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Production, allocation, and stemwood growth efficiency of *Pinus taeda* L. stands in response to 6 years of intensive management

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Abstract

Loblolly pine (*Pinus taeda* L.) is a highly plastic species with respect to growth responses to forest management. Loblolly pine is the most planted species across the southern United States, a region with the most expansive and intensively managed forest plantations in the world. Management intensity, using tools such as site preparation and fertilization, is increasing greatly in scope over time. To better define to the productive potential of loblolly pine under intensive management, the influence of 6 years of management with weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (irrigation with a fertilizer solution) (WIF), or weed control plus irrigation, fertigation, and pest control (WIFP) since plantation establishment on stand productivity in loblolly pine was examined. The site is located near Bainbridge, GA (30°48′N latitude and 84°39′W longitude) and is of medium quality (site index = 18 m, base age 25). Increasing management intensity greatly accelerated stand development and biomass accumulation. At age 6 total production (above plus belowground) was nearly doubled from 50 to 93 Mg ha^{-1} in WIFP stands compared to W stands, and standing stem biomass increased from 24 Mg ha^{-1} in W stands to 48 Mg ha^{-1} in response to WIFP treatment. Stem current annual increment (CAI) peaked at age 5 in the WIF and WIFP stands at 17–18 Mg ha^{-1} per year at a basal area between 18 and 21 m^2 ha^{-1}. Year to year variation in CAI was better explained by previous-year leaf area index (LAI) than current-year LAI. Maximum stemwood production in loblolly pine was achieved through large increases in LAI and small decreases in allocation to woody roots (tap + coarse roots) versus woody shoots (stem + branches) associated with intensive treatments.

Keywords: Loblolly pine; Fertilization; Irrigation; Current annual increment

1. Introduction

Intensive management of loblolly pine (*Pinus taeda* L.) plantations using fertilization, competition control, and superior genotypes can increase productivity at least up to three-fold (Borders and Bailey, 2001). Over the past several decades, increasing rates of production have been documented, and thus the genetic potential of loblolly pine for growth is still unknown. Increased productivity has been mostly ascribed to enhancement of leaf area index (LAI) but also to reduced allocation belowground (Cannell, 1985). The progression of aboveground net primary production with stand development is closely coupled

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with LAI, but the timing and magnitude of maximum current annual stemwood biomass increment (CAI) may vary with management intensity. While the age-related decline in forest stand production is well documented (Assmann, 1970; Ryan et al., 1997), potential maximum productivity under very intensive silviculture is less predictable, especially in species where short rotations are possible.

Reductions in CAI that occur with increasing stand development have been attributed to many factors including increased maintenance respiration, decreased leaf area efficiency, greater hydraulic limitations, reduced nutrient availability, changes in allocation among tissues, crown abrasion, and tree mortality (Smith and Long, 2001), and reductions in CAI may occur as early as age 5 in *Pinus* plantations (Forrest and Ovington, 1970). Reductions in stemwood growth at age 8 in an intensively managed loblolly pine plantation following curtailment of fertilizer treatment led Jokela and Martin (2000) to hypothesize that stemwood growth decline following peak LAI in lobolly pine was in response to increasing nutrient limitation. Similarly, Piatek and Allen (2001) concluded that the forest floor was a sink for N and P in a mid-rotation loblolly pine stand. Evidence indicates that the root:needle ratio and fine root production may increase with stand development (Vanninen and Makela, 1999; Makkonen and Helmisaari, 2001). However, the mechanism(s) inducing declines in CAI is still equivocal. In addition, increased fine root biomass in response to fertilization has been reported (Majdi, 2001), although relative allocation to fine root biomass can actually decrease (Albaugh et al., 1998).

The overall objective of this study was to examine the effects of 6 years of intensive silviculture on stand development in loblolly pine. Here, the influence of silvicultural manipulation of nutrient and water availability, and pest control on stand dynamics, aboveground and belowground biomass, and stemwood growth efficiency of loblolly pine is reported. This work builds on growth and leaf physiological data reported at the individual tree-level during the first 4 years of plantation growth (Samuelson, 1998; Samuelson et al., 2001). Specific hypotheses tested were that greater management intensity decreases allocation to fine roots and that stemwood growth efficiency will be maintained by the addition of nutrients and water.

2. Methods

2.1. Experimental design and treatments

The 15 ha research site was established and maintained by International Paper Inc. in the Upper Coastal Plain 22 km west of Bainbridge, GA (30°48′N latitude and 84°39′W longitude) in January 1995. The site was previously used for agriculture for several decades. Soils were classified as well-drained Grossarenic Paleudults. Depth to the argillic horizon was 102 cm. Prior to study installation, soil pH, organic matter, cation exchange capacity, available P, and textural class at the 0–15 cm depth were 5.7, 1.6%, 3.0 cmol(+) kg^{-1}, 23.3 mg kg^{-1}, and sandy loam, respectively. Site index base age 25 for the native site was 18 m.

In August 1994, soils were ripped to a 45 cm depth with a single-shank subsoiler and disc-harrowed the following November to eliminate soil compaction. Herbaceous vegetation was removed using a broadcast spray of glyphosate herbicide (1.5% solution in water) applied in July and September 1994. Loblolly pine seedlings were assigned to 0.20 ha treatment plots within a block and hand-planted using a 2.4 m× 3.7 m spacing in January 1995. Two treated buffer rows surrounded each treatment plot. Four open-pollinated, improved, second generation families of loblolly pine were planted on separate sub-plots within a treatment plot. One family was examined throughout this study. Excluding buffer rows, the measurement plot was 0.026 ha with 28 sample trees (planting density 1070 trees ha^{-1}). Treatment plots were arranged in a randomized complete block design with four treatments and three replicates. The following treatments were applied since plantation establishment and randomly assigned to treatment plots within the three blocks:

- W: complete weed control maintained using a broadcast application of sulfometuron (0.1 kg active ingredient ha^{-1}) and several directed applications of glyphosate (1.5% solution in water) throughout the summer.
- WI: weed control plus drip irrigation (Netafim Irrigation Inc., Altamonte Springs, FL). Drip lines ran along tree rows on the south side of each tree. Yearly additions were 341 mm in 1995, 210 mm in 1996, 266 mm in 1997, 310 mm in 1998, 1127 mm in 1999, and 1127 mm in 2000.

- WIF: weed control plus drip irrigation and fertigation (addition of a fertilizer solution to the irrigation water) with NH_4NO_3, and urea (45 kg N ha^{-1} in 1995, 87 kg N ha^{-1} in 1996, 135 kg N ha^{-1} in 1997, 112 kg N ha^{-1} in 1998, 79 g N ha^{-1} in 1999, and 79 g N ha^{-1} in 2000), H_3PO_4 (11 kg P ha^{-1} in 1995, 22 kg P ha^{-1} in 1996, 33 kg P ha^{-1} in 1997, 112 kg P ha^{-1} in 1998, 20 kg P ha^{-1} in 1999, and 20 kg P ha^{-1} in 2000) and K_2O (45 kg K ha^{-1} in 1995, 87 kg K ha^{-1} in 1996, 130 kg K ha^{-1} in 1997, 90 kg K ha^{-1} in 1998, 79 kg K ha^{-1} in 1999, and 79 kg K ha^{-1} in 2000). Addition of fertilizer to the irrigation water began in May and continued through October.
- WIFP: weed control plus irrigation, fertigation, and pest control. Fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*) controlled with applications of triadimefon fungicide. Nantucket pine tip moth (*Rhyacionia frustana*) controlled with applications of permethrin or acephate insecticides.

2.2. Procedures

Foliar N concentrations were determined for tissue collected in July or August of each respective year. One sample was collected from each plot–treatment combination and consisted of needles collected from a minimum of two trees per plot.

One tree from each plot was randomly selected for harvest during the week of 11–13 December 2000. Trees were felled at the ground line, stored in coolers at 5 °C, separated by leaf, branch (dead and live), and stem, and oven-dried.

To determine the standing crop of fine roots in May and December 2000, soil cores were removed from one 3.6 m long linear transect in each plot. Transect locations within a plot were randomly chosen in May and were located adjacent to the harvest tree in December. Transects were equidistant between two trees within a row, perpendicular to the row, and traversed the inter-row space. Seven cores 15 cm in diameter down to a 15 and 30 cm depth were removed at 60 cm intervals along each transect. Thus, one sample was collected from the center location (in between the two trees within a row) and six samples were collected between rows (three on each side of the center sample spaced at 60 cm intervals). The irrigation drip line was located between the center and first 60 cm sample on the south side of each row. A total of 168 cores from each sampling period were placed on ice and returned to the laboratory for processing. Cores were washed and live fine roots (2 mm or less) were separated from the soil using a #14 mesh sieve. Roots were oven-dried at 65 °C for 72 h and weighed. The influence of sampling location and soil depth was examined on transect-level fine root mass, reported in g m^{-2}. Stand-level fine root mass was determined by summing fine root mass to the 30 cm depth and averaging across sample locations, a reasonable approach as the soil profile is literally devoid of rocks.

Coarse roots (>2 mm) were extracted from a 1 m × 1 m pit excavated around each harvest tree in December 2000. Soil was loosened in each pit using compressed air and removed by hand, and all roots were removed down to a 60 cm depth. After coarse roots were removed, the entire taproot of each sample tree was dug out of the soil by hand and with a backhoe.

All samples were oven-dried at 65 °C to a constant weight. Stand-level biomass (leaf, branch, stem mass) was calculated for each plot and year (1996–2000) using allometric equations and inventory data for the 28 tree plots collected in December of each year. Allometric equations (Table 1) were developed by year across treatments from whole-tree harvests conducted in 1996 (Samuelson, 1998), 1997 and 1998 (Samuelson et al., 2001), and 2000. Biomass was predicted for each tree and summed yearly for each 28 tree plot. Aboveground net primary production was calculated from the yearly increment in the sum of leaf, branch, and stem biomass. Stand-level stem mass was used to calculate current annual increment (CAI, the yearly increment in mass) and mean annual increment (MAI, mass/age). Leaf mass was converted to one-sided LAI using a specific leaf area of 59.5 cm^2 g^{-1} (Samuelson et al., 2001).

Stand-level taproot mass and coarse root mass in 2000 were predicted using allometric equations developed for all treatments combined (Table 1). Stand-level coarse root mass was determined by summing all size classes and assuming the majority of coarse roots were located within the excavation pit.

2.3. Statistical analyzes

Because a factorial experimental design was not used, the individual and interactive effects of nutrients,

Table 1
Parameter estimates for the general regression model logmass (kg per tree) = $a + b$log diameter), where diameter (cm) is at ground-line (age 2) or breast height (1.6 m), developed for loblolly pine grown under intensive management for 6 years

Dependent variable	Age (years)	a	b	$P > F$	MSE	R^2
Leaf	2	−3.460	2.081	<0.001	0.015	0.95
	3	−1.357	1.406	<0.001	0.044	0.71
	4	−4.526	2.572	<0.001	0.050	0.79
	5 and 6	−4.221	2.231	<0.001	0.038	0.77
Branch	2	−5.310	2.560	<0.001	0.079	0.84
	3	−1.779	1.470	<0.001	0.093	0.55
	4	−4.741	2.762	<0.001	0.069	0.76
	5 and 6	−3.272	2.081	<0.001	0.053	0.68
Stem	2	−5.295	2.709	<0.001	0.021	0.96
	3	−1.012	1.207	<0.001	0.002	0.77
	4	−3.788	2.583	<0.001	0.018	0.92
	5 and 6	−2.910	2.349	<0.001	0.005	0.97
Tap root	6	−2.276	1.742	0.003	0.054	0.59
Coarse root	6	−4.950	2.211	0.006	0.102	0.55

Models for aboveground mass are based on 12 trees harvested each sampling year. Tap and coarse roots were harvested only at age 6.

water, and pest control could not be tested. Treatment effects at age 6 on aboveground biomass, belowground biomass, foliar N concentration, live crown length, tree height, standing stem biomass, and LAI were tested using a randomized complete block design. A three-way ANOVA with block, depth, location, and treatment as main effects was used to analyze the fine root data. Duncan's multiple range test was used to separate treatment means. Main or interactive effects were considered significant at the $\alpha = 0.05$ level. The analysis of variance was performed on log-transformed data when needed to satisfy heterogeneity of variance assumptions (non-transformed values are always reported). Linear functions were fit to the relationship between CAI and LAI. Differences in slope coefficients between treatments were tested using dummy variables.

3. Results

3.1. Growing conditions

Average yearly precipitation and temperature for the region are 1257 mm and 18.9 °C, respectively (Ruffner, 1980). Since plantation establishment, yearly and growing season (March–October) precipitation (Fig. 1a) ranged between 869–1463 and 531–855 mm, respectively, with the highest mean temperature occurring in July (Fig. 1b).

3.2. Stand development

At age 6, average tree height was greatest in response to the WIFP treatment, but live crown length was similar among treatments despite greater stand development in the more intensive treatments (Fig. 2a and b). The live crown ratio (crown length/tree height) at age 6 was 75, 66, 63, and 60% in response to W, WI, WIF, and WIFP treatments, respectively. Thus, increasing intensity of treatment resulted in the crown climbing higher above ground level from 1.9 m in the W treatment to 4.2 m in the WIFP stands. Initial planting density was 1070 trees ha^{-1} and three trees were removed from each plot for sampling over the 6-year study. Stand basal area at age 6 was 25 m^2 ha^{-1} in WIFP stands compared to approximately 15 m^2 ha^{-1} in W stands (Fig. 2c). The total number of trees lost to mortality across all three blocks within a treatment was 0, 1, 1, and 4 in the W, WI, WIF, and WIFP treatments, respectively. The number of trees in the larger diameter classes increased with increasing intensity of treatment (Fig. 3).

Foliar N concentrations over the life of the stand ranged between 11 and 16 mg g^{-1}, and were below the critical level of 12 mg g^{-1} (Allen, 1987) at age 3 in all

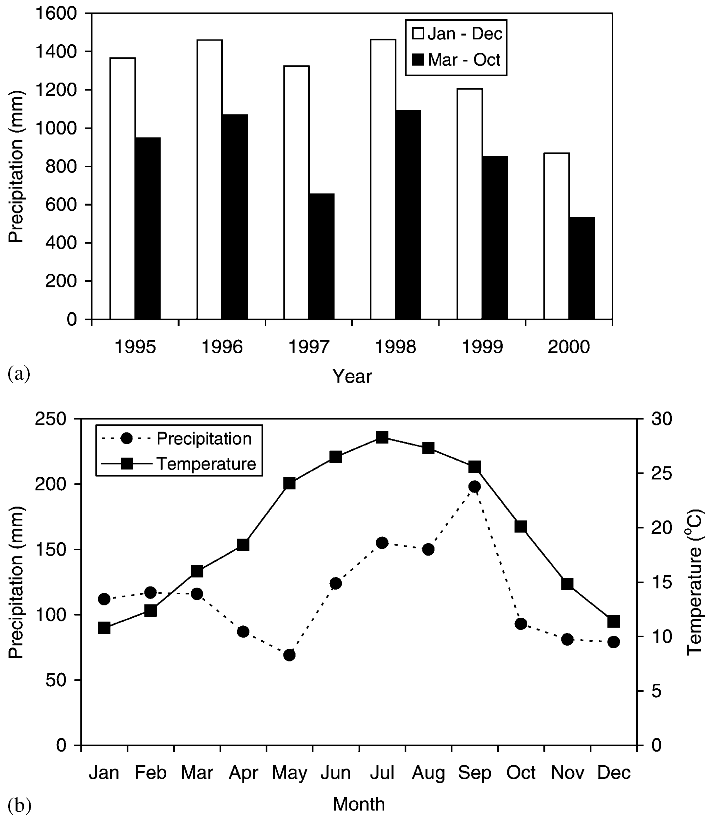

Fig. 1. Yearly and growing season precipitation (a), and average monthly temperature and precipitation (b) for International Paper Inc., Bainbridge, GA from 1995 to 2000 (Southeast Regional Climate Center).

treatments (Fig. 4). At age 6, no significant treatment differences in foliar N concentration were observed, but a trend ($P = 0.11$) towards higher N concentration in the WIFP treatment relative to the WI treatment was detected (WIFP = 16 mg g^{-1} and WI = 13 mg g^{-1}).

Treatment effects on standing stem biomass increased over the life of the plantation, and at age 6 stem biomass was greatest (48 Mg ha^{-1}) in the WIFP treatment (Fig. 5a). LAI (projected) increased with increasing management intensity and at age 6 was increased from 2.8 m^2 m^{-2} in the W stands to 5.4 m^2 m^{-2} in response to WIFP treatment (Fig. 5b).

CAI was highest at age 5 in the WIF and WIFP stands at a basal area between 18 and 21 m^2 ha^{-1}, and CAI appeared to be approaching MAI at age 6 in WIFP stands (Fig. 6a and b). No significant relationship between CAI and current-year LAI was observed for any treatment or with all treatments pooled (data not shown). In contrast, CAI was linearly related to previous-year LAI in all treatments and previous-year LAI explained between 71 and 80% of the variation in CAI, but no significant treatment differences in slope coefficients were detected (Fig. 7).

3.3. Aboveground mass

In general, increasing intensity of treatment successively increased aboveground biomass over the life of the stand (Fig. 8). In all treatments, aboveground biomass was increased approximately four times from ages 3 to 6 to a maximum of 72.3 Mg ha^{-1} in WIFP stands. Greater allocation to branches and foliage than stem was observed at ages 3 and 4, in contrast to greater allocation to stem than foliage and branches at ages 5 and 6. Differences in allocation to stem, branches, or foliage between treatments within any given year were small. At age 6, total aboveground biomass was highest in the WIFP and WIF treatments

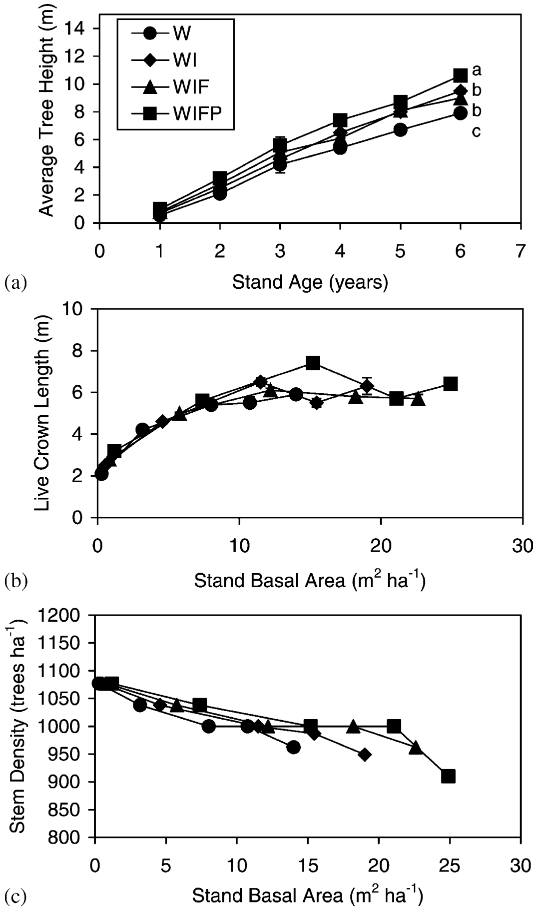

Fig. 2. Average tree height in relation to stand age (a), and live crown length (b) and stem density (c) in relation to stand basal area of loblolly pine in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation, and pest control (WIFP). Standard error bars represent plot to plot variation. Different letters denote significant differences among treatments at age 6.

and greater in the WI than W treatment. Dead branch biomass at age 6 increased with increasing stem diameter (Fig. 9).

3.4. Belowground mass

3.4.1. Fine roots

Despite the irrigation line present in three out of the four treatments, no significant differences in fine root mass were observed between similar transect locations based on distance from the center on either measurement date (data not shown). Therefore, fine root data were averaged across similar locations to represent a center location (between the two trees within a row), and an inner (0.6 m from the center location), middle (1.2 m from the center location), and outer (1.8 m from the center location) location.

In May 2000, significant main effects of location, treatment, and depth on fine root mass were observed, but no interactions were significant ($P > 0.400$). Fine root mass was greatest in the center location (Fig. 10a), significantly greater in the WI treatment compared to the WIFP treatment (Fig. 10c), and lower in the 15–30 depth than in the 0–15 cm depth (data not shown).

In December 2000, a significant ($P = 0.016$) interaction between depth and treatment was detected for fine root mass; fine root mass was lower in the 15–30 cm depth than in 0–15 cm depth in all treatments except the W treatment (Fig. 10b). No other interactions were observed. Fine root mass decreased from the center to the outermost locations (Fig. 10a), and was significantly greater in the WIFP treatment than in the WIF and W treatments, and greater in the WI treatment than in the WIF treatment (Fig. 10c).

Stand-level fine root mass, determined by summing fine root mass to the 30 cm depth and averaging across sample locations, was not significantly ($P = 0.747$) influenced by treatment, and values ranged from 1.8 Mg ha^{-1} in the W treatment to 1.8, 2.0 and 2.7 Mg ha^{-1} in the WIF, WIFP, and WI treatments, respectively, in May 2000. In December 2000, stand-level fine root mass was significantly increased in response to WIFP treatment (1.7 Mg ha^{-1}) compared to the W treatment (0.9 Mg ha^{-1}), but no significant ($P = 0.194$) treatment differences in stand-level fine root allocation relative to total belowground mass were observed (Fig. 11a). Stand-level fine root allocation relative to leaf mass was not significantly ($P = 0.202$) different among treatments (Fig. 11b).

3.4.2. Coarse roots and tap roots

Coarse root mass was significantly increased by WI and WIFP treatment relative to the W treatment, and greater in the WIFP treatment than in the WI treatment (Fig. 11a). Coarse root mass ranged from 2.2 Mg ha^{-1} in the W treatment to 4 Mg ha^{-1} in the WIFP treatment. Tap root mass was significantly increased from 9.2 Mg ha^{-1} in the W treatment to 15.2 Mg ha^{-1} in the WIFP treatment, and WI treatment increased tap

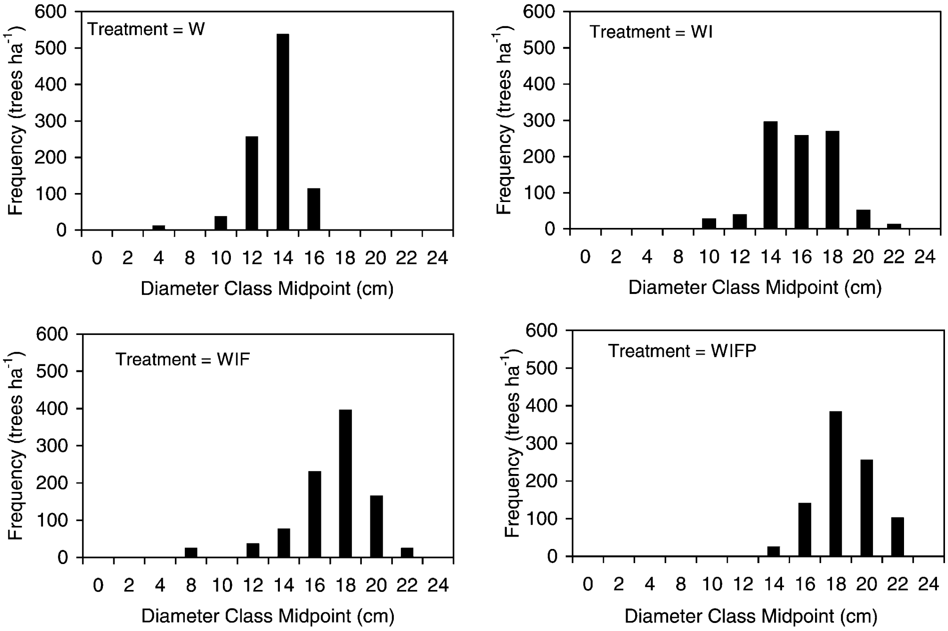

Fig. 3. Living diameter distribution of 6-year-old loblolly pine stands in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control, irrigation, fertigation, and pest control (WIFP).

root mass relative to the W treatment (Fig. 11a). No significant differences in relative allocation to tap root were observed among treatments (Fig. 11a). Allocation to woody root relative to woody shoot significantly decreased with increasing intensity of treatment from 35% in the W treatment to 31% in the WIFP treatment (Fig. 11b).

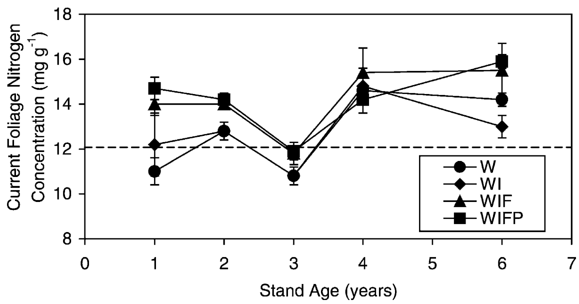

Fig. 4. Foliar nitrogen concentration of loblolly pine in relation to stand age in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation, and pest control (WIFP). The line indicates the 12 mg g^{-1} critical level for loblolly pine (Allen, 1987).

4. Discussion

On this southern Georgia site, maximum aboveground net primary production of intensively managed loblolly pine was 25 Mg ha^{-1} per year at age 4. This value is higher than the maximum of 15–20 Mg ha^{-1} per year reported for 6–23-year-old slash pine (*Pinus elliottii* Engelm.) and 7–9-year-old loblolly pine (Gholz et al., 1991; Jokela and Martin, 2000), and 17 Mg ha^{-1} per year observed for 50-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Gower et al., 1992), but lower than the 39 Mg ha^{-1} per year reported for 13-year-old Monterey pine (*Pinus radiata* D. Don) (Snowdon and Benson, 1992). After six growing seasons, increasing management intensity greatly accelerated stand development (e.g. LAI and the decrease in CAI from ages 5 to 6) and aboveground biomass accumulation (maximum of 72 Mg ha^{-1}) relative to other reports on intensively managed loblolly pine. For example, aboveground biomass accumulation was 50 Mg ha^{-1} in 6-year-old loblolly pine planted on a 1.8 m × 3.6 m spacing and managed with repeated fertilization and weed control (Jokela and Martin, 2000). King et al. (1999) reported maximum

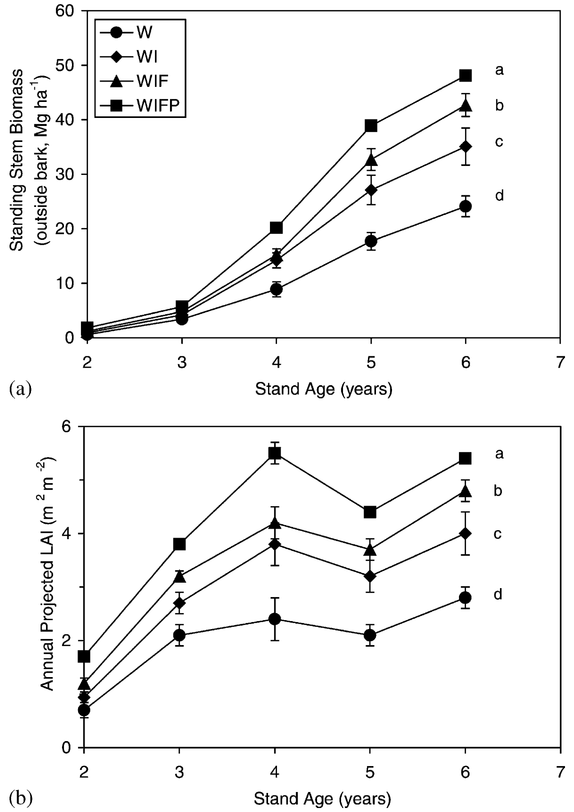

Fig. 5. Standing stem biomass (a) and projected LAI (b) vs. stand age of loblolly pine stands in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation, and pest control (WIFP). Standard error bars represent plot to plot variation. Different letters denote significant differences among treatments at age 6.

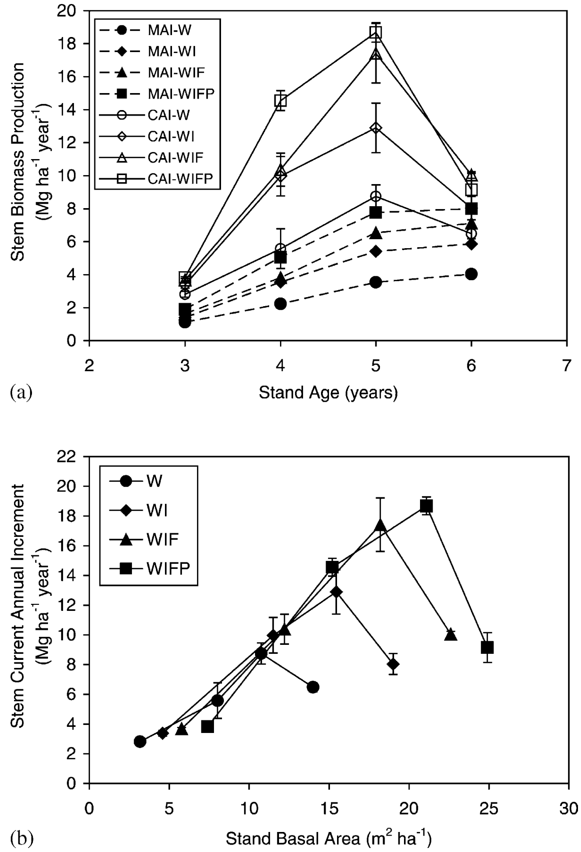

Fig. 6. Mean annual increment (MAI) or current annual increment (CAI) vs. (a) stand age or (b) stand basal area of loblolly pine stands in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation, and pest control (WIFP). Standard error bars represent plot to plot variation.

aboveground and belowground biomass accumulation of 44 and 13.6 Mg ha^{-1}, respectively, in response to irrigation plus fertilization in an 11-year-old loblolly pine plantation stocked at 1260 stems ha^{-1}. LAI increased with management intensity to values unprecedented in the southeastern US, and previous-year LAI was strongly related to CAI. Although biomass accumulation was greater in our study than in King et al. (1999) because of greater LAI, belowground allocation patterns were similar between studies, indicating that these metrics might be stable across sites. Allocation to tap root, coarse root, and fine root relative to total belowground mass was 75, 18 and 7%, respectively, in response to fertilization with irrigation (King et al., 1999) compared to 72, 20 and 8%, respectively, in our stands under the most intensive treatment. In contrast, in our study, stands in the WIFP treatment allocated more to stem and less to foliage and branch compared to the King et al. (1999).

Relative to the W treatment, aboveground mass, tap root mass, and coarse root mass were approximately doubled by the most intensive treatment. Across all treatments, belowground mass was 22–25% of total mass, estimates that are likely biased downward due to assumptions on course root lateral extent and fine root horizontal extent. Our estimates of total belowground mass are larger than the 12% reported by Naidu et al. (1998) based on regression equations developed from loblolly pine trees from a range of diameters and canopy locations in unmanaged plantations. However,

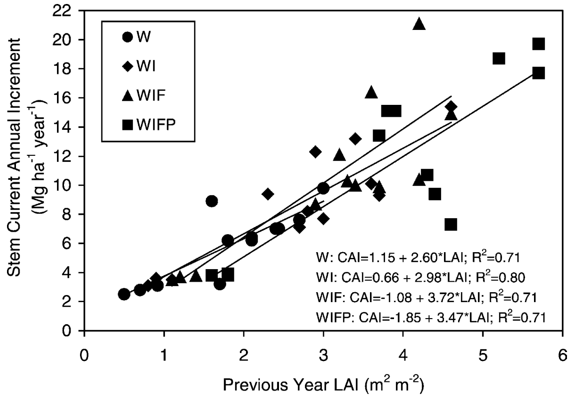

Fig. 7. Stem current annual increment in relation to previous-year projected leaf area index (LAI) of loblolly pine stands in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation, and pest control (WIFP). Symbols represent individual plot values from ages 3 to 6.

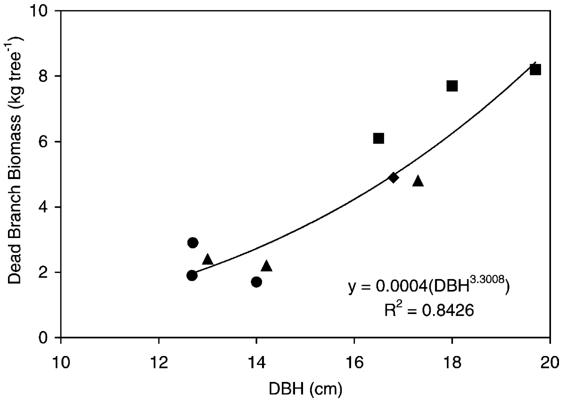

Fig. 9. Relationship between dead branch biomass and diameter at breast height for 6-year-old loblolly pine in response to weed control (circles), weed control plus irrigation (diamonds), weed control plus irrigation and fertigation (triangles), and weed control plus irrigation, fertigation, and pest control (squares). Symbols represent one tree harvested from each plot.

Van Lear and Kapeluck (1995) found that 20% of total biomass was partitioned to roots in a 48-year-old loblolly pine plantation. Maximum belowground accumulation of 36–39 Mg ha^{-1} has been reported for loblolly pine plantations ranging in ages from 15 to 48 years (Wells et al., 1975; Pehl et al., 1984; Van Lear and Kapeluck, 1995). Our estimates of belowground biomass, ranging from 12 to 21 Mg ha^{-1} at only age 6, reflect the very high productivity achieved in this experiment.

Results reported here are notably similar to a study on the effects of management intensity on growth of

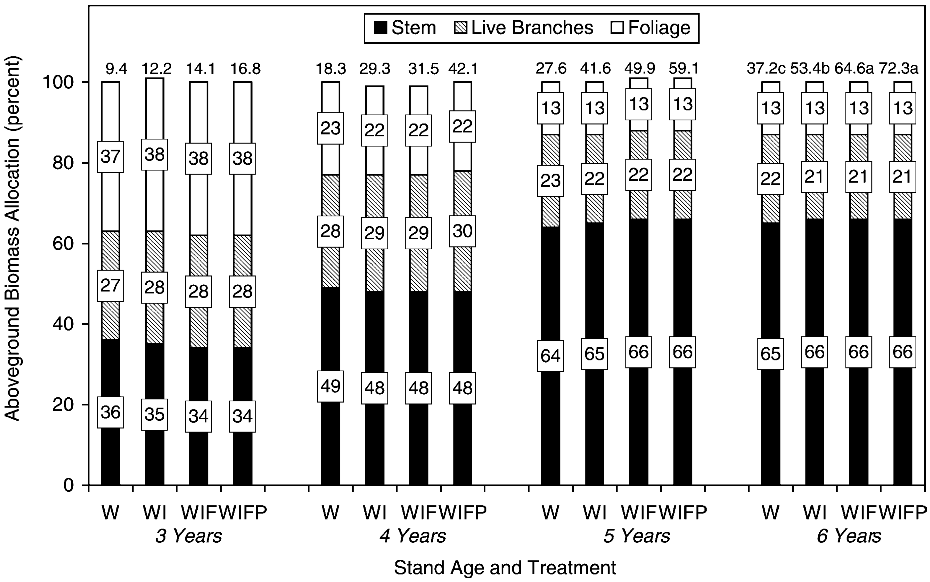

Fig. 8. Stand-level allocation of aboveground mass to foliage, branch and stem from ages 3 to 6 of loblolly pine stands in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation, and pest control (WIFP). Percentages of each component are indicated, and absolute standing aboveground mass (Mg ha^{-1}) is indicated above each bar. Different letters denote significant differences among treatments at age 6.

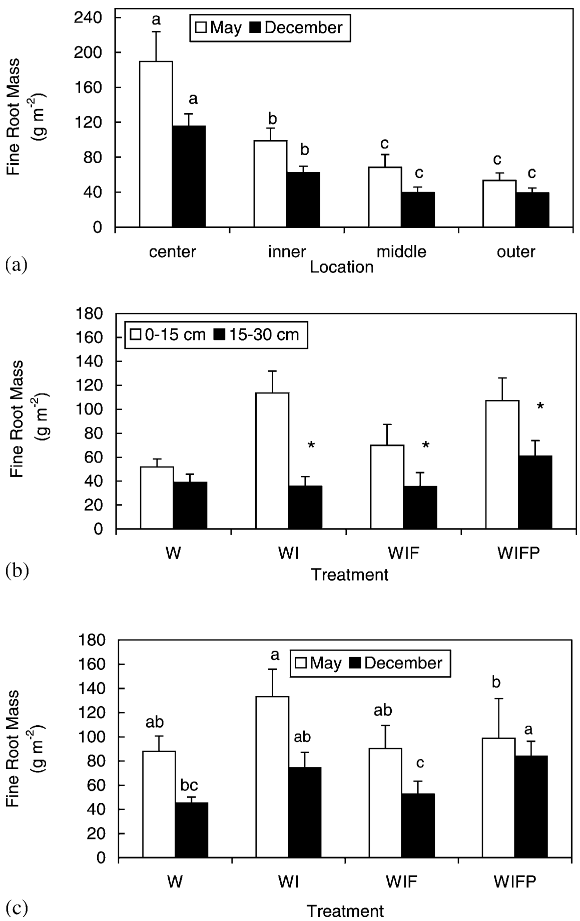

Fig. 10. Fine root mass of 6-year-old loblolly pine in response to (a) soil location in May and December 2000, (b) soil depth by treatment in December 2000, and (c) treatment in May and December 2000. Treatments were weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation, and pest control (WIFP). Locations were between two trees within a row (center), and 0.6 m (inner), 1.2 m (middle), and 1.8 m (outer) from the center location. Different letters or '*' denote significant differences among locations, soil depths, or treatments. Note: statistical analysis based on log-transformed fine root mass.

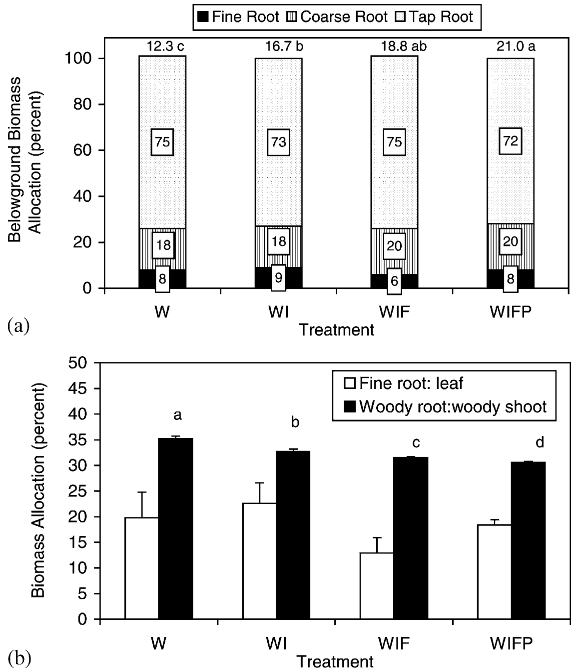

Fig. 11. Allocation of total belowground mass in (a), and (b) allocation to fine root mass (stand-level, measured in December 2000) relative to leaf mass, and to total woody root mass (coarse + tap root) relative to woody shoot mass (branch + stem) in 6-year-old loblolly pine stands in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation, and pest control (WIFP). In (a), absolute standing belowground mass (Mg ha^{-1}) is indicated above each bar, and percentages of each component are indicated. Different letters denote significant differences among treatments. Trees were harvested in December 2000.

loblolly pine in Florida, in that a maximum in periodic annual increment (PAI) of 14 Mg ha^{-1} per year at a basal area of 23 m^2 ha^{-1} was observed in 8-year-old loblolly pine in response to fertilization plus competition control (Jokela and Martin, 2000) compared to our maximum CAI of 18 Mg ha^{-1} per year at a basal area of 21 m^2 ha^{-1} in WIFP stands. Jokela and Martin (2000) concluded that the decline in PAI after peak LAI was a result of N limitations following cessation of fertilizer treatment. However, in our study foliar N was not limiting after age 3 and the decline in CAI at age 6 was strongly correlated to LAI of the previous year. Because the majority of stem growth occurs before current-year-foliage is no longer a carbon sink (Harkin, 1962; Radoglou and Teskey, 1997; Tang et al., 1999), 1-year-old foliage is important in providing the carbon for stem growth in the spring (Chung and Barnes, 1980). Previous-year foliage is also responsible for recharging the labile carbon pool during the non-growing season, and this labile carbon pool is critical for maintaining mid-summer growth rates when carbon demand can outpace carbon gain due to high temperature, and soil and atmospheric drought stress (Sampson et al., 2001). Previous work on this site established the importance of leaf area rather than leaf-level physiology in determining maximum productivity in young loblolly pine (Samuelson, 1998; Samuelson et al., 2001), and this work demonstrates the importance of LAI of the previous year in defining stand-level productive potential under intensive management.

Dougherty et al. (1995) reported that annual leaf biomass production in loblolly pine was strongly correlated to the average mean temperature from June to September, the period of rapid needle expansion in the canopy, and a 2 °C increase in average temperature reduced annual leaf biomass production by 27% in 11–17-year-old loblolly pine. Average mean temperature from June to September decreased from 27.8 °C in 1998 (age 4) to 26.1 °C in 1999 (age 5), but reductions in LAI ranging from 12 to 22% were observed from ages 4 to 5. Lower LAI at age 5 may be in response to peak LAI at age 4 and a shifting of the live crown after canopy closure, rather than a function of climate. In the most intensively managed stands, LAI at ages 4 and 6 was between 4 and 5.5 $m^2\ m^{-2}$, a theoretical optimum for maximum productivity in loblolly pine (Gholz, 1986). Crown closure was evident in all treatments except the control by age 4, and at age 6 the crown ratio was smaller and dead branch biomass was greater in the more developed stands. Thus, shifts in LAI from ages 4 to 6 were possibly due to changes in canopy architecture associated with canopy closure (Smith and Long, 2001), mainly the loss of foliage in the lower canopy and redistribution of foliage to the upper canopy. Similarly, Xu and Harrington (1998) observed an upward shift of crown foliage of loblolly pine with increasing LAI from 3 to 5 $m^2\ m^{-2}$ in response to greater shading among individuals. Leaf area of upper but not lower crown shoots increased 64% 6 years after fertilization in 13-year-old loblolly pine (Tang et al., 1999). Although the canopy was rising rapidly most likely because of increased shading of lower foliage, LAI remained relatively steady, indicating that LAI has not, to this point, overshot a maintainable maximum and then declined. In addition, although CAI and MAI appear near convergence at age 6 in WIFP stands (a similar convergence of PAI and MAI at 8 Mg ha^{-1} per year was reported for intensively managed loblolly pine at age 12 by Jokela and Martin (2000)), it is unclear if MAI has culminated in WIFP stands given the strong relationship between CAI and previous-year LAI.

We had hypothesized that increased availability of water and nutrients would decrease allocation to fine roots and thus maintain stemwood growth efficiency. Stemwood growth efficiency, defined as the slope of the relationship between CAI and previous-year LAI, ranged from 2.6 to 3.7 Mg ha^{-1} per year previous-year LAI^{-1} when calculated over the life of the plantation. Stemwood growth efficiency was maintained in the more developed stands most likely in response to the upward shift in crown foliage rather than to changes in relative allocation to fine roots. Treatment effects on fine root mass were inconsistent and reductions in woody root mass relative to woody shoot mass in response to intensive silviculture were small and likely a function of ontogeny. In contrast, on a more nutrient limiting site, Maier and Kress (2000) observed lower fine root mass in fertilized than in unfertilized 11-year-old loblolly pine trees during most of the year including winter, and on the same site fertilization increased net production and turnover of fine roots (King et al., 2002). As of yet, we have no information on the impacts of intensive management at this site on fine root turnover, which represents a major component of belowground carbon use.

In summary, 6 years of intensive management since plantation establishment greatly accelerated stand development and above and belowground production in loblolly pine. Management intensity had a large impact on LAI and little effect on carbon allocation patterns. The strong relationship between CAI and LAI of the previous year demonstrates the continuing importance of LAI in defining maximum productivity in intensively managed loblolly pine plantations.

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