998 (ages 7 and 11–17 years). On the unthinned plots, total height of 25% of the measurement trees was recorded at ages 7 and 11–15 years, and total height of 100% of the measurement trees was recorded at ages 16 and 17 years. On the thinned plots, total height of all measurement trees was quantified at ages 7 and 11–17 years. Height to the base of the live crown was measured, and live-crown length was calculated at ages 16 and 17 years. Trees were measured between January and April. Survival (%), stand density (trees $ha^{-1}$), mean dbh (cm), frequencies of trees in 2 cm diameter classes, stand basal area ($m^2$ $ha^{-1}$), mean tree height (m), and mean live-crown length (m) between ages 11 and 17 years were calculated for each measurement plot.

## 2.4. Biomass

For trees at age 7 years and between ages 11 and 15 years without total height measurements, total tree height was predicted by year and plot using an equation developed from the model:

$$\ln(Y) = B_0 + \left(B_1\left(\frac{1}{X}\right)\right) \quad (1)$$

where $Y$ is the total tree height (ft) and $X$ the dbh (in.). Values of predicted total height were corrected for transformation bias (Snowdon, 1991). Using dbh and either actual or predicted total height, inside-bark dry stem biomass per tree was predicted by an equation from Baldwin and Feduccia (1987). Stem mass before thinning at age 7 years was expressed as a function of the stem mass after thinning at age 7 years, trees $ha^{-1}$ removed by row thinning, and residual trees $ha^{-1}$. Standing stem mass was defined as the inside-bark dry stem mass of live trees at the end of the growing season, and gross stem mass was calculated as standing stem mass plus the inside-bark dry stem mass removed by the two thinnings and lost to natural mortality. Both standing and gross stem mass are expressed as Mg $ha^{-1}$. Gross values of current and mean annual increments were calculated for each measurement plot for each year. Current annual increment (CAI) was calculated as the difference between standing stem mass at the beginning of the growing season and standing stem mass at the end of the growing season plus the stem mass that was removed by thinning or lost to natural mortality in this time interval. Gross mean annual increment (MAI) is the gross stem mass divided by stand age. Growth values are expressed as Mg $ha^{-1}$ per year.

Foliage and branch mass were estimated at ages 14 and 17 years. Foliage mass (Mg $ha^{-1}$) was estimated by collecting needle fall in four randomly placed traps (0.92 $m^2$) in each measurement plot following the procedures of Vose and Allen (1988) and Dougherty et al. (1995). Biweekly collections were oven-dried at 65 °C to equilibrium and weighed. Foliage mass produced per year was determined as the sum of monthly needle-fall dry weights during the subsequent phenological year (April–March). Foliage mass was calculated as the sum of needle-fall dry weights produced in two consecutive phenological years and expressed as Mg $ha^{-1}$.

At age 14 years, total tree height, height to the base of the live crown, and dbh of two randomly chosen dominant or codominant trees and two randomly chosen intermediate trees per measurement plot were recorded. At age 17 years, these dimensions were measured on all trees. Live-crown length was calculated as the difference between total tree height and height to the base of the live crown, and live-crown ratio was calculated as live-crown length divided by total tree height. With live-crown ratio, branch mass per tree was estimated using an equation from Baldwin et al. (1997). Branch mass per hectare (Mg $ha^{-1}$) was calculated as the product of mean tree branch mass and number of live trees per hectare.

Outside-bark stem mass of individual trees was estimated with dbh and both actual and predicted total height at age 14 years and actual total height at age 17 years using an equation from Baldwin and Feduccia (1987). Total outside-bark stem mass was defined as the sum of individual tree values expressed as Mg $ha^{-1}$ for each measurement age. Total aboveground biomass (Mg $ha^{-1}$) was calculated as the sum of foliage, branch, and outside-bark stem mass, and percentages of aboveground biomass components relative to the total were determined.

### 2.4.1. *Wood quality*

Specific gravity (SG) of individual growth rings and the ratio of earlywood and latewood widths (ELW) per growth ring were determined using increment cores. For ages 11–17 years, one core was extracted at dbh from two or three randomly chosen measurement trees per plot with breast height diameters within ±1.27 cm of the quadratic mean diameter of the plot. Increment cores were air dried at room temperature, mounted, sanded, and cross-dated using techniques described by Stokes and Smiley (1968) and Fritts (1976). Earlywood and latewood ring widths were measured to the nearest 1 μm using a microscope. Ring SG was predicted by the equation:

$$Y = 0.3084867 + 0.0045681(X) \quad (2)$$

where $Y$ = SG and $X$ the percentage of latewood ring width (Alexander Clark III, personal communication). Mean SG and ELW were calculated per growth ring of all increment cores. Values of SG and ELW in years that trees had breast height diameters within ±1.27 cm of the plot mean quadratic diameter were averaged by plot.

### 2.4.2. *Mineral nutrition*

Foliar mineral nutrient concentrations were determined at ages 14–17 years on two of the replications. Samples for mineral nutrition were collected during December and January from three dominant or codominant trees by removing foliage from the upper and lower one-third of the crowns. Samples were collected from 1995 to 1998 and pooled by crown level and plot. Foliage was freeze-dried and ground in a Wiley mill (20-mesh). Foliar N concentration (mg $g^{-1}$) was determined with a LECO CNS-2000 elemental analyzer (LECO Corporation, St. Joseph, MI); foliar P concentration (mg $g^{-1}$) was determined by colorimetry (John, 1970); and foliar K concentration (mg $g^{-1}$) was determined by atomic absorption spectrophotometry (Isaac and Kerber, 1971).

### 2.4.3. *Projected leaf area index and stemwood growth efficiency*

Using values of specific projected leaf area (SLA) (g $m^{-2}$) for each treatment that were determined at age

14 years (Yu et al., 1999), the monthly loss of projected leaf area from the canopy was calculated as the mass of needle fall per $m^2$ of ground area divided by SLA and expressed as $m^2\ m^{-2}$ per month. Annual leaf area produced during the subsequent phenological year was calculated from yearly needle-fall leaf areas. Annual peak leaf area index (LAI) ($m^2\ m^{-2}$) was calculated as the sum of leaf areas produced in two consecutive phenological years. Stemwood growth efficiency was calculated as CAI (Mg $ha^{-1}$ per year) divided by LAI ($m^2\ m^{-2}$).

### 2.5. Statistical analyses

The normal distribution of each variable was evaluated by the Shapiro–Wilk statistic (SAS, 1991). Data associated with six variables required transformation to natural logarithms to establish normality (ELW, foliar P and K concentrations, CAI, MAI, and LAI). Stem density, stand basal area, standing stem mass, gross stem mass, CAI and MAI between ages 11 and 17 years were analyzed using a completely random design with repeated measures. Repeated measurements were the age of trees since planting. Treatments were two levels each of thinning and fertilization. Live-crown length at age 17 years was analyzed using a completely random design with factorial combinations of the thinning and fertilization treatments. The SG and ELW produced between ages 1 and 17 years, total aboveground biomass and percentages of outside-bark stem, branch and foliage mass at ages 14 and 17 years, and LAI and stemwood growth efficiency between ages 12 and 18 years were analyzed similarly. Foliar N, P, and K concentrations were analyzed using a randomized complete block, split-split-plot design with two blocks that were delineated by slope. Whole plots were levels of thinning and fertilization. Subplots were crown level and age. Main and interaction effects were considered significant at $P \leq 0.05$ unless otherwise noted. Treatment combinations are: C (unfertilized–unthinned), F (fertilized–unthinned), T (unfertilized–thinned), and FT (fertilized–thinned). Significantly different treatment means were compared with the least significant difference test at $P \leq 0.05$ (Steel and Torrie, 1980).

Nonlinear equations to predict CAI as a function of LAI were estimated using dummy variables to distinguish treatments. We deleted the least significant dummy variables until all coefficients in the model were significant ($P \leq 0.05$). The best equation was the cumulative form of the Weibull function:

$$Y = \alpha(1 - \exp(\beta X^{\lambda})) \quad (3)$$

with the parameters $\alpha$, $\beta$ and $\lambda$ as potential functions of dummy variables for treatments. We estimated the equation by a robust regression characterized by a $\Psi$ function with $a$, $b$, and $c$ parameters of 1.0, 2.0 and 5.0 (Hampel et al., 1986). The parameter estimates were only slightly different from those obtained by ordinary least-squares regression.

For each level of thinning, the linear relationship between CAI and LAI at ages 12–18 years was evaluated by ordinary least-squares regression. The slope of the regression equations between CAI and LAI were considered significant at $P \leq 0.05$.

## 3. Results

### 3.1. Annual and monthly water balance

Between ages 11 and 17 years, mean annual precipitation was 1435 mm $\pm$ 18% (coefficient of variation), mean annual potential evapotranspiration (PET) was 1049 mm $\pm$ 6.0%, and mean annual actual evapotranspiration (AET) was 869 mm $\pm$ 7% with averages of 64% of annual precipitation, 92% of annual PET, and 91% of annual AET occurring in March–October, respectively (Fig. 1A). Annual water deficit ranged between 69 mm at age 11 years and 343 mm at age 17 years. For all years, the entire annual water deficit accrued during May–September (Fig. 1B). Annual water deficits between ages 15 and 17 years were 145% higher than between ages 11 and 14 years.

### 3.2. Stand development

#### 3.2.1. Tree height

Fertilization was the only treatment that exhibited a significant effect on mean tree height throughout the study (first table in Appendix A). Mean tree height was significantly affected by stand age with a steady increase in mean tree height as stand age increased (Fig. 2). Significant interactions between thinning and stand age, and between fertilization and stand age were found. These responses resulted from different

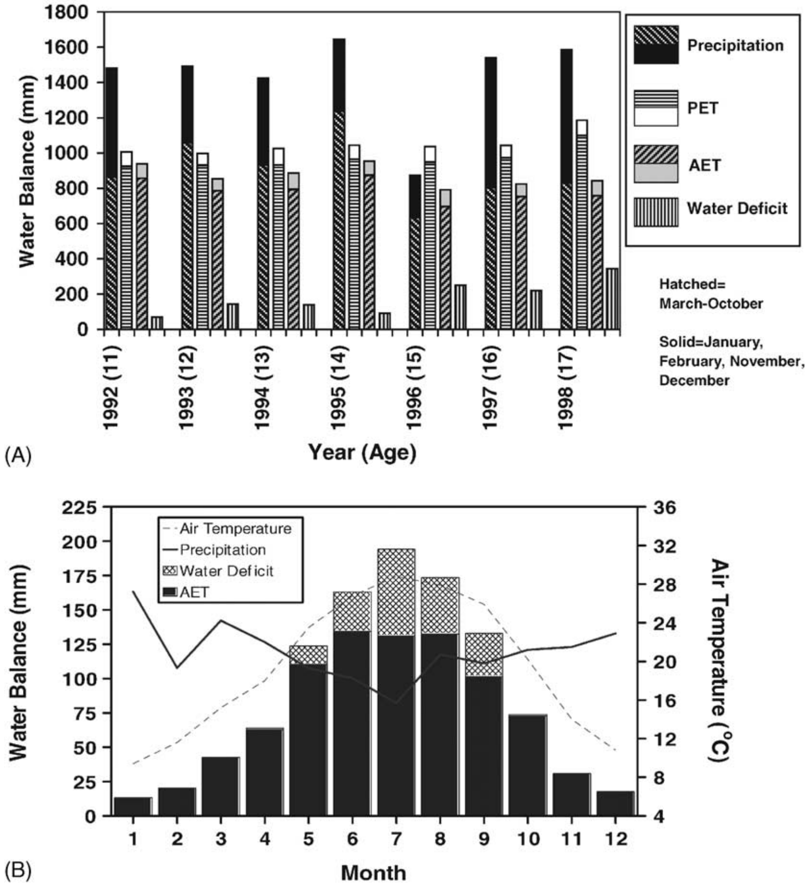


Fig. 1. Annual (A) and mean monthly (B) water balance of plantation loblolly pine between ages 11 and 17 years in Rapides Parish, LA. Precipitation and air temperature were used to calculate actual evapotranspiration (AET) and water deficit by the method of Thornthwaite and Mather (1955). Monthly PET is equivalent to the sum of monthly AET and monthly water deficit.

rates of increase in mean tree height with stand age and the effects of either thinning or fertilization. By age 11 years, for example, thinning at age 7 years resulted in reduced mean tree height growth. This response to thinning continued through age 12 years. After age 12 years, mean tree height growth was no longer reduced by thinning. On the thinned plots, absence of a thinning effect on mean tree height occurred at basal areas between 18.3 $m^2 ha^{-1}$ at age 13 years and 20.0 $m^2 ha^{-1}$ at age 17 years. Between ages 13 and 17 years, mean tree height was stimulated by fertilization. The positive effect of fertilization on mean tree height between ages 13 and 17 years was reflected as an increase in apparent site index from 20.3 to 22.4 m at age 17 years.

### 3.2.2. Stem density and stand basal area

Stem density and stand basal area were significantly affected by thinning, and stand basal area was significantly affected by fertilization (first table in Appendix A). Overall, stem density decreased and stand basal area increased significantly with stand age (Fig. 3). On the unthinned plots, fertilization resulted in less stem density and tree survival and higher stand basal area, but did not affect the relationship between stem density and stand basal area. Furthermore, stem density began to decrease at a consistent basal area of approximately 42 $m^2 ha^{-1}$ on the unthinned plots regardless of fertilization treatment. On the thinned plots, the relationship between stem density and stand basal area was similar before

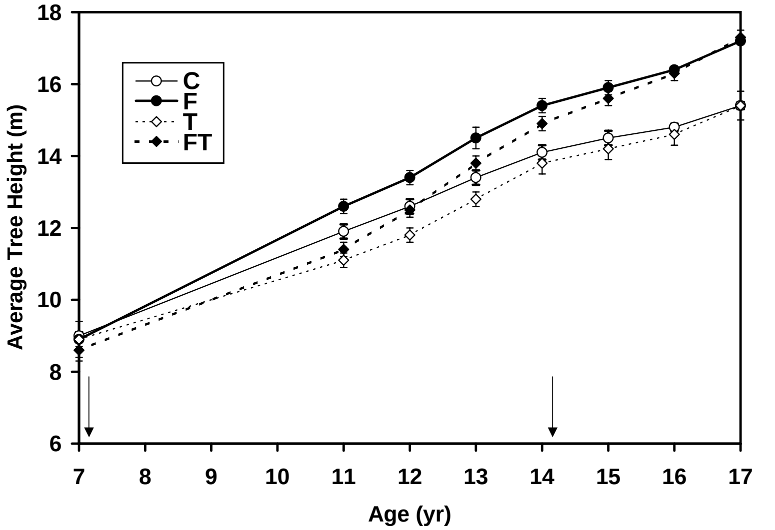


Fig. 2. Mean tree height (m) of plantation loblolly pine between ages 7 and 17 years in response to four silvicultural treatments in Rapides Parish, LA. Silvicultural treatments are unthinned and unfertilized (C), unthinned and fertilized at ages 7 and 14 years (F), thinned at ages 7 and 14 years and unfertilized (T), and thinned and fertilized at ages 7 and 14 years (FT). Arrows note the time of treatment application and bars represent the standard error of the means.

and after rethinning with minor reductions in stem density caused by ice and lightning damage and constant increases in stand basal area regardless of fertilization treatment (Fig. 3B).

### 3.2.3. Diameter distribution

By the end of this study, both thinning and fertilization affected diameter distributions within these plots. The primary effect of both treatments was to produce a greater percentage of larger diameter trees (Fig. 4). On the unthinned plots, for example, the median dbh for the unfertilized and fertilized trees was 14 and 16 cm, respectively. This indicates that by age 17 years, most of the trees on the unthinned plots were pulpwood size (14.0–19.1 cm dbh; Harris, 2001) regardless of fertilization treatment. Tree mortality occurred within the

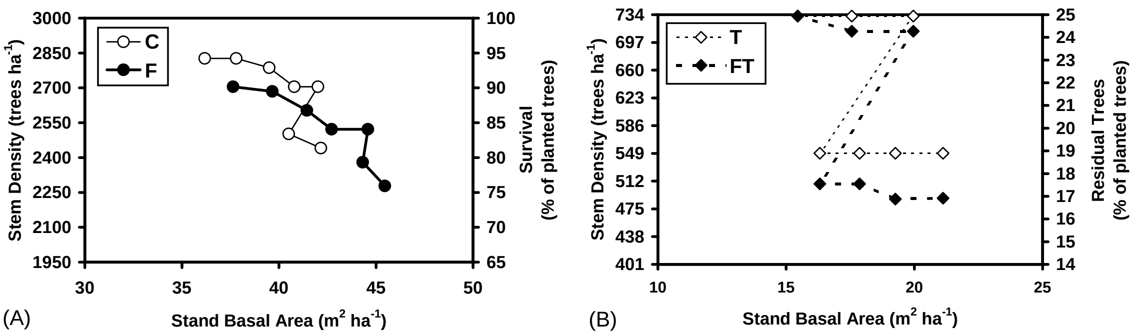


Fig. 3. Relationships between (A) stem density (trees $ha^{-1}$), stand basal area ($m^2\ ha^{-1}$) and percentage of trees surviving on the unthinned plots (unthinned and unfertilized (C); unthinned and fertilized at ages 7 and 14 years (F)), and (B) stem density (trees $ha^{-1}$), stand basal area ($m^2\ ha^{-1}$) and percentage of planted trees remaining as residual trees on the thinned plots (thinned at ages 7 and 14 years and unfertilized (T); thinned and fertilized at ages 7 and 14 years (FT)). Trees are plantation loblolly pine between ages 11 and 17 years in Rapides Parish, LA.

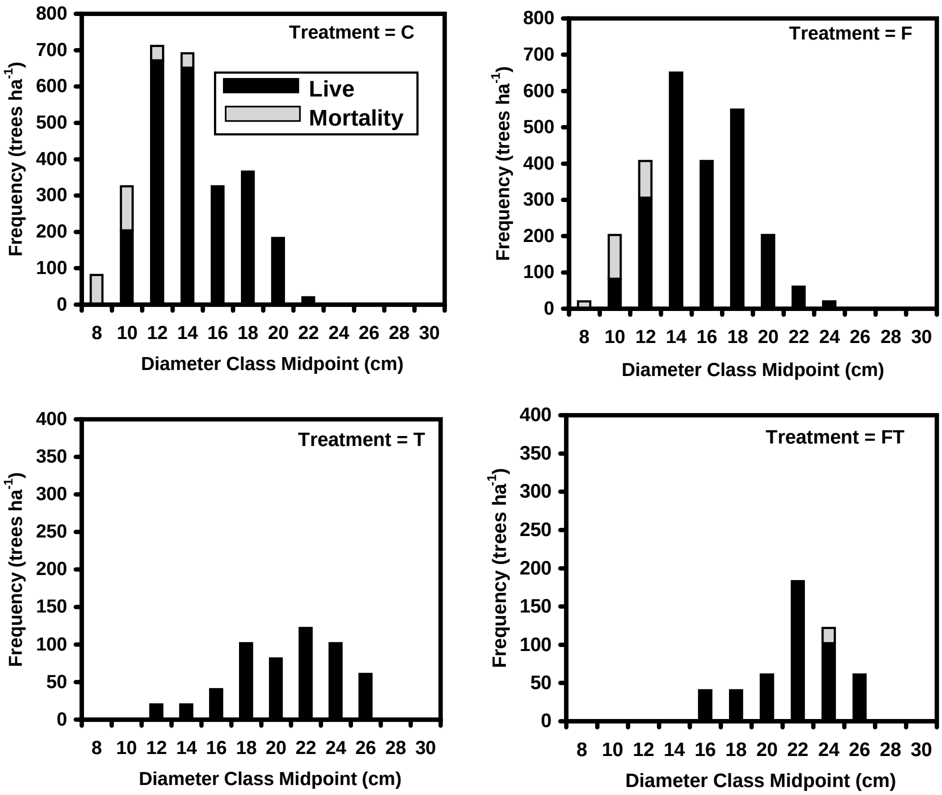


Fig. 4. Diameter distribution of live loblolly pine trees at age 17 years (black bars), and mortality during the 16th and 17th years (gray bars) in response to four silvicultural treatments in Rapides Parish, LA. Silvicultural treatments are unthinned and unfertilized (C), unthinned and fertilized at ages 7 and 14 years (F), thinned at ages 7 and 14 years and unfertilized (T), and thinned and fertilized at ages 7 and 14 years (FT).

lower 50 and 33% of the diameter distribution on the C and F plots, respectively. Because most tree mortality on the unthinned plots occurred in the smaller and less valuable diameter classes, the value lost per volume of tree mortality was lower than if tree mortality occurred in larger diameter classes. Within the thinned plots, trees in the smaller diameter classes did not die during the study period. Lightning killed the trees within the 24 cm diameter class on the FT plots.

Thinning was effective in shifting the entire diameter distribution to the larger diameter classes, and therefore, potentially increasing value per unit of volume (Fig. 4). Without fertilization, more than 50% of the trees in the thinned plots attained chip-and-saw size (19.1–29.2 cm dbh) by age 17 years (Harris, 2001). With fertilization, however, greater than 70% of the trees in the thinned plots attained chip-and-saw size by age 17 years.

#### 3.2.4. Live-crown length

Mean live-crown length at age 17 years was significantly affected by thinning ($P = 0.0001$) with values of 4.2 and 7.8 m on the unthinned and thinned plots, respectively (Fig. 5). Fertilization had no significant effect on live-crown length. This information suggests that managing stand density is an important factor in manipulating crown vigor and tree growth potential.

### 3.3. Stand productivity and stem characteristics

#### 3.3.1. Aboveground biomass production

Throughout this study, both gross and standing stem mass changed significantly with stand age (second table in Appendix A). Stand age effects on gross and standing stem mass resulted from nearly constant increases in both variables with stand age across all

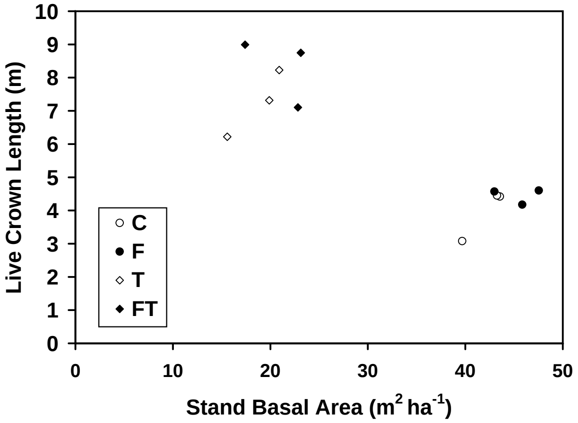


Fig. 5. Relationship between live-crown length (m) and stand basal area ($m^2\ ha^{-1}$) of 17-year-old plantation loblolly pine in response to four silvicultural treatments in Rapides Parish, LA. Silvicultural treatments are unthinned and unfertilized (C), unthinned and fertilized at ages 7 and 14 years (F), thinned at ages 7 and 14 years and unfertilized (T), and thinned and fertilized at ages 7 and 14 years (FT).

treatment combinations (Fig. 6). Thinning directly affected these variables with the removal of growing stock at ages 7 and 14 years—the likely reason thinning significantly interacted with stand age. By age 17 years, the T and FT plots produced 69 and 61% of the gross stem mass that occurred on the C and F plots, respectively. Fertilization also significantly affected gross and standing stem mass during this observation period, and there was a significant interaction between fertilization and stand age for both variables. Fertilization increased gross and standing stem mass across the range of basal areas occurring between ages 11 and 17 years on both the unthinned (37–44 $m^2\ ha^{-1}$) and thinned (14–20 $m^2\ ha^{-1}$) plots. By age 17 years, fertilization led to increases in gross and standing stem biomass of 27.1 and 25.2 Mg $ha^{-1}$ on the unthinned plots, and increases in gross and standing stem mass of 17.0 and 12.4 Mg $ha^{-1}$ on the thinned plots, respectively.

Gross values of CAI and MAI varied significantly with stand age (second table in Appendix A). Values of CAI at age 17 years were as high as the maximum values of 6.6–15.0 Mg $ha^{-1}$ per year observed earlier in the rotation at age 13 years (Fig. 7). This indicates that stand growth potential did not decline with stand age between 12 and 17 years. For gross MAI, the significant stand age effect is due to nearly constant increases in MAI with stand age for all treatment combinations. While thinning and fertilization significantly affected CAI and MAI, thinning effects on CAI and fertilization effects on MAI changed significantly with stand age. Except for CAI responses to thinning at age 16 years, thinning significantly reduced CAI by 36–44% between ages 12 and 17 years. At age 16 years, thinning had no significant effect on CAI. Between ages 11 and 17 years, values of MAI were reduced by an average of 32% in response to thinning. Fertilization increased CAI at all ages by an average of

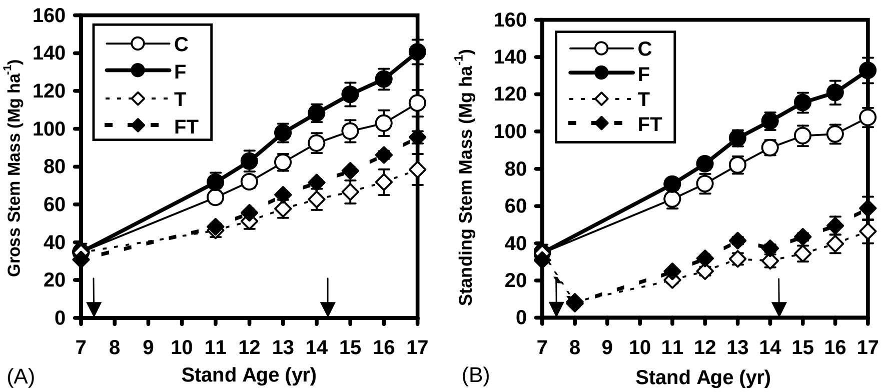


Fig. 6. Gross (A) and standing (B) stem mass (inside bark) (Mg $ha^{-1}$) of plantation loblolly pine between ages 7 and 17 years in response to four silvicultural treatments in Rapides Parish, LA. Silvicultural treatments are unthinned and unfertilized (C), unthinned and fertilized at ages 7 and 14 years (F), thinned at ages 7 and 14 years and unfertilized (T), and thinned and fertilized at ages 7 and 14 years (FT). Arrows note the time of treatment application and bars represent the standard error of the means.

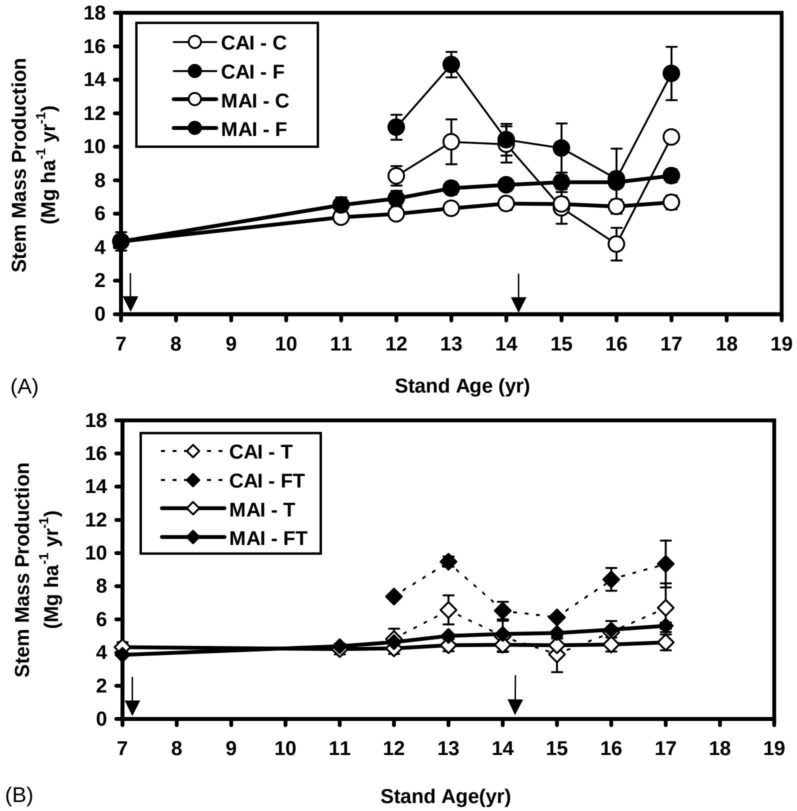


Fig. 7. Current (CAI) and mean (MAI) annual increment (Mg $ha^{-1}$ per year) of plantation loblolly pine stem biomass (inside bark) between ages 11 (MAI) or 12 (CAI) and 17 years on (A) unthinned plots (unthinned and unfertilized (C); unthinned and fertilized at ages 7 and 14 years (F)), and (B) thinned plots (thinned at ages 7 and 14 years and unfertilized (T); thinned and fertilized at ages 7 and 14 years (FT)) in Rapides Parish, LA. Arrows note the time of treatment application and bars represent the standard error of the means.

45% on the unthinned plots and 48% on the thinned plots. The rate of increase in MAI with stand age varied for each treatment, which is probably responsible for the significant two-way interaction between fertilization and stand age.

### 3.4. Wood quality

Both SG and ELW differed significantly by ring age but not by thinning or fertilization treatment (third table in Appendix A). When averaged among treatment combinations, values of SG were higher at ring ages of 6, 11, and 12 years and lower at ring ages of 14, 15, and 17 years when compared to SG in other years (Fig. 8A). Ring age was inversely related to chronological age (i.e., a ring age of 19 years was produced when trees were 1-year-old). Values of ELW were higher at ring ages of 14, 15, and 17 years and lower at ring ages of 6, 11, and 12 years (Fig. 8B). A significant interaction between fertilization and ring age was detected for both SG and ELW. However, fertilization did not significantly affect SG or ELW within a ring age. From ring age 12 years to ring age 2 years, SG and ELW exhibit no clear trend. Thus, with regard to these criteria, and because SG increased and ELW decreased at ring ages of 11 and 12 years, wood quality appeared to achieve mature characteristics by the age of 8 years. This is consistent with the results of Clark and Saucier (1989), and Clark and Schmidtling (1989) who reported that the period of juvenile wood formation for loblolly pine is 6–8 years on the Gulf Coastal Plain.

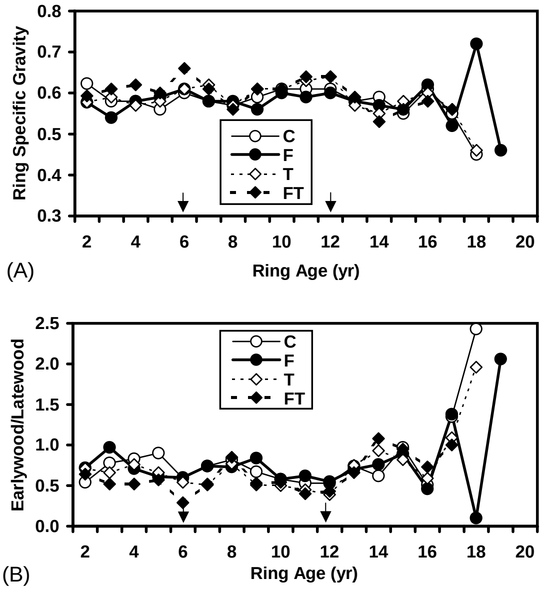


Fig. 8. Mean ring specific gravity (A) and ratio between earlywood and latewood (B) of growth rings from increment cores of 20-year-old loblolly pine trees in response to four silvicultural treatments in Rapides Parish, LA. Silvicultural treatments are unthinned and unfertilized (C), unthinned and fertilized at ages 7 and 14 years (F), thinning at ages 7 and 14 years and unfertilized (T), and thinned and fertilized at ages 7 and 14 years (FT). Ring 19 is located at the center of the stem. Arrows note the time of treatment application.

### 3.5. Basic ecophysiological relationships

#### 3.5.1. Mineral nutrition

Foliar concentrations of N, P, and K were significantly affected by interaction between fertilization and stand age (fourth table in Appendix A). Before refertilization at age 14 years, foliar N concentrations on the unfertilized and fertilized plots were 12.2 and 11.2 mg $g^{-1}$, and 1 year after refertilization they were 13.4 and 15.2 mg $g^{-1}$, respectively (Table 2). A significant three-way interaction among thinning, fertilization, and stand age indicated that at age 14 years, foliar N concentrations on the C and F plots were not significantly different, but those on the T and FT plots were significantly different (Fig. 9). Two years after refertilization, foliar N concentrations were similar on the fertilized and unfertilized plots, but after 3 years, foliar N concentrations were 3% less on the fertilized plots (12.3 mg $g^{-1}$) than on the unfertilized plots (12.7 mg $g^{-1}$).

Table 2
Mean foliar mineral nutrient concentrations of the loblolly pine plantation during the dormant season in central Louisiana between ages 14 and 17 years in response to two levels of fertilization[a]

| Stand age (years) | Level of fertilization[b] | N (mg $g^{-1}$) | P (mg $g^{-1}$) | K (mg $g^{-1}$) |
|---|---|---|---|---|
| 14 | UF | 12.2 d | 0.67 f | 3.6 e |
| 14 | F | 11.2 e | 0.96 c | 3.9 de |
| 15 | UF | 13.3 bc | 0.80 de | 4.0 cd |
| 15 | F | 15.2 a | 1.40 a | 4.8 a |
| 16 | UF | 14.3 ab | 0.83 d | 4.4 bc |
| 16 | F | 13.9 b | 1.30 a | 4.8 ab |
| 17 | UF | 12.7 c | 0.75 e | 4.1 cd |
| 17 | F | 12.3 d | 1.20 b | 4.8 ab |

[a] Means within a column followed by a different letters are significantly different at $P \leq 0.05$ by the least significant difference test.

[b] UF, unfertilized; F, fertilized at ages 7 and 14 years.

Before refertilization at age 14 years, foliar P concentrations were significantly greater on the fertilized plots (0.96 mg $g^{-1}$) than on the unfertilized plots (0.67 mg $g^{-1}$) (Table 2). During the 2-year period after refertilization, foliar P concentrations averaged 0.82 and 1.35 mg $g^{-1}$ on the unfertilized and fertilized plots, respectively. In the third year after refertilization, however, foliar P concentrations began to decline with values that were only 90 and 92% of foliar P concentrations on the unfertilized and fertilized plots, respectively, at age 16 years.

Before refertilization, foliar K concentration was 3.8 mg $g^{-1}$ and was unaffected by the fertilization treatment (Table 2). However, during the 3-year period after refertilization, foliar K concentrations on the unfertilized and fertilized plots were significantly different and averaged 4.2 and 4.8 mg $g^{-1}$, respectively.

Foliar P concentrations were significantly affected by thinning with a small reduction on the thinned plots (unthinned: 0.97 mg $g^{-1}$; thinned: 0.92 mg $g^{-1}$) (fourth table in Appendix A). A significant interaction between thinning and stand age affected foliar K concentrations. In the second and third year after thinning, foliar K concentrations were 15% less on the thinned plots (4.1 mg $g^{-1}$) than on the unthinned (4.8 mg $g^{-1}$) plots.

Foliar N concentration was significantly affected by crown level (fourth table in Appendix A) with higher

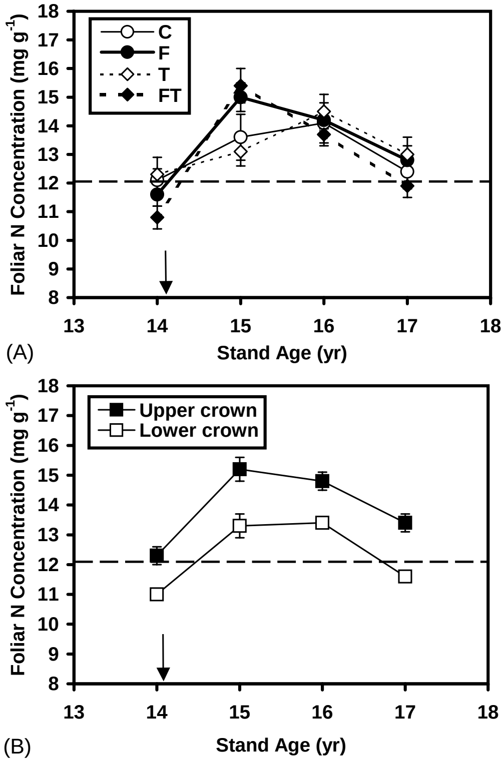


Fig. 9. Nitrogen concentration (mg $g^{-1}$) of current-year foliage of plantation loblolly pine between ages 14 and 17 years (A) in response to four silvicultural treatments and (B) in two crown levels in Rapides Parish, LA. Silvicultural treatments are unthinned and unfertilized (C), unthinned and fertilized at ages 7 and 14 years (F), thinned at ages 7 and 14 years and unfertilized (T), and thinned and fertilized at ages 7 and 14 years (FT). Crown levels are the upper and lower one-third of the live crown. The foliar nitrogen concentration of 12 mg $g^{-1}$ represents the critical level at which nitrogen becomes limiting to loblolly pine growth. Arrows note the time of treatment application and bars represent the standard error of the means.

values in the upper crown (13.9 mg $g^{-1}$) than in the lower crown (12.4 mg $g^{-1}$) (Fig. 9B). Foliar P concentrations were significantly affected by an interaction between crown level and fertilization. On the unfertilized plots, foliar P concentrations were significantly less in the upper crown (0.73 mg $g^{-1}$) than in the lower crown (0.79 mg $g^{-1}$). Foliar P concentrations were also significantly affected by an interaction between crown level and stand age with a decrease in the lower crown from 1.09 to 0.94 mg $g^{-1}$ between ages 16 and 17 years. Foliar K concentration was significantly affected by an interaction between crown level and thinning with lower values in the upper crown (3.99 mg $g^{-1}$) than in the lower crown (4.84 mg $g^{-1}$) on the unthinned plots.

### 3.5.2. Standing aboveground biomass

The standing aboveground biomass was significantly greater at age 17 years than at age 14 years, regardless of treatment (fifth table in Appendix A). Thinning significantly reduced standing aboveground biomass, and fertilization significantly increased it. Averaged across both stand ages, standing aboveground biomass was 55% lower on the thinned plots (72 Mg $ha^{-1}$) than on the unthinned plots (159 Mg $ha^{-1}$), and it was 20% higher on the fertilized plots (126 Mg $ha^{-1}$) than on the unfertilized (105 Mg $ha^{-1}$) plots.

## 3.6. Aboveground biomass distribution

Percentages of standing aboveground biomass allocated to stem, branch, and foliage mass were significantly affected by stand age (fifth table in Appendix A). Between ages 14 and 17 years, the relative amount (%) of standing aboveground biomass allocated to stem mass increased by 4%, while those allocated to branch and foliage mass each decreased by 2% (Fig. 10). Across the 2 years, thinning significantly increased the relative distribution of biomass to foliage and branches by 4 and 6%, respectively, and decreased that to the stem by 10%. Fertilization did not significantly shift the relative distribution of stem, branch, and foliage mass. Percentages of standing aboveground biomass allocated to stem and branch mass ($P = 0.0574$ and 0.0157, respectively) were significantly affected by an interaction between thinning and stand age. Between ages 14 and 17 years on the unthinned plots, the percentage of standing aboveground biomass allocated to the stem increased from 82 to 87% and that allocated to branches decreased from 9 to 6%. In contrast, between ages 14 and 17 years on the thinned plots, the percentage of standing aboveground biomass allocated to the stem increased from 72 to 75% but that allocated to branches was unchanged at 14%.

## 3.7. Projected leaf area index

The effects of thinning and fertilization on LAI were significant (sixth table in Appendix A). Across the

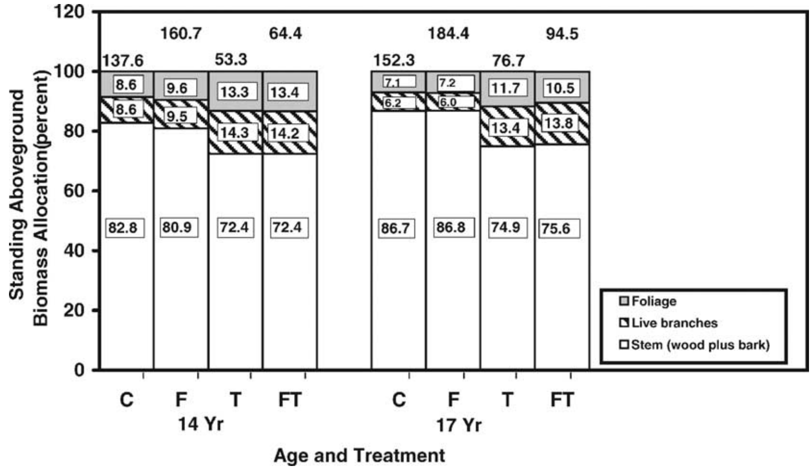


Fig. 10. Distribution of standing aboveground dry biomass (%) of 14- and 17-year-old plantation loblolly pine in response to four silvicultural treatments in Rapides Parish, LA. Numbers within bars are percentages of dry biomass as foliage, live branches and stem (outside bark). Numbers above bars are the absolute standing crop of the three aboveground biomass components combined. Silvicultural treatments are unthinned unfertilized (C), unthinned and fertilized at ages 7 and 14 years (F), thinned at ages 7 and 14 years and unfertilized (T), and thinned and fertilized at ages 7 and 14 years (FT).

7-year study period, mean LAI on the unthinned plots was 5.1 $m^2\,m^{-2}$, and that on the thinned plots was 3.4 $m^2\,m^{-2}$. During this time, fertilization increased LAI on the unthinned plots by 43% from 4.2 to 6.0 $m^2\,m^{-2}$, and on the thinned plots by 23% from 3.0 to 3.7 $m^2\,m^{-2}$. Stand age did not have a significant main effect on LAI. This suggests that before retreatment at age 14 years, LAI had achieved equilibrium values for one or more treatments (Fig. 11). Rethinning at age 14 years caused a significant interaction between thinning and stand age. On the unthinned plots, LAI at age 15 years was significantly greater than LAI at all stand ages except ages 14 and 16 years. On the thinned plots, LAI at age 15 years was significantly less than that at stand ages 13, 14 and 16–18 years.

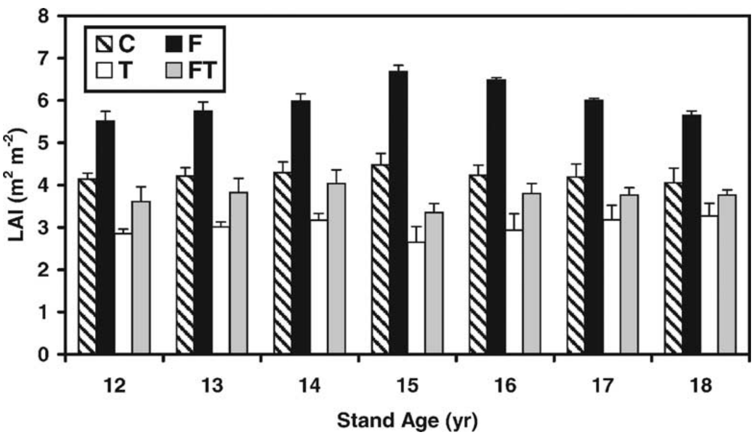


Fig. 11. Annual peak projected leaf area index ($m^2\,m^{-2}$) of plantation loblolly pine between ages 12 and 18 years in response to four silvicultural treatments in Rapides Parish, LA. Silvicultural treatments are unthinned and unfertilized (C), unthinned and fertilized at ages 7 and 14 years (F), thinned at ages 7 and 14 years and unfertilized (T), and thinned and fertilized at ages 7 and 14 years (FT). Bars represent the standard error of the means.

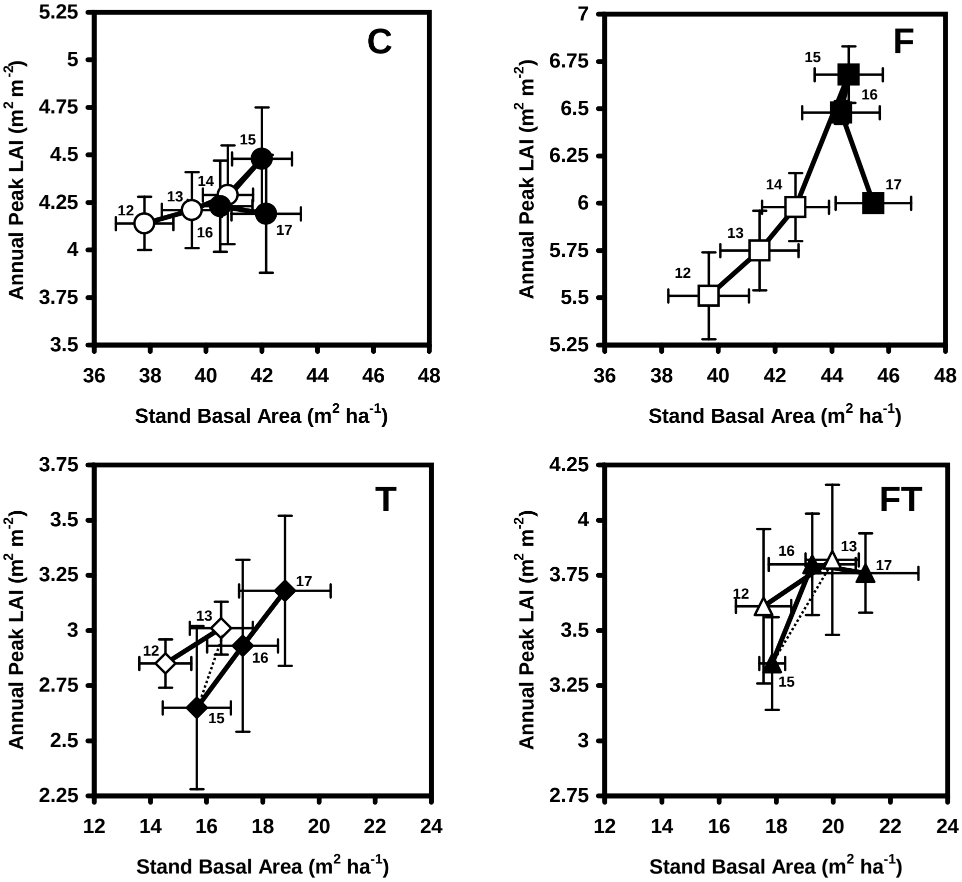


Fig. 12. Relationship between annual peak projected leaf area index ($m^2\ m^{-2}$) and stand basal area ($m^2\ ha^{-1}$) of loblolly pine between ages 12 and 17 years in response to four silvicultural treatments in Rapides Parish, LA. Silvicultural treatments are unthinned and unfertilized (C), unthinned and fertilized at ages 7 and 14 years (F), thinned at ages 7 and 14 years and unfertilized (T), and thinned and fertilized at ages 7 and 14 years (FT). Unfilled and filled symbols represent data before and after the reapplication of treatments, respectively, at age 14 years. Stand age is noted beside the symbols. Tree dbh was not measured immediately before thinning at age 14 years, so stand basal area at age 14 years was not available on the thinned plots. Bars represent the standard error of the means.

### *3.8. Relationship between LAI and stand basal area*

On the unthinned plots between ages 12 and 15 years, LAI increased with stand basal area (Fig. 12). At age 15 years, maximum values of LAI (C: 4.5 $m^2\ m^{-2}$; F: 6.7 $m^2\ m^{-2}$) were attained at stand basal areas of 42 and 45 $m^2\ ha^{-1}$ on the C and F plots, respectively. In the subsequent year, decreases in both LAI (C: 5.6%; F: 3.0%) and stand basal area (C: 3.6%; F: 0.6%) occurred. Between ages 16 and 17 years, increases in stand basal area from 40.5 to 42.2 $m^2\ ha^{-1}$ on the C plots and from 44.3 to 45.5 $m^2\ ha^{-1}$ on the F plots occurred with maintenance of LAI at 4.2 $m^2\ m^{-2}$ on the C plots and a 7.7% decrease in LAI from 6.5 to 6.0 $m^2\ m^{-2}$ on the F plots.

During the second year before and after retreatment on the thinned plots, LAI increased with stand basal area (Fig. 12). In the third year after retreatment, increases in stand basal area from 17.3 to 18.8 $m^2\ ha^{-1}$ on the T plots and from 19.3 to 21.1 $m^2\ ha^{-1}$ on the FT plots occurred with an increase in LAI from 2.9 to 3.2 $m^2\ m^{-2}$ on the T plots and maintenance of LAI at 3.8 $m^2\ m^{-2}$ on the FT plots.

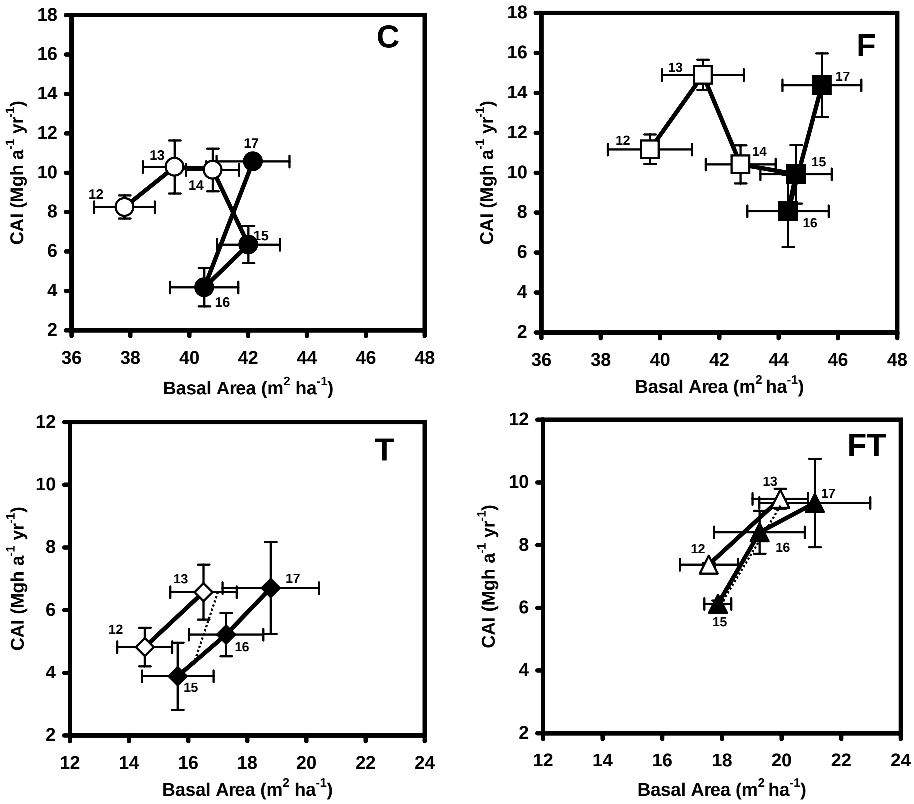


Fig. 13. Relationship between stem current annual increment (Mg ha$^{-1}$ per year) and basal area (m$^2$ ha$^{-1}$) of loblolly pine between ages 12 and 17 years in response to four silvicultural treatments in Rapides Parish, LA. Silvicultural treatments are unthinned and unfertilized (C), unthinned and fertilized at ages 7 and 14 years (F), thinned at ages 7 and 14 years and unfertilized (T), and thinned and fertilized at ages 7 and 14 years (FT). Unfilled and filled symbols represent data before and after the reapplication of treatments, respectively, at age 14 years. Stand age is noted beside the symbols. Tree dbh and height were not measured immediately before thinning at age 14 years, so stand basal area and CAI data at age 14 years were not available on the thinned plots. Bars represent the standard error of the means.

### *3.9. Relationship between CAI and stand basal area*

Relationships between CAI and stand basal area were similar for the unfertilized and fertilized plots within each level of thinning (Fig. 13). By age 13 years, CAI reached 10.3 and 14.9 Mg ha$^{-1}$ per year, and basal areas were 39.5 and 41.5 m$^2$ ha$^{-1}$ on the C and F plots, respectively. Between ages 13 and 15 years, CAI decreased from 10.3 to 6.3 Mg ha$^{-1}$ per year and from 14.9 to 9.9 Mg ha$^{-1}$ per year on the C and F plots, respectively, and stand basal area increased from 39.5 to 42.0 m$^2$ ha$^{-1}$ and from 41.5 to 44.6 m$^2$ ha$^{-1}$ on the C and F plots, respectively. Between ages 15 and 16 years, further declines in CAI (C: 34%; F: 19%) occurred together with losses in stand basal area (C: 4%; F: 1%). After this 3-year period of decline, CAI increased from 4.2 to 10.6 Mg ha$^{-1}$ per year and from 8.1 to 14.4 Mg ha$^{-1}$ per year on the C and F plots, respectively, and stand basal area increased from 40.5 to 42.2 m$^2$ ha$^{-1}$ and from 44.3 to 45.5 m$^2$ ha$^{-1}$ on the C and F plots, respectively, between ages 16 and 17 years. On the thinned plots, CAI increased from 4.8 to 6.6 Mg ha$^{-1}$ per year and from 7.4 to 9.5 Mg ha$^{-1}$ per year on the T and FT plots, respectively, and basal area increased from 14.5 to 16.5 m$^2$ ha$^{-1}$ and from 17.6 to 20.0 m$^2$ ha$^{-1}$ on the T and FT plots, respectively, between ages 12 and 13 years. Rethinning at age 14 years reduced CAI and stand basal area between ages 13 and 15 years. Between ages 15 and 17 years, pre-thinning values of CAI were attained with 72 and 20% increases in CAI and stand basal area, respectively, on the T plots and 53 and 18% increased in CAI and stand basal area, respectively, on the FT plots.

### 3.10. Relationship between CAI and LAI

With data from all four treatment combinations, our final model to predict CAI from LAI is

$$CAI = 11.769(1 - \exp(-0.0507\,LAI^{2.349})) \quad (4)$$

(Fig. 14A). The root mean squared error of the equation is 2.325 Mg ha$^{-1}$ per year, and the corrected $r^2$ is 0.46. The equation is asymptotic, suggesting that CAI will increase with LAI up to some point after which additional LAI provides a negligible increase in CAI. For our data, CAI increases negligibly after LAI exceeds 5 m$^2$ m$^{-2}$; however, we have little data at a LAI of 5 m$^2$ m$^{-2}$, so this threshold may not be well established. On the unthinned plots, fertilization allowed LAI to surpass 6 m$^2$ m$^{-2}$. As LAI exceeded 5 m$^2$ m$^{-2}$, however, CAI appeared to plateau at 10 Mg ha$^{-1}$ per year. On the thinned plots, fertilization increased both LAI and CAI, but appeared to widen the range of CAI at any given of LAI. Although stand basal area was 54% lower on the FT plots than on the C plots, values of CAI were similar.

Across the treatment combinations, there was no consistent relationship between stand age and CAI, and CAI varied two- to four-fold at any given LAI (Fig. 14B). Much of this variance seemed to be due to year-to-year fluctuations in stand conditions. For example, extreme drought at age 15 years was associated with reduced and more variable CAI at ages 15 and 16 years than at ages 13, 17 and 18 years. This suggests that our model would be improved by adding a variable to account for the occurrence and severity of drought.

Within each thinning treatment, a significant quadratic relationship was found between CAI and LAI. On the unthinned plots, this relationship is $CAI = -23.521 + 12.07(LAI) - 1.0425(LAI^2)$ ($r^2 = 0.2506$, $P = 0.0036$). It is characterized by substantial variation in CAI for any given value of LAI. Lower values of both LAI and CAI occurred on the C plots than on the F plots (Fig. 15A). On the thinned plots, this relationship is $CAI = -24.728 + 16.579(LAI) - 2.058(LAI^2)$ ($r^2 = 0.6136$, $P = 0.0001$) (Fig. 15B). In the T and FT plots, the variability of CAI is reduced for all levels of LAI compared with the C and F plots (Figs. 14 and 15). This suggests that year-to-year variation in CAI increases as stand basal area and LAI increase.

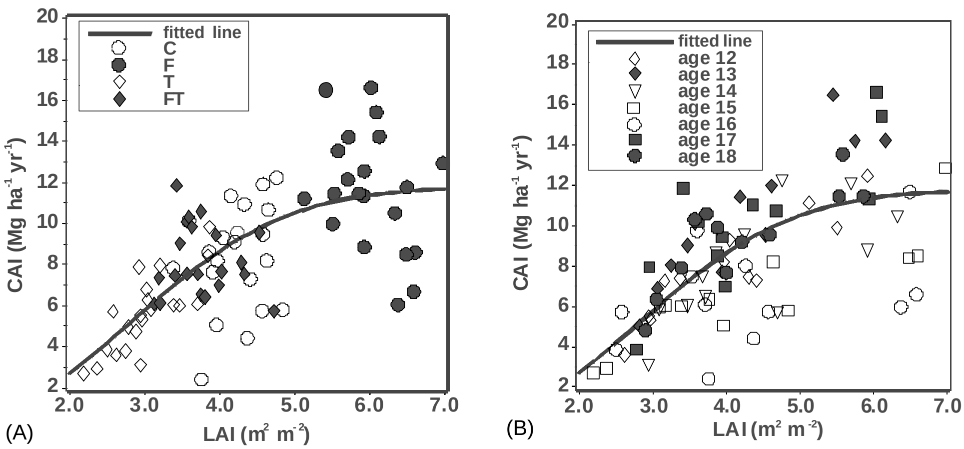


Fig. 14. Relationships between stem current annual increment (Mg ha$^{-1}$ per year) and annual peak projected leaf area index (m$^2$ m$^{-2}$) of loblolly pine between ages 12 and 18 years (A) in response to four silvicultural treatments, and (B) by stand age in Rapides Parish, LA. Silvicultural treatments are unthinned and unfertilized (C), unthinned and fertilized at ages 7 and 14 years (F), thinned at ages 7 and 14 years and unfertilized (T), and thinned and fertilized at ages 7 and 14 years (FT). Tree dbh and height were not measured immediately before thinning at age 14 years, so CAI at age 14 years was not available on the thinned plots.

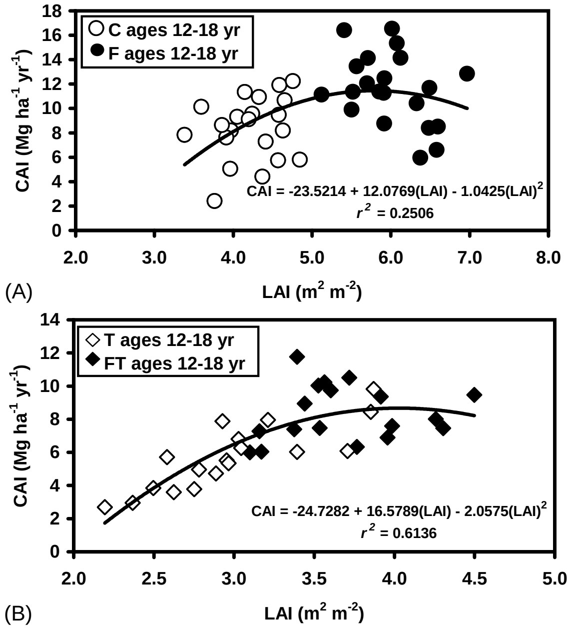


Fig. 15. Relationships between stem current annual increment (Mg ha$^{-1}$ per year) and annual peak projected leaf area index (m$^2$ m$^{-2}$) of loblolly pine between ages 12 and 18 years in Rapides Parish, LA (A) on the unthinned plots (unthinned and unfertilized (C); unthinned and fertilized at ages 7 and 14 years (F)), and (B) on the thinned plots (thinned at ages 7 and 14 years and unfertilized (T); thinned and fertilized at ages 7 and 14 years (FT)). Tree dbh and height were not measured immediately before thinning at age 14 years, so CAI at age 14 years was not available on the thinned plots.

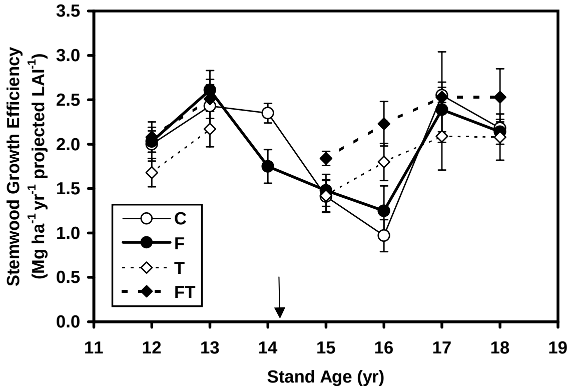


Fig. 16. Stemwood growth efficiency (Mg ha$^{-1}$ per year LAI$^{-1}$) of loblolly pine between ages 12 and 18 years in response to four silvicultural treatments in Rapides Parish, LA. Silvicultural treatments are unthinned and unfertilized (C), unthinned and fertilized at ages 7 and 14 years (F), thinned at ages 7 and 14 years and unfertilized (T), and thinned and fertilized at ages 7 and 14 years (FT). Tree dbh and height were not measured immediately before thinning at age 14 years, so growth efficiency at age 14 years was not available on the thinned plots. Bars represent the standard error of the means.

### *3.11. Growth efficiency*

Growth efficiency varied significantly with stand age but with no consistent trend (sixth table in Appendix A). The highest values of GE occurred at ages 13, 17, and 18 years, and the lowest values occurred at ages 15 and 16 years (Fig. 16). Interaction between thinning and stand age significantly affected GE with a significantly higher GE on the thinned plots than on the unthinned plots at age 16 years. The FT plots between ages 15 and 18 years provided the most consistently high GE.

## 4. Discussion

Production of loblolly pine on a West Gulf Coastal Plain site was affected by stand density, soil nutrition, and climate during the 7-year period between ages 11 and 17 years. Specifically, the effects of light, mineral nutrient, and water availabilities on foliage production appeared partially responsible for the dynamics of aboveground biomass production, CAI, and biomass distribution among stemwood, branches, and foliage. Stand environment also appeared to influence stand productivity, especially in years of extreme drought such as age 15 years when values of CAI at ages 15 and 16 years were low.

Two conditions of our study made it possible to investigate the mechanisms by which loblolly pine stand productivity responded to silvicultural- and climate-induced changes in foliage production. First, reapplication of the fertilization treatments midway through our 7-year observation period allowed us to study stand productivity responses before and after leaf area responses to N and P addition on a N- and P-deficient site. Second, the last 3 years of our study were characterized by annual water deficits that were 145% higher than in the prior 4 years. This permitted observation of plantation loblolly pine productivity in four stand environments during an initial 4-year period of low water deficit followed by 3 years of extreme drought.

### 4.1. Stand development

Distinct differences in the proportion of aboveground biomass allocated to stem, branch, and foliage components between ages 14 and 17 years indicate that individual trees in our unthinned plots were light-limited. On these plots, biomass distributed to the stem increased from 82 to 87% and biomass distributed to the foliage was unchanged across the study between ages 14 and 17 years. Although the proportion of branch mass was unchanged on the thinned plots, that on the unthinned plots decreased from 9 to 6% during this 4-year period (Fig. 10). The simultaneous occurrence of higher relative biomass distribution to the stem, lower relative biomass distribution to the branches and a 10% decrease in stem density from 2613 to 2359 trees $ha^{-1}$ between ages 14 and 17 years suggests that the unthinned plots experienced natural pruning and thinning in response to light levels below the light compensation point. Stand densities also indicate that the unthinned plots were very dense even at the start of our study; at age 11 years, the relative stand density indices of the C and F plots were 85 and 86%, respectively, greatly exceeding the value of 50% associated with the initiation of density-related mortality in loblolly pine stands (Dean and Baldwin, 1993).

Fertilization in fully stocked stands has been observed to stimulate the mortality of trees in the suppressed crown class of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations (Mitchell et al., 1996). Fertilization appears to have had the same effect in the unthinned plots of this study. Whereas tree mortality in the C plots was distributed among all diameter classes below the median diameter class, tree mortality in the F plots was concentrated in the three smallest diameter classes (Fig. 4). One mechanism responsible for the increase in suppression-related mortality with fertilization may be greater extinction of light through the canopy as a result of higher leaf area (Gholz et al., 1991). Smaller canopy gaps and more rapid colonization of canopy gaps by new foliage may have increased canopy-level light-use efficiency and therefore, resulted in a positive effect of fertilization on stand productivity.

### 4.2. Stand productivity

Previous research has documented the positive effects of fertilization on plantation loblolly pine aboveground productivity (Vose and Allen, 1988; Colbert et al., 1990; Haywood and Burton, 1990; Haywood and Tiarks, 1990; Dalla-Tea and Jokela, 1991; Haywood et al., 1997; Albaugh et al., 1998; Jokela and Martin, 2000; Borders and Bailey, 2001; Retzlaff et al., 2001; Samuelson et al., 2001). We also found that fertilization increased aboveground stand productivity. By age 17 years, fertilization increased gross stem mass by 27.1 Mg $ha^{-1}$ (24%) on the unthinned plots and by 17.0 Mg $ha^{-1}$ (22%) on the thinned plots. The magnitude of this difference increased with stand age (Fig. 6). Tree height and diameter class distribution also show that the effect of fertilization on stand productivity increased with stand age. Specifically, fertilization increased tree height by 0.7 m (6%) and 0.3 m (3%) at age 11 years, and by 1.8 m (12%) and 1.9 m (12%) at age 17 years on the unthinned and thinned plots, respectively. By age 17 years, fertilization also increased the proportion of trees in higher diameter classes on both the unthinned and thinned plots. Similar temporal patterns of loblolly pine productivity in response to fertilization have been reported (Haywood et al., 1997; Jokela and Martin, 2000; Borders and Bailey, 2001).

### 4.3. Basic ecophysiological relationships

#### 4.3.1. Foliage production and stand productivity

Positive effects of fertilization on pine productivity have been linked to increases in net photosynthesis and foliage production (Sheriff et al., 1986; Vose and Allen, 1988; Vose et al., 1994; Murthy et al., 1997; Albaugh et al., 1998; Jokela and Martin, 2000). However, the response of loblolly pine net photosynthesis to fertilization is inconsistent. Murthy et al. (1997) found that fertilization stimulated loblolly pine net photosynthesis. Others have found no effect of fertilization on loblolly pine net photosynthesis (Samuelson, 1998;

Samuelson et al., 2001; Maier et al., 2002). At our study site, Tang et al. (1999) also found that loblolly pine net photosynthesis at age 13 years was not affected by fertilization. Teskey et al. (1994) suggest that these inconsistent responses are due to the maintenance or creation of nutrient imbalances after fertilization.

At our study site, fertilization increased LAI, and positive relationships between CAI and LAI, and between stand basal area and LAI, were apparent. Similar to the findings of other scientists (Vose and Allen, 1988; Colbert et al., 1990; Vose et al., 1994; Albaugh et al., 1998; Jokela and Martin, 2000; Samuelson et al., 2001), greater total tree photosynthesis resulting from increased leaf area appears to be the most likely variable driving stand production at our study site. Further evaluation of leaf area and stand production relative to annual trends in stem density, water deficit, and foliar nutrition provide insight into the ecophysiological processes controlling loblolly pine production over the 7-year period of our study.

Annual trends in stand basal area and CAI on the unthinned plots illustrate interactive effects of water deficit and fertilization on stand productivity between ages 11 and 17 years. Between ages 11 and 15 years, for example, progressive increases in basal area of 5.8 $m^2$ $ha^{-1}$ (16%) and 6.9 $m^2$ $ha^{-1}$ (18%) on the C and F plots coincided with small amounts of annual mortality (C: 122 trees $ha^{-1}$ (4.3%); F: 183 trees $ha^{-1}$ (6.8%)). In the subsequent year, 1996, 42% less precipitation (874 mm) fell than the annual average precipitation of the previous 4 years (1511 mm) (Fig. 1). The resulting high annual water deficit coincided with increased tree mortality and resulted in 7.5 and 5.6% decreases in stem density between ages 15 and 16 years on the C and F plots, respectively. By age 17 years, positive trends in stand basal area growth were resumed on the C and F plots, but a net gain in stand basal area between ages 15 and 17 years was apparent only on the F plots (Fig. 3). Between ages 14 and 16 years, declining trends in CAI were also apparent on both the C and F plots (Fig. 7). However, CAI of the F plots decreased more slowly than CAI of the C plots.

Density-driven competition for light, water, and mineral nutrients may have led to declines in stand basal area and CAI on the unthinned plots. We hypothesize that fertilization curbed the chronic N and P deficiencies that limited foliage production on the unthinned plots, and therefore, increased values of LAI on the F plots compared to the C plots. We further propose that refertilization at age 14 years hastened foliage production and led to a more rapid recovery of positive stemwood growth on the F plots compared to the C plots.

Refertilization at age 14 years also appeared to slow the rate of CAI decline on the thinned plots between ages 13 and 15 years (Fig. 7). Again, reestablishment of foliar N and P sufficiency, and maintenance of higher values of LAI with refertilization at age 14 years probably stimulated canopy-level carbon fixation so that negative trends in stand productivity were less severe on the FT plots than on the T plots. Furthermore, the small size of our treatment plots seemed to result in some fertilizer drift from the treated to the untreated plots, which increased foliar N, P, and K after refertilization on the C and T plots (Table 2). Responses to fertilization in this study may have been more pronounced if fertilizer drift was eliminated.

### 4.4. Foliage production and wood quality

Interaction between water deficit and fertilization may have had a minor effect on wood quality. Specifically, small but distinct decreases in ELW and increases in SG were observed at ring ages of 6, 11, and 12 years (Fig. 8). These ring ages coincided with the application of thinning and fertilization treatments at ages 7 and 14 years, and an extreme drought at age 15 years. An increase in evaporative demand caused by either foliage production in response to fertilization or drought, may have created water stress conditions that hastened the transition from earlywood to latewood production. Similarly, Cregg et al. (1988) observed that an increase in evaporative demand and a decrease in water availability promoted the latewood initiation of loblolly pine on a southeastern Oklahoma site. Alternatively, lower ELW and higher SG could be attributed to extension of latewood growth during the fall of years with treatment-induced increases in light, water and mineral nutrient availabilities. These ring age effects were short-lived, however, and had little effect on overall wood quality.

### 4.5. Mineral nutrition

In our study, fertilization with N and P was done at ages 7 and 14 years using operational application guidelines and methods (Tiarks, 1982; Shoulders and Tiarks, 1983). Immediately before refertilization at age 14 years, dormant-season foliar N and P concentrations were 11.2 and 0.96 mg $g^{-1}$, respectively (Table 2). These foliar N and P values are below the critical concentrations of 12.0 mg $g^{-1}$ N and 1.0 mg $g^{-1}$ P for loblolly pine (Allen, 1987; Schultz, 1997). Refertilization increased foliar N but this effect decreased over time and foliar N approached the critical value of 12.0 mg $g^{-1}$ by age 17 years. Although foliar P averaged among crown levels appeared sufficient at this time, by age 17 years, foliar P in the lower crown approached the critical value of 1.0 mg $g^{-1}$ P which was primarily due to a reduction in foliar P from 1.27 to 0.99 mg $g^{-1}$ on the FT plots between ages 16 and 17 years. When drought reduces the acquisition of water and mineral nutrients by roots, less P may be distributed to foliage in the lower crown than the upper crown, or P may be preferentially mobilized from lower crown foliage to support the P needs elsewhere in the crown. Wells and Allen (1985) note that loblolly pine growth rates generally return to prefertilized rates 5–8 years after N addition, and Pritchett and Gooding (1975) suggest that refertilization with P may be required every 15 years on Coastal Plain sites. At our site, high rates of aboveground growth show the potential need for more frequent N and P application than generally recommended. Specifically, N additions may be needed as often as every 3 years while P additions may be needed every 3–5 years.

We also found that by age 14 years, the foliar K concentrations of all four treatments approached the critical value of 3.5 mg $g^{-1}$ recommended by Allen (1987) for loblolly pine. However, foliar K of all four treatments was sufficient for the 3-year period after refertilization. In a nearby loblolly pine study, a negative relationship between foliar K and tannin concentration was observed with N and P fertilization but was absent on the unfertilized plots (Sword et al., 1998). Sword et al. (1998) also found that without herbaceous weed control, available K in the soil decreased. This information indicates that with intensive forest management on the West Gulf Coastal Plain, the supply of K may need more attention in the future.

### 4.6. Growth efficiency and the relationship between stand productivity and LAI

Several studies have documented an increase in loblolly pine GE in response to fertilization (Colbert et al., 1990; Albaugh et al., 1998; Jokela and Martin, 2000). Similar to Samuelson et al. (2001), we found no significant effect of fertilization on loblolly pine GE. We did, however, observe a non-significant trend for higher GE on the FT plots compared to the T plots at ages 15 and 16 years (Fig. 16). Extreme drought at age 15 years and its effect on the variation associated with CAI at ages 15 and 16 years may have precluded detection of a concurrent effect of fertilization on the GE of the thinned plots.

Throughout our 7-year study, stand conditions that led to mortality on the unthinned plots and stand conditions that allowed the trees on the thinned plots to better endure high water deficit appeared to be the primary factors that affected GE. On the unthinned plots, for example, decreases in GE between ages 13 and 15 years occurred as tree mortality caused a decrease in CAI and an increase in LAI with the growth of new foliage into canopy gaps (Fig. 16). Higher GE on the thinned plots than on the unthinned plots at age 16 years was due to stand conditions that led to increases in both CAI and LAI on the thinned plots during the 2-year period after rethinning. We suggest that thinning allowed the residual trees to better endure the poorer growing conditions that occurred in 1996.

When CAI and LAI from across our study site were combined, stand productivity appeared to be largely determined by leaf area. We found a common regression line across all four treatments (Fig. 14A). Our estimation of an asymptotic relationship between LAI and CAI differs from the simple linear relationships found by Jokela and Martin (2000) and Albaugh et al. (1998), although the maximum LAI in those studies was less than in ours. At our study site, CAI did not increase linearly with LAI except over a relatively narrow range of LAI (i.e., 2–4 $m^2$ $m^{-2}$). Harper (1977, pp. 315–318) describes the relationship between LAI and yield as a parabola truncated at a suboptimal maximum. There may be a small decrease in our data between LAI of 6 and 7 $m^2 m^{-2}$, but we would need more observations at LAI greater than 6 $m^2 m^{-2}$ to reliably estimate such a curve. Dean and Baldwin (1996) observed similar results for a loblolly pine plantation in southwestern Louisiana.

Considering the combined data from the unthinned and thinned plots, there seems to be little reason to maintain LAI over 5 $m^2 m^{-2}$. However, additional data at LAI values of 5 $m^2 m^{-2}$ are needed to validate this proposition. Sampson et al. (1998) indicated that the optimal LAI for loblolly pine is in the range of 3.0–3.5 $m^2 m^{-2}$, but this was based upon a simulation model rather than actual data. Jarvis and Leverenz (1983) suggested that increasing LAI over 6 $m^2 m^{-2}$ would negligibly affect the interception of radiation. From a practical standpoint, this information indicates that LAI may be a useful guide in stand density management. Also, the CAI–LAI relationship could be used as an index of site quality. By knowing LAI and measuring CAI at a fixed point in time, one could specify site productivity with a suite of CAI–LAI curves. A significant problem would be normalizing CAI across stand conditions such as climate, age, and stand ontogeny. The CAI–LAI relationship then could be used in both stand density management and site quality evaluation.

The classical progression of LAI through time is characterized by an increase to a peak followed by a gradual decrease (Jarvis and Leverenz, 1983; Kozlowski et al., 1991, pp. 116–117). Our highest values of LAI are 6.7 and 6.5 $m^2 m^{-2}$ for the F plots at ages 15 and 16 years, respectively. On these plots, LAI decreased to 6.0 $m^2 m^{-2}$ by age 17 years and CAI increased from 8.1 to 14.4 Mg $ha^{-1}$ per year between ages 16 and 17 years. New foliage growth on the F plots between ages 15 and 17 years did not balance the loss of LAI during this 3-year period. We suggest that density-related mortality associated with high water deficit and subsequent foliage growth into canopy gaps increased canopy-level light-use efficiency and resulted in higher CAI at age 17 years than at ages 15 and 16 years.

Jokela and Martin (2000) produced different regression lines for the CAI–LAI relationship of loblolly pine at different ages. In our study while age is clearly important, it appears that year-to-year stand conditions conducive to high GE affected the CAI–LAI relationship rather than stand age, per se. Values of GE at ages 13, 17, and 18 years were higher than those at the other ages and in these years, the relationship between LAI and CAI was more linear than when all data were combined (Fig. 14B). Again, stand conditions promoting density-related mortality, and tolerance of high water deficit seemed to be the key factors that influenced both GE and the CAI–LAI relationship.

On the thinned plots alone, relationships between LAI and stand productivity between ages 15 and 17 years indicate that carbon gain and relative carbon distribution may have changed after refertilization. When compared to the T plots, the FT plots exhibited higher values of LAI at age 15 years (26%) and at age 16 years (30%) (Fig. 11). However, between ages 15 and 17 years, basal area gains (T: 3.1 $m^2 ha^{-1}$; FT: 3.3 $m^2 ha^{-1}$), and CAI gains (T: 2.8 Mg $ha^{-1}$; FT: 3.2 Mg $ha^{-1}$) on these plots were similar (Figs. 12 and 13). This suggests that although loblolly pine productivity is a function of LAI (Vose and Allen, 1988; Colbert et al., 1990; Vose et al., 1994; Albaugh et al., 1998; Jokela and Martin, 2000; Samuelson et al., 2001), this relationship is not linear. The regression equations that describes the relationship between CAI and LAI on our thinned plots show that CAI and LAI were directly related until a LAI of approximately 3.5 $m^2 m^{-2}$ (Fig. 15B). Values of LAI greater than 3.5 $m^2 m^{-2}$ were associated with little change in CAI. Perhaps as LAI exceeded 3.5 $m^2 m^{-2}$ on our thinned plots, crown structural and foliage density responses to fertilization reduced photosynthetically active radiation and carbon fixation in the lower canopy. Alternatively, stand conditions such as high water deficit and increased evaporative demand could have decreased canopy-level carbon fixation or caused a shift in carbon distribution among plant components.

## 5. Conclusions

Our research results support the overall conclusion that leaf area is an important factor that controls loblolly pine productivity. Stand conditions, however, altered this relationship at our study site in two ways. First, stand conditions that reduced GE apparently introduced variability into the relationship between CAI and LAI. Second, we found an asymptotic rather than simple linear relationship between CAI at LAI. Specifically, when data from all treatment combinations were considered, CAI increased linearly with LAI between 2 and 4 $m^2 m^{-2}$, but values of LAI greater than 5 $m^2 m^{-2}$ did not seem to benefit stemwood growth. Furthermore, on the thinned plots, it appeared that there was little increase in CAI at LAI greater than 3.5 $m^2 m^{-2}$.

Stand conditions associated with density-related mortality in response to competition for light and water, and nutrition-limited foliage growth appeared to be the primary factors controlling GE and the variability and asymptotic nature of the CAI–LAI relationship at our study site. The thinning treatment improved stand conditions by increasing light availability. This led to greater live-crown lengths, larger tree diameters, and maintenance of vigorous growth as indicated by CAI–MAI and standing aboveground biomass relationships. Fertilization affected stand conditions by increasing the availability of N, P, and K, which had a strong positive effect on foliage production and subsequently, stand productivity. We also observed a subtle effect of fertilization on stand development that may have increased productivity. Specifically, with fertilization, tree mortality occurred among trees of lower diameter, and the smaller size of the associated canopy gaps may have facilitated higher canopy-level light-use efficiency as new foliage was produced in response to fertilization.

Although the general relationship between leaf area and loblolly pine productivity is well-founded our research results indicate that this relationship varies by stand conditions. Light limitations to this relationship occur across the loblolly pine range and are initially remedied by weed control and later by thinning. However, mineral nutrient and water limitations that affect this relationship may be site- or region-specific. For example, we found that N, P, and K sufficiencies at our study site required fertilization more often than is generally recommended. Furthermore, canopy-level carbon fixation may have been reduced in response to large evaporative demands caused by interaction between higher water deficit and leaf area growth in response to refertilization. Because a static relationship between leaf area and loblolly pine productivity does not appear to universally apply to all sites and all ages, further research is needed to better define this relationship in the western Gulf region and across the range of loblolly pine.

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## Appendix A

Probabilities of a greater *F*-value for the stand development variables of the loblolly pine plantation in central Louisiana between ages 14 and 17 years in response to two levels each of thinning and fertilization at ages 7 and 14 years

| Effect | Degrees of freedom | Tree height | Stem density | Stand basal area |
|---|---|---|---|---|
| Thinning (T) | 1 | 0.1960 | 0.0001 | 0.0001 |
| Fertilization (F) | 1 | 0.0081 | 0.1532 | 0.0427 |
| T × F | 1 | 0.8979 | 0.3446 | 0.9696 |
| Age (A) | 6 | 0.0001 | 0.0001 | 0.0001 |
| T × A | 6 | 0.0004 | 0.0001 | 0.0001 |
| F × A | 6 | 0.0001 | 0.8644 | 0.8988 |
| T × F × A | 6 | 0.9948 | 0.9303 | 0.4705 |

Probabilities of a greater *F*-value for the stand productivity variables of the loblolly pine plantation in central Louisiana between ages 14 and 17 years in response to two levels each of thinning and fertilization at ages 7 and 14 years

| Effect | Degrees of freedom | Gross stem mass | Standing stem mass | log(CAI[a])[b] | log(MAI[a])[b] |
|---|---|---|---|---|---|
| Thinning (T) | 1 | 0.0001 | 0.0001 | 0.0025 | 0.0002 |
| Fertilization (F) | 1 | 0.0209 | 0.0151 | 0.0071 | 0.0322 |
| T × F | 1 | 0.4221 | 0.3680 | 0.7278 | 0.7982 |
| Age (A) | 6 | 0.0001 | 0.0001 | 0.0001 | 0.0001 |
| T × A | 6 | 0.0001 | 0.0001 | 0.0001 | 0.2975 |
| F × A | 6 | 0.0001 | 0.0013 | 0.0795 | 0.0001 |
| T × F × A | 6 | 0.9794 | 0.4627 | 0.7200 | 0.7893 |

[a] CAI, current annual increment; MAI, gross mean annual increment.
[b] To establish normality, analyses of CAI and MAI were conducted on values that were transformed to natural logarithms.

Probabilities of a greater $F$-value for wood quality variables of two or three trees of quadratic mean diameter (±1.27 cm) per plot of the loblolly pine plantation in central Louisiana in response to two levels each of thinning and fertilization at ages 7 and 14 years. Data associated with 3- to 19-year-old growth rings were included in the analysis

| Effect | Degrees of freedom | SG[a] | log(ELW[a])[b] |
|---|---|---|---|
| Thinning (T) | 1 | 0.2959 | 0.2834 |
| Fertilization (F) | 1 | 0.3265 | 0.2168 |
| T × F | 1 | 0.6595 | 0.7909 |
| Ring age (R) | 16 | 0.0001 | 0.0001 |
| T × R | 15[c] | 0.1599 | 0.0717 |
| F × R | 15 | 0.0001 | 0.0001 |
| T × F × R | 14 | 0.9003 | 0.9246 |

[a] SG, ring specific gravity; ELW, ratio of earlywood and latewood ring widths.
[b] To establish normality, analysis of ELW was conducted on values that were transformed to natural logarithms.
[c] Degrees of freedom reflect missing data at tree ring ages of 18 and 19 years.

Probabilities of a greater $F$-value for foliar mineral nutrient concentrations of the loblolly pine plantation during the dormant season in central Louisiana between ages 14 and 17 years in response to two levels each of thinning and fertilization at ages 7 and 14 years

| Effect | Degrees of freedom | $N$ | log($P$)[a] | log($K$)[a] |
|---|---|---|---|---|
| Block | 1 | 0.1957 | 0.1554 | 0.2191 |
| Crown (Cr) | 1 | 0.0246 | 0.1986 | 0.0864 |
| Age (A) | 3 | 0.0010 | 0.0015 | 0.0331 |
| Cr × A | 3 | 0.8702 | 0.0048 | 0.6505 |
| Thinning (T) | 1 | 0.2752 | 0.0329 | 0.0117 |
| Fertilization (F) | 1 | 0.7290 | 0.0001 | 0.0031 |
| T × F | 1 | 0.0439 | 0.9462 | 0.0709 |
| T × Cr | 1 | 0.5377 | 0.2951 | 0.0067 |
| F × Cr | 1 | 0.0762 | 0.0216 | 0.3174 |
| T × F × Cr | 3 | 0.7927 | 0.2062 | 0.9764 |
| T × A | 3 | 0.8912 | 0.8268 | 0.0001 |
| F × A | 3 | 0.0001 | 0.0036 | 0.0153 |
| T × F × A | 3 | 0.0377 | 0.5421 | 0.4242 |
| T × Cr × A | 3 | 0.8320 | 0.6918 | 0.1677 |
| F × Cr × A | 3 | 0.5020 | 0.9111 | 0.0556 |
| T × F × Cr × A | 3 | 0.5273 | 0.7405 | 0.0189 |

[a] To establish normality, analyses of $P$ and $K$ were conducted on values that were transformed to natural logarithms.

Probabilities of a greater $F$-value for total aboveground biomass and percentages of stem (outside bark), branch and foliage mass of 14- and 17-year-old plantation loblolly pine in central Louisiana in response to two levels each of thinning and fertilization at ages 7 and 14 years

| Effect | Degrees of freedom | Total | Stem | Branch | Foliage |
|---|---|---|---|---|---|
| Thinning (T) | 1 | 0.0001 | 0.0001 | 0.0001 | 0.0002 |
| Fertilization (F) | 1 | 0.0153 | 0.7435 | 0.6386 | 0.9804 |
| T × F | 1 | 0.3656 | 0.4306 | 0.8387 | 0.4150 |
| Age (A) | 1 | 0.0001 | 0.0001 | 0.0016 | 0.0008 |
| T × A | 1 | 0.1004 | 0.0574 | 0.0157 | 0.7472 |
| F × A | 1 | 0.0922 | 0.1784 | 0.7095 | 0.2124 |
| T × F × A | 1 | 0.7943 | 0.5109 | 0.3250 | 0.8470 |

Total: total standing aboveground biomass; Stem: percentage of standing aboveground biomass allocated to outside-bark stem mass; Branch: percentage of standing aboveground biomass allocated to branch mass; Foliage: percentage of standing aboveground biomass allocated to foliage mass.

Probabilities of a greater *F*-value for annual peak leaf area index and stemwood growth efficiency of the loblolly pine plantation in central Louisiana between ages 12 and 18 years in response to two levels each of thinning and fertilization at ages 7 and 14 years

| Effect | Degrees of freedom | log(LAI)[a] | Growth efficiency |
|---|---|---|---|
| Thinning (T) | 1 | 0.0001 | 0.7924 |
| Fertilization (F) | 1 | 0.0008 | 0.3507 |
| T × F | 1 | 0.2652 | 0.2607 |
| Age (A) | 6 | 0.1368 | 0.0001 |
| T × A | 6 | 0.0001 | 0.0001 |
| F × A | 6 | 0.5109 | 0.2417 |
| T × F × A | 6 | 0.8380 | 0.8835 |

[a] To establish normality, analysis of LAI was conducted on values that were transformed to natural logarithms.

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