Growth and physiology of loblolly pine in response to long-term resource management: defining growth potential in the southern United States

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Abstract: Leaf physiology and stem growth were assessed in loblolly pine (*Pinus taeda* L.) in response to 10 to 11 years of treatment with weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), or weed control plus irrigation, fertigation, and pest control (WIFP) to determine whether increased resource availability can push productivity of loblolly pine closer to its biological growth potential expressed in favorable, exotic environments. Maximum basal area and stem biomass were 41 $m^2 \cdot ha^{-1}$ and 172 $Mg \cdot ha^{-1}$, respectively, in response to fertigation. Stemwood biomass production was positively and linearly related to basal area. Belowground woody biomass was highest in the WIF and WIFP treatments and averaged 50 $Mg \cdot ha^{-1}$, but the W and WI treatments exploited a greater area of soil with low-density coarse roots. Fertigation increased foliar nitrogen concentration and foliage biomass, but treatment had no effect on leaf physiological parameters or growth efficiency. Comparison with growth rates reported for loblolly pine in Hawaii revealed that loblolly pine grown in its native range can produce the high yields observed in exotic environments when stands are below maximum carrying capacity.

Résumé : Dans le but de déterminer si une augmentation de la disponibilité des ressources peut rapprocher la productivité du pin des marais (*Pinus taeda* L.) de son potentiel biologique de croissance observé dans des environnements exotiques favorables, la physiologie foliaire et la croissance de la tige ont été mesurées 10 à 11 ans après l'application des traitements suivants : maîtrise de la végétation concurrente (V), maîtrise de la végétation concurrente et irrigation (VI), maîtrise de la végétation concurrente, irrigation et fertigation (VIF) et maîtrise de la végétation concurrente, irrigation, fertigation et contrôle des ravageurs (VIFR). À la suite de la fertigation, les valeurs maximales de surface terrière et de biomasse de la tige atteignaient respectivement de 41 $m^2 \cdot ha^{-1}$ et 172 $Mg \cdot ha^{-1}$. La production en biomasse de la tige était positivement et linéairement reliée à la surface terrière. Les plus fortes valeurs de biomasse ligneuse des racines ont été observées dans les traitements VIF et VIFR et atteignaient en moyenne 50 $Mg \cdot ha^{-1}$, mais les traitements V et VI exploitaient un plus grand volume de sol avec une plus faible densité de grosses racines. La fertigation a provoqué une augmentation de la concentration foliaire en azote et de la biomasse foliaire, mais ce traitement n'a eu aucun effet sur les paramètres physiologiques des feuilles et sur l'efficacité de la croissance. Une comparaison avec les taux de croissance publiés pour le pin des marais dans l'État d'Hawaii, aux États-Unis, montre que le pin des marais qui croît dans son aire de répartition naturelle peut produire les hauts rendements observés dans des environnements exotiques lorsque les peuplements n'excèdent pas la capacité maximale de support du milieu.

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Introduction

The southern United States produces 60% of the Nation's timber products and more timber than any other country in the world (Prestemon and Abt 2002). In part, the role of the southern United States as the woodbasket of the world is due to increasing productivity of pine plantations, in particular loblolly pine (*Pinus taeda* L.) (Prestemon and Abt 2002), as a result of improved genetic stock and use of more intensive management practices, such as repeated fertilization and competition control (Johnsen et al. 2001; Fox et al. 2004). Despite great gains in productivity of loblolly pine in response to more intensive silviculture, growth rates in Hawaii, Brazil, and South Africa indicate that biological expression of growth potential in loblolly pine's native range has not been fully realized (Jokela et al. 2004). As an example, volume and basal area in a 35-year-old plantation in Hawaii were 1300 $m^3 \cdot ha^{-1}$ and 100 $m^2 \cdot ha^{-1}$, respectively,

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and mean annual increment (MAI) was 40 $m^3 \cdot ha^{-1} \cdot year^{-1}$ at age 20 years (Harms et al. 2000). In contrast, maximum carrying capacity for closed-canopy stands in the southeastern United States has been estimated at 45–48 $m^2 \cdot ha^{-1}$ (Jokela et al. 2004). Adegbidi et al. (2002) among others (Samuelson et al. 2004*a*; Allen et al. 2005; Will et al. 2006) have suggested that increased resource availability may produce yields observed in exotic environments. For instance, Borders and Bailey (2001) found that annual fertilization and weed control of loblolly pine in Georgia increased volume MAI to 34 $m^3 \cdot ha^{-1} \cdot year^{-1}$, which approached yields (37 $m^3 \cdot ha^{-1} \cdot year^{-1}$) reported for loblolly pine in South Africa.

Large gains in leaf area and growth on nutrient limited sites in response to fertilization are common in conifers in the southern United States (Fox et al. 2007). Jokela et al. (2004) identified soil nutrient availability as the dominant driver of stand leaf area and subsequent productivity of loblolly pine from a synthesis of seven long-term experiments in the southern United States spanning a wide range of soil and climate conditions and stand ages. To a lesser degree, soil water availability and evaporative demand may influence leaf area and leaf retention (Teskey et al. 1987; Dougherty et al. 1995), and fertilization may increase vulnerability to drought stress by reducing the root to leaf area ratio (Ewers et al. 2000). Water availability in addition to fertilization may be important in supporting exceptionally high leaf area and achieving maximum productivity in climates with high vapor pressure deficit and high temperatures during the growing season (Teskey et al. 1987; Gholz et al. 1990; Sampson and Allen 1999; Samuelson and Stokes 2006). Greatly accelerated growth rates in loblolly pine in response to fertilization and increased soil water availability indicate that amelioration of nutrient and water deficiencies can significantly alter productivity and patterns of stand development (Borders and Bailey 2001; Samuelson et al. 2004*a*).

Whether high production rates can be sustained over the long-term by increased resource availability is unclear (Adegbidi et al. 2002). Jokela et al. (2004) concluded that growing space limitations would limit fertilizer responses once basal area exceeds 35 $m^2 \cdot ha^{-1}$. Similarly, Will et al. (2002) determined that annual fertilization had a continued and positive effect on current annual increment (CAI) and leaf biomass of loblolly pine from 7 to 13 years of age, but growth efficiency declined once basal area surpassed 37 $m^2 \cdot ha^{-1}$. No decline in CAI and growth efficiency over time was reported from ages 7 to 16 years in fertilized and irrigated loblolly pine stands because of low mortality and little variation in relative growth rate across tree size classes (Albaugh et al. 2004). However, once basal area reached 35 $m^2 \cdot ha^{-1}$ at age 17 years, mortality increased in fertilized plots (Albaugh et al. 2006*a*).

This paper presents long-term growth responses of loblolly pine to continuous resource management to determine whether improved genetic stock, fertilization, irrigation, and weed control can produce growth rates in loblolly pine comparable with those observed in favorable, exotic environments (Neary et al. 1990). The objectives of this study were to (*i*) assess long-term growth and ecophysiological responses to resource availability, and (*ii*) determine the degree to which increased resource availability can push productivity of loblolly pine closer to its biological growth potential. Leaf-level physiology, stand dynamics, and above- and below-ground biomass were examined in loblolly pine after 10–11 years of management with weed control, irrigation, fertigation, and pest control.

Materials and methods

Study design

The 15 ha research site was located in the Upper Coastal Plain 22 km west of Bainbridge, Georgia (30°48′N, 84°39′W) and maintained by International Paper, Inc. Mean annual precipitation and 24 h temperature for the region are 1257 mm and 18.9 °C, respectively (Ruffner 1980). The site was previously used for agriculture for several decades. Soils were classified as well-drained Grossarenic Paleudults, and 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(+)$\cdot kg^{-1}$, 23.3 $mg \cdot kg^{-1}$, and sandy loam, respectively. Estimated site index base age 25 years 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 controlled using a broadcast spray of glyphosate herbicide (1.5% solution in water) applied in July and September 1994. Loblolly pine seedlings were hand-planted using 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 subplots within a block-treatment plot. Growth and physiology of only family 7-56 was presented in this study as well as in previous research on this plantation conducted up to age 6 years (Samuelson 1998; Samuelson et al. 2001, 2004*a*, 2004*b*; Samuelson and Stokes 2006). Excluding buffer rows, the measurement plot for an individual family subplot was 0.026 ha with 28 sample trees. Treatment plots were arranged in a randomized complete block design with four treatments and three blocks. The treatments identified below were applied since plantation establishment (see Table 1 for details): (*i*) complete weed control (W); (*ii*) weed control plus drip irrigation (WI); (*iii*) weed control, drip irrigation, and fertigation (WIF); and (*iv*) weed control, drip irrigation, fertigation, and pest control. In the W treatment, complete weed control was maintained using a broadcast application of sulfometuron (0.1 kg active ingredient$\cdot ha^{-1}$) and several directed applications of glyphosate (1.5% solution in water) throughout the summer. The WI treatment used weed control plus drip irrigation (Netafim Irrigation, Inc., Altamonte Springs, Florida) from drip lines that ran along tree rows on the south side of each tree. Watering was done from March through December. Irrigation was applied daily, and the system was programmed to apply 6.25 $mm \cdot day^{-1}$. From 2001, the irrigation ran every day the system was operational regardless of precipitation amounts. The rationale was to ensure that there was no or minimal water stress on irrigated plots on this well-drained soil. The drip system did not function for most of 2004 but was operational beginning July 2005. In addition to weed control and drip irrigation for the WIF treatment, fertiga-

Table 1. Annual water balance and irrigation additions in weed control plus irrigation, weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation, and pest control (WIFP) treatments and fertilizer additions in WIF and WIFP treatments.

Year	PET (mm)	Precipitation (mm)	Irrigation (mm)	N ($kg \cdot ha^{-1}$)	P ($kg \cdot ha^{-1}$)	K ($kg \cdot ha^{-1}$)
1995			341	45	11	45
1996	944	938	210	87	22	87
1997	908	951	266	135	33	130
1998	961	997	310	112	20	90
1999	833	597	1127	79	20	79
2000	794	614	1127	79	20	79
2001	635	1014	1575	111	28	111
2002	964	927	1575	113	28	113
2003	876	985	1575	132	37	132
2004	958	927	381	49	12	49
2005	943	1306	1016	38	10	38

Note: Potential evapotranspiration (PET) and precipitation data were from the Georgia Automated Environmental Monitoring Network (www.GeorgiaWeather.com) for Attapulgus, Georgia, approximately 21 km from the study site.

Table 2. Summary of ANOVA degrees of freedom and *p* values for family (7-56 and a Florida family) and management treatment effects on stand characteristics of loblolly pine.

Source of variation	Numerator df	DBH	Height	Live crown length	Basal area	Volume
Block	2	0.016	0.018	0.014	0.014	0.009
Treatment	3	<0.001	<0.001	0.002	<0.001	<0.001
Whole-plot error	6					
Family	1	0.005	<0.001	0.539	0.853	0.312
Family × treatment	3	0.573	0.616	0.773	0.116	0.219
Split-plot error	8					

tion (addition of a fertilizer solution to the irrigation water) with NH_4NO_3, and urea, H_3PO_4 and K_2O was applied. Addition of fertilizer to the irrigation water ran from May through October with additions spread evenly throughout the 6 months. Fertilizer was injected daily. The only record of micronutrient fertilization is the application of 0.21 $kg \cdot ha^{-1}$ of elemental copper in 1997. Soil nutrient concentrations were measured before planting and described in Samuelson (1998). Finally, in the WIFP treatment, pest control was added to weed control, irrigation, and fertigation. Fusiform rust (*Cronartium quercuum* (Berk.) Miyabe ex Shirai, f. sp. *fusiforme* (Hedgc. & N. Hunt) Burdsall & G. Snow) was controlled with applications of triadimefon fungicide from 1995 to 2000. Nantucket pine tip moth (*Rhyacionia frustana* (Comstock)) was controlled with applications of permethrin or acephate insecticides during the growing season from 1995 to 2005. Insect damage was monitored the first 4 years, and tip moth damage defined by the percentage of damaged shoots was as much as two times greater in treatments lacking pest control during high infestation periods (Nowak and Berisford 2000).

Aboveground biomass and growth

Plot inventories were made annually through age 11 (2006). These inventories included diameter at breast height (DBH), total height and live crown length of all living trees in each measurement plot. Above- and below-ground biomass was measured at age 10 years. In the current study to limit tree removal from family 7-56 plots, we harvested sample trees from a different family (from Florida) with similar stand characteristics just to develop surrogate allometric equations for use with family 7-56. To justify applying allometric equations developed from the Florida family to family 7-56, stand characteristics were compared between the two families using analysis of variance for a split-plot design with treatment as main plots and family as subplots. Stand merchantable volume (to a top diameter limit of 5 cm) was calculated with individual tree volume equations from Pienaar et al. (1987). No significant interaction between family and treatment was detected for any growth variable at age 10 years (Table 2), indicating that the two families responded similarly to management intensity. Family 7-56 had greater height (16.2 m versus 15.6 m) and DBH (21.4 cm versus 20.8 cm) than the Florida family, but live crown length, basal area, and volume were similar between families (Table 2).

One tree from each plot representing mean plot DBH was harvested during the week of 17 January 2005 from the Florida family. Trees were felled at the groundline, and all branches (foliage + branch) were immediately weighed after cutting. One sample branch from each whorl in the live crown of each tree was randomly selected and stored in a cooler at 5 °C until processing. Foliage was removed from sample branches, and foliage and branch mass were measured after oven-drying to a constant mass at 65 °C. To estimate total foliage mass for a felled sample tree, regression equations were developed by sample tree between foliage dry mass and total branch green mass and height to the branch whorl. Total branch mass of a sample tree was estimated from regression equations for relationships between branch dry mass and branch diameter developed for each sample tree.

Table 3. Regression equations between biomass and tree size for loblolly pine developed using the Florida family.

Regression equation	n	$P > F$	R^2
Leaf mass = 3.428 + 0.00055(DBH^2 × LCL)	12	0.002	0.623
Branch mass = –54.110 + 1.376(DBH) + 5.121(LCL)	12	0.002	0.701
Log(stem mass) = –4.806 + 1.085(log(DBH^2) × H)	24	<0.001	0.986

Note: Data were pooled across treatments. Equations for leaf and branch mass were based on trees harvested at age 10 years, and the equation for stem mass was based on trees harvested at ages 6 and 10 years. Mass was measured in kilograms per tree; diameter at breast height (DBH) was measured in centimetres; and height (H) and live crown length (LCL) were measured in metres.

The bole was cut into 1.2 m sections. A disk was cut from every 1.2 m section, and green stem sections and disks were weighed on site. Relationships between disk dry mass and disk green mass were developed by sample tree to predict the dry mass (including bark) of each 1.2 m section. The dry mass of each section was summed by sample tree.

Allometric equations between total tree stem, leaf, or branch mass and DBH, live crown length, or height were developed by pooling across treatments, because of the low sample size (Table 3). As such, we assumed that the relationship between biomass and tree size parameters did not change with treatment and differences in live crown length would take into account potential treatment differences in relationships between foliage or branch biomass and tree size. Individual tree stem mass (including bark) for years 6–11 was estimated using an allometric equation developed from the combined data from this harvest and from a harvest at age 6 using family 7-56 (Samuelson et al. 2004*a*) (Table 3). Stem biomass for age 6 years from Samuelson et al. (2004*a*) was recalculated using the new allometric equation.

Stand-level leaf, branch, and stem biomass at the end of the 10th growing season and stem biomass for years 6–11 were calculated using the allometric equations and annual inventory data for family 7-56. Biomass components were predicted for each tree and summed for each 28 tree plot. Stand-level stem mass was used to calculate CAI (yearly increment in stem mass) and MAI (mass/age). Leaf area index (LAI) was measured with a LAI-2000 plant canopy analyzer (LI-COR Inc., Lincoln, Neb.) on one date in May, July, and August over 3 years, from ages 8–10 years. Growth efficiency in years 8–10 was calculated as CAI divided by LAI averaged over May–August. Crown density was calculated as the quotient of mean individual tree foliage biomass and live crown length.

Belowground biomass

Ground-penetrating radar (GPR) has been shown to be a rapid means of detecting tree roots and measuring lateral root mass in well-drained, electrically resistive soils (Butnor et al. 2001, 2003; Cox et al. 2005; Stover et al. 2007). We collected root data with GPR using two separate procedures: (*i*) linking radargrams to destructively sampled soil cores to calibrate the system and provide a correlation between actual harvested root mass and a radar-derived index of root reflectance (Butnor et al. 2003; Stover et al. 2007), and (*ii*) collecting radar data in series of parallel transects around each sample tree to add a spatial dimension to the GPR survey and applying the calibration developed using the first procedure to give a measure of root mass per unit area of soil. Surface-based radars used in reflection mode only measure lateral root mass and are unable to measure taproot mass. For both procedures, an SIR-2000 GPR system equipped with a model 5100 high-frequency antenna (1.5 GHz) and an encoder wheel (Geophysical Survey Systems, Inc., North Salem, N.H) was used during the week of 17 January 2005 to collect all of the field data. The antenna was through-mounted on to a wooden runner (skateboard deck) to glide over the soil surface with minimal rocking and maintain close contact with the soil. A 16 in. (1 in. = 2.54 cm) encoder wheel was attached to the rear of the runner to link the density of data collection to the distance traveled along a transect.

Within each block treatment combination, a 3.6 m transect was established equidistant between trees and perpendicular to rows. Seven sample points were located 60 cm apart along each transect. One pass was made with the 1.5 GHz antenna on a transect, and the location of each sample point on the radargram was marked. Once GPR sampling was complete, a 15 cm diameter soil core was collected to a depth of 30 cm at each point. Live coarse roots (>2 mm diameter) were separated from soil using a standard No. 14 mesh sieve and washed with water. The roots were oven-dried at 65 °C for 72 h and weighed to determine total coarse root biomass. Because it is difficult to delineate root diameter when the orientation of roots is unknown (Butnor et al. 2001; Barton and Montagu 2004), total live coarse root biomass for the entire 30 cm core was correlated to GPR results. Raw GPR data were processed using the method described by Stover et al. (2007); the only difference was the omission of the Kirchoff migration step, which had been previously found to be unnecessary at this site (Butnor et al. 2003). GPR analysis provided a relative index of root mass density which was scaled to megagrams per hectare using 84 soil cores and linear regression.

Within each block treatment combination, eight trees were selected for detailed root mass analysis (two rows of four adjacent live trees) for a total of 96 trees. After the litter was raked aside, an area of 7.5 m^2 was scanned around each tree using 10 parallel transects spaced 0.25 m apart. The GPR survey took 1.5 days to complete and imaged a total of 720 m^2 of forest floor with a collection density equivalent to 21 900 soil cores (15 cm). The survey data from each tree was converted to megagrams per hectare of live coarse root mass with the core correlation. Data summarization and spatial analysis for each 7.5 m^2 plot was performed with Surfer 8.0 (Golden Software Inc., Golden, Colo.). For the purpose of estimating total belowground biomass, taproot plus adjacent coarse root mass within a 1 m^2 area directly beneath each tree was modeled using a linear equation developed by Johnsen et al. (2004), ($y = 1.956 + (0.2166280114 \times$ aboveground mass), $R^2 = 0.98$) and combined with radar estimates of lateral root mass measured outside the 1 m^2 area.

Leaf physiology

Leaf-level physiology was measured over a 3 day period between 09:00 and 16:00 on one block per day beginning 13 October 2004 (age 10 years). Loblolly pine typically has light-saturated photosynthetic rates (A_{sat}) in October equivalent to or greater than rates observed in summer (Gough et al. 2004*a*). All measurements were made on current-year, first-flush foliage. Leaf A_{sat} was measured on one fascicle each from upper and lower canopy positions on three to five randomly selected trees in each treatment plot using two portable gas exchange systems (LI-COR 6400; LI-COR Inc., Lincoln, Neb.). The order of measurement for each treatment plot within a block was random, but all trees in a plot were measured before moving to the next treatment plot. The canopy was accessed using a portable lift. During measurements, leaf chamber conditions were maintained at 25 °C and 1800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetically active radiation (PAR), vapor pressure deficit <1 kPa, and reference [CO_2] of 38 Pa. Measurements were made on detached fascicles within several minutes of removing shoots from the canopy (Maier et al. 2002). After gas exchange measurements, needle length and diameter were measured, and dry mass was determined. Needles were oven-dried to a constant mass at 65 °C ($\approx$48 h), weighed, and ground in a Wiley mill. Leaf mass per unit area (LMA) was calculated as the ratio of needle dry mass to total surface area, where surface area is based on needle length, diameter, and taper (Maier et al. 2004). Foliar nitrogen concentration per unit leaf mass (N_m) or leaf area (N_a) was determined using a Carlo-Erba analyzer (model NA 1500; Fison Instruments, Danvers, Mass.).

Photosynthetic response to internal CO_2 partial pressures (A–pC_i curves) was evaluated during the same sampling period on detached current-year shoots (Maier et al. 2002) using two additional gas-exchange systems (LI-COR 6400; LI-COR Inc., Lincoln, Neb.). Measurement of A and pC_i were made over a range of eight external CO_2 partial pressures (10, 18, 28, 37, 57, 80, 150, and 200 Pa). Leaf cuvette conditions were maintained near 25 °C, 1800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PAR, and vapor pressure deficit <1 kPa. A curve took approximately 30 min to complete, and leaf stomatal conductance changed less than 20% during measurements (data not shown, but see Maier et al. (2002)). Carboxylation efficiency (V_{cmax}) and maximum rate of electron transport (J_{max}) were determined for each shoot using the Farquhar biochemical model of photosynthesis (Farquhar et al. 1980) and the approach described in Ellsworth et al. (2004).

Statistical analysis

Because a factorial design was not used, the individual and interactive effects of nutrients, water, and pest control could not be tested. Measurements of physiological and tree-level characteristics were averaged across trees and plot averages were used in the analyses. The SAS general linear methods analysis of variance (ANOVA) procedure for a randomized complete block design with three blocks was used to test for treatment effects (SAS version 9.1; SAS Institute Inc., Cary, N.C.). Analysis of leaf physiological variables included crown location (upper and lower) as an additional class variable. The ANOVA for area of soil occupied by roots included discrete intervals of root mass density. Homogeneity of variance and normality assumptions were tested for each analysis. All variables were found to be normally distributed with equal variances, and no transformations were made. CAI, MAI, growth efficiency, and LAI were analyzed by repeated measures and the mixed model procedure (PROC MIXED; SAS Inc., Cary, N.C.). The covariance structure for each variable was determined using the bias-corrected Akaike information criterion (Burnham and Anderson 1998), and the autoregressive covariance structure was selected for all variables. In all tests, treatment effects were considered significant at $\alpha \leq 0.05$, and differences between treatments were determined using Tukey's paired comparison procedure. The relationship between CAI and basal area was analyzed on data pooled across treatments and years 3–11 by general linear modeling with the GENMOD procedure (SAS version 9.1, Cary, N.C.), which adjusts regression estimates using the correlation estimate for repeated measures of the same subject (Hartz et al. 2001).

Results

Leaf physiology

No significant treatment $\times$ crown location interactions were detected for any physiological parameter (Table 4). Mean foliar N_m was highest in WIF and WIFP treatments (17.8 $mg \cdot g^{-1}$) and was 36% greater than in WI and W trees (Table 4). There were no treatment effects on foliar LMA; as a result, treatment effects on N_a were similar to N_m. Management treatment had no significant effect on A_{sat}, V_{cmax}, or J_{max}. Upper canopy sun foliage had significantly higher N_m, N_a, LMA, A_{sat}, V_{cmax}, and J_{max} than lower canopy shade foliage.

Aboveground growth

Management treatment had a significant influence on DBH ($p < 0.001$), height ($p < 0.001$), basal area ($p < 0.001$), and volume ($p < 0.001$) at age 11 years. DBH and volume were highest in WIF and WIFP stands and higher in WI than W stands (Fig. 1; Table 5). Across the WIF and WIFP treatments, mean DBH and volume were 24 cm and 341 $m^3 \cdot ha^{-1}$, respectively. Basal area was 41 $m^2 \cdot ha^{-1}$ in WIF stands and greater in WIF than in WI and W stands (Fig. 1). Height was greatest in the WIFP treatment (18 m) (Fig. 1). A total of three trees were removed from each plot (115 $trees \cdot ha^{-1}$) for biomass sampling from ages 1 through 6 years. By age 11 years, actual cumulative mortality was 39, 51, 51 and 141 $trees \cdot ha^{-1}$ in W, WI, WIF, and WIFP treatments, respectively. At age 11 years, stem density declined to 820 $trees \cdot ha^{-1}$ in the WIFP treatment compared with 910–923 $trees \cdot ha^{-1}$ in the other treatments (Fig. 1).

Stand-level stem and total aboveground biomass at age 10 years were highest in WIF and WIFP treatments and greater in the WI than W treatment (Table 5; Fig. 2). Branch biomass was similar among the WI, WIF, and WIF stands and lowest in the W treatment (Table 5). Leaf biomass was higher in the WIF and WIFP treatments relative to W stands

Table 4. Effects of management treatment on leaf physiological parameters and crown characteristics of loblolly pine family 7-56 and associated ANOVA *p* values.

	N_m (mg·g^{-1})	N_a (g·m^{-2})	LMA (g·m^{-2})	A_{sat} (µmol·m^{-2}·s^{-1})	V_{cmax} (µmol·m^{-2}·s^{-1})	J_{max} (µmol·m^{-2}·s^{-1})	Foliage mass (kg·tree^{-1})	Live crown length (m)	Crown density (kg·m^{-1})
Treatment									
W	13.1±1.5b	1.0±0.2b	74.3±5.3	5.5±0.9	36.3±2.4	47.4±4.0	5.0±0.05c	8.0±0.2c	0.64±0.01
WI	13.2±5.0b	1.0±0.2b	69.6±5.0	4.3±0.8	33.9±3.1	45.9±3.4	5.7±0.15b	9.5±0.4b	0.61±0.01
WIF	17.3±1.9a	1.2±0.2ab	67.0±3.6	5.3±0.7	38.0±2.6	46.7±3.6	6.3±0.03a	9.9±0.1ab	0.64±0.01
WIFP	18.4±1.1a	1.4±0.2a	73.7±4.9	5.6±0.9	34.8±1.6	44.1±1.9	6.6±0.11a	10.4±0.2a	0.64±0.01
Crown location									
Upper	17.5±1.0a	1.4±0.1a	81.9±1.4a	6.7±0.5a	38.7±1.2a	50.5±2.3a			
Lower	13.5±1.4b	0.8±0.1b	61.8±1.0b	3.7±0.3b	32.8±1.7b	41.7±1.2b			
P > *F*									
Block	<0.001	<0.001	0.835	<0.001	0.675	0.212	0.044	0.592	0.941
Treatment	0.001	0.001	0.149	0.0862	0.610	0.822	<0.001	0.002	0.250
Location	<0.001	<0.001	<0.001	<0.001	0.020	0.004			
Treatment × location	0.623	0.567	0.342	0.852	0.501	0.275			

Note: Values are means ± SEs at age 10 years. Parameter values among treatments or between crown locations with different letters are significantly different ($\alpha = 0.05$). N_m, foliar nitrogen concentration per unit leaf mass; N_a, foliar nitrogen concentration per unit leaf area; LMA, leaf mass per unit area; A_{sat}, light saturated rate of net photosynthesis; V_{cmax}, carboxylation efficiency; J_{max}, maximum electron transport; W, weed control; WI, weed control plus irrigation; WIF, weed control plus irrigation and fertigation; WIFP, weed control plus irrigation, fertigation, and pest control.

(Table 5). Mean maximum total aboveground biomass at age 10 years was 173 Mg·ha^{-1} with stem biomass comprising the majority of aboveground mass. At age 11 years, mean stem mass was 172 Mg·ha^{-1} in the WIF and WIFP treatments.

Stemwood biomass production (CAI) was higher at ages 10 and 11 years than at ages 8 and 9 years, and MAI increased with stand age (Fig. 2; Table 6). No interaction effects between treatment and stand age were detected for MAI or CAI. MAI increased successively with irrigation and fertilization. CAI was highest in WIF stands (25.6 Mg· ha^{-1}·year^{-1}), similar between WIFP and WI stands, and lowest in W stands. A linear relationship between stemwood biomass production and basal area was observed (Fig. 2).

Mean LAI was highest in year 8 and was similar among treatments (5.3 m^2·m^{-2}; Table 6). Individual tree foliage mass increased consecutively with irrigation and fertigation to a mean of 6.4 kg·tree^{-1} in WIF and WIFP stands (Table 4). When foliage mass was standardized by live crown length, crown density was similar among treatments (Table 4). Growth efficiency, defined as the ratio of annual stemwood biomass production to LAI, was highest at age 10 years and not significantly different among treatments (Table 6).

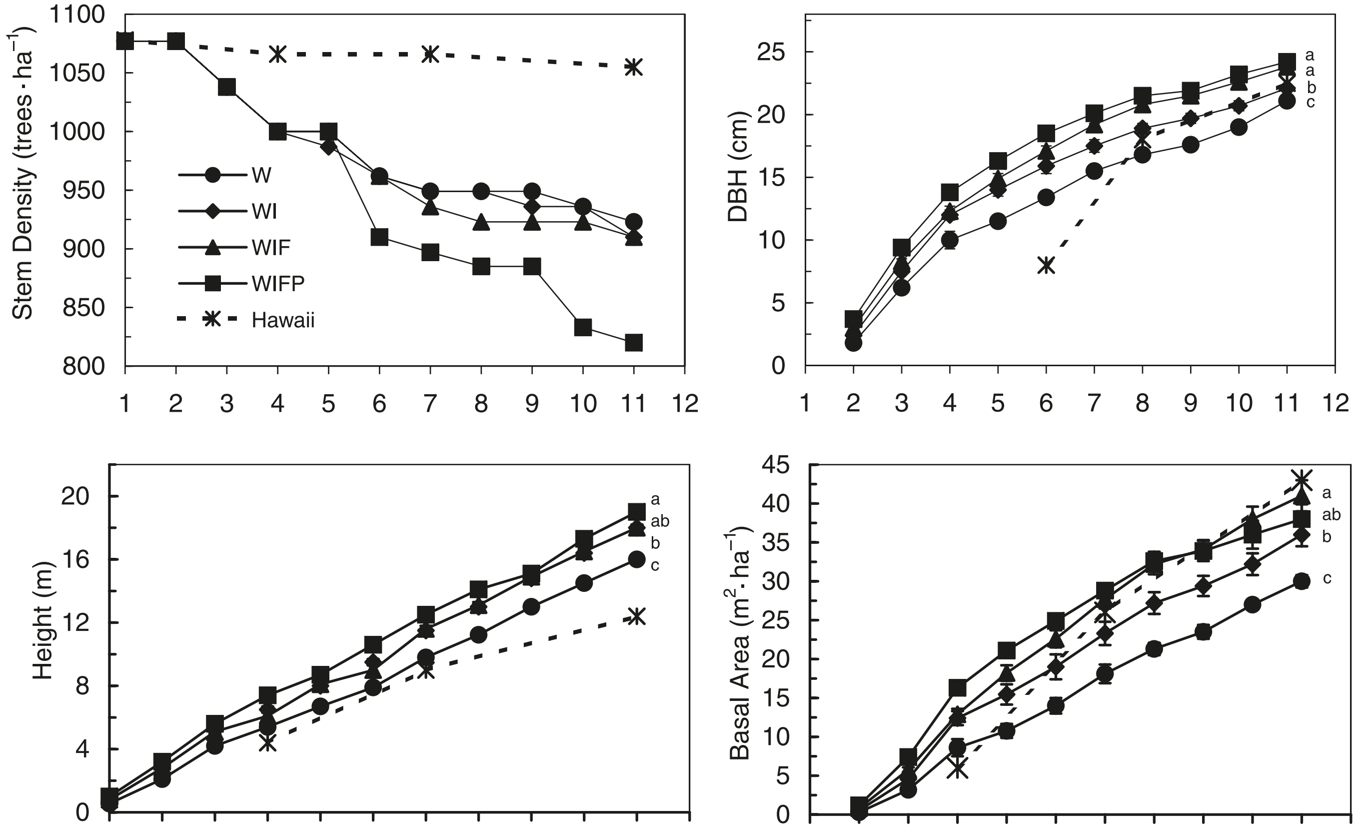
Belowground biomass

Root reflectance measured using GPR was highly correlated with results from soil cores (root mass (g·m^2) = 12.44 + 0.00815 × (GPR reflectance), $R^2 = 0.80$) and radar-derived root data were expressed on a mass per unit area basis. No differences in lateral coarse root mass outside the 1 m^2 area were observed across the treatments (Table 5). Total belowground woody mass was estimated by combining model predicted estimates of taproot mass plus adjacent coarse roots within a 1 m^2 area directly beneath each tree (Johnsen et al. 2004) with GPR measures of lateral root mass. Treatments receiving fertigation (WIF and WIFP) had the highest belowground mass followed by the WI and W treatments, and treatment differences were largely driven by modeled taproot plus coarse root mass within 1 m^2. Allocation to total woody belowground mass relative to total mass (above- and below-ground) was highest in the W treatment and successively decreased with irrigation and irrigation plus fertigation. The minimum coarse root density consistently detected with GPR was 600 g·m^{-2}. Root mass density was divided into 17 intervals from 600 to 4200 g·m^{-2}. Significant treatment ($p < 0.001$), root mass density interval ($p < 0.001$), and treatment × density ($p = 0.013$) effects were observed. The area of soil in the plantation occupied by roots with density between 600 and 1200 g·m^{-2} was higher in W and WI than in WIF and WIFP treatments (Table 7). No significant treatment effects were observed in the nine highest root density intervals (>2200 g·m^{-2}), which accounted for <1% of the total area (data not shown). This analysis revealed that treatments without fertilizer showed a greater area of soil occupied by relatively low-density roots (<1200 g·m^{-2}).

Discussion

Maximum standing stem biomass accumulation rate, 172 Mg·ha^{-1} by age 11 years, is among if not the highest documented for loblolly pine in the southern United States. At 6 years of age, stem biomass in WIFP stands (Samuelson et

Fig. 1. Influence of management intensity on mean stand characteristics of loblolly pine family 7-56. Data from years 1–6 are from Samuelson et al. (2004*a*). Growth of loblolly pine in Hawaii was adapted from Harms et al. (2000). Error bars are SEs. Different letters indicate significant (α = 0.05) differences between treatments at age 11. W, weed control; WI, weed control plus irrigation; WIF, weed control plus irrigation and fertigation; WIFP, weed control plus irrigation, fertigation, and pest control.



al. 2004*a*) was similar to the 40 Mg·ha^{-1} reported for 6-year-old loblolly pine stands planted on a wet site and managed with annual fertilization plus weed control (Borders et al. 2004). By age 11 years, stem biomass in Borders et al. (2004) was 120 Mg·ha^{-1} (inside bark). Although annual stemwood biomass increment of loblolly pine has been shown to peak at basal areas from 20 to 35 m^2·ha^{-1} (Jokela et al. 2004), stemwood increment in this study was linearly related to basal area, and basal area exceeded 40 m^2·ha^{-1} at age 11 years. Basal area in the WIF and WIFP treatments was below the maximum carrying capacity of 45–48 m^2·ha^{-1} estimated for closed-canopy stands in the southern United States (Jokela et al. 2004). Although irrigation increased stem and total above- and below-ground biomass, for the most part, the addition of fertilization to the irrigation water resulted in the greatest growth. Irrigation additions combined with ambient precipitation greatly exceeded potential evapotranspiration (Table 1), and it was assumed that drip irrigation was a surrogate for nonlimiting soil water availability. However, sites with greater water holding capacity may show greater growth response to irrigation.

Increasing management intensity typically results in increased leaf area (Jokela et al. 2004; Samuelson et al. 2004*a*), which likely increases productivity directly by increasing gross primary productivity (GPP). Although large increases in LAI with increasing resource availability were observed up to age 6 years (Samuelson et al. 2004*a*), peak LAI from ages 8–10 years was similar among treatments. It is possible that we were unable to detect treatment differences in LAI using the LI-COR LAI-2000 plant canopy analyzer. Sampson and Allen (1995) demonstrated that increased foliage overlap decreased the ability of the analyzer to accurately estimate LAI in loblolly pine and underestimation of LAI increased as LAI increased (Sampson et al. 2003). Individual tree foliage mass was highest in WIF and WIFP stands, and stand-level foliage mass was higher in WIF and WIFP stands than in W stands, in part because of increased live crown length. Therefore, light attenuation was possibly greater in fertilized stands; to maintain equal growth efficiency, fertilized stands may have made adjustments in morphology or photosynthetic capacity. However, fertilization did not increase photosynthetic capacity despite significant treatment effects on foliar N_m and N_a. These results are consistent with those reported for the same stands at age 4 years (Samuelson et al. 2001). As suggested by Samuelson et al. (2001), this may be in part due to the high soil N availability. Foliar N_m was >13.0 mg·g^{-1} in nonfertilized trees, which is considerably higher than what is considered the optimum for growth (Allen 1987). Additionally, the relationship between A_{sat} and N_a can vary with season and foliage age (Maier et al. 2002), which may reflect phenological differences in the partitioning of leaf N between photosynthetic proteins and more easily transportable forms (e.g., amino acids). Even on sites where N is limiting, typical sites for loblolly pine plantations, it appears that N fertilization only increases A_{sat} ephemerally (Murthy

Table 5. Effects of management treatment on standing volume and biomass of loblolly pine family 7-56 and associated ANOVA *p* values.

	Volume ($m^3 \cdot ha^{-1}$)	Stem mass ($Mg \cdot ha^{-1}$)	Branch mass ($Mg \cdot ha^{-1}$)	Leaf mass ($Mg \cdot ha^{-1}$)	Total aboveground mass ($Mg \cdot ha^{-1}$)	Taproot + coarse root mass ($Mg \cdot ha^{-1}$)*	Lateral coarse root mass ($Mg \cdot ha^{-1}$)†	Total belowground mass ($Mg \cdot ha^{-1}$)‡	Root/total (%)§
Treatment									
W	226.8±4.3c	85.6±1.8c	12.2±0.6b	4.7±0.1b	102.6±2.2c	24.2±0.5c	10.4±0.2	34.5±0.37c	24.8±0.3a
WI	296.9±12.7b	119.1±6.3b	21.7±2.2a	5.4±0.2ab	146.1±8.4b	33.0±1.7b	11.0±0.2	44.0±2.0b	23.1±0.3b
WIF	348.4±13.2a	143.9±5.9a	25.4±1.1a	5.8±0.2a	175.2±7.3a	39.6±1.6a	10.0±0.1	49.6±1.7a	22.2±0.1c
WIFP	333.0±17.2a	142.6±9.0a	26.0±2.0a	5.5±0.3a	174.0±11.0a	39.3±2.4a	10.3±0.2	49.7±2.5a	22.2±0.1c
P > *F*									
Block	0.006	0.010	0.165	0.064	0.019				0.034
Treatment	<0.001	<0.001	0.001	0.014	<0.001	<0.001	0.450	<0.001	<0.001

Note: Values are means ± SEs. Values among treatments with different letters are significantly different ($\alpha = 0.05$). Biomass was measured at age 10 years, and volume was measured at age 11 years. See Table 4 for treament abbreviations.

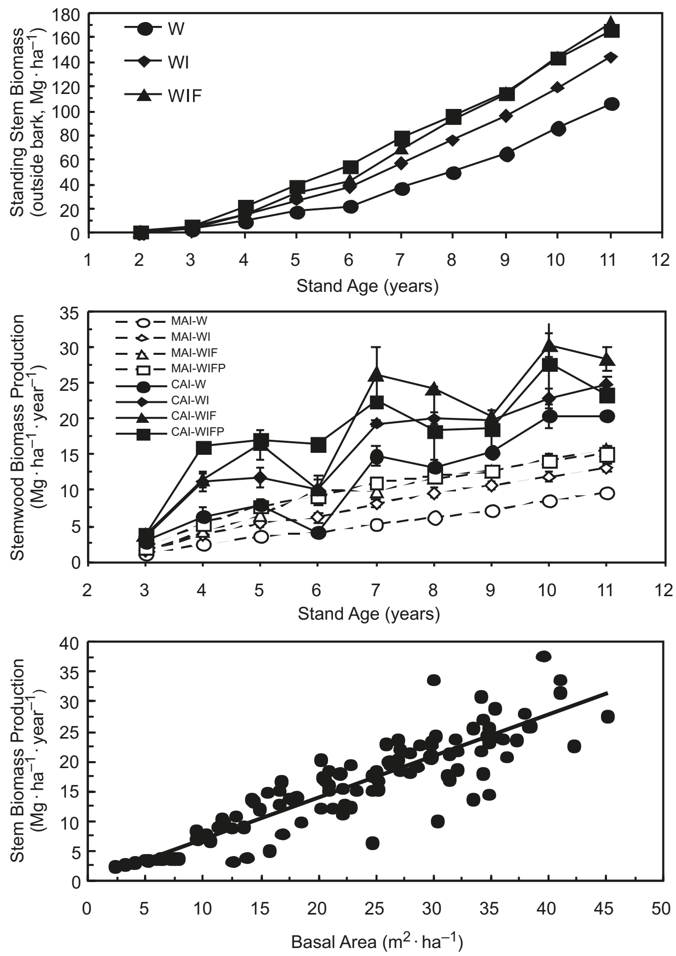
*Total mass of taproots and all coarse roots within a 1 m^2 area directly beneath each tree.

†Measured with ground-penetrating radar (GPR) outside the 1 m^2 area.

‡Taproot plus adjacent coarse root mass and lateral root mass outside the 1 m^2 area measured with GPR.

§Ratio of total belowground woody mass to total above- plus below-ground mass.

Fig. 2. Influence of management treatment on mean cumulative stemwood biomass and stemwood biomass production in loblolly pine family 7-56, and the relationship between stemwood biomass production and basal area. Data from years 1–6 were adapted from Samuelson et al. (2004*a*). Error bars are SEs. CAI, current annual increment; MAI, mean annual increment. See Fig. 1 for treatment abbreviaitons.



et al. 1996; Gough et al. 2004*a*, 2004*b*). Treatments did not alter leaf mass per unit area, but other potential impacts on crown and shoot structure that influence radiation capture (Stenberg et al. 1994) were not measured.

Total belowground woody mass ranged between 11 and 19 $Mg \cdot ha^{-1}$ at age 6 (Samuelson et al. 2004*a*) and increased to 34–50 $Mg \cdot ha^{-1}$ at age 10. Estimates of total belowground woody biomass are lower than those predicted by Albaugh et al. (2006*b*), who found a strong relationship between total coarse root mass (taproot plus coarse root) and stem mass. Using the linear function from Albaugh et al. (2006*b*), predicted belowground mass with 144 $Mg \cdot ha^{-1}$ of stem mass was 72 $Mg \cdot ha^{-1}$ compared with the 50 $Mg \cdot ha^{-1}$ we estimated using Johnsen et al. (2004) in combination with GPR measurements of lateral coarse root mass. It should be noted that the equation from Johnsen et al. (2004) was calculated using data from across a large range of stand ages, productivities, and standing biomass and included our data at age 6 years and that from Albaugh et al. (2006*b*) and Van Lear and Kapeluck (1995). Our estimates of total belowground mass are comparable with the 58 $Mg \cdot ha^{-1}$ of belowground woody bio-

Table 6. Effects of management treatment and stand age on stem mean annual increment (MAI) and current annual increment (CAI), leaf area index (LAI), and growth efficiency of loblolly pine family 7-56 and associated ANOVA p values.

	MAI ($Mg{\cdot}ha^{-1}{\cdot}year^{-1}$)	CAI ($Mg{\cdot}ha^{-1}{\cdot}year^{-1}$)	LAI ($m^2{\cdot}m^{-2}$)*	Growth efficiency ($Mg{\cdot}ha^{-1}{\cdot}year^{-1}{\cdot}LAI^{-1}$)†
Treatment				
W	7.4±0.4c	16.8±0.9c	4.7±0.2	3.6±0.4
WI	10.5±0.5b	21.2±0.8b	5.0±0.2	4.2±0.2
WIF	12.6±0.6a	25.6±1.2a	5.8±0.2	4.4±0.3
WIFP	13.1±0.5a	22.1±1.8b	5.8±0.4	4.0±0.8
Stand age (years)				
7	8.6±0.7e	20.7±1.5ab		
8	9.9±0.7d	18.9±1.8b	5.7±0.2a	3.3±0.3b
9	10.8±0.7c	18.5±0.9b	5.2±0.2b	3.6±0.2b
10	12.3±0.8b	25.4±1.8a	5.0±0.2b	5.2±0.5a
11	13.2±0.9a	23.7±0.9a		
P > *F*				
Treatment	<0.001	<0.001	0.124	0.296
Year	<0.001	<0.001	0.008	0.005
Treatment × year	0.3799	0.877	0.156	0.780

Note: Values are means ± SEs. Values among treatments or ages with different letters are significantly different (α = 0.05). See Table 4 for treatment abbreviations.

*LAI was calculated as the mean over the months of May, July, and August and measured using a LAI-2000 plant canopy analyzer.

†Growth efficiency was calculated as the ratio of CAI to LAI.

Table 7. Effects of management treatment on percent area of forest floor occupied by coarse roots of loblolly pine family 7-56 and associated ANOVA p values for treatment effects by root mass density interval.

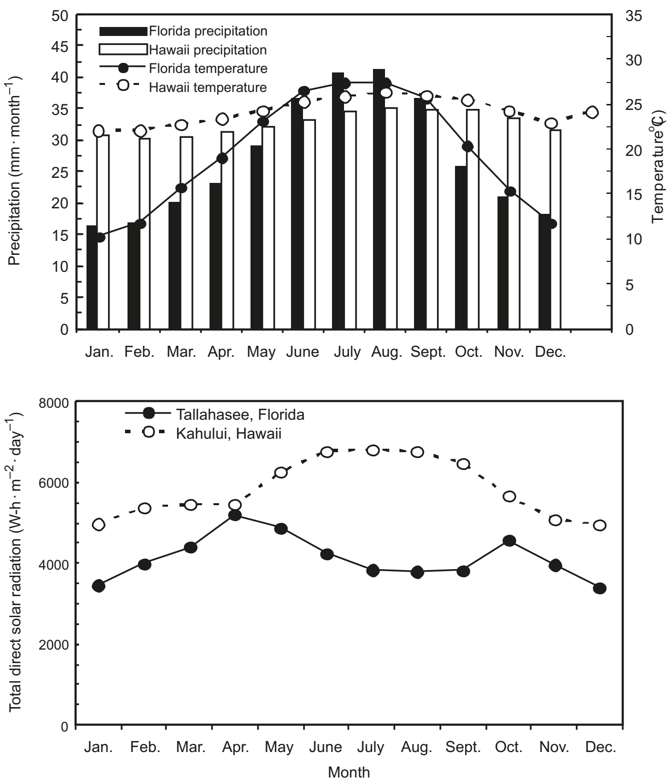
	Root mass density interval ($g{\cdot}m^{-2}$)							
	600–800	800–1000	1000–1200	1200–1400	1400–1600	1600–1800	1800–2000	2000–2200
Treatment								
W	32.3±0.9a	15.9±0.8a	9.5±0.7a	6.2±0.6	4.0±0.5	2.4±0.4b	1.2±0.3b	0.7±0.2
WI	26.8±1.3b	14.5±1.0a	9.8±0.5a	6.8±0.5	5.1±0.5	3.6±0.4a	2.2±0.3a	1.3±0.3
WIF	22.0±0.9c	10.7±0.5b	7.5±0.4b	5.9±0.4	3.9±0.3	2.4±0.3b	1.5±0.2b	1.0±0.2
WIFP	22.0±1.3c	10.8±0.8b	7.4±0.4b	6.1±0.4	4.8±0.5	3.4±0.4a	2.1±0.3a	1.1±0.2
P > *F*								
Block	0.022	0.752	0.257	0.002	<0.001	0.042	0.128	0.050
Treatment	<0.001	<0.001	<0.001	0.460	0.065	0.005	0.012	0.070

Note: Values are means ± SEs. The minimum detectable root density with GPR was 600 $g{\cdot}m^{-2}$. No significant treatment effects were observed in the nine highest root density intervals, which accounted for <1% of the total area, and these intervals were omitted from this table. Values among treatments with different letters are significantly different (α = 0.05) within a density interval. See Table 4 for treatment abbreviations.

mass measured in a 23-year-old loblolly pine plantation with a similar basal area (Miller et al. 2006). Although no absolute differences in lateral coarse root mass outside the 1 m^2 area were observed in the current study, the W and WI treatments exploited a significantly greater area of soil with relatively low-density coarse roots (<1200 $g{\cdot}m^{-2}$) than treatments receiving fertilizer. This new application of GPR was able to show that enhanced root proliferation was most pronounced at lower root densities. The data collected with GPR in a matter of days was equivalent to destructively harvesting and quantifying roots from 720 m^2 of forest floor.

There is still some question as to which management activities have the potential to alter allocation to roots. The 22%–25% proportion in allocation to belowground woody mass as a percentage of total mass was within the range reported for loblolly pine: 19% in 23-year-old stands (Miller et al. 2006), 20%–23% in 8- to 11-year-old stands (King et al. 1999), and 18% for 48-year-old stands (Van Lear and Kapeluck 1995). In contrast to our results, fertilization plus irrigation treatment beginning at age 8 years resulted in a small but significant increase in woody root allocation at age 11 years in a loblolly pine plantation in the Carolina Sand Hills (King et al. 1999). The allocation of mass to roots in loblolly pine follows a general pattern of decreasing with age across a range of soils and management regimes (Retzlaff et al. 2001). Small but significant reductions in coarse root allocation in this study may be an indirect response to accelerated stand development (Coyle and Coleman 2005). On our site, there is no evidence that fertilization greatly altered dry matter partitioning to roots (Samuelson et al. 2004*a*, 2004*b*). However, at year 6, fertilization did decrease carbon loss via soil CO_2 efflux (Samuelson et al. 2004*b*). This is consistent with the premise that soil fertility may alter carbon allocation by reducing its rapid transport belowground (Johnsen et al. 2007), which results in additional increases in wood production (Oren et al. 2001; McCarthy et al. 2006; Palmroth et al. 2006).

Fig. 3. Mean precipitation, daily 24 h temperature, and daily direct solar radiation by month at Tallahassee, Florida, and Kahului, Hawaii (National Solar Radiation Database, National Renewable Energy Laboratory, rredc.nrel.gov). Values are 30 year monthly means (1961–1990). Tallahassee, Florida is approximately 64 km from the study site. The Hawaii study was located on the northeastern side of Maui (20°49′N, 156°17′W) (Whitesell 1970). Kahului, Hawaii, is on Maui (20°54′N, 156°26′SW).



Did more intensive silviculture push productivity of loblolly pine closer to its biological growth potential? Comparison of growth rates between this study and a study in Hawaii, on the northeastern side of Maui (Harms et al. 1994, 2000), revealed that DBH and basal area of WIF and WIFP stands at age 11 years were similar to Hawaii stands of the same age and similar spacing (3.0 m × 3.0 m) but of unknown seed origin (Fig. 1). Mean DBH in WIF and WIFP stands was 24 cm compared with a mean of 22 cm in Hawaii, and tree height was 7 m higher in WIFP trees than in Hawaii trees. Maximum basal area was 41 $m^2 \cdot ha^{-1}$ at age 11 years compared with the 43 $m^2 \cdot ha^{-1}$ in Hawaii stands, and maximum volume was 340 $m^3 \cdot ha^{-1}$ compared with approximately 300 $m^3 \cdot ha^{-1}$ in Hawaii. Actual mortality in WIF stands was relatively low but still higher than the cumulative 10 $trees \cdot ha^{-1}$ observed in Hawaii (Fig. 1). An increase in mortality in WIFP stands after basal area exceeded 35 $m^2 \cdot ha^{-1}$ and a decrease in CAI in WIFP compared with WIF stands was possibly because of greater early height growth and subsequent wind damage to crowns in WIFP stands. A higher number of broken tops were recorded in WIFP stands with approximately 50% of mortality due to broken tops compared with only one tree in WIF stands. Storms with high winds frequent the area (www.srh.noaa.gov). It is unclear if mortality would accelerate once maximum carrying capacity is reached.

DeBell et al. (1989) attributed basal areas of 85–100 $m^2 \cdot ha^{-1}$ in loblolly pine stands in Hawaii to high site index, favorable environmental conditions, rapid growth of individual trees, and low competition-related mortality. Harms et al. (1994) proposed that low mortality and rapid growth were a result of long crowns with high leaf area, high foliar nutrient concentrations, ample soil moisture, light penetration deep into the canopy, long growing season length, and lack of disease and pests. Of these factors, intensive management provided foliar N_m similar to the 17 $mg \cdot g^{-1}$ reported for upper canopy foliage of Hawaii trees (Harms et al. 1994), high soil moisture availability (Samuelson et al. 2004*b*), and control of aboveground pests to age 5 years. Although the growing season in southern Georgia is long and mild winter conditions facilitate photosynthesis (Samuelson and Stokes 2006), environmental conditions for year-round photosynthate production are likely most favorable in Hawaii. For example, in addition to as much as 40% higher mean daily direct solar radiation during summer months in Hawaii, mean monthly precipitation and mean daily 24 h temperatures from November through March were higher in Hawaii than in Tallahassee, Florida, approximately 64 km from the site (Fig. 3). Harms et al. (1994) attributed increases in flush number and needle length of Hawaii trees compared with loblolly pine in South Carolina to climatic differences and year-round photosynthesis. In addition, high stocking in Hawaii stands was ascribed to a two-tiered canopy structure and positive carbon balance in subdominant trees as a result of crown extension into the main canopy, high solar radiation intensities, moderate temperatures, and ample soil moisture (Harms et al. 1994). Projected LAI, calculated from foliage mass, of Hawaii stands at age 26 was 9.1 $m^2 \cdot m^{-2}$ (Harms et al. 1994), which greatly exceeds the theoretical maximum of 6 $m^2 \cdot m^{-2}$ previously proposed for loblolly pine (Jokela et al. 2004; Samuelson et al. 2004*a*).

In summary, 11 years of intensive resource management of loblolly pine resulted in DBH, basal area, and volume similar to or greater than values reported for loblolly pine of the same age and planting density in Hawaii. These results indicate that loblolly pine grown in the southern United States can produce the high yields observed on favorable, exotic locations when stands are below maximum carrying capacity. Short-rotation plantations, perhaps used to produce biofuels, would better exploit the genetic potential of loblolly pine, because stands would be harvested before reaching carrying capacity. High basal area and volume production in older loblolly pine stands in Hawaii are likely a result of low mortality and exceptionally high LAI. Interactions between site and climatic factors and physiological processes that control mortality require further study.

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