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Stand development and production dynamics of loblolly pine under a range of cultural treatments in north-central Florida USA

Timothy A. Martin*, Eric J. Jokela

School of Forest Resources and Conservation, Box 110410, University of Florida, Gainesville, FL 32611-0410, USA

Abstract

The objectives of this study were to examine the effects of stand development and soil nutrient supply on processes affecting the productivity of loblolly pine (*Pinus taeda* L.) over a period approximately equal to a pulpwood rotation (18 years). The experiment consisted of a 2×2 factorial combination of complete and sustained weed control and annual fertilization treatments (C: control treatment, F: fertilization, W: weed control, FW: combined fertilization and weed control), located on a Spodosol in north-central Florida, USA. The reduction of soil nutrient limitations through fertilization or control of competing vegetation resulted in dramatic increases in almost every measure of productivity investigated, including height (19.7 m in the FW treatment versus 12.5 m in the C treatment at age 18 years), basal area (FW = 44.2 $m^2\,ha^{-1}$, F = 39.6 $m^2\,ha^{-1}$, W = 36.6 $m^2\,ha^{-1}$, C = 19.9 $m^2\,ha^{-1}$ at age 16 years), stemwood biomass accumulation (114 Mg ha^{-1} in FW versus 42.8 Mg ha^{-1} in C at age 18 years), foliar nitrogen concentration (1.53% in plots receiving fertilization versus 1.06% in unfertilized plots at age 17 years) and leaf area index (age 16-year peak projected of approximately 3.3 at age 9–10 years in F and FW plots, 2.5 in the W treatment and 1.5 in the C plots). Cultural treatments also decreased the growth ring earlywood/latewood ratio, and accelerated the juvenile wood to mature wood transition. While soil nutrient supply was a major determinant of productivity, production changes that occurred within treatments over the course of stand development were equally dramatic. For example, between age 8 and 15 years, stemwood PAI in the FW treatment declined by 275%; similarly large reductions occurred in the F and W treatments over the same time period. The reductions in PAI in the treated plots were linearly related to stand BA, suggesting the decline in productivity was associated with the onset of inter-tree competition. Responses of stemwood PAI to re-fertilization treatments at age 15 years suggests that the declines in growth and growth efficiency with time were partially attributable to nutrient limitations.
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Keywords: Fertilization; Competition; Growth efficiency; Leaf area development; Even-aged stands; Growth declines; Vegetation control

1. Introduction

The natural range of loblolly pine (*Pinus taeda* L.) is extensive, encompassing 15 southern and mid-Atlantic states from Florida to Delaware and west to eastern Texas and southeastern Oklahoma, USA. Loblolly pine is the most important commercial species in this region, and it is found on more than 13 million ha and a variety of soil types (Sheffield and Knight, 1982; Schultz, 1997).

Over the last three decades, considerable investments have been made in applied research programs with loblolly pine, emphasizing site preparation, understory competition control, fertilization, thinning,

* Corresponding author. Tel.: +1-352-846-0866; fax: +1-352-846-1277.
E-mail address: tamartin@ufl.edu (T.A. Martin).

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pest relationships, wood quality, growth and yield, and genetic tree improvement as a basis for developing sound management strategies for this species (Schultz, 1997; Martin, 1997). Intensive silvicultural practices have been commonly applied to both increase stand productivity and reduce rotation lengths throughout its native range. For example, although loblolly pine is generally adapted to the relatively infertile soils of this region, it has long been known that growth responses due to fertilizer additions, particularly nitrogen (N) and phosphorus (P), are biologically and economically justifiable (Pritchett and Smith, 1972; Pritchett and Comerford, 1982; Jokela and Stearns-Smith, 1993). Recent estimates indicate that approximately 2.35 million ha of loblolly pine were fertilized between 1969 and 1998 (NCSFNC, 1999). Woody and herbaceous competition control treatments have also been routinely used to enhance survival and growth (Creighton et al., 1987; Shiver et al., 1990; Miller et al., 1991; Jokela et al., 2000).

A large number of process-level research investigations have similarly been conducted to understand the production ecology and ecophysiology of loblolly pine (e.g., Bormann, 1953; Brix, 1962; Kinerson et al., 1974; Teskey et al., 1987; Dalla-Tea and Jokela, 1994; Albaugh et al., 1998; Ellsworth, 2000; Samuelson et al., 2001; Will et al., 2001). Nevertheless, the impacts of intensive management practices on processes affecting stand development and productivity are still inadequately understood for this species because comprehensive experiments that span the range from establishment to maturity (e.g., pulpwood rotations) are limited.

In 1983, the Intensive Management Practices Assessment Center (IMPAC), located at the University of Florida, designed and established a study to evaluate the biological growth potential of loblolly and slash (*Pinus elliottii* var. *elliottii*) pines. A factorial combination of treatments, including annual fertilizer applications and sustained elimination of understory competition was used to manipulate growth limiting environmental factors (Swindel et al., 1988). This experiment, established at the southern limit of the commercial range of loblolly pine in the southeastern USA, has been extensively studied over the last 18 years to document the effects of nutrient amendments and understory competition control on biomass accumulation and distribution, leaf area development, canopy light interception, growth efficiency and nutrient cycling processes (Swindel et al., 1988, 1989; Neary et al., 1990; Colbert et al., 1990; Dalla-Tea and Jokela, 1991; Escamilla et al., 1991; Polglase et al., 1992a,b,c,d; Grierson et al., 1998, 1999; Martin, 2000; Jokela and Martin, 2000).

Comparative studies that examine variation in growth performance for a range of silvicultural treatments and site types are essential for improving our ability to assess biological growth potential, understand growth strategies, and responsiveness to management inputs (Adegbidi et al., 2002). The objectives of this paper are to synthesize results from the IMPAC experiment and address the long-term effects of intensive silvicultural treatments on processes affecting the productivity of loblolly pine stands growing on Spodosols in north-central Florida. To accomplish this objective, we examined and compared patterns of stand development, biomass accumulation and distribution, wood quality characteristics, and ecophysiological relationships associated with leaf area and growth efficiency among four silvicultural treatments over an 18-year period. A secondary objective of this paper is to examine the effects of late-rotation fertilizer application on stand dynamics and productivity. Earlier reports demonstrated that nutrient availability was the primary limiting factor (Neary et al., 1990) for this site because irrigation did not enhance pine growth (Swindel et al., 1988). Later work (Jokela and Martin, 2000) documented large declines in productivity associated with stand development, and hypothesized that this decline might be partially attributable to nutrient limitations.

2. Materials and methods

2.1. Site description

The study site is located approximately 10 km north of Gainesville, FL, USA (29°40′N, 82°20′W) at an elevation of about 45 m. The topography is nearly flat, with less than 0.5 m relief across the area (<1% slope). In May 1981, a wildfire destroyed a 4-year-old slash pine plantation that occupied the site. During the summer of 1982 the area was again site prepared by roller drum chopping and single-pass bedding. Genetically improved (first generation, open-pollinated) 1-year-old

loblolly pine seedlings were hand-planted at a 1.8 m × 3.6 m spacing in January, 1983 (Swindel et al., 1988). Understory plants were those common to lower Coastal Plain flatwoods sites, with gallberry (*Ilex glabra* (L.) Gray), sawtooth palmetto (*Serenoa repens* (B.) Small.), fetterbush (*Lyonia lucida* (Lam.) K. Koch), staggerbush (*Lyonia ferruginea* (Walt.) Nutt.), wax myrtle (*Myrica ceriferea* L.), blueberries (*Vaccinum* spp.), St. John's-wort (*Hypericum fasciculatum* Lam.) and runner oak (*Quercus pumila* Walt.) being the dominant woody species. Herbaceous species also commonly present were broomsedges (*Andropogon* spp.) and panic grasses (*Panicum* spp. and *Dicanthelium* spp.).

The soils are poorly drained and classified as sandy, siliceous, hyperthermic Ultic Alaquods (Pomona fine sands; Soil Survey Staff, 1998). In a typical profile, the diagnostic spodic horizon, with an intermittent ortstein layer, occurs at 20–50 cm, and the argillic horizon at 90–120 cm. The water table fluctuates within 12–50 cm from the surface at least once during the growing season. The soil nutrient reserves are inherently low (Grierson et al., 1999), as the A horizon is comprised predominantly of quartz sand that has both low organic matter content (16.7 g kg^{-1}) and cation exchange capacity (<5 $cmol_c$ kg^{-1}). Double acid extractable P levels ranged from about 1.3 mg kg^{-1} in the A horizon to 2.0 mg kg^{-1} in the Bh horizon (Colbert, 1988).

The climate is subtropical and humid, with mean annual temperatures in January and July averaging 14 and 28 °C, respectively (NOAA, 1989). The frost-free growing season is 290 days. The soil water holding capacity of a 100 cm soil profile is 260 mm, calculated from the difference between field capacity (−0.033 MPa soil water potential) and permanent wilting point (−1.5 MPa soil water potential) from moisture release curves generated for similar soils (H.L. Gholz, personal commun., 2002). The long-term average annual precipitation at the site is 1350 mm. Annual precipitation between 1984 and 2000 averaged 1203 mm, ranging from 871 mm in 2000 to 1480 mm in 1997 (Fig. 1A). Thornthwaite AET exceeded precipitation in 8 of the 17 years for which detailed meteorological data were available (Fig. 1A). On a monthly basis, precipitation tends to be highest in the summer months, with dry periods occurring in April–May and November–December (Fig. 1B).

2.2. Experimental design and treatments

The study consisted of three replicates of a 2 × 2 factorial of complete and sustained understory competition control, and annual fertilizer application arranged in a randomized block design (Swindel et al., 1988). Treatment plots were about 820 m^2 in size, with interior measurement plots being 260 m^2 (40 trees). An untreated, two-row planted buffer separated all plots. Understory vegetation was controlled using herbicides and mechanical methods from age 1 to 10 years (1983–1993) (Neary et al., 1990). At this point, tree canopy development prevented encroachment of understory plants onto treated plots. Fertilizers were applied annually from 1983 to 1993 in 30 cm semicircular bands around the base of each tree. Over the 10-year treatment period, total elemental application rates for those plots receiving fertilizer additions were approximately: N (360 kg ha^{-1}), P (143 kg ha^{-1}), K (317 kg ha^{-1}), Ca (108 kg ha^{-1}), Mg (72 kg ha^{-1}), S (72 kg ha^{-1}), Mn (3 kg ha^{-1}), Fe (3 kg ha^{-1}), Zn (3 kg ha^{-1}), Cu (0.5 kg ha^{-1}), and B (0.5 kg ha^{-1}). The control plots did not receive either the fertilizer or understory competition control treatments. Fertilizer applications were again applied annually during the 16th–18th growing seasons (1998–2000). Elemental application rates over these 3 years totaled approximately: N (738 kg ha^{-1}), P (86 kg ha^{-1}), K (112 kg ha^{-1}), Mn (1.1 kg ha^{-1}), Fe (2.2 kg ha^{-1}) Zn (0.9 kg ha^{-1}), Cu (0.5 kg ha^{-1}), and B (0.5 kg ha^{-1}). These later fertilizer rates were intended to offset reductions in growth that were attributed to soil nutrient limitations (Jokela and Martin, 2000). All plots remained unthinned over the duration of the study. Treatment abbreviations used throughout this paper will hereafter be referred to as—C: control (no fertilizer or weed control), F: fertilization, W: weed control/herbicide, and FW: fertilizer + weed control.

2.3. Sampling procedures

2.3.1. Biomass and leaf area estimation

Total tree and component aboveground biomass prediction equations were developed separately by treatment at age 4 and 13 years. Destructive sampling procedures and allometric equation development at

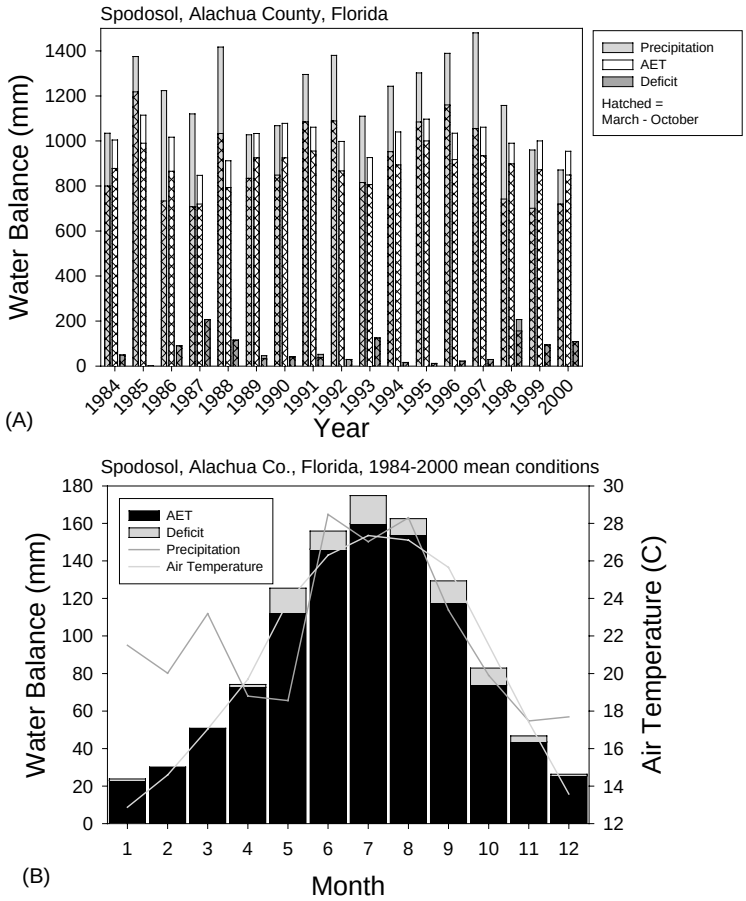

Fig. 1. Summary of climate conditions for Alachua County, Florida. (A) Annual and growing season (March–October) precipitation, AET and deficit from 1984 to 2000. (B) Mean monthly air temperature, precipitation, AET and deficit.

age 4 years ($n = 36$ trees) and 13 years (n=40 trees) were reported in Colbert et al. (1990) and Jokela and Martin (2000), respectively.

Pine litterfall was collected monthly for each treatment and replication beginning at age 6 years and continuing through age 18 years from six circular litter traps (0.7 m^2) installed in each plot (Dalla-Tea and Jokela, 1991). Leaf area index (LAI) was calculated from litterfall and logistic models of foliage accretion as described by Kinerson et al. (1974) and Dougherty et al. (1995). Litterfall data were corrected for senescence-related biomass reductions (14% for loblolly pine; Dalla-Tea, 1990) and were converted to projected leaf area using specific leaf area estimates (0.00366 $m^2\ g^{-1}$; Dalla-Tea and Jokela, 1991).

2.3.2. *Foliar nutrient levels*

Foliage samples were collected from the upper third of the crown from four dominant and codominant trees per plot during the 1989, 1996 and 2000 dormant seasons (October–March). Nitrogen was determined using a semimicro-Kjeldahl method (Wilde et al., 1979) or C–N elemental analyzer (NCS 2500, CE Elantech, Lakewood, NJ). Tissue solution samples were analyzed for total P on a spectrophotometer using the ascorbic acid-antimony reduced phosphate method following a wet digestion procedure (H_2SO_4–30% H_2O_2; Murphy and Riley, 1962).

2.3.3. *Woody quality*

Wood quality sampling was carried out by Rockwood (1997). Briefly, samples were taken from one

disease-free tree from each of the lower- through upper-1/5 of the DBH range in two replicates of each of the four treatments, for a total of 40 trees. Bark-to-bark 12 mm cores were taken from each sample tree near BH, and measurements were made following the methods of Clark and Saucier (1989). Specific gravity for each annual ring was calculated as $Sg = 0.3084867 + 0.0045681(\%\text{latewood})$ (A. Clark, personal commun.).

2.3.4. Inventory and statistical analyses

Diameter (1.3 m) and height of all living trees within the measurement plots were measured annually (except during years 8 and 12) during the dormant season and used to estimate basal area, changes in stem density, and site index. In addition, the biomass prediction equations were applied to the inventory data to estimate dry matter accumulation and distribution (Mg ha^{-1}), stemwood periodic annual increment (PAI; Mg ha^{-1} per year) and mean annual increment (MAI; Mg ha^{-1} per year) over time. Specifically, stemwood PAI was calculated as

$$\text{PAI} = \sum B_{t2} - \sum B_{t1} + \sum_{t1}^{t2} M \quad (1)$$

where B_{ti} is the biomass at time i, and $\sum_{t1}^{t2} M$ is the summed biomass of trees that died during the interval between $t1$ and $t2$ ("Approach 2" of Clark et al., 2001). This approach minimizes underestimates of PAI that can result when large trees die in small plots (Clark et al., 2001). It should be noted that there may be some uncertainty associated with biomass estimates from the later stand ages, since allometric equations were developed at age 13 years. However, the alternative of utilizing equations for older trees developed on another site would likely introduce even greater uncertainty. Corrections for logarithmic bias were made on all biomass estimates (Baskerville, 1972). Growth efficiency (i.e., annual production/leaf area) was computed to examine ontogenetic and treatment effects on growth processes.

Analysis of variance for a factorial design was used to test for treatment effects on growth parameters. When two-way interactions were significant, the differences between means of individual treatment combinations were tested using pairwise t-tests, with P-values adjusted using the Tukey–Kramer method to control the family confidence coefficient (Neter et al., 1990). All statistical analyses were conducted using the SAS statistical package (SAS, 1996).

3. Results

3.1. Stand development

3.1.1. Height, basal area development and mortality trends

Height growth was asymptotic for all treatments and at age 18 years averaged about 12.5 and 19.7 m for the C and FW treatments, respectively (Fig. 2). Tree heights for the single factor treatments (F = 19.1 m, W = 17.3 m) were significantly greater than the C, but did not differ from each other or the combined FW treatment. When expressed as site index (base age 25 years) (Pienaar and Shiver, 1980), the non-treated (C) plots averaged about 16 m compared to 25 m for the FW plots.

Basal area accretion was directly related to the intensity of the imposed silvicultural treatments. The FW treatment accrued the highest level of basal area, peaking at 44.2 m^2 ha^{-1} at age 16 years, and then declining to 41.6 m^2 ha^{-1} by age 18 years. With the exception of the C treatment, that was still slowly aggrading (C = 19.9 m^2 ha^{-1}), basal areas for the W and F treatments also reached maximum levels at age

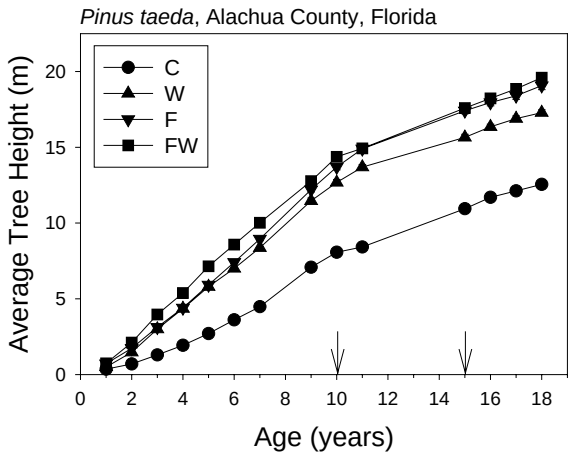

Fig. 2. Changes in average tree height with age for control (C), weed control (W), fertilization (F) and combination (FW) treatments. Arrows at 10 and 15 years indicate the cessation and resumption of fertilization treatments, respectively.

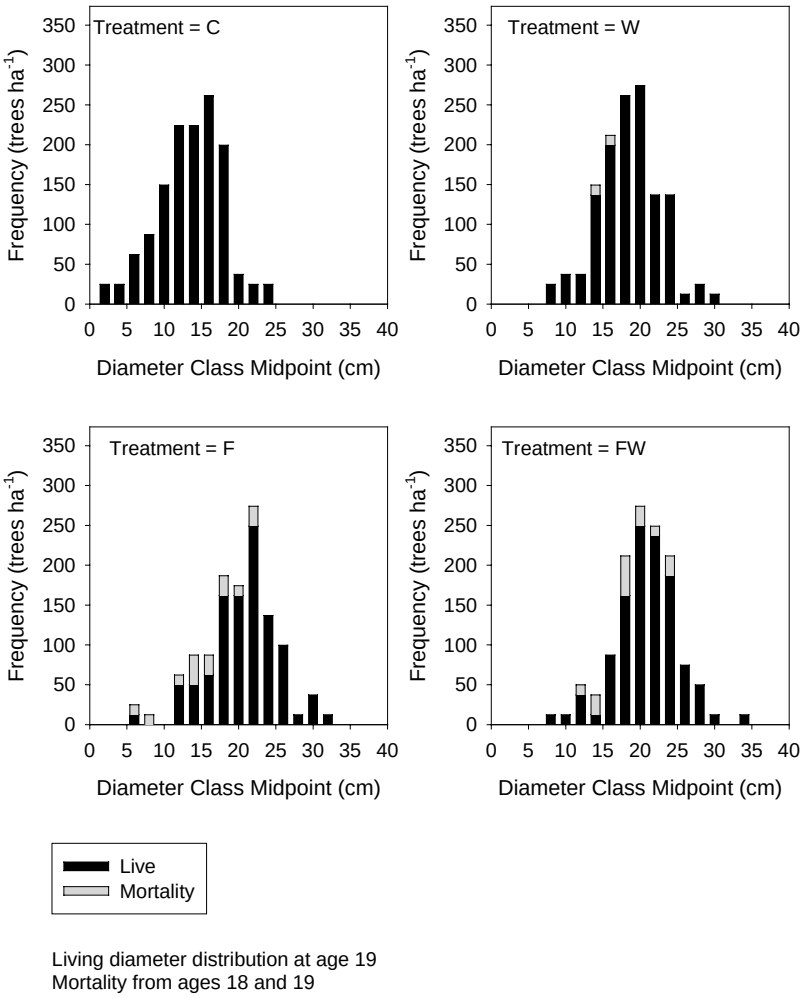

Fig. 3. Diameter distributions of live trees at age 19 years for control (C), weed control (W), fertilization (F) and combination (FW) treatments. Shaded portion of bars shows diameter distribution of trees that died at age 18 and 19 years.

16 years ($W = 36.6\ m^2\ ha^{-1}$, $F = 39.6\ m^2\ ha^{-1}$). Diameter distributions for all treatments were skewed toward larger trees, with the skewness increasing with treatment intensity (e.g., skewness = 0.49, 0.65, 1.06 and 0.98 for the C, W, F and FW treatments, respectively, Fig. 3). The range in DBH also increased slightly in treatments that received fertilizer, with ranges of approximately 22 cm in both the C and W treatments, and about 26 cm in the F and FW treatments (Fig. 3).

In general, the greatest degree of self-thinning, as evidenced by cumulative mortality levels, was associated with the fertilizer (F, FW) treatments (Fig. 3). At the last inventory, cumulative mortality rates for the C, W, F, and FW treatments were 10.8, 12.5, 22.5, and 17.5%, respectively, with most mortality occurring in the lower and average diameter classes (e.g., 5–25 cm). Mortality levels on the treated plots became especially pronounced as the basal areas approached 30–40 $m^2\ ha^{-1}$ (Fig. 4), apparently in response to the upper limits of stocking supported at this site and the diminished levels of light received by the lower crown class trees. This effect was also apparent in live crown lengths that varied between 5 and 8 m among the four treatments (Fig. 5). In general, as levels of basal area and site resources increased so did live crown length.

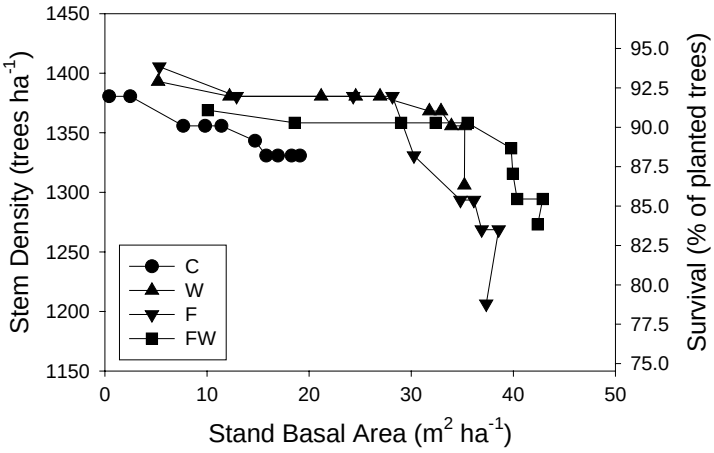

Fig. 4. Variation in stem density and stand basal area between the age of 4 and 18 years for control (C), weed control (W), fertilization (F) and combination (FW) treatments. Each point is the mean of three replicate plots for one inventory date.

3.2. Stand productivity and stem characteristics

3.2.1. Standing stemwood biomass versus age

Growth responses due to silvicultural treatments were large and consistent over time for both gross and standing stemwood biomass accumulation (Fig. 6). The fertilizer and weed control main effects were still highly significant ($P < 0.01$) at age 18 years, along with the fertilizer × weed control interaction ($P < 0.05$; less than additive). Sigmoidal growth curves fitted to the plot level data showed treatment differences in the maximum biomass accumulation parameter, but similar shape coefficients among treatments (Fig. 6, third table in Appendix A). Gross stemwood biomass accumulation averaged 124 Mg ha^{-1} for the combined FW treatment compared to 43 Mg ha^{-1} for the untreated control (~2.9-fold response; Fig. 6). Although stemwood biomass for all silvicultural treatments were greater than the control, no significant differences were found between the F and W treatments ($P = 0.442$), which averaged about 115 and 95 Mg ha^{-1}, respectively. Similarly, the single factor treatments did not differ significantly from the FW treatment during this later inventory period. Regression analyses using a logistic model showed comparable results, although the maximum biomass accumulation parameter for the FW treatment was significantly greater than for the single factor treatments (third table in Appendix A). The most pronounced differences between standing crop and gross stemwood biomass accumulation were found with the F and FW treatments, reflecting the effects of density-related mortality (Figs. 3 and 4). For example, gross stemwood biomass accumulation was 12% greater than net accumulation in the F treatment, but <1% greater in the C treatment.

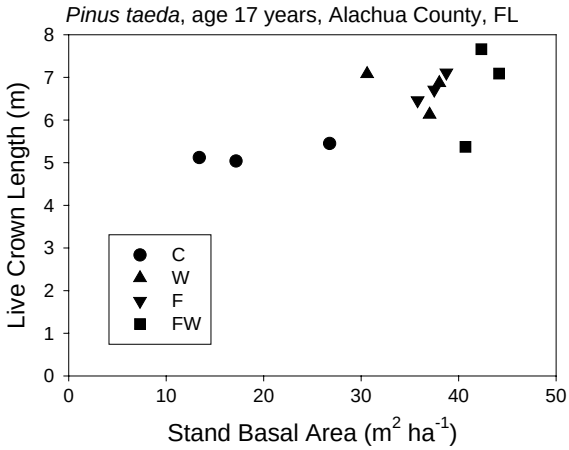

Fig. 5. Live crown length and stand basal area for the control (C), weed control (W), fertilization (F) and combination (FW) treatments at age 17 years. Each point represents one of three replicate plots.

3.2.2. MAI and PAI versus age

The dynamics of stemwood production were significantly affected by the silvicultural treatments.

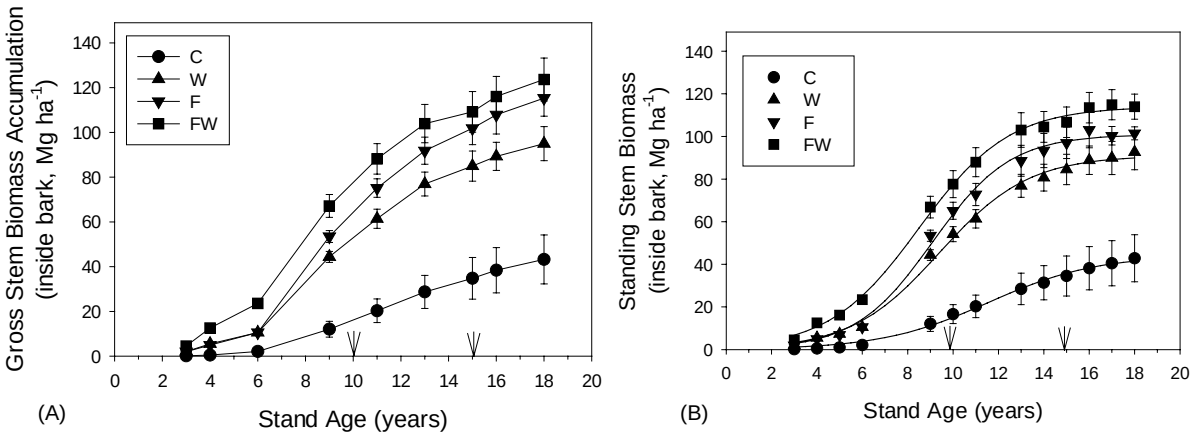

Fig. 6. Gross (A) and standing (B) stemwood biomass (dry mass, inside bark, no branches) vs. stand age for control (C), weed control (W), fertilization (F) and combination (FW) treatments. Gross stemwood biomass accumulation represents total cumulative stemwood biomass production, inclusive of mortality. Each point is the mean of three replicate plots, error bars are standard errors. Lines in (B) are logistic equations fitted to the plot-level data (third table in Appendix A). Arrows at 10 and 15 years indicate the cessation and resumption of fertilization treatments, respectively.

Fertilizer and W main effects for MAI were highly significant ($P < 0.001$) over the entire study period, as was the F × W interaction (less than additive; $P < 0.05$). MAI for the combined FW treatment was significantly greater than all treatments through age 9 years, although by age 13 years differences among the F, W, and FW treatments diminished (Appendix A). Stemwood MAI culminated (~8 Mg ha^{-1} per year) on the FW treatment at age 13 years, but had not yet reached a maximum on the C treatment (2.4 Mg ha^{-1} per year) at age 18 years (Fig. 7). Peak MAI for the single factor treatments similarly occurred at age 13 years and averaged 6.8 and 5.9 Mg ha^{-1} per year, respectively, for the F and W treatments.

In comparison, stemwood PAI for the FW treatment culminated at about age 8 years (14.3 Mg ha^{-1} per year) and then declined rapidly (~275%) to 3.8 Mg ha^{-1} per year at 15 years following curtailment (age 10 years) of the annual fertilizer treatment. A similarly timed peak and decline in PAI occurred

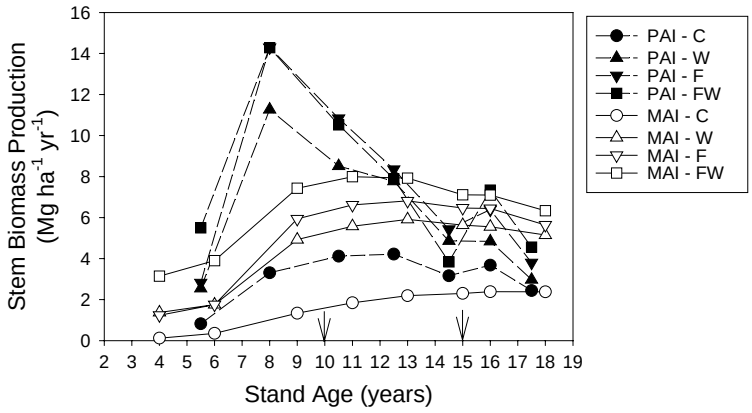

Fig. 7. Mean and periodic annual increment of stemwood biomass for control (C), weed control (W), fertilization (F) and combination (FW) treatments. Each point is the mean of three replicate plots. Arrows at 10 and 15 years indicate the cessation and resumption of fertilization treatments, respectively.

with the F and W treatments. PAI for the C treatment, however, peaked at age 13 years (4.2 Mg ha^{-1} per year) and then declined to 2.4 Mg ha^{-1} per year at age 18 years. When the fertilizer treatments (F, FW) were reinstated at age 15 years, PAI for the treated plots increased (e.g., FW = 3.8 Mg ha^{-1} per year (age 15 years) versus 7.3 Mg ha^{-1} per year (age 16 years)) and the main effect due to F was significant ($P < 0.05$) from age 16 to the last inventory period. By contrast, the main effect due to W was no longer significant after age 11 years.

3.2.3. Earlywood (EW)/latewood (LW) ratio and ring specific gravity

The impacts of intensive management and accelerated stand development on wood quality attributes were summarized in Rockwood (1997) and are shown in Fig. 8. In general, the EW/LW ratio decreased with ring age for all treatments. The treated plots tended to have a higher percentage of latewood than the C treatment at all ages except year 5, although the only significant treatment effect on the EW/LW ratio or ring specific gravity (which was linearly derived from EW/LW) occurred at age 6 years; at this point, the EW/LW ratio was significantly higher in the C treatment (3.59) than in the W treatment (1.88) (Fig. 8). McAlister and Powers (1992) suggested that the transition from juvenile to mature wood occurred in southern pines when LW values exceeded 50%. Accordingly, loblolly began to produce mature wood between the 7th and 9th year, which generally corresponded with ring specific gravities exceeding 0.5.

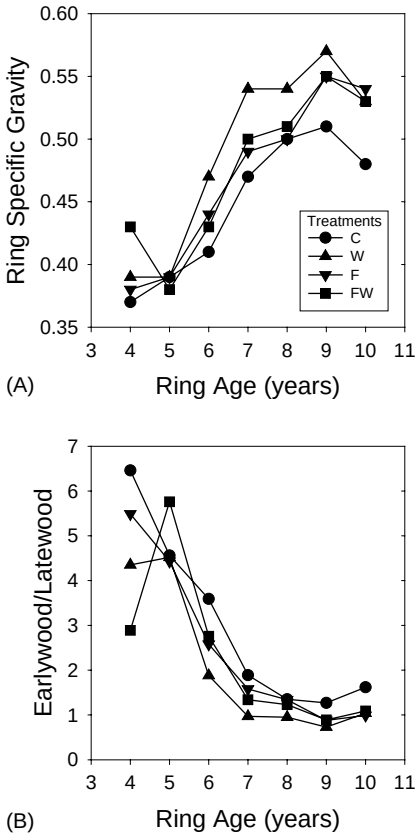

Fig. 8. Variation in ring specific gravity (A) and earlywood/latewood ratio (B) with ring age for control (C), weed control (W), fertilization (F) and combination (FW) treatments. Each point is the mean of three replicate plots.

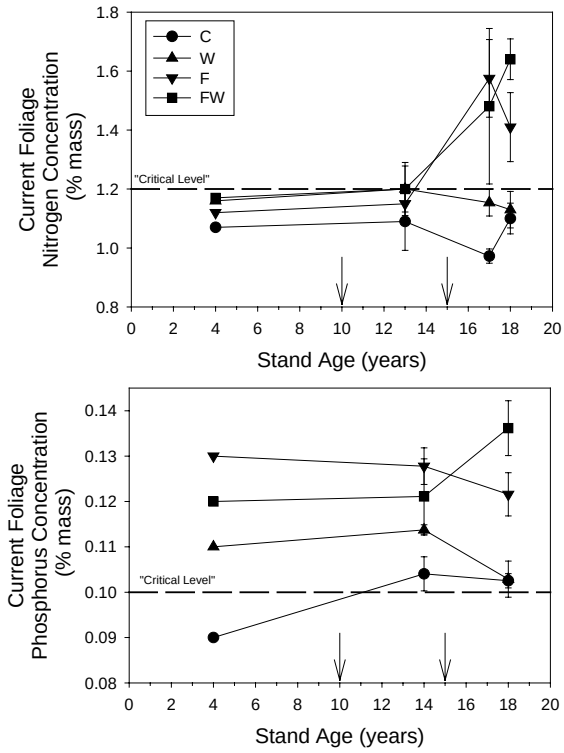

Fig. 9. Dormant season (October–March) nitrogen concentration (by mass) of current-year foliage for control (C), weed control (W), fertilization (F) and combination (FW) treatments. Error bars represent standard errors. Arrows at 10 and 15 years indicate the cessation and resumption of fertilization treatments, respectively.

3.3. Ecophysiological relationships

3.3.1. Foliar nutrients

Foliar nutrient sampling prior to age 13 years was limited, but indicated that despite annual fertilization, foliar N concentrations remained near or below the critical level of 1.20% (Jokela et al., 1991). For example, Colbert (1988) reported that foliar N levels at age 4 years averaged 1.07, 1.16, 1.12 and 1.17% for the C, W, F and FW treatments, respectively. At age 13 years, 3 years after cessation of the fertilization treatments, no significant treatment effects were found, with N concentrations of current-year needles averaging 1.16% (Fig. 9). At age 17 years, 2 years after the resumption of fertilization, a significant ($P = 0.0143$) fertilizer main effect was detected; N concentrations of fertilized plots averaged 1.53% compared to 1.06% for those plots not receiving fertilizer additions. Similar results persisted through age 18 years.

In contrast to N, foliar P levels in most treatments remained somewhat above the critical level (0.10%) for most of the experiment (Fig. 9). Silvicultural treatments did, however, influence foliar P concentrations, with significant fertilizer main effects detected both before and after retreatment (second table in Appendix A). At age 14 years, fertilized plots showed a 13.8% increase in foliar P over unfertilized plots (0.124% versus 0.109%), while the difference at age 18 years was 25% (0.129% versus 0.103%). Results for 1-year old needles were similar to the observations for current year needles for all time periods for both N and P (data not shown).

3.3.2. Dry matter distribution patterns

Treatment main effects and interactions on dry matter distribution patterns (e.g., stemwood, bark, branches, foliage) were examined using destructive harvest data (Fig. 10). At age 13 years, the main effects of fertilizer (F) and weed control (W) on biomass distribution patterns were highly significant for all tree components. In general, a small, but consistent treatment response was observed among biomass components, with the C treatment being significantly different from the W, F, and FW treatments; no differences in distribution patterns were found among the W, F, and FW treatments. For example, biomass distribution patterns between the C and an average of the other three treatments (W, F, FW) were—stemwood: 63.0% versus 66.0%, bark: 10.3% versus 8.6%, live branches: 17.7% versus 18.8%, and foliage: 8.8% versus 7.0%. Similar to that observed at age 4 years for this same site (Colbert et al., 1990), the magnitude of the interactions between silvicultural treatments were small (less than additive), but statistically significant ($P < 0.01$) for all biomass components, suggesting a lack of independence between these two treatments. In other words, the magnitudes of the changes in biomass distribution due to fertilizer additions were dependent on the associated level of weed control.

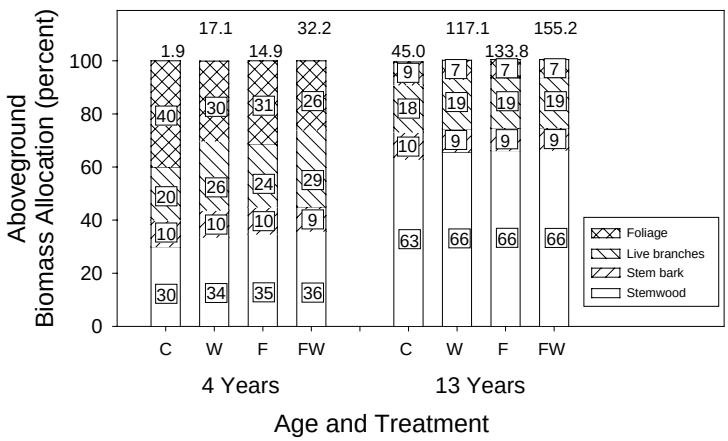

Fig. 10. Distribution of standing aboveground biomass for control (C), weed control (W), fertilization (F) and combination (FW) treatments at 4 and 13 years. Values above bars represent total aboveground biomass accumulation (Mg ha^{-1}) for that age and treatment, and values in boxes within bars represent the fraction of total biomass (in %) in that particular component.

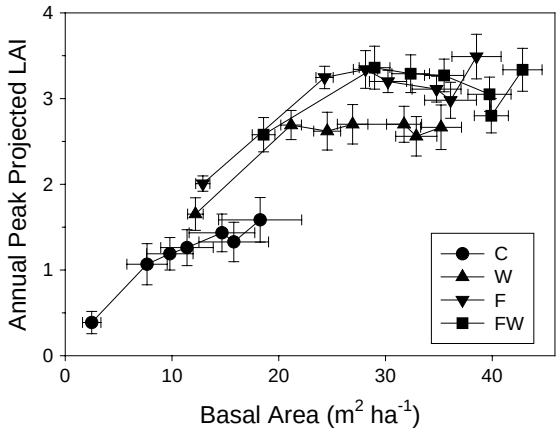

Fig. 11. Peak projected LAI vs. stand basal area for control (C), weed control (W), fertilization (F) and combination (FW) treatments. Age 6, 9, 10, 11, 13, 14 and 16 years are plotted. Error bars are standard errors.

3.3.3. Relationships among basal area, LAI and growth

Because basal area is an effective surrogate for the progression of stocking and inter-tree competition with stand age, plots of annual peak projected LAI versus basal area (Fig. 11) and stem PAI versus basal area (Fig. 12) give insight into the changes in these parameters that occur with stand development.

Peak projected LAI in the fertilized treatments (F and FW) increased rapidly with increasing basal area to a peak of approximately 3.3 at age 9–10 years and 20–25 m^2 ha^{-1} BA (Fig. 11). After this peak, LAI in both treatments declined through age 14 by approximately 15%, even as BA continued to increase to 35–40 m^2 ha^{-1}. After the re-fertilization treatment, LAI in the F and FW treatments responded dramatically, increasing by an average of 18% between age 14 and 16 years (3.0–3.5 in the F treatment, 2.8–3.4 in the FW treatment). LAI in the W treatment also peaked at age 9 years and 20 m^2 ha^{-1} BA, but remained relatively constant through age 16 years at a lower LAI of approximately 2.5, as BA increased to 35 m^2 ha^{-1}. The C treatment showed an increase in LAI with BA, but the levels of LAI and BA attained remained considerably below the other treatments, and did not appear to be leveling off as of age 16 years.

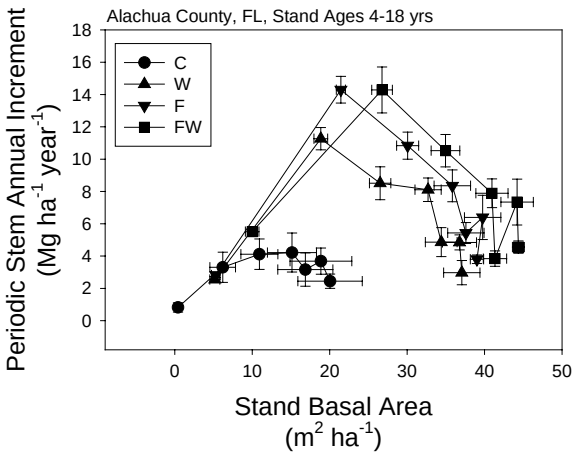

Fig. 12. Periodic annual increment of stemwood biomass vs. stand basal area for age 4–6, 6–9, 9–11, 11–13, 13–15, 15–16 and 16–18 years. Error bars are standard errors.

Stemwood PAI was very dynamic relative to stand BA in the F, W and FW treatments (Fig. 12). As stand BA in these treatments increased from 5–10 to 20–25 m^2 ha^{-1}, PAI increased almost three-fold, from 2–5 to 10–15 Mg ha^{-1} per year. After this peak, however, PAI in the F, W and FW treatments declined linearly as BA continued to accumulate. Indicator variable regression showed that the slope of this decline was the same among the F, W and FW treatments, while the y-intercept of the FW treatment regression was significantly higher than the F and W treatments ($R^2 = 0.66-0.73$, analysis not shown). In contrast to the results observed in the more intensively managed treatments, stemwood PAI of the C treatment remained relatively steady at 3–4 Mg ha^{-1} per year as stand BA increased from 5 to 20 m^2 ha^{-1}.

Stemwood PAI was a strong function of LAI, but the nature of this function changed with stand development (Fig. 13). Indicator variable regression showed that the slope of this relationship changed significantly with each successive time period, declining in each measurement period from 3.79 Mg ha^{-1} per year per LAI at age 7–9 years, to 1.35 Mg ha^{-1} per year per LAI at age 14–15 years, with a slight increase to 1.62 Mg ha^{-1} per year per LAI at age 16 years following re-fertilization. Within a time period, LAI explained from 94.1 to 99.4% of the variation in PAI.

3.3.4. Growth efficiency

In general, growth efficiency (GE) was highest for age 6–9 years, and declined in each period thereafter (Fig. 14). Only in years 6–9 was there a treatment

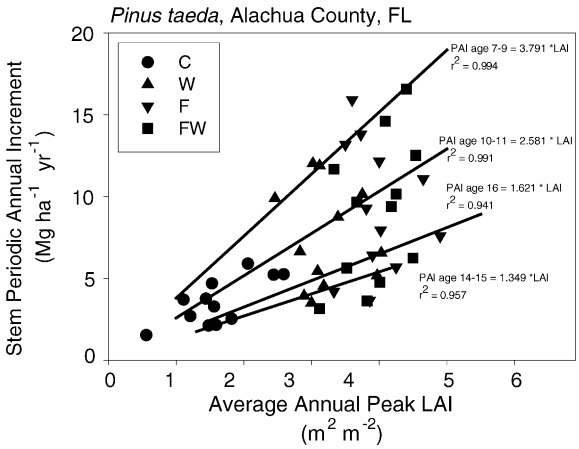

Fig. 13. Stemwood periodic annual increment vs. average annual peak projected LAI for several stages in stand development. Slopes of all lines are significantly different from one another.

effect on growth efficiency, when a significant F × W interaction ($P = 0.0038$) occurred. This interaction resulted from the fact that while the F and W treatments had higher GE than the C treatment (3.95 Mg ha^{-1} per year per LAI versus 3.05 Mg ha^{-1} per year per LAI, respectively), GE of the FW treatment (3.61 Mg ha^{-1} per year per LAI) was not significantly different from the control. By age 13–15 years, 3–5 years after the cessation of fertilization, growth efficiency had declined to 1.38 Mg ha^{-1} per year per LAI (averaged across treatments). For age 15–16 years, the year following the resumption of fertilization treatments, there was a slight increase in average GE to 1.65 Mg ha^{-1} per year per LAI, although there were still no statistically detectable treatment effects.

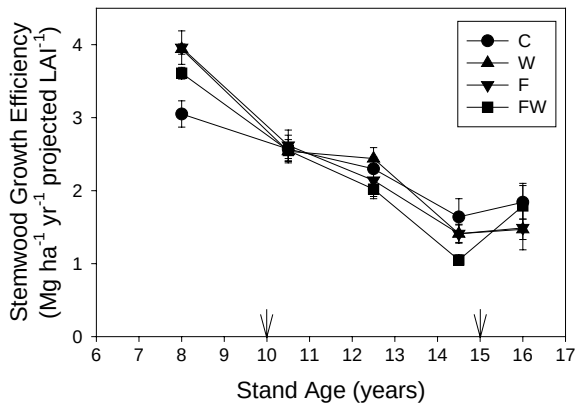

Fig. 14. Stemwood growth efficiency vs. stand age. Arrows at 10 and 15 years indicate the cessation and resumption of fertilization treatments, respectively.

4. Discussion

4.1. Stemwood growth and stand development

Investigations at this site (Colbert et al., 1990; Dalla-Tea and Jokela, 1994; Jokela and Martin, 2000; current study), as well as a number of others (Vose and Allen, 1988; Haywood et al., 1997; Tissue et al., 1997; Albaugh et al., 1998; Samuelson, 1998), demonstrate that throughout its natural range, the growth of loblolly pine is generally nutrient limited. In the current study, the amelioration of soil nutrient limitations either through fertilizer additions or understory competition control resulted in dramatic increases in almost every measure of productivity investigated, including height (Fig. 2), basal area (Fig. 4), stemwood biomass accumulation and production (Figs. 6 and 7), foliar nutrient concentrations (Fig. 9) and LAI (Fig. 11).

While soil nutrient supply was a major determinant of productivity in this experiment, production changes that occurred within treatments over the course of stand development were equally dramatic. For example, between age 8 and 15 years, stemwood PAI in the FW treatment declined by 275%; similarly, large reductions occurred in the F and W treatments over the same time period in these unthinned stands (Fig. 7). These reductions in PAI in the treated plots were linearly related to stand BA (with statistically identical slopes for the declining portion of the PAI versus BA regression for the three treatments, Fig. 12), suggesting the decline in productivity was associated with the onset of inter-tree competition. The intercepts of the PAI versus BA regression in the W, F and FW treatments trended upward in that order, with the intercept of the FW treatment being significantly higher than in the W and F treatments. These trends imply that the increase in management intensity associated with the change from W to F to FW treatments resulted in concomitant increases in the carrying capacity of the site, allowing the more intensively managed treatments to maintain higher stemwood PAI at any given level of stand BA, particularly later in stand development (Fig. 12).

Increases in productivity in response to silvicultural treatments such as weed control and fertilizer additions are often viewed as being the result of an acceleration of stand developmental processes (Miller, 1981). In this conceptual model, treated and untreated stands are assumed to be moving along similar growth trajectories, with the treated stands progressing more rapidly along the growth curve, and arriving at a specified endpoint (e.g., culmination of MAI) at an earlier chronological age than untreated stands. Our data indicated that MAI culminated 5 years earlier in the treated plots than in the C stands (Fig. 7), suggesting that stand development was indeed accelerated in the F, W and FW treatments. However, this analogy may be limited in its ability to explain stand dynamics responses when fertilizer additions and weed control are intensively applied, as in this study. For example, the treated plots (F, W and FW treatments) differed greatly from the control plots in the shape and magnitude of the functions relating stem density to stand BA (Fig. 4), stemwood PAI to stand age (Fig. 7), stand LAI to stand BA (Fig. 11) and stemwood PAI to stand BA (Fig. 12). Regression analyses using a logistic model showed that standing stemwood biomass in all treatments had accumulated to within 5% of the maximum by age 18 years (Fig. 7, third table in Appendix A). This implies that stemwood biomass of the C plots will never reach the magnitude achieved in the other treatments, presumably because fertilizer and understory competition control treatments changed inherent site quality, i.e., site index (Fig. 2). Albaugh et al. (1998) observed similar disparities in stand structure and function between control and intensively fertilized stands. In summary, the effects of large alterations in soil nutrient supply in this study were manifested partially through changes in the rate of stand development, but primarily through apparent shifts in the structure and function of stands growing on the altered sites.

4.2. Implications for density management

The patterns of density-related mortality (Fig. 4) and PAI declines (Fig. 12) in this study suggest that for the management regimes in the F, W and FW treatments, thinning to maintain stand BA below 20–25 $m^2\,ha^{-1}$ would maximize PAI, while minimizing "self-thinning" losses. These BA levels correspond to the maximum stocking levels indicated in Dean and Baldwin's (1993) loblolly pine density management diagram.

4.3. Stemwood growth efficiency

Many studies in southern pines (Vose and Allen, 1988; Colbert et al., 1990; Albaugh et al., 1998; Samuelson et al., 2001) and other species (Smith and Long, 1989; Heilman et al., 1996; Beadle, 1997; Carlyle, 1998) have demonstrated strong relationships between productivity and LAI. In contrast, few studies have documented changes in this relationship with stand development. In the present study, LAI at any one point in time explained greater than 94% of the variation in stemwood PAI in the same time interval (Fig. 13). However, the slope of the PAI versus LAI relationship changed by almost a factor of 3 from age 7–9 to age 14–15 years. The resulting variation in GE (Fig. 14) shows that stand developmental stage and applied management regime must be considered whenever the relationship between productivity and LAI is assessed.

The large declines in GE with stand development were driven almost entirely by reductions in PAI rather than changes in LAI. For example, while PAI in the FW treatment declined by over 73% between 6 and 9 years and 13–15 years (from 14.3 to 3.8 Mg ha^{-1} per year, Fig. 7), LAI in the same treatment over the same time period changed by less than 8% (from 3.9 to 3.7, Fig. 11). Similarly, both the W and F treatments showed relatively constant LAI (Fig. 11) during the period in stand development when PAI was declining (Fig. 7). These patterns are consistent with the early observations of Kira and Shidei (1967), who demonstrated that for a range of even-aged forests in the western Pacific, net primary production (NPP) tended to decline as stands aged, while leaf biomass (and presumably LAI) reached a plateau soon after canopy closure.

Subsequent research has shown that the patterns of declining growth and relatively constant LAI after canopy closure are almost universally observed for even aged forests throughout the world (Ryan et al., 1997), although the mechanisms driving these patterns have not been elucidated. Ryan et al. (1997) reviewed hypothesized mechanisms for this phenomenon, which include: increases in the ratio of respiring to

photosynthesizing tissue in aging trees that reduces carbon available for growth; size-related increases in xylem hydraulic resistance that results in higher stomatal limitations to carbon gain in aging trees; declines in soil nutrient supply due to nutrient immobilization or slowed N mineralization in stands with aggrading stand and forest floor biomass; increased mortality in aging stands; allocation of carbon to reproduction at the expense of growth in maturing stands; and age-related changes in gene expression and inherently slower growth in older tissue.

Jokela and Martin (2000) hypothesized that the reductions in GE observed in this experiment resulted in part from nutrient limitations in combination with increased maintenance respiration costs. In order to address the nutrient limitation portion of this hypothesis, the study was re-fertilized at age 15 years. Foliar nutrient concentrations (Fig. 9) and leaf area (Fig. 11) responded rapidly and dramatically to the re-treatment. The response of stemwood biomass PAI to the re-treatment was statistically significant (Fig. 7, first table in Appendix A), but was small relative to the LAI response. As a result, there was no change in GE after the re-fertilization treatment (Fig. 14, first table in Appendix A). The small but detectable increase in stemwood PAI and LAI after re-fertilization indicates that nutrient limitations may have played a role in the observed decline in production. However, these fertilization responses in reality did little to alter the overarching pattern of growth declines associated with increased stand basal area in the F, W and FW treatments (Fig. 12). Binkley et al. (1995) similarly concluded that in even-aged *Pinus contorta* stands, nutrition was only partially responsible for observed growth declines with stand development.

It should be noted that the initiation of the re-fertilization treatment coincided with the start of a severe drought in the region. Annual precipitation in the three years following the re-fertilization treatment (1998, 1999 and 2000) was 1158, 960 and 871 mm, respectively, representing reductions of 14–35% below the long-term average precipitation of 1350 mm. Physiological measurements in similar stands in the area showed severe water stress responses during this time period (T.A. Martin, unpublished data), suggesting that growth responses to the re-fertilization treatment may have been partially constrained by soil water deficits.

4.4. Tree- and stand-level responses

Smith and Long (2001) hypothesized that the post-peak LAI decline in growth observed in most even aged forests is an emergent stand dynamics property, independent of individual tree responses. Specifically, they stated that "Reduced individual tree growth is not responsible for the early decline in stand level production", citing as support Assmann's (1970) observations that growth of individual trees in a population tends to continue increasing even as stand-level growth begins to decline.

In order to examine individual tree growth patterns in relation to stand growth in our experiment, we graphed stemwood biomass PAI for dominant (largest: 15% of trees by DBH), co-dominant (middle: 70% of trees) and intermediate/suppressed (smallest: 15% of trees) trees (Fig. 15). This analysis showed that the peak and subsequent decline in PAI observed in the stand level data (Fig. 7) directly coincided with the patterns observed in all three size classes at the tree level (Fig. 15). Similar patterns of stand- and tree-level growth have been observed in developing *Populus* stands (DeBell et al., 1997). In our experiment, where mortality was relatively low throughout the course of the study (Fig. 4), the onset of density-related competition resulted in decreased individual tree growth, which was directly propagated to the stand level (Figs. 7 and 15). The exact physiological mechanisms which cause individual tree growth to decline at this point in stand development remain unclear, although nutrient limitations (current study, Binkley et al., 1995) appear to play a role, at least in some pine forests. Further elucidation of these mechanisms remains a pressing issue for forest biologists (Ryan et al., 1997).

4.5. Dry matter distribution

Data for these stands at age 4 years (Colbert et al., 1990) and 13 years (Jokela and Martin, 2000) demonstrate the effects of both nutrition and stand development on dry matter distribution in foliage, branches, stem bark, and stemwood (Fig. 10). Ontogenetic or stand developmental effects on distribution are apparent between the two sampling years, showing greatly reduced fraction of dry matter in foliage by age 13 years, a result of accumulating woody biomass in stem, bark and branches in larger trees. Nutritional impacts

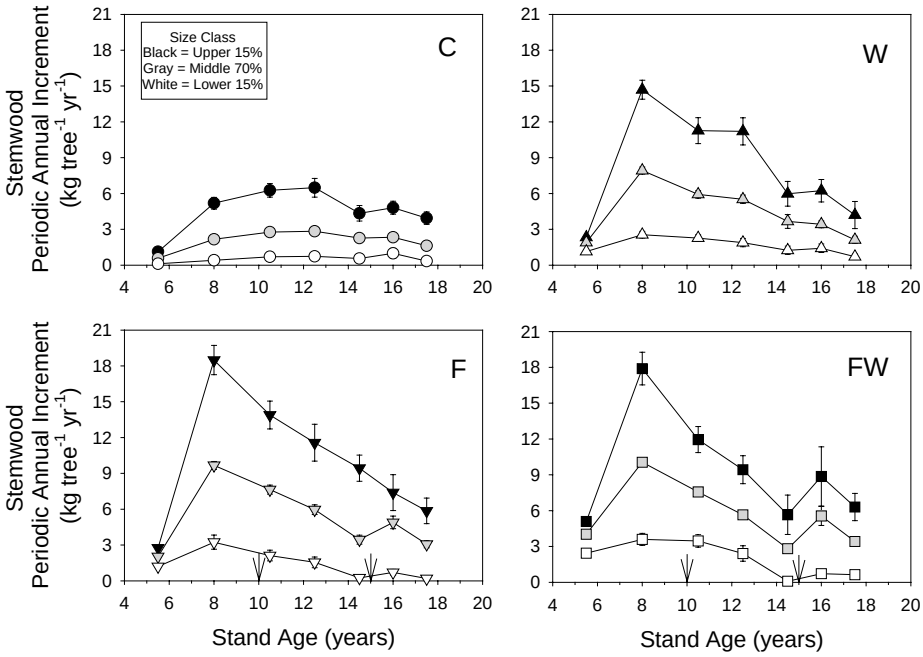

Fig. 15. Average individual tree stemwood periodic annual increment for trees in the upper 15%, middle 70% and lower 15% of the DBH distribution. Arrows at 10 and 15 years indicate the cessation and resumption of fertilization treatments, respectively.

were also apparent at both 4 and 13 years, with the treated plots (F, W and FW treatments) showing significantly different biomass distribution than the C treatments. In general, treated plots showed greater accumulation of woody biomass as a percent of total than did the C treatments, again reflecting the effects of tree size on this measure of biomass accumulation.

4.6. Wood quality

The intensive silvicultural treatments tended to have lower earlywood/latewood ratios (EW/LW) than the C treatment (Fig. 8), although this effect was only statistically significant at age 6 years (Rockwood, 1997). This culturally induced shift in EW/LW resulted in the treated plots reaching the threshold for juvenile to mature wood transition (50% latewood) at a ring age of approximately 8 years, while the C trees had not reached this point by age 10 years. The juvenile to mature wood transition generally occurs earlier as latitude decreases, due to extended growing seasons which allow increased production of latewood (Baker and Langdon, 1990; Clark and Saucier, 1991). It is likely that a similar phenomenon was induced by culture in this study, with the trees in the treated plots growing longer into the fall than the C trees, resulting in increased latewood percentage and decreased juvenile to mature wood transition age (Cooksey, 1986; Neary et al., 1990). This cultural effect on EW/LW could have considerable economic implications, as wood quality of intensively managed trees is an increasingly important consideration for southern forest managers (Cregg et al., 1988).

5. Conclusions

5.1. Summary of results

Management prescriptions developed to enhance the productivity and sustainability of loblolly pine stands in the southern USA have relied upon an extensive and integrated research foundation based on comprehensive, long-term regional experiments. The current study has summarized stand development and production relationships for a loblolly pine plantation growing at the southern limit of its native commercial range on seasonally wet Spodosols, a

dominant soil type in this region. Rotation-long measurements demonstrated that intensive management practices that increased soil nutrient availability (e.g., fertilization, understory competition control) dramatically altered the structure and function of these systems. In particular, the treated plots (F, W and FW treatments) varied greatly from the control plots in the shape and magnitude of the functions relating stem density to stand BA, stemwood PAI to stand age, LAI to stand BA, and stemwood PAI to stand BA. Although small but detectable increases in stemwood PAI and LAI occurred following re-fertilization, the responses only slightly counteracted the strong growth decline associated with increased stand basal area in the F, W and FW treatments following peak leaf area development.

5.2. Research needs

Ryan et al. (1997) summarized a number of hypotheses to explain the almost universal pattern of post-peak LAI growth declines in even-aged forests. While our results suggest that this decline in even-aged loblolly pine stands may be partially attributable to nutritional factors, it is clear that additional mechanisms are also important. Potential factors that might be responsible for growth declines in southern pine systems include: shifts in carbon allocation from above- to belowground (especially fine root) production; increases in the ratio of respiring to photosynthesizing tissue in aging trees that reduces carbon available for growth; limits on root system expansion and growth due to physical restrictions such as fluctuating water tables or hardpan layers; and decreased canopy carbon gain due to self-shading in lower canopy layers. Although detailed and expensive ecophysiological investigations will be necessary to test these additional hypotheses, the information gained should provide valuable and fundamental insights into the nature of a number of important stand dynamics questions. For instance, knowledge of the mechanism underlying even-aged stand growth declines should contribute directly to an understanding of the nature of competition-induced mortality associated with the −3/2 self-thinning law. It is likely that the same mechanisms will also be related to the causes of variation in site carrying capacity or stockability, as indicated by shifts in the intercept of the −3/2 self-thinning line (e.g., Harms et al., 1994, 2000). These insights into the production ecology and physiology of even-aged forests are critical to our ability to predict growth performance under a range of management and environmental scenarios, and to identify and ameliorate environmental limits to productivity.

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Appendix A. Statistical summaries

Summary of ANOVA *P*-values for parameters calculated on a multi-year basis

Parameter	Source	Period (years)						
		4–6	6–9	9–11	11–13	13–15	15–16	16–18
PAI	F	**<0.0001**	**0.0001**	**0.0018**	0.0781	0.4539	**0.0442**	**0.0176**
	W	**<0.0001**	**0.0042**	0.0644	0.1143	0.9435	0.3630	0.2298
	F × W	0.0502	**0.0041**	**0.0386**	0.0546	0.0717	0.9266	0.8252
Growth efficiency	F	–	0.0927	0.8709	0.1768	0.1023	0.9489	–
	W	–	0.1182	0.7841	0.9637	0.0958	0.9009	–
	F × W	–	**0.0038**	0.8847	0.5064	0.6822	0.2195	–

Significant *P*-values (<0.0500) are shown in bold type.

Summary of ANOVA *P*-values for parameters calculated on a yearly basis

Parameter	Source	Stand age (years)											
		2	3	4	6	9	11	13	14	15	16	17	18
Height	F	**<0.0001**	–	**<0.0001**	**<0.0001**	–	–	–	–	–	**0.0005**	–	**0.0007**
	W	**0.0002**	–	**<0.0001**	**0.0001**	–	–	–	–	–	**0.0084**	–	**0.0109**
	F × W	0.0626	–	**0.0053**	**0.0095**	–	–	–	–	–	**0.0161**	–	**0.0353**
Current foliage N concentration	F	–	–	–	–	–	–	0.6726	–	–	–	**0.0143**	**0.0010**
	W	–	–	–	–	–	–	0.3327	–	–	–	0.7319	0.1708
	F × W	–	–	–	–	–	–	0.6621	–	–	–	0.2729	0.3168
Current foliage P concentration	F	–	–	–	–	–	–	–	**0.0257**	–	–	–	**0.0003**
	W	–	–	–	–	–	–	–	0.7355	–	–	–	0.1517
	F × W	–	–	–	–	–	–	–	0.1589	–	–	–	0.1654
MAI or standing biomass	F	–	**0.0003**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0003**	–	**0.0006**	**0.0006**	–	**0.0008**
	W	–	**0.0003**	**<0.0001**	**<0.0001**	**0.0002**	**0.0009**	**0.0022**	–	**0.0051**	**0.0058**	–	**0.0036**
	F × W	–	0.4231	0.0980	**0.0337**	**0.0302**	**0.0454**	**0.0440**	–	**0.0328**	**0.0397**	–	**0.0407**
Gross biomass	F	–	**0.0003**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0002**	–	**0.0005**	**0.0005**	–	**0.0006**
	W	–	**0.0003**	**<0.0001**	**<0.0001**	**0.0002**	**0.0008**	**0.0024**	–	**0.0080**	**0.0089**	–	**0.0110**
	F × W	–	0.4231	0.0980	**0.0260**	**0.0315**	**0.0276**	**0.0312**	–	**0.0311**	**0.0378**	–	**0.0450**

Significant *P*-values (<0.0500) are shown in bold type.

Parameters of the logistic equation describing the patterns of standing stemwood biomass versus time shown in Fig. 6

Treatment	Y_{max}	b	k	Years to reach 95% Y_{max}
C	44.2 a	−4.89 a	0.42 a	18.5
F	100.9 b	−5.32 a	0.58 a	14.1
W	91.0 b	−4.80 a	0.51 a	15.2
FW	114.0 c	−4.28 a	0.50 a	14.4

The equation was of the form: $Y = Y_{max}/(1 + \exp(-b - kx))$. Parameters within a column not followed by the same letter are significantly different ($P < 0.05$).

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