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Long term growth responses of loblolly pine to optimal nutrient and water resource availability

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Abstract

A factorial combination of four treatments (control (CW), optimal growing season water availability (IW), optimum nutrient availability (FW), and combined optimum water and nutrient availability (FIW)) in four replications were initiated in an 8-year-old *Pinus taeda* stand growing on a droughty, nutrient-poor, sandy site in Scotland County, NC and maintained for 9 years. Results for the first 4 years after treatment initiation at this study were first reported by Albaugh et al. [For. Sci. 44 (1998) 317]. The site is primarily nutrient limited and all measured stand parameters (height, basal area, leaf area index, live crown length, stem mass accumulation, current annual stem mass increment) were increased with fertilization throughout the study period. Irrigation effects were also positive for these parameters but the increases were much smaller than those found with fertilization. For example, 9 years after treatment initiation, standing stem mass was increased 100 and 25% by fertilization and irrigation, respectively, while current annual increment of stem biomass production was increased 119 and 23% by fertilization and irrigation, respectively. Interestingly, stem density (stems ha^{-1}) was not significantly affected by treatment in any year of the study. Growth efficiency (stem mass increment per unit leaf area index) was 1.9 $\mathrm{Mg\,ha}^{-1}$ per year per LAI for CW and influenced by treatment with IW, FW, and FIW achieving growth efficiencies of 2.4, 2.7 and 2.9 $\mathrm{Mg\,ha}^{-1}$ per year per LAI, respectively. Growth efficiency appeared to be relatively stable in the last 4 years of the study. Ring specific gravity was measured in the third, fourth, and fifth years after treatment initiation. An average reduction in ring specific gravity of 7.5% was observed with fertilization while irrigation had little effect on specific gravity in any year measured. The continuation of high growth rates with no observable growth decline in the treated stands throughout the 9-year study may be a function of the age of the stands when treatments were initiated (8 years), the very poor initial nutrient and moisture availability, and/or the application of an ongoing optimum nutrient regime at the site. The fertilized plots are now at or near an age and a size when a commercial harvest would be feasible. For the stand conditions at this site, then, the optimum nutrient availability plots have achieved high productivity throughout the economic life of the stand without measurable declines in stand productivity.

Keywords: Nutrients; Irrigation; Stand productivity; Long term responses; Loblolly pine

1. Introduction

Intensive management of pine plantations is now the norm in the southeastern United States as forest managers have become more aware of the opportunities to improve production through the manipulation

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of resource availability (Allen et al., 2001). Soil preparation, deployment of genetically improved planting stock, vegetation control, and nutrient amendments are all tools used in intensive silviculture. The application of these tools is grounded on the knowledge that productivity is largely dependent on resource availability, especially nutrients and water, and on the understanding of how nutrient and water availability interact with prevailing climatic conditions to determine production potential. This understanding is, at least in part, still developing as most studies examining resource availability and its potential for intensive management are based on relatively short term results (5 years or less). A need exists to examine and synthesize longer term effects of site resource manipulation on stand ecophysiological parameters.

Improving resource availability in SE US pine plantations can dramatically increase stand productivity as leaf area is often well below the optimum for maximum light interception and consequently optimum production (Vose and Allen, 1988; Colbert et al., 1990; Albaugh et al., 1998; Sampson and Allen, 1999; Jokela and Martin, 2000). From an ecophysiological perspective, change in resource availability may affect stand structure, carrying capacity, growth efficiency, and wood properties. Stand structure is thought to follow a regular pattern of development from planting through a period of self-thinning as the stand reaches maturity and previous evidence suggested that nutrient additions hastened this process (Miller, 1981). More current evidence indicates that improved resource availability may allow trees to grow larger per unit area before self-thinning begins (Morris and Myerscough, 1991) and that improved resource availability does not always accelerate development of within stand size hierarchies (Nilsson et al., 2002). As stands age, growth has been observed to reach a peak and then decline (Assman, 1970). Several causes for this decline in productivity have been proposed including reductions in resource availability (especially nutrients; Binkley et al., 1995), increased hydraulic resistance (Mencuccini and Grace, 1996), increased respiratory losses or changes in aboveground and belowground carbon allocation (Ryan et al., 1997; Binkley et al., 2002), Clearly leaf area and growth efficiency (production per unit of light interception) can be improved with resource additions (Linder, 1987; Albaugh et al., 1998; Samuelson et al., 2001); however, it is uncertain whether improved resource availability can totally eliminate productivity declines associated with stand age (Binkley et al., 2002). Wood density would be expected to decrease with nutrient additions due to proportionately less production of late wood (Hattenschwiler et al., 1996). Zobel and van Buijenen (1989) found that while nitrogen fertilization initially decreased wood density, 5–10 years after fertilization density returned to the same level it would have been in the absence of fertilizer. This may not be the case when fertilization is maintained through time. Roderick and Berry (2001) noted the link between wood density and the hydraulic conductivity of stems where less dense wood will have more space for water since the density of cell wall material is relatively constant. Understanding the linkages among resource availability, stand structure, carrying capacity, growth efficiency, and wood quality will be necessary to extrapolate our current knowledge on highly productive stands forward into the future.

The long term studies available indicate potential productivity for loblolly pine when planted outside the southern US that is much higher (basal area up to 100 m^2 ha^{-1}) than currently being achieved in the SE US (Harms et al., 2000). Unfortunately, our knowledge of the ecophysiological processes needed to exploit this potential in the SE US is based on relatively short term results (Albaugh et al., 1998; Samuelson et al., 2001; Colbert et al., 1990). Consequently, our understanding of how improved resource availability may alter or delay the onset of self-thinning, reduced stand growth, reduced growth efficiency and altered wood properties will be key to fully understanding the impact of current intensive management practices. It may be possible that improved resource availability for an extended period may delay the expected growth reductions past a point of economic consequence (i.e. they occur after a stand would normally be cut). What becomes critical is not just the understanding of these processes but a quantification of their timing under different resource availability regimes.

Our objectives in this study were to understand how ecophysiological responses in loblolly pine may change with time under different resource availability regimes. Specifically, we examined stand structure, growth efficiency and wood quality on a site where a treatment induced range of nutrient and water availability had been maintained for 9 years.

2. Methods

2.1. Study site

The study was established in the Sandhills of Scotland County, NC, USA (35°N latitude, 79°W longitude) on a flat, infertile, somewhat excessively drained soil (sandy, siliceous, thermic Psammentic Hapludult). Annual precipitation averages 1220 mm (40-year average), and is well distributed through out the year although extended droughts are possible during the growing season. Average annual summer (June–August) temperature is 26 °C (40-year average) and average annual winter temperature (December, January and February) is 7 °C with an average of 303 frost-free days. The site was hand planted on a 2.5 m × 3 m spacing with loblolly pine in 1985 after felling of the previous natural longleaf pine (*P. palustris* Mill.) stand and application of Velpar^{TM} grid balls (17 kg ha^{-1}). Loblolly pine site index at installation was estimated at 16 m (25 years). Earlier results from this study were reported in Albaugh et al. (1998).

Sixteen 50 m × 50 m (0.25 ha) treatment plots with 30 m × 30 m measurement plots centered in the treatment plot were established in January 1992 in the 8-year-old stand. Through plot selection and thinning, initial mean tree height, diameter, stand basal area, volume, LAI, and density (1176 stems ha^{-1}) were similar (no statistically significant differences detected) in all plots prior to treatment imposition. A 10 m buffer separated the treatment plots and in the two cases where the buffer was less than 10 m, a 150 cm deep trench between the treatment plots was dug, lined with plastic and refilled. Also, in 1998, a similar trench was dug between all treatment plots to stop roots from growing into adjacent plots. Complete control of non-pine vegetation in the treatment plots has been maintained since 1992 through a combination of mechanical and chemical (glyphosate) methods.

Treatments were a 2 × 2 factorial combination of nutrition and water additions replicated four times. The four treatments were, then, control (CW), irrigation (IW), fertilization (FW) and the combination of fertilization and irrigation (FIW) where all treatments received complete vegetation control.

The fertilizer treatments, which began in March 1992, were: (1) optimum nutrition through fertilization or (2) no addition. Optimum nutrition was defined as (1) maintaining a foliar nitrogen (N) concentration of 1.3%, (2) maintaining foliar macronutrient concentration:N concentration ratios of 0.10 for phosphorus (P), 0.35 for potassium (K), 0.12 for calcium (Ca), and 0.06 for magnesium (Mg), and (3) maintaining foliar boron (B) levels greater than 12 ppm. Annual assessments of stand nutritional status were completed in January by collecting 20 fully elongated fascicles from the first flush foliage on a primary lateral branch in the upper one-third of the live crown of five trees in each plot. All samples were pooled within a plot, dried to a constant weight at 65 °C, weighed, ground, and analyzed for nitrogen using a CHN analyzer. Fertilizer was applied annually in the spring as needed to meet the target and was continued through 2000.

Water treatments, which began in April 1993, were: (1) natural precipitation and (2) natural precipitation plus irrigation applied to meet the target soil water content level. From 1993 to 1999, irrigation events were targeted to maintain soil water content at greater than 3.0 cm soil water content in the surface 50 cm of soil (40% available water content) as determined from volumetric soil water content measured with time domain reflectometry (TDR) (Topp and Davis, 1985; Albaugh et al., 1998). The soil moisture target was based on evidence suggesting that 40% of the available soil water content may be a biologically meaningful threshold for photosynthesis and growth (Myers and Talsma, 1992). In 1999, new pumping equipment allowed irrigation to occur continuously; however, the soil moisture target was not achieved even with daily irrigation. Consequently, in 2000, the target goal was set as applying 650 mm of additional water evenly distributed during the growing season (March–November) to each irrigated plot. This amount approximated the maximum added to the irrigated plots in any 1 year except 1999. The irrigation system consisted of Rainbird irrigation nozzles positioned on 35 cm risers spaced 10 m × 10 m apart on a head-to-head design. During each irrigation event 2.5 cm of water was added to the plot.

Rainfall (Campbell Scientific TE525 tipping bucket rain gauge) and air temperature (Campbell Scientific HMP45C temperature and relative humidity probe) were measured at a weather station on site. Potential and actual evapotranspiration (PET and AET, respectively) were calculated using Thornthwaite and Mather (1957). The monthly water deficit was calculated as the difference of PET and AET.

2.2. *Estimation of basal area*

In December of each year, from 1991 (prior to treatment) to 2000, measurements of diameter at breast (1.4 m) height (D), height (H), and live crown length (L) and assessments of mortality were made on all trees in each measurement plot (~100 trees per plot). Basal area was calculated for each tree, summed to the plot level, and scaled to determine basal area per hectare.

2.3. *Estimation of biomass production and allocation*

Stand level biomass (dry weight) estimates for foliage, branch wood, stem wood, and coarse root (>2 mm diameter) components were calculated from age and treatment specific whole tree regression equations applied to all trees and then scaled to an area basis for each plot. The whole tree regression equations were developed following the methods presented in Albaugh et al. (1998) and were based on destructive harvests. Destructive sampling of tree components was completed in February of 1992 (prior to treatment and only aboveground components), 1994, 1996, and 1998 on 16 trees in each year. Trees were selected to represent the range in H and D by treatment at the time of sampling. All trees were cut at ground level, separated into stem wood, branch wood and foliage and dried at 65 °C to a constant weight. Stem bark to stem wood ratio was measured on each destructively harvested tree in 1996. Three 5 cm disks (at D, base of the 1996 growth and half way between these points) were selected and the bark was separated from the wood prior to drying. No significant treatment or height related differences were observed in the bark to wood ratio. In 1994 (seven trees), 1996 (16 trees), and 1998 (16 trees), all coarse roots found in a square meter centered on the tree stump down to 50 cm in the soil, and the entire tap root were removed and dried at 65 °C to a constant weight. Trees sampled in 1992 were selected from trees removed prior to treatment imposition to equilibrate spacing and stand density among plots. In 1994, 1996, and 1998 trees were selected from within the treatment plots, but they represented less than 3% of trees in the plots. Consequently, removal of harvested trees had minimal impact on other stand measurements (e.g. LAI).

Fine root biomass was estimated from core samples collected each month in each plot and scaled to an area basis. Stand level dry weight fine root (<2 mm diameter) biomass estimates were calculated by scaling soil core data to an area basis for each plot. In 1993 and 1994, all live and dead loblolly pine roots were removed and dried from 20, 6.6-cm diameter × 10-cm deep cores collected in each plot (Mignano, 1995). Samples were scaled to a 50-cm depth using Mignano's (1995) root distribution assessments. In 1995 and 1996, the same procedures were followed; however, only five, 15.2-cm diameter × 15-cm deep cores were sampled in each plot. No fine root sampling was conducted between 1997 and 2000 so the 1996 measurements were used in subsequent years to estimate fine root mass. Measured fine root mass and production fluctuated a relatively small amount compared to other plant components (stem, foliage, branch, coarse roots) from 1992 to 1996. Fine root mass represented less than 4% of total plant mass in 1996. Consequently, we expect a relatively small amount of error with this assumption.

Production estimates for stem wood, branch, tap root and coarse root biomass for a given year were calculated as the difference between the biomass estimate for the following year and the given year for these components. For example, the 1993 production estimate for stem wood biomass was the difference between the 1994 and 1993 biomass estimate for stem wood. Foliage production was the estimate from the biomass regression directly because only one cohort of foliage is found on the trees in January when the assessments were completed.

Standing stem mass was determined on a dry mass inside bark basis, and included no branches. Gross stem wood biomass was calculated as standing stem biomass plus stem biomass of all mortality to date (i.e. dead trees were carried forward in the gross inventory).

Current annual increment (CAI) of stem biomass was calculated as

$$\text{increment} = \sum \text{stem biomass}_{t2} - \sum \text{stem biomass}_{t1} + \sum_{t1}^{t2} \text{mortality}$$

where stem biomass$_{ti}$ is standing stem biomass at time i, and $\sum_{t1}^{t2}$mortality is the summed stem wood biomass of trees that died during the interval between time 1 and time 2 (Clark et al., 2001).

2.4. Stem density and early wood: late wood ratio

Ring specific gravity was measured for 1994, 1995, and 1996 using cores from trees in the treatment plot but not the measurement plot (Mann, 1999). Percentage late wood was estimated using the equation:

$$\text{LW} = \frac{\text{SG} - 0.308}{0.00457}$$

where LW is the percentage late wood and SG the specific gravity (Alex Clark, personal communication). Early wood was calculated as 1 − LW.

2.5. Leaf area index

Stand leaf area index (LAI) (projected) was estimated monthly from March 1992 to December 1997, in each of the 16 treatment plots using the Li-Cor LAI2000 plant canopy analyzer (Li-Cor, 1991). For each month in each plot, 20 LAI measurements along a transect on the south side of the plot were made at a height of 60 cm between 07:00 and 10:00 EST using a 90° view cap. Simultaneously, above canopy light measurements were collected in an open field adjacent to the study site where the light sensor had an unobstructed view of the sky. The 20 measurements were averaged to estimate monthly plot LAI and the unadjusted maximum monthly LAI measures recorded for each plot for each year were used as our estimates of peak LAI. To better estimate peak LAI and reduce the number of measurements each year in 1998, 1999, and 2000, peak LAI was determined as the maximum Li-Cor LAI measurements completed on five dates during the period from the middle of August until the end of September.

2.6. Statistical analyses

The statistical significance of the fertilization, irrigation, and fertilization by irrigation interaction effects were determined using analysis of variance (SAS, 1988). All significance levels were <0.05.

3. Results

3.1. Treatment and site characterization

In the 9 years since study establishment, approximately 100 kg ha^{-1} per year of elemental N were added to the fertilized plots (Table 1) to achieve the

Table 1
Nutrient and water additions to treatment plots from 1992 to 2000

Year	Nutrient additions (kg ha^{-1})							Water additions[a] (mm)	
	N	P	K	Ca	Mg	S	B	Non-irrigated	Irrigated
1992	224	56	112	134	56	0	1.7	866	866
1993	82	50	113	0	56	120	0.0	735	1403
1994	112	0	0	0	0	0	0.0	885	1052
1995	56	28	56	24	34	74	1.1	990	1591
1996	112	11	56	10	0	15	1.1	922	1361
1997	134	0	0	0	0	0	0.0	751	1321
1998	56	6	0	0	0	0	0.0	989	1612
1999	69	0	0	0	0	0	0.0	987	3130
2000	56	6	0	0	0	0	0.4	812	1317
Total	902	157	337	168	146	208	4		

[a] Water additions from 1 March to 31 October each year. No irrigation in 1992, equipment problems resulted in low irrigation in 1994, near continuous irrigation was completed in 1999.

desired average foliage N level of 1.35%. Other nutrients (K, S, Ca, P, Mg, B) were added at lower rates to maintain the desired nutrient ratios. The average nutrient concentration:N concentrations for the 9 years of treatment were 0.09 for P, 0.34 for K, 0.08 for Ca and 0.05 for Mg, which were all slightly under our target ratios. On average, from 1993 to 2000, more than 700 mm of irrigation water were added annually in each of the irrigated plots. In 1994, only 167 mm of water was added due to equipment limitations and in 1999, as noted in the methods, new pumping equipment allowed the addition of 2100 mm of irrigation water to each plot in an attempt to meet the original treatment goals. The average annual water deficit during the study period was 128 mm per year (Fig. 1A). In 1993, the largest annual water deficit was observed when the difference between potential and actual evapotranspiration was 239 mm. On average, a seasonal water deficit was observed from March to November and coincided with the growing season while the highest average deficits occurred in June with 37 mm per month of water deficit (Fig. 1B).

3.2. Stand development

Average height on the CW plots increased from 3.4 m in 1991 to 8.7 m in 2000 (Fig. 2). By 2000,

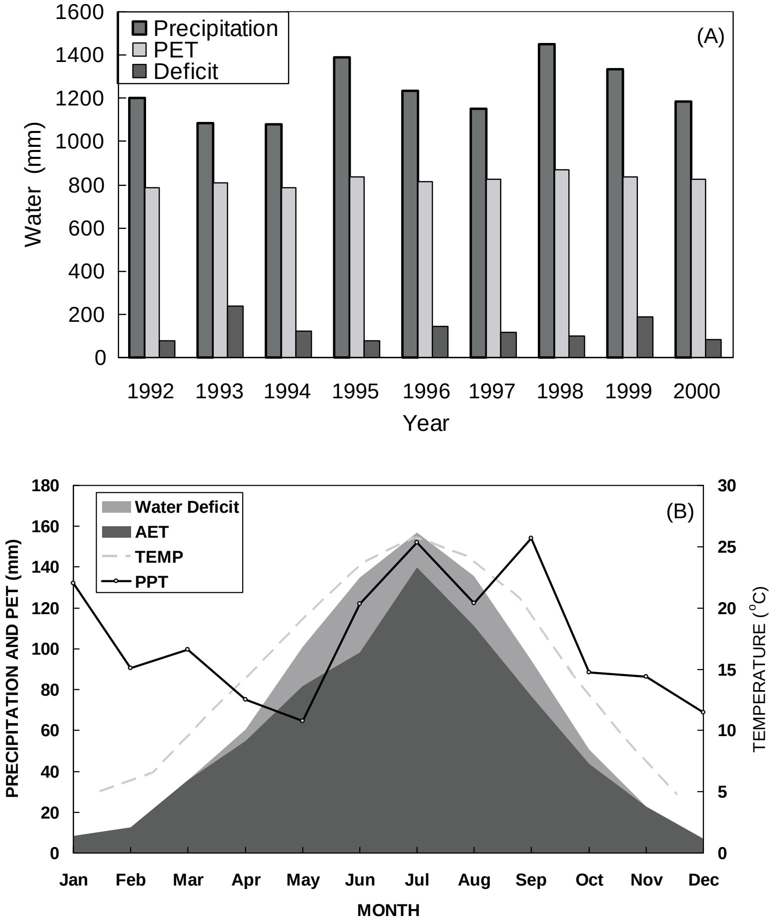

Fig. 1. (A) Precipitation, potential evapotranspiration and estimated water deficit (PET minus actual evapotranspiration) for each year of the study. Evapotranspiration estimates from Thornthwaite and Mather (1957). (B) Monthly mean (mean from each month for the years 1992–2000) precipitation, ambient air temperature, AET, and water deficit.

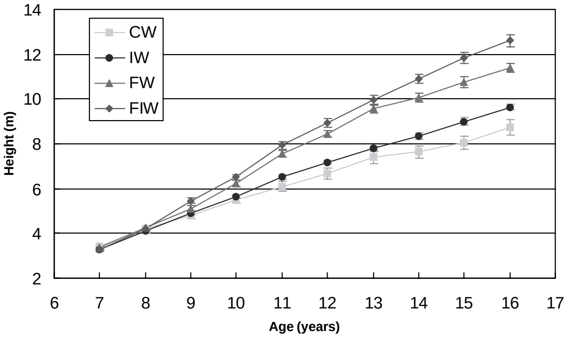

Fig. 2. Mean tree height of all trees in the measurement plot. Height was measured in December of each year from age 8 to 16. Error bars are ±1 S.E.

average height had significantly increased 2.8 and 1.1 m in fertilized and irrigated plots, respectively (Fig. 2 and Table 2). By 2000, fertilization had increased average diameter by 4 cm (Fig. 3). Irrigation had little effect on the diameter distribution. Virtually no mortality was observed until 1999 and 2000 and then the trees that died were in the smaller diameter classes (Fig. 3). Basal area increased 645% in the CW plots during the 9 years of the study (Table 3). At the end of 2000, basal area was 71% greater on the fertilized plots (treatments FW and FIW) (33 $m^2 ha^{-1}$) than on non-fertilized plots (treatments CW and IW) (19 $m^2 ha^{-1}$) and this difference was statistically significant (Tables 2 and 3 and Fig. 4). Irrigation did not significantly affect basal area. No significant treatment effects on stem density were observed (Table 2 and Fig. 4). Live crown length in the CW plots increased 75% from 3.1 m in 1991 to 5.5 m in 2000 (Fig. 5). Fertilization and irrigation significantly increased live crown length by 1.2 and 0.5 m, respectively, by 2000 (Table 2 and Fig. 5). All treatments followed a similar trajectory in live crown length development up to a basal area of 15 $m^2 ha^{-1}$ (Fig. 5). Greater than a basal area of 15 $m^2 ha^{-1}$, live crown length appears to have reached a maximum of 5.3 m in the CW plots. The maximum live crown lengths for the other treatments were 6.0, 6.7 and 7.3 m for the IW, FW, and FIW treatments, respectively.

3.3. *Stand productivity and stem characteristics*

Gross stem mass accumulation and standing stem mass were nearly identical due to low mortality observed in the plots since treatment establishment (Fig. 6A and B). Standing stem mass increased 737% during the 9 years of the study (Fig. 6B). By 2000, fertilization and irrigation both significantly increased standing stem mass 119 and 23%, respectively (Fig. 6B and Table 2). The standing stem mass growth response for fertilization and irrigation applied alone or in combination continued to increase through 2000 (the trends through time diverged) (Fig. 6B). Consequently, treatment trends for mean annual increment also continued to diverge through 2000 (Fig. 7). On the CW plots CAI increased 162% from 1992 to 2000 and with a steady increase throughout the entire study period. Fertilization and irrigation both significantly increased CAI by 99 and 26%, respectively, at age 16 in 2000 (Fig. 7 and Table 2). Current annual stem mass increment quadrupled in the fertilized plots during the first 4 years after treatment initiation. In 1996, at age 12, CAI in the treated plots (IW, FW, and FIW) was

Table 2
Summary of statistical significance (prob > *F*) of treatment effects and coefficient of variation (CV) for stand parameters in 2000, 9 years after treatment initiation

Parameter	Effect			CV
	Fertilizer	Irrigation	Fertilization × irrigation	
Height	<0.001	0.001	0.538	4.5
Basal area	<0.001	0.052	0.895	10.5
Stocking	0.861	0.688	0.556	7.0
Live crown length	<0.001	0.001	0.391	3.0
Standing stem mass	<0.001	0.018	0.547	14.1
Current annual stem increment	<0.001	0.014	0.546	15.6
Foliar nitrogen concentration	<0.001	0.063	0.139	4.6
Total biomass accumulation	<0.001	0.044	0.698	13.1
Peak leaf area index	<0.001	0.014	0.304	8.3

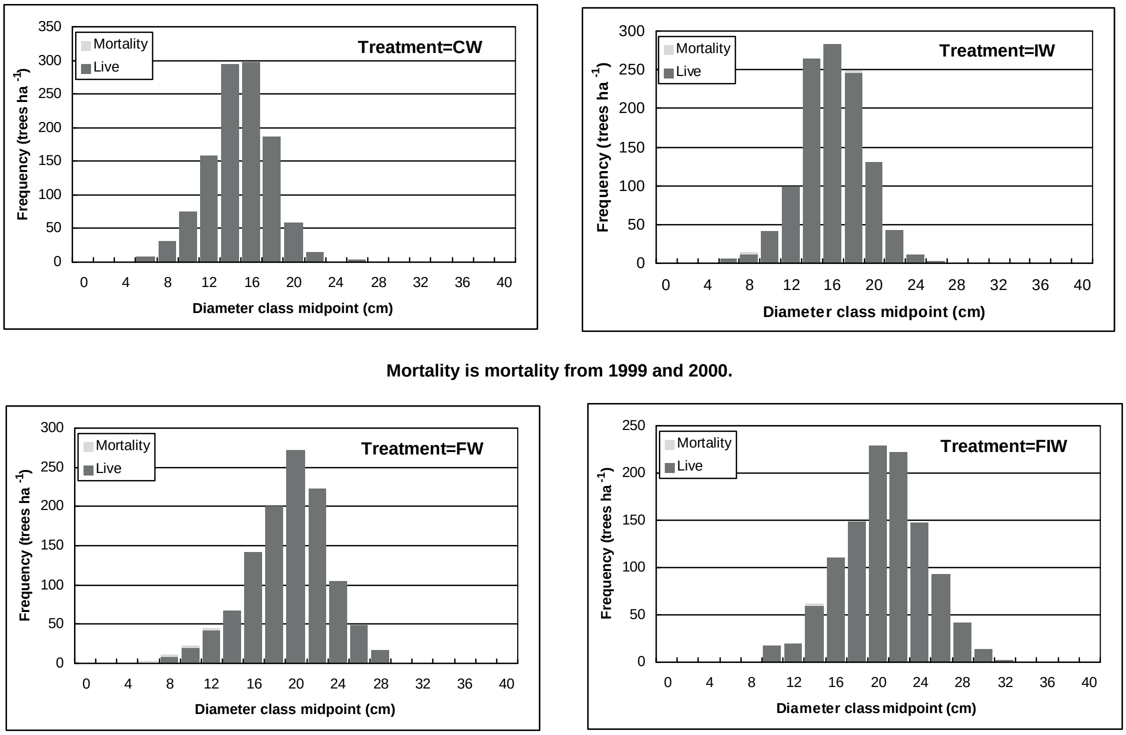

Fig. 3. Diameter distribution is shown for each treatment in 2000 by 2 cm size classes. Mortality includes trees that died in 1999 and 2000.

less than the previous year most likely a result of damage related to a hurricane in September 1996. The most obvious damage to the trees was the loss of foliage and smaller branch material that occurred after peak LAI was measured. These losses resulted in a reduction in diameter growth for the year and consequently a reduction in CAI. The CW plots were largely unaffected by the storm possibly because the smaller individual tree crowns did not touch even with high winds. All the treated plots recovered the next year when CAI was greater than the year prior to the hurricane. During the last 4 years of the study, CAI in the FW and FIW plots was relative stable at about 8 and 10 Mg ha^{-1} per year, respectively (Fig. 7).

Table 3
Stand basal area and S.E.

Year	Age	Control		Irrigated		Fertilized		Fertilization + irrigation	
		m^2 ha^{-1}	S.E.	m^2 ha^{-1}	S.E.	m^2 ha^{-1}	S.E.	m^2 ha^{-1}	S.E.
1991	7	2.4	0.2	2.1	0.2	2.2	0.1	2.1	0.2
1992	8	4.2	0.3	3.9	0.3	5.1	0.1	4.9	0.4
1993	9	6.1	0.4	6.1	0.3	8.7	0.2	9.3	0.9
1994	10	8.2	0.6	8.5	0.3	13.1	0.3	13.9	1.1
1995	11	10.1	0.7	11.0	0.4	17.1	0.4	18.3	1.5
1996	12	11.7	0.8	12.9	0.5	20.3	0.5	21.7	1.6
1997	13	13.3	0.9	15.1	0.5	23.5	0.5	25.5	1.7
1998	14	14.9	1.0	16.9	0.6	26.7	0.7	28.7	1.9
1999	15	16.2	1.0	18.9	0.7	29.2	0.8	31.9	2.1
2000	16	17.7	1.0	21.0	0.8	31.7	0.7	34.6	2.3

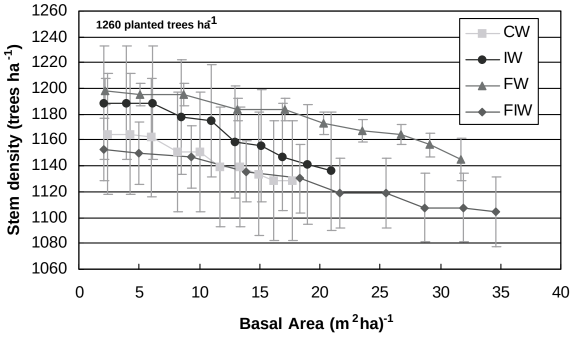

Fig. 4. Stand density and basal area by treatment are shown for 1992–2000. All plots were planted at 1260 stems per hectare. Error bars are ±1 S.E.

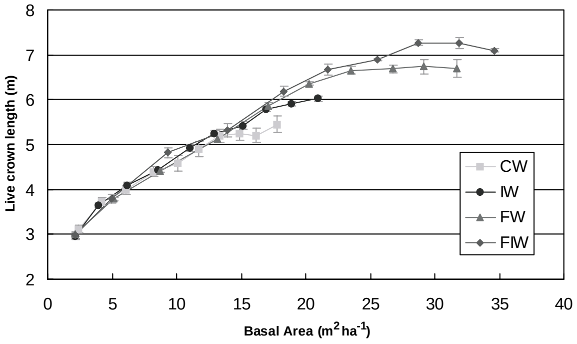

Fig. 5. Live crown length measured from the top of the tree to the height of the lowest living branch is shown with basal area for all years of the study. Error bars are ±1 S.E.

Ring specific gravity was measured for age 10, 11 and 12 in the third, fourth and fifth years after treatment initiation, respectively. Fertilization reduced ring specific gravity 9.0, 7.2 and 6.4% at ages 10, 11, and 12, respectively (Fig. 8A, and Mann, 1999). Irrigation had little effect on specific gravity. Ring specific gravity increased with age in all treatments but this increase was greater in the fertilized plots for the 3

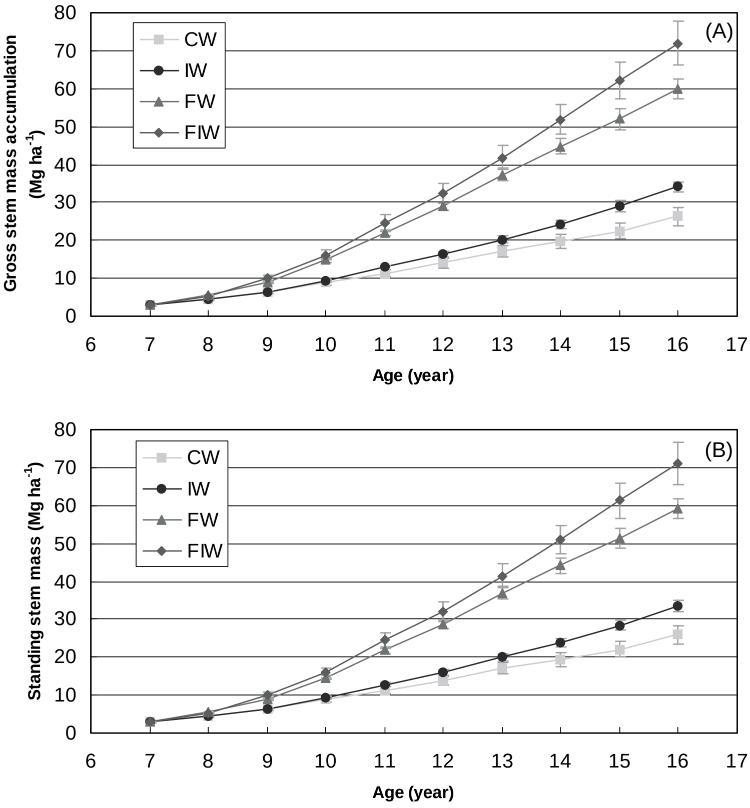

Fig. 6. Gross (A) and standing (B) stem wood biomass (dry mass, inside bark, no branches) vs. stand age by treatment. Gross stem wood biomass is: standing stem biomass + stem biomass of all mortality to date (i.e. dead trees are carried forward in the inventory). Error bars are ±1 S.E.

years measured. From age 10 to 12 ring specific gravity increased 11% in the fertilized plots but only increased 8% in the non-fertilized plots. Early wood:late wood ratio was measured for the same ages as ring specific gravity. Fertilization increased the early wood:late wood ratio 53, 40 and 35% at ages 10, 11, and 12, respectively (Fig. 8B, and Mann, 1999). Irrigation had little effect on the early wood:late wood ratio. By 1996 the non-fertilized plot had about a one to one ratio of early wood to late wood, while the fertilized plots continued to produce about 40% more early wood than late wood. However, during the 3 years we measured, the early wood:late wood ratio in the fertilized plots was declining at a faster rate than that observed in the non-fertilized plots.

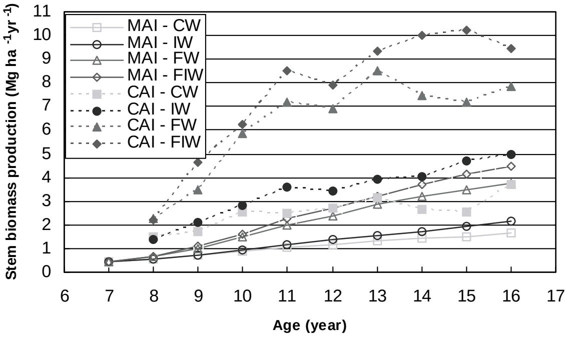

Fig. 7. Mean and current annual increment of stem biomass by treatment vs. stand age. Current annual increment calculated as: increment $= \sum \text{stem biomass}_{t2} - \sum \text{stem biomass}_{t1} + \sum_{t1}^{t2} \text{mortality}$ where stem biomass$_{ti}$ is stand stem biomass at time i, and $\sum_{t1}^{t2}$mortality is the summed stem wood biomass of trees that died during the interval between time 1 and time 2.

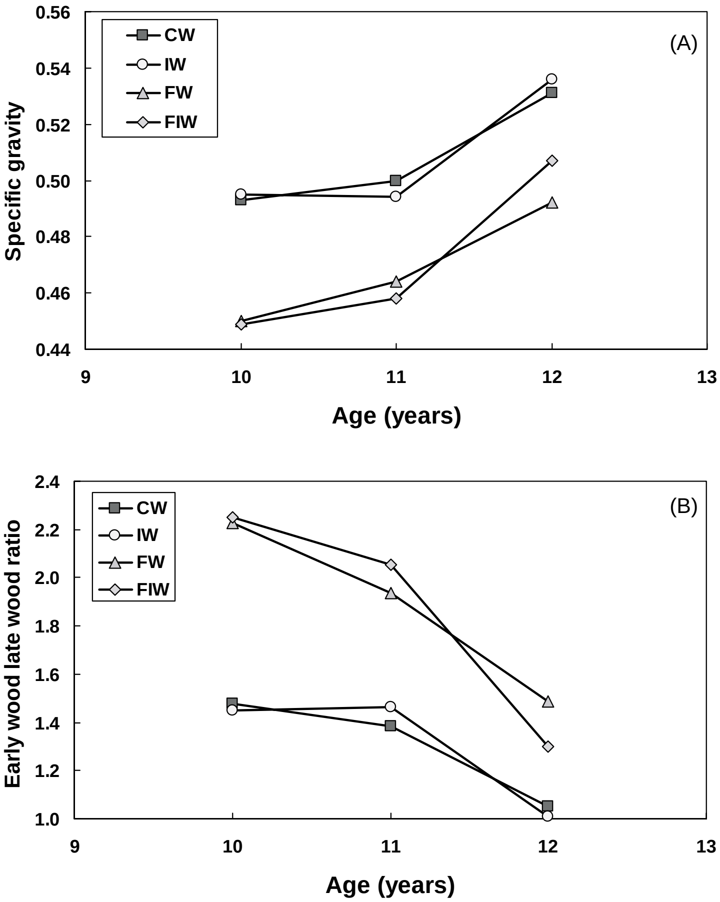

Fig. 8. Ring specific gravity and early wood:late wood ratio by treatment versus stand age. Early wood:late ratio is calculated from the equation $\%\text{LW} = (\text{SG} - 0.308)/0.00457$ where %LW is percent latewood and SG is specific gravity. Early wood percentage is $1 -$ late wood percentage.

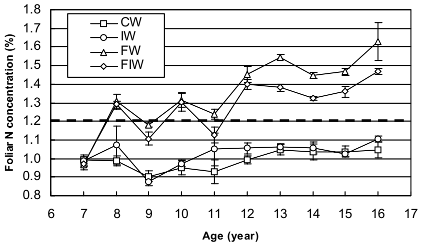

Fig. 9. Foliar nitrogen concentration by treatment vs. stand age. Concentration is from foliage collected in January each year. Critical value of 1.2% is shown as dashed line. Error bars are ±1 S.E.

3.4. Ecophysiological relationships

Foliar N concentrations in the non-fertilized plots remained fairly stable throughout the study period at 1.0% N. Fertilization significantly increased foliar N concentration 44% in 2000 (Fig. 9 and Table 2). Irrigation did not significantly affect foliar N concentration. Foliar N concentration in the fertilized plots dropped below the 1.2% critical value in 1993 and 1995 when we reduced N additions to avoid a N to Mg imbalance. Despite repeated applications of Mg in

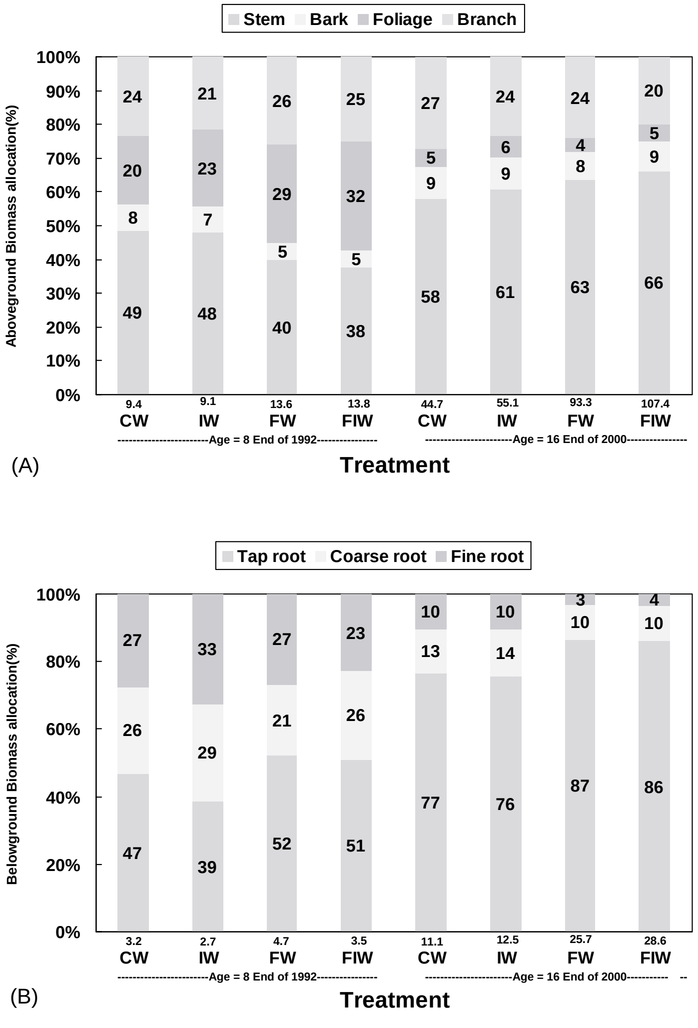

Fig. 10. Aboveground (Panel A) and belowground (Panel B) biomass allocation by component for the first (1992) and the last (2000) year of the study. Values listed above each treatment name are the total aboveground or belowground biomass (Mg ha^{-1}) for that year and treatment combination. Values in the bars are the percentage of the total aboveground or belowground biomass found in that component for the given year and treatment.

1992 and 1993, the Mg levels had dropped, in some plots, to less than 0.05% during the early years of the study; however, no macro- or micro-symptoms of Mg deficiency were observed. In subsequent years, additions of magnesium sulfate (Sophomag) resulted in elevated foliar Mg concentrations and allowed application of more N to the stands to achieve the target for foliar N concentration of 1.3%.

Total biomass (aboveground plus belowground) accumulation increased in the CW plots from 12.7 Mg ha^{-1} in 1992 to 55.7 Mg ha^{-1} in 2000 (340%) (Fig. 10A and B). By 2000, fertilization and irrigation significantly increased accumulated total biomass by 107 and 16%, respectively (Fig. 10A and B and Table 2). Across all treatments, the proportion of aboveground biomass found in foliage decreased dramatically from 26% in 1992 to 5% in 2000, while the proportion found in stem wood increased from 44 to 62% over the same time period. A similar shift from ephemeral tissue (foliage and fine root) to more permanent tissue (stem wood and tap root) was observed in the belowground components where fine root as a proportion of belowground biomass dropped from 28 to 7% from 1992 to 2000, while tap root increased from 47% in 1992 to 82% in 2000.

Peak LAI on the CW plots increased from 0.8 m^2 m^{-2} in 1992 to 1.8 m^2 m^{-2} in 2000 (125%) (Fig. 11). During 2000, fertilization and irrigation significantly increased peak LAI 59% and 14%, respectively (Figure 11 and Table 2) (Fig. 11 and Table 2). The relationship between peak LAI and basal area were similar for CW and IW plots with both treatments following a similar trajectory throughout the study. The FW and FIW plots share a similar trajectory until 1995 when the FIW continue to increase in both peak LAI and basal area faster than the FW plots. Peak LAI has stabilized in the FW and FIW plots with the FIW plots maintaining about 0.5 LAI more than the FW plots at basal areas greater than 15 m^2 ha^{-1}. The FW plots achieve a given level of basal area about 1 year after the FIW plots. The patterns found with peak LAI and basal area for the different treatments are similar to the CAI and basal area relationships (Fig. 12).

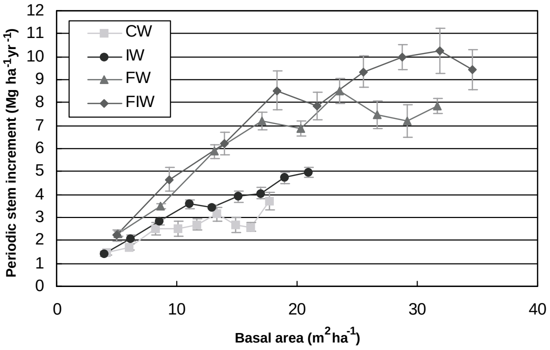

Fig. 12. Current annual stem mass increment vs. basal area for each year of the study. See Fig. 7 for description of calculations. Error bars are ±1 S.E.

In the CW plots 1.89 Mg ha^{-1} per year of stem mass was produced for one unit of peak LAI (Fig. 13). Growth efficiency (stem mass produced per unit of peak LAI) increased 32, 15 and 53% with fertilization, irrigation and fertilization plus irrigation (Fig. 13).

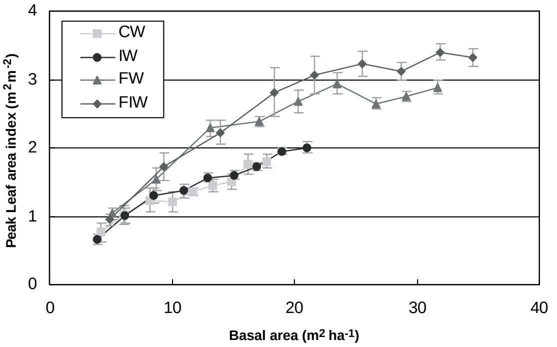

Fig. 11. Projected peak leaf area index by treatment vs. basal area for each year of the study. Leaf area was measured with a Li-Cor LAI2000 Plant Canopy Analyzer in September of each year. Error bars are ±1 S.E.

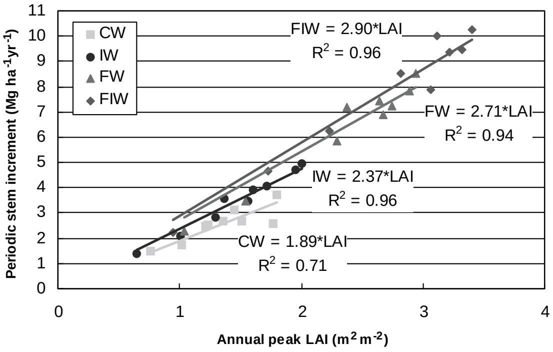

Fig. 13. Current annual stem mass increment vs. projected peak leaf area index for each year of the study by treatment. Regression lines are fit with a zero intercept.

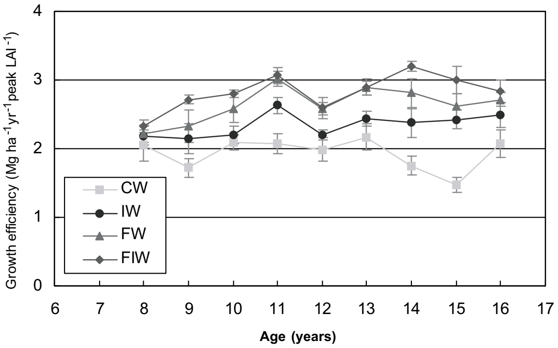

Fig. 14. Mean treatment growth efficiency vs. stand age. Growth efficiency is current annual increment as described in Fig. 7 divided by the peak LAI for that year. Error bars are ±1 S.E.

Growth efficiency increased on the treated plots (IW, FW, and FIW) from 1992 until 1995 when the stands were 11 years old (Fig. 14). In 1996, at age 12, all the treated plots experienced a decrease in growth efficiency most likely due to the hurricane event described previously. From age 13 until 16, the last year reported, slight increases and decreases in growth efficiency were observed for all treatments with no clear trend through time (Fig. 14).

4. Discussion

The strong positive responses to added nutrients were not surprising given the relatively low initial LAI and the low foliar N and B concentrations. Our results compare favorably with studies, from the SE US and other parts of the world, that have examined nutrient additions in stands where resource limitations were evident (Linder, 1987; Vose and Allen, 1988; Allen, 2001; Colbert et al., 1990; Bergh et al., 1998; Jokela and Martin, 2000; Samuelson et al., 2001; Carlyle, 1998). Significant treatment responses due to fertilization were observed at this site in the very first year after treatment initiation (Albaugh et al., 1998). After treatments began in 1992, the peak LAI (and hence the stand productivity) with improved nutrient availability increased for the first 5 years (Albaugh et al., 1998) and then remained at a high level for the next 4 years of the study. Interestingly, 9 years after the treatments were initiated there were no indications that current increment will diminish in the fertilized treatments. Apparently, the factors which may result in stand growth reductions with age (Ryan et al., 1997; Harms et al., 2000) have not had a measurable impact at this time. In the future, we should be able to observe which factors are important in any growth reductions that may occur.

The relatively small growth increase in response to irrigation was surprising given the annual soil water deficit of 128 mm which occurred mostly during the growing season. Our results contrast with results from Linder et al. (1987) and Pereira et al. (1994) who found large responses to irrigation in *P. radiata* in Australia and *E. globulus* in Portugal. These sites experienced annual soil water deficits in excess of 400 mm and drought resulted in significant and early loss of foliage and tree mortality. In our driest year (1993), the water deficit was only 239 mm per year and the fertilized trees had achieved an LAI of about 1.5. Even though the driest year in our study was much less severe than the one from Linder et al. (1987), there may be other factors that help mitigate the effect of drought in *Pinus taeda* for this site. There was a large volume of soil exploited by the roots since the sandy soil offered relatively little resistance to root penetration as we commonly found 15 mm diameter coarse roots at depths of 3 m in the profile during our root excavations. The 1200 mm per year of precipitation at our site was well distributed so that the lowest average monthly precipitation was 60 mm per month in May. The evaporative demand (vapor pressure deficit) may be relatively low due to fairly high humidity levels observed during the growing season (Manogaran, 1973). Lastly, Ewers et al. (1999) found that fertilization improved water use efficiency—allowing growth to continue in the fertilized stands even though water availability may have been low. The combination of these factors may have contributed to limit the influence of irrigation on the growth of these stands. It remains to be seen how the trees will respond should more severe drought conditions occur.

Clearly the trees on this site responded more to improved nutrient availability than to improved water availability for every parameter measured; consequently, we believe the site is primarily limited by nutrients rather than water. Samuelson et al. (2001) also found that improved nutrient availability had a greater impact on growth efficiency than improved water availability for loblolly pine. Hebert and Jack's

(1998) examination of *P. taeda* growth along a precipitation gradient in east Texas suggested that site fertility may be a stronger determinant of stand LAI (and hence productivity) than water availability even in areas traditionally considered water limited. In light of these results, it becomes apparent that our traditional thinking regarding water limited sites needs to be re-examined.

The treatments we applied resulted in stands with very different structures. At age 16 (the last year with data presented), the FIW plots had about three times as much total standing biomass and accumulated stem mass, and about twice as much basal area as the CW plots at the same age, even though there were no significant differences in the number of stems per hectare between treatments. Average diameter in the FIW plots was 4 cm larger than the CW plots and the largest diameter trees in the FIW plots were 6 cm larger than the largest diameter trees in the CW plots (Fig. 3). Height and live crown length were about 50% greater in the FIW plots compared to the CW plots. Albaugh et al. (1998) indicated it may be more appropriate to examine treatment differences when the stands were at the same developmental state rather than the same age. The FIW plots at age 11 and the CW plots at age 16 had similar basal area (18.3 and 17.7 $m^2\ ha^{-1}$, respectively) and stand density (1130 and 1128 stems ha^{-1}, respectively). Interestingly, several other assessments of stand conditions were similar for the age 11 FIW plots and the age 16 CW plots. For example, height (7.9 m for FIW and 8.7 m for CW), live crown length (6.2 m for FIW and 5.5 m for CW), gross stem mass accumulation (24.6 Mg ha^{-1} for FIW and 26.2 Mg ha^{-1} for CW), standing stem mass (24.4 Mg ha^{-1} for FIW and 25.9 Mg ha^{-1} for CW), and total biomass accumulation (60.3 Mg ha^{-1} for FIW and 55.7 Mg ha^{-1} for CW) were similar. However, some differences were observed in this comparison. Foliage biomass as a percentage of the total standing biomass was greater in the FIW plots where foliage represented 19% of total standing biomass compared to only 8% for the CW plots. In keeping with this finding, FIW LAI was 2.8 compared to 1.8 $m^2\ m^{-2}$ on the CW plots. While this shift to foliage biomass came largely at the expense of stem wood, the current annual stem mass increment was more than two times greater in the FIW plots (8.5 Mg ha^{-1} per year) than in the CW plots (3.7 Mg ha^{-1} per year). Consequently, these stands, while similar in size at these ages, were on very different growth trajectories: one highly productive (FIW) and the other only marginally so (CW).

Given the marked differences in stand development from the CW to the FIW treatment, it was somewhat surprising to find no significant differences in stand density due to treatment. Little mortality was observed in any treatment through the 9 years of the study. Nilsson et al. (2002) found an unusually small amount of variation in relative growth rate across tree size classes at this site and attributed this result to increased biomass partitioning to aboveground components (stem wood) in smaller trees in the fertilized plots and noted that the broadcast fertilization probably resulted in more equal access to limiting resources among all tree size classes. They also noted that few small trees in the fertilized plots had been overtopped by their neighbors so that competition for light at that time was not a critical factor. In their analysis of *P. taeda* growth in Hawaii where basal areas of 100 $m^2\ ha^{-1}$ were observed, Harms et al. (1994) attributed the high stockability to a combination of high sun angle, high solar radiation intensity, long growing season, favorable soil conditions, high foliar nutrients, and freedom from pests. In a subsequent paper regarding the results from the Hawaiian study, Harms et al. (2000) recommended identifying methods to increase the number of trees per unit area that can be grown to a desired size as a way to improve productivity of *P. taeda* grown in its natural range. Of the environmental and site conditions mentioned above, only the foliar nutrient levels were experimentally manipulated in this study and at this time it appears that the optimum nutritional treatment applied to these stands has made an impact on the number of trees of a given size that can be grown per unit area. The more equal access to limiting resources among all tree size classes and the optimum nutrient regime may allow for trees to compete more evenly for light and allow all trees to maintain their position with in the canopy. It will be interesting to observe how long this situation will be maintained in the future.

Growth efficiency increased with increased resource availability (Fig. 14) in agreement with Samuelson et al. (2001) but not Jokela and Martin (2000). From 1992 through 1995, growth efficiency steadily increased in the fertilized stands. After 1995, growth efficiency was fairly stable in all treatments except for 1996 when hurricane induced foliage loss reduced growth efficiency for 1 year in the fertilized plots. After 1996, we observed no clear decline or increase in growth efficiency in any treatment for the remainder of the study. Our measures of LAI may be in error as the LICOR may underestimate LAI at higher LAI levels (Sampson and Allen, 1995). However, based on calculations from the destructive harvests, the LAI estimates from all treatments appeared to do a reasonable job of estimating true LAI (Sampson et al., 2003).

One would expect that reduced growth efficiency as a result of limited nutrition would not be a factor in the fertilized plots; however as per previous studies, hydraulic resistance might have increased due to the taller stems. In the non-fertilized plots, low nutrient availability would be expected to play an important role in any potential age related decline since this site is already nutrient limited, while hydraulic problems would be less important because the trees are smaller and growing slower. Acclimation to well-drained conditions, via increased fine root biomass and decreased root hydraulic conductivity (Ewers et al., 1999, 2000) appear to have balanced water demand with a morphological system well-tuned to supply this demand. Since we have not observed a growth efficiency decline in any treatment at this time, it may be that the trees have not reached the size or age when these issues may become important. Our results support Mencuccini and Grace's (1996) observations that clear reductions in growth efficiency did not occur until about age 20 in *P. sylvestris*. However, before age 15 in managed loblolly and slash (*P. elliottii*) pine plantations Jokela and Martin (2000 and this issue) observed large reductions in growth efficiency. In contrast to this study, their sites were not fertilized annually. Regular applications of balanced fertilizer appear to maintain the biological potential for high growth efficiency. Continued evaluations will assess how long high growth efficiency can be maintained.

Reductions in ring specific gravity due to fertilization and the increase in ring specific gravity with age are similar to trends noted in Roderick and Berry (2001) but different from those found by Van Lear et al. (1973). Van Lear et al. found no decrease in specific gravity with fertilization on a nutrient poor Piedmont site; however, the magnitude of pine growth response to fertilization in their study was much smaller than that observed here. The observed changes in ring specific gravity in our study were relatively minor. For example, the ring specific gravity in the fifth year after fertilization was approximately the same in the fertilized plots as that found in the third year of the study in control plots. The effect of fertilization on ring specific gravity appeared first as reduction in specific gravity and then the fertilized trees display the same pattern of increasing specific gravity with age after a lag of about 2 years. This is in agreement with the observations of Zobel and van Buijenen (1989). Given the limited measurements of ring specific gravity, it is difficult to draw conclusions about the effect of treatments over a long period of time. Certainly this is an area that warrants further investigation. However, given the relatively small absolute effect of fertilization on ring specific gravity even under the intensive fertilization regime provided, it appears unlikely that fertilization will alter wood properties so much as to render them unusable for current product mixes.

Our results were largely a continuation of the trends reported by Albaugh et al. (1998) in their examination of treatment responses in the first 4 years after treatment at this site. The patterns of stand development and productivity observed in 1995 (the last year of analysis reported in Albaugh et al. (1998) and the fourth of 9 years reported in this paper) have continued through 2000 with little change. The longevity of response may be a function of the age of the stands when treatments were initiated (8 years), the very poor nutrient availability, and/or the application of an optimum nutrient regime at the site. The fertilized plots are now at or near an age and a size when a commercial harvest is feasible. For the stand conditions at this site, then, the optimum nutrient availability plots have achieved high productivity throughout the economic life of the stand (given that application of the treatment occurred at age 8) without any measurable decline in stand productivity. A nearby stand of *P. taeda* with the same soil and site conditions as this stand has been treated with a similar optimal nutrient availability regime since planting and fertilization responses through age 6 have been dramatic (McKeand et al., 2000). Continued research at these sites will further our understanding of the growth potential and longevity of response for *P. taeda* on this poor droughty soil.

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