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Effect of complete competition control and annual fertilization on stem growth and canopy relations for a chronosequence of loblolly pine plantations in the lower coastal plain of Georgia

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Abstract

Stem growth, developmental patterns and canopy relations were measured in a chronosequence of intensively managed loblolly pine stands. The study was located on two distinct sites in the lower coastal plain of Georgia, USA and contained a factorial arrangement of complete control of interspecific competition (W) and annual nitrogen fertilization (F). The W treatment increased growth rate for several years, while the F treatments led to sustained growth increases. The combination of the W and F treatments resulted in more than 180 Mg ha⁻¹ stem biomass production at age 15 which is more than double the production of control treatment. Stem biomass production is continuing to increase through age 15 as indicated by the current annual increment in stem biomass continuing to exceed the mean annual increment in stem biomass. The F treatment decreased wood quality by decreasing whole tree latewood specific gravity from 0.565 to 0.535 and by lengthening the transition from juvenile to mature wood from 4 to 5 years. Increased rates of stem growth in response to cultural treatments were largely mediated by increased leaf area, with strong functional relationships between leaf area index and current annual increment. However, growth efficiency (stem production per unit of leaf area) decreased with stand age. These results indicate that nutrient amendments are necessary for sustaining high rates of stand development on relatively nutrient poor lower coastal plain soils.

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1. Introduction

Intensive management of pine plantations in the southern United States has been of keen interest to many researchers over the past two decades. Many field studies were installed since the late 1970s to understand and quantify the response of southern pine

plantations to vegetation control, fertilization, mechanical soil treatments and interactions of all of these treatments on a wide array of sites (e.g. Pienaar and Shiver, 1993; Miller et al., 1995; Allen, 1987; Gent et al., 1986). The goal of these studies has been to quantify the response of silvicultural treatments at different sites and parameterize growth and yield models. The large growth increases associated with these field studies has led to adoption of practices such as fertilization and aggressive competition control

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(Goetzl, 1998; Moffat et al., 1998). More recently, the mechanisms driving growth differences associated with silvicultural treatments have been explored. Here, the hope is to elucidate the causes for increased growth in order to parameterize process models, extrapolate empirical studies to new sites and novel conditions, and increase site specificity of silvicultural recommendations.

In 1987, a study was begun in the lower coastal plain of Georgia on the Dixon State Forest near Waycross, GA, USA to determine the growth response of loblolly pine (*Pinus taeda* L.) to annual nitrogen fertilization and complete control of competing vegetation. These extreme treatments were chosen to determine the biological potential of loblolly pine, monitor long-term changes in growth associated with environmental change, and serve as a research platform for mechanistic studies. Since 1987, additional stands have been installed (1989 and 1993) that permit a chronosequence research approach. The growth rates of the more intensively managed stands (fertilization + competition control) are some of the fastest reported in the southeastern United States (Borders and Bailey, 2001). The outstanding growth rates, the replication in time and space, and continuous application of treatments since planting make this an ideal research platform to study growth and yield as well as to examine the relationships between leaf area dynamics and growth.

The objective of this paper is to report and summarize the long-term findings from this study. Important attributes relate to stand growth (height, mean annual increment, current annual increment), stand characteristics (basal area, leaf area index, foliar nitrogen status, wood density, aboveground biomass partitioning), and functional relationships between stand attributes (basal area versus stand density, basal area versus live crown, basal area versus leaf area index, stand growth versus leaf area index). Previous papers have been published from this research platform (Borders and Bailey, 2001—stand growth at age 9; Will et al., 2002—relationship between leaf biomass and stem biomass; Munger et al., 2003—leaf level physiology). However, the results presented in this paper are not presented elsewhere and provide a synopsis of the effects of the extreme treatments over time on a number of important stand attributes and relationships.

2. Materials and methods

The study was established on two separate sites in the lower coastal plain of Georgia on the Dixon State Forest near the city of Waycross in Ware County, GA, USA (31°15'N latitude, 82°24'W longitude). Both sites were established on recently cut-over forested areas that had been harvested approximately 1.5 years before initial plot establishment in the winter of 1987.

One site, known as the Waycross “wet” site is poorly to somewhat poorly drained and contains primarily pelham (loamy, siliceous, thermic arenic paleaquult) in association with rigdon soil series (sandy, siliceous, thermic oxyaquic alorthod) (Table 1). Pelham is a wet ultisol while rigdon is a spodosol. This association indicates that spodic horizons are present but not predominant across the landscape. The other site, known as the Waycross “dry” site is well drained to moderately well drained and has soils that are predominantly bonifay (loamy, siliceous, thermic grossarenic plinthic paleudult) in close association with blanton soil series (loamy, siliceous, thermic grossarenic paleudult) (Table 1). The defining features are >100 cm of sand for both series with plinthite being present for bonifay. Both sites are typical of the lower coastal plain of Georgia and have slopes of <1%. Base age 25 site index (based on nonintensively managed control plots measured at age 15) for these two sites is 23.5 and 24.8 m (Harrison and Borders, 1996) for the wet and dry sites, respectively.

The climate in this area is characterized by long, hot, humid summers, with an average maximum July temperature of 33.2 °C and winters that are cool and fairly short, with an average January low temperature of 4.1 °C. Average annual precipitation is about 130 cm.

The mean monthly water balance for the period of growth (1987–2001) indicates that stored soil moisture is depleted in May and June and that water deficits are generally encountered during the late growing season months of July, August, and September (Fig. 1). During these months average precipitation inputs exceed 90 mm and thus help meet transpirational demands. On an annual basis, transpirational deficits were encountered in all years other than 1992. The highest deficit was encountered in 1995 (425 mm) and in 3 of the last 4 years while Georgia has been suffering a drought deficits have exceeded 240 mm.

Table 1

Soil characteristics for plots within the consortium for accelerated pine productivity studies (CAPPS) located in the Dixon State Forest, in Waycross, GA (31°15'N, 82°24'W)

Component	Location	
	Wet site	Dry site
Taxonomic family	Loamy, siliceous, subactive, thermic arenic paleaquults	Loamy, siliceous, subactive, thermic, grossarenic plinthic paleudults
Site index (m at base age 25)	21.3 (70 ft.)	19.8 (65 ft.)
Texture of A horizon	Loamy sand	Sand to loamy sand
Texture of B horizon	Loam	Sandy loam
Depth to argillic (cm)	60–70	120–140
Slope (%)	0–5	0–12
Drainage class	Poorly drained	Well drained
Plant available water (mm)	120	80
pH ^a	3.83 ± 0.17	4.67 ± 0.15
Organic carbon ^b (%)	1.78 ± 0.09	1.01 ± 0.11
Available P ^c (mg/kg)	1.97 ± 0.82	5.4 ± 4.5

Soil chemical parameters are for a 0–10 cm layer and represent means and I.S.D. from six control plots.

^a Soil pH is measured in DI water with a 1:2 mass to volume ratio.

^b Organic carbon was determined by dry combustion.

^c Available P was estimated using a Mehlich I extract.

In general, these sandy coastal plain soils, even those that contain an argillic horizon, are not able to supply sufficient soil moisture to fully meet transpirational demands during the warm months of the latter growing season. However, on the wet site, trees have easy access to the relatively high water table during most of the growing season.

At each site (wet and dry), two blocks composed of four 0.15 ha plots were installed on each planting date (1987, 1989, 1993). Within each 0.15 ha treatment plot, we established an interior 0.05 ha measurement plot and identified all the trees on this plot with a unique number. In each block of four plots, the following treatments were randomly assigned:

- W herbicide used to control all herbaceous and woody competing vegetation throughout the life of the study;
- F fertilize as follows—first two growing seasons: 280 kg ha⁻¹ DAP + 112 kg ha⁻¹ KCl in the spring and 56 kg ha⁻¹ of NH₄NO₃ mid-summer. In subsequent growing seasons: 150 lbs/ac NH₄NO₃ early to mid-spring. At age 10, 336 kg ha⁻¹ NH₄NO₃ + 140 kg ha⁻¹ triple super phosphate. At age 11, 560 kg ha⁻¹ super rainbow (10-10-10) with micronutrients + 168 kg ha⁻¹ NH₄NO₃ early

spring. At age 12 forward 336 kg ha⁻¹ NH₄NO₃ early spring;

- FW Both F and W treatments;
- C Control treatment: no other treatment following a spot rake, pile and bed mechanical site preparation treatment (same site preparation as performed for all treatments).

Improved 1–0 loblolly pine seedlings were hand planted at the equivalent of 1660 trees/ha. Each planting spot was double planted to help insure that 1 year survival was adequate. Genetically improved, open pollinated 7–56 (North Carolina State University Tree Improvement Cooperative) were planted. Seedlings were produced at the nursery near Bellville, GA which was previously owned by Union Camp Corporation and which is currently owned by International Paper Company. At the end of the first growing season all planting spaces that contained two living seedlings had one seedling removed. Thus, our data reflect expected survival and development from age 1 forward. The weed control treatment eliminated all vegetation other than the planted pines during the study so that the pines would grow free of competition throughout stand development. In the early spring of years 1, 2 and 3, we evenly broadcast 114 g/ha

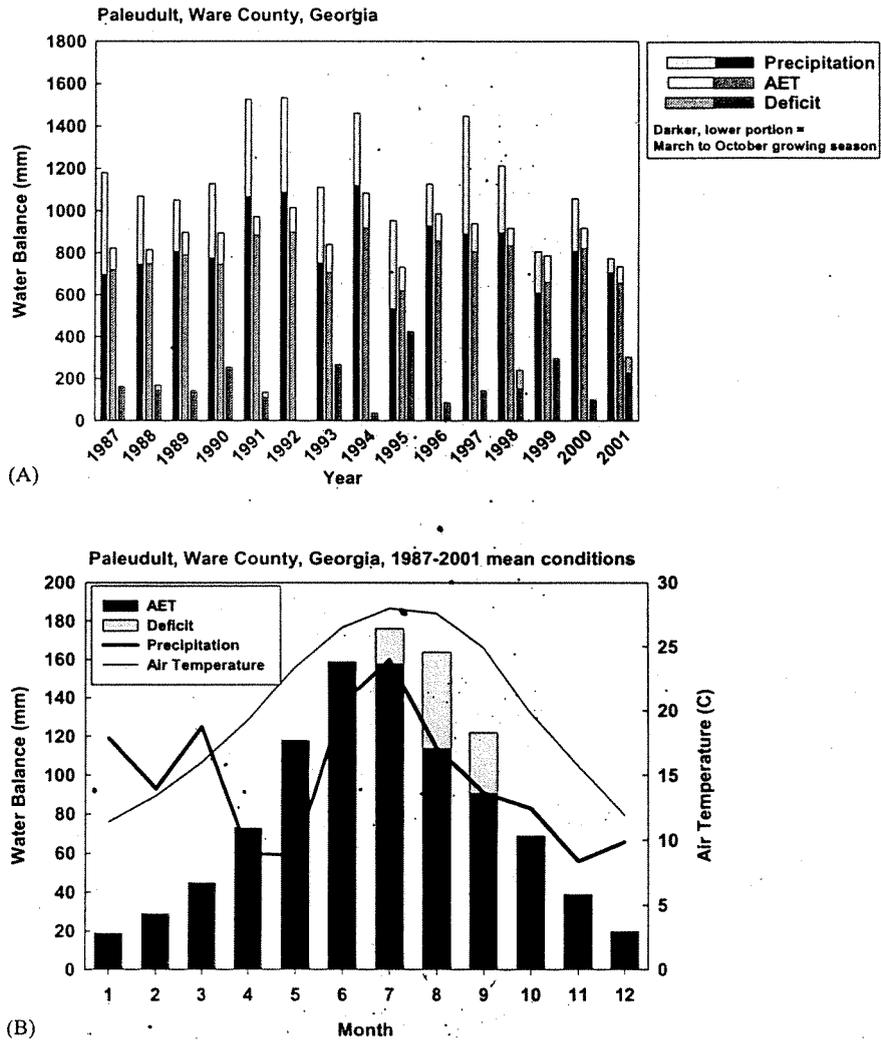


Fig. 1. Water balance estimates for plots within the consortium for accelerated pine productivity studies (CAPPS) located in the Dixon State Forest, Waycross, GA. Climatological data for 1987–2001 are from Alma, GA approximately 18 miles north of Waycross (Georgia Automated Environmental Monitoring Network, 2001). Potential evapotranspiration was estimated using the approach of Thornthwaite and Mather (1957) and soil moisture storage was taken as 100 mm for the upper 1 m of soil. Annual precipitation, actual evapotranspiration (AET), and water deficit for all years of plantation growth are in (A) and mean monthly values over the course of the experiment are in (B).

of sulfomethuron methyl (Oust[®]) over the site using a four wheel all terrain vehicle. Follow up treatments with directed sprays of glyphosate occurred in mid-summer of each year. After the third year the crowns of the pines had closed and we limited additional herbicide treatments to directed sprays of glyphosate as needed. All fertilizer applications were broadcast over the site by hand using a cyclone spreader.

The oldest trees in our study were planted during the winter of 1987. For this time replicate we have 15-year measurements available for individual tree and plot development. However, for some measurements such as nutrient concentrations and leaf area, we present data taken during an intensive sampling period conducted during 1999 on the chronosequence when the stand ages were 6-, 10-, and 12-years.

Total height and height to live crown of each tree was measured annually. Additionally, we measured basal diameter on all trees <1.37 m in height and diameter at breast height on all trees ≥ 1.37 m in height. Site specific taper, weight and volume equations were developed from 192 destructively sampled trees (four trees per plot) harvested during the winter of 1998–1999 (Zhang et al., 2002). These equations were used to develop unit area estimates of dry biomass for each treatment. Detailed analysis of disks that were removed from each stem starting at the base on 2.44 m intervals was used to investigate specific gravity and other wood characteristics along the stem.

Leaf area was calculated using litter traps. Litter was collected from five randomly placed, 0.75 m diameter, round litterfall traps per plot at approximately 6-week intervals between March 1999 and March 2001. Litter collected from each plot was pooled, put into paper bags, and dried at 60 °C. Pine leaf litter was separated from the rest of the sample and weighed. Specific area of the litter (all-sided basis) was determined individually for all plots. The amount that fresh needles shrank before abscission was determined empirically and used to convert litter area to that of fresh needles. Loblolly pine in the southeastern US generally keeps its needles for a year-and-a-half, such that needles abscising during a given year are those that developed the previous year. Leaf area generally peaks in August or September. Therefore, to calculate peak LAI during 1999, we summed the litter collections between August 1999 and March 2001. All-sided values were divided by π to convert to a projected area basis.

Foliar nitrogen concentration was determined from samples taken from six locations in the upper and middle canopy on the trees harvested during the dormant season of 1998–1999 (same trees as described above). Needles were placed on ice in the field and stored at 4 °C in the laboratory until they were processed. Foliage was dried at 64 °C and then ground. Nitrogen concentration was determined using a NC2100 CNS analyzer (CE Elantech Inc., Lakewood, NJ, USA).

Stand development patterns are presented separately for the dry and wet sites since development on the wet site was faster than on the dry site. For each site, the stand development data from the oldest plots were analyzed as a factorial arrangement of the F and

W treatments with repeated measures. For measurements taken on the chronosequence (foliar nitrogen concentration, leaf area index, growth efficiency), data were combined for the wet and dry sites and analyzed as a split-plot ANOVA where site served as the replicate, stand age was the whole-plot factor, and the factorial combination of F and W were split-plot factors. Because treatment blocks of the same age were established adjacent to one another at a given site within a location, i.e. age was not randomized within sites, they were averaged before analysis. Ratios were log transformed as necessary.

3. Results

3.1. Stand development

Stand development was based through age 15 measurements from the 1987 time replicate. The younger aged stands (planted in 1989 and 1993) developed very similarly to the 1987 replicate. On the dry site, average height ranged from approximately 15 m for the control treatment to 21 m for the F and FW treatments with the W only treatment at about 17 m (Fig. 2). At age 15, average height for the F and FW treatments did not differ significantly from one another whereas both the F and FW treatments were significantly different from the C and W treatments ($P < 0.0001$). On the Wet site, the order of treatments for age 15 average height was the same, with the C treatment approximately 14 m, the FW and F treatments at about 22 m and the W only treatment at about 15 m (Fig. 2). On both sites the F only treatment had slower height development than the W only treatment through age 5 or 6 years. Starting at about age 5, height development slowed dramatically on the W only treatment plots while it increased for the F only treatments. In fact, at age 5 the FW and W treatment average heights were greater than the C and F treatments (P value 0.004), however, by age 10 the FW and F treatments were not statistically different from one another while they were larger than the W treatment ($P < 0.0001$).

Stand basal area development proceeded very quickly for the F and FW treatment plots on both sites (Fig. 3). These two treatments approached their maximum carrying capacity and were exhibiting a

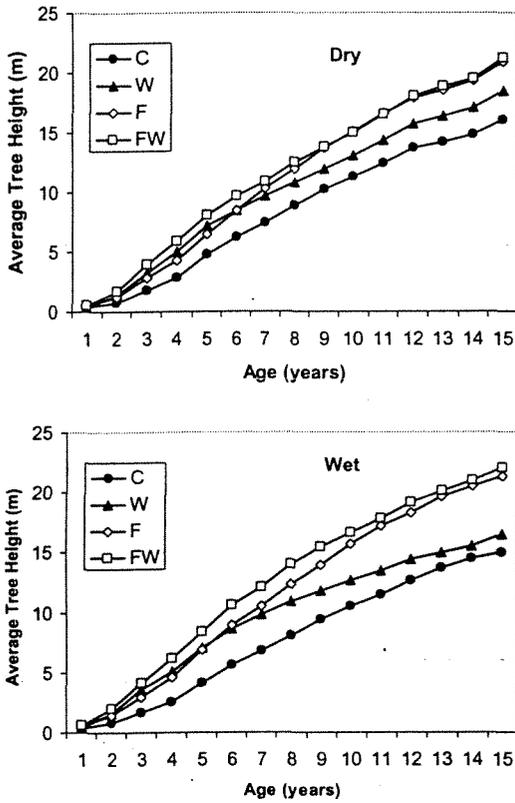


Fig. 2. Average height through 15 growing seasons for loblolly pine stands on the lower coastal plain. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation.

decrease in stems per hectare density by age 15, while the W and C plots had substantially lower levels of basal area and had not begun to show a substantial decrease in stems per hectare density. Average stem diameter at breast height (dbh) (diameter outside bark at 1.37 m from the base) for the four treatments at each location clearly shows that the F and FW treatments resulted in the largest diameter trees by age 15 (Table 2). In fact, average dbh at age 15 ranges from 15 cm for the C treatment to 20 cm for the FW treatment on the dry site and from 14 cm for the C treatment to 21 cm for the FW treatment on the wet site. These differences were not only statistically significant ($P < 0.0001$) but may be operationally

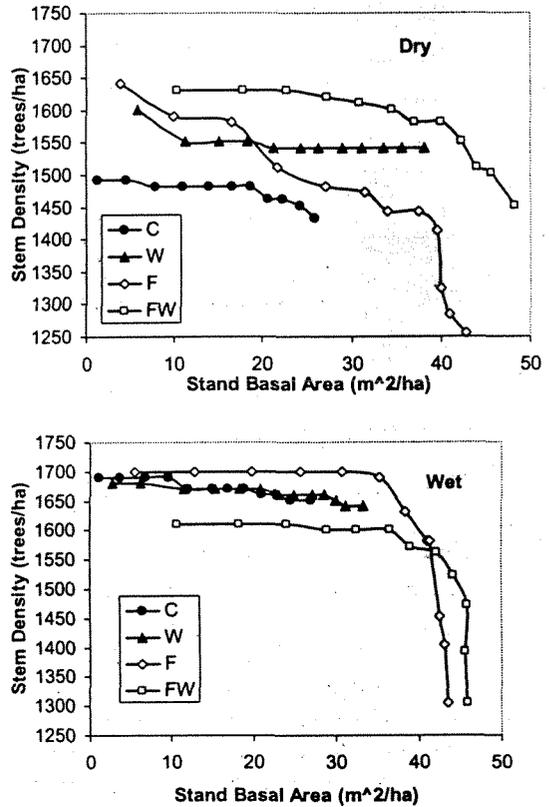


Fig. 3. Stem density vs. stand basal area for loblolly pine stands on the lower coastal plain. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation.

Table 2
Average dbh at age 15 for loblolly pine on the lower coastal plain

Treatment	Average dbh at age 15 (cm)	
	Dry site	Wet site
C	14.9 (2.4)	14.0 (0.5)
W	17.4 (0.6)	15.7 (0.8)
F	20.4 (0.4)	20.2 (0.1)
FW	20.4 (1.0)	20.8 (0.3)

C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation (standard error in parentheses).

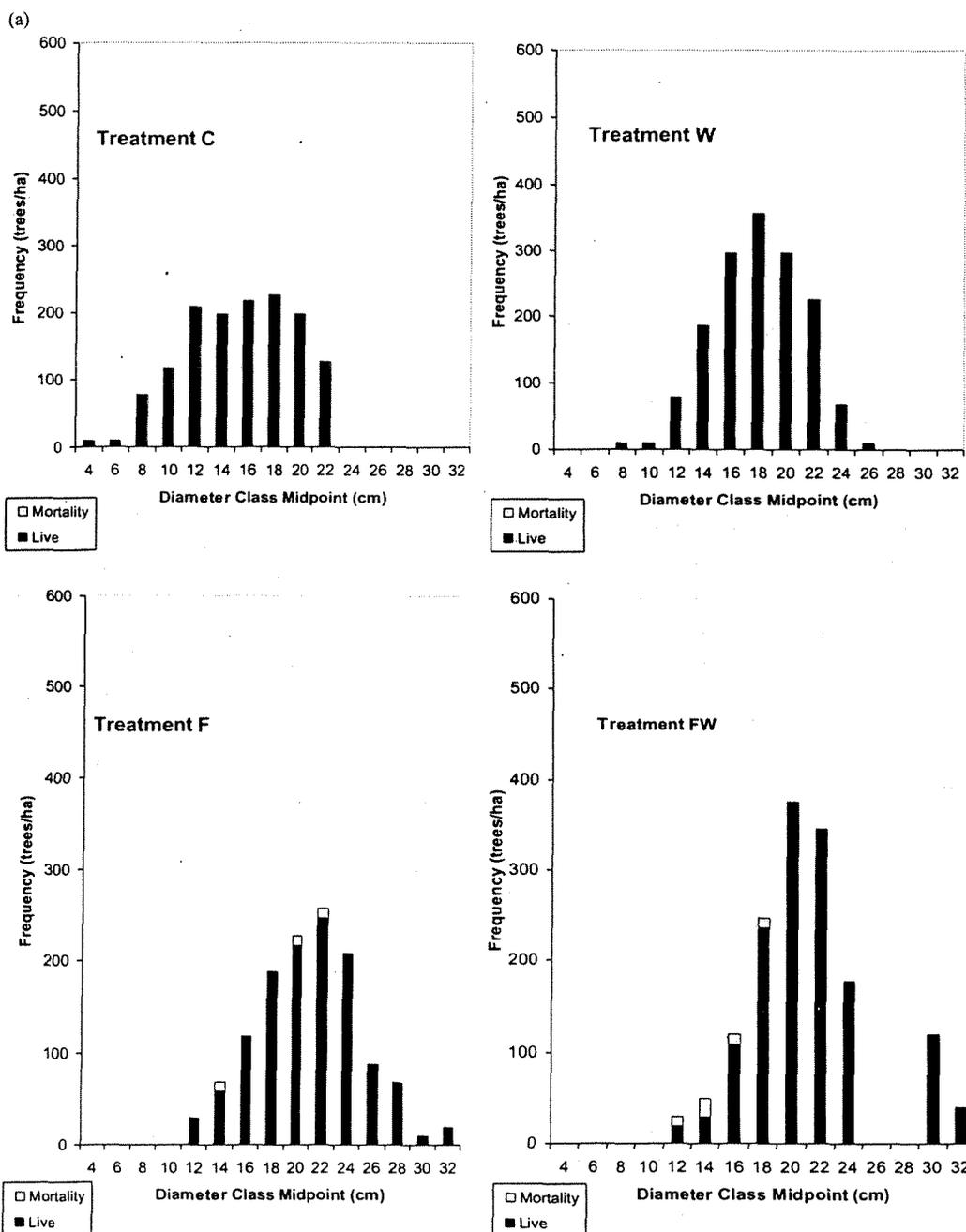


Fig. 4. (a) Diameter distribution bar graphs by treatment for loblolly pine on the lower coastal plain dry site. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation. (b) Diameter distribution bar graphs by treatment for loblolly pine on the lower coastal plain dry site. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation.

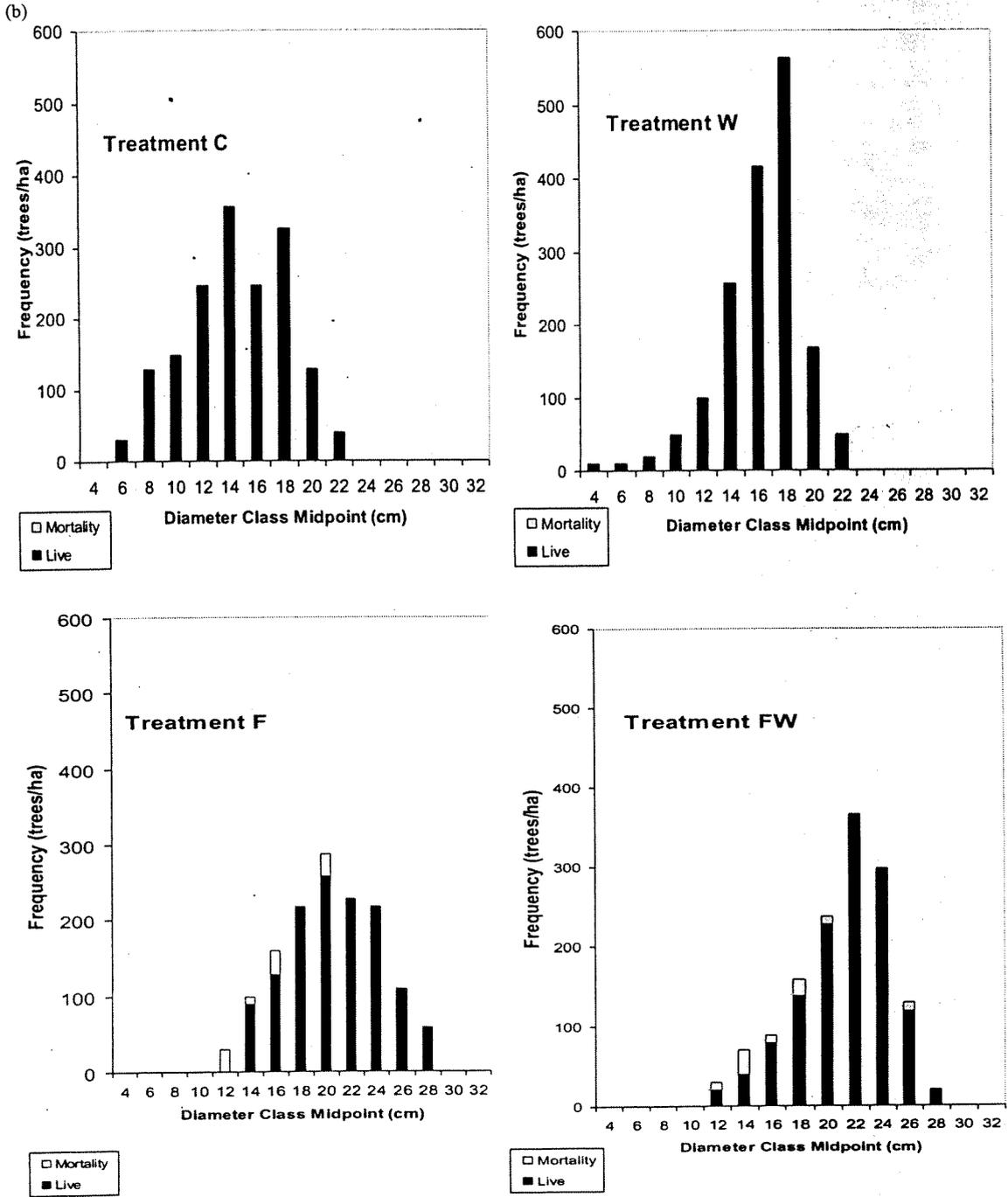


Fig. 4. (Continued).

significant as well in that in that many stems on the FW treatment were large enough to be considered for use as solid wood products rather than, as fiber products. The diameter distribution for the F and FW treatments shifted to the right with approximately half of the stems larger than or equal to 20 cm while <10% of the stems in the C and W treatments were ≥ 20 cm by age 15 (Fig. 4).

Live crown length is related to the amount of photosynthetic area available for tree growth. In general, average crown length followed a typical growth pattern, increasing relatively quickly early in stand development and stabilizing as the stand basal area increased (Fig. 5). There was quite a bit of variability in live crown length from year to year. However, it appeared that average crown length did not vary tremendously by treatment when plotted versus stand basal area.

3.2. Stand productivity and stem characteristics

Stem wood biomass at age 15 as well as gross stem wood biomass production (standing biomass plus biomass of stems that died during the life of the stand) shows that the addition of fertilizer almost doubled production relative to the control treatment on the dry site and more than doubled production on the wet site (Fig. 6). At both sites, competition control without fertilization resulted in moderate increases in biomass production that occurred early in stand development and were maintained through age 15. As for stand basal area development, the F treatment initially lagged behind the W treatment, but surpassed the W treatment by age 6 on the dry site and by age 5 on the wet site. Total standing biomass at age 15 for the FW treatment on both the dry and wet sites was approximately 180 Mg ha^{-1} compared to approximately 85 and 75 Mg ha^{-1} for the C treatment on the dry and wet sites, respectively (differences are statistically significant with a $P < 0.0001$). Age 15 standing stem biomass production for the W treatment was approximately 120 Mg ha^{-1} on the dry site but only 100 Mg ha^{-1} on the wet site (both values are statistically significantly different from the FW treatment with a $P < 0.0001$). Stem biomass production has continued to increase through age 15 and is expected to continue to increase for the next several years. In fact, the current annual increment continues

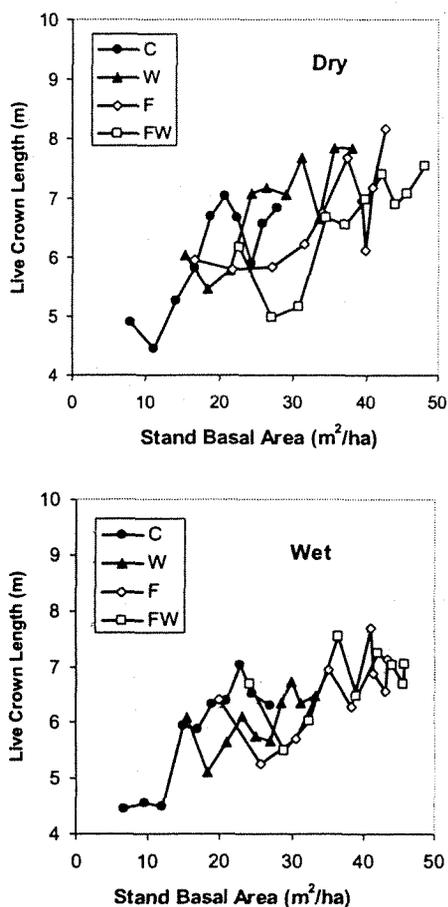


Fig. 5. Average live crown length vs. stand basal area for loblolly pine on the lower coastal plain. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation.

to be higher than mean annual increment for all treatments (Fig. 7). For example, in the FW treatment the current annual increment is approximately 25 and 17 Mg ha^{-1} for the dry and wet sites, respectively, while the mean annual increment is currently about 11 and 12 Mg ha^{-1} for the same dry and wet plots, respectively.

Plots of ring specific gravity over ring age from pith show that W alone did not effect length of juvenility or ring specific gravity when compared to C (Fig. 8). However, fertilization (F alone and FW treatments) increased length of juvenility from 4 to 5 years. The

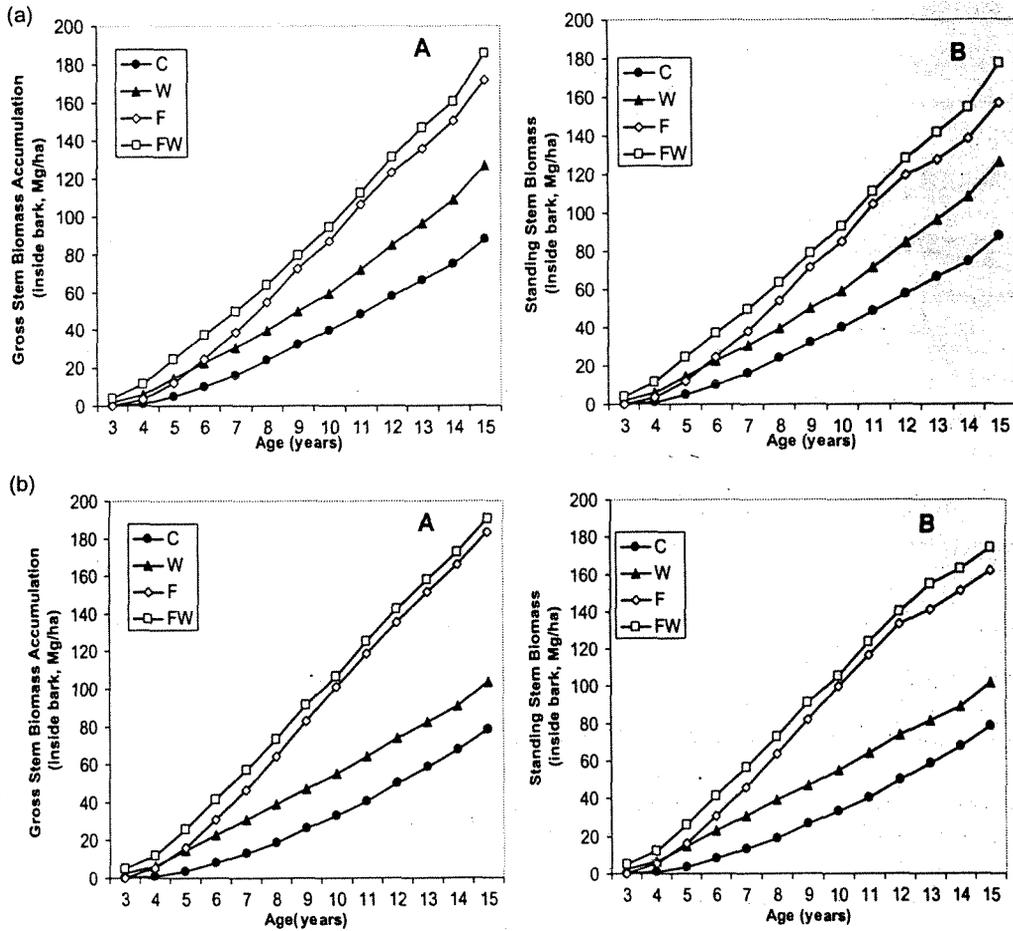


Fig. 6. (a) Gross (A) and standing (B) stem wood biomass (dry mass, inside bark, no branches) vs. stand age for the loblolly pine on the lower coastal plain of Georgia for the dry site. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation. (b) Gross (A) and standing (B) stem wood biomass (dry mass, inside bark, no branches) vs. stand age for loblolly pine on the lower coastal plain of Georgia for the wet site. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation.

fixed species definition method was used to differentiate juvenile wood from mature wood. Specifically, the transition from juvenile wood to mature wood is defined as the year that total ring specific gravity is >0.48 and the percent latewood is $>40\%$ for two consecutive annual growth rings. The F and FW treatments also exhibited significantly reduced latewood specific gravity of 0.535 compared to 0.565 ($P = 0.05$) for C and W treatments based on a whole tree weighted average latewood specific gravity mea-

sure. There were no treatment differences detected in earlywood specific gravity which was approximately 0.4 for all treatments. Furthermore, no treatment differences were found in the earlywood/latewood ratio for these trees. Since the earlywood/latewood ratio did not change with treatment it appears that high annual nitrogen fertilization may have increased tracheid formation of earlywood and late wood but reduced cell wall thickening thus, leading to lower latewood specific gravity.

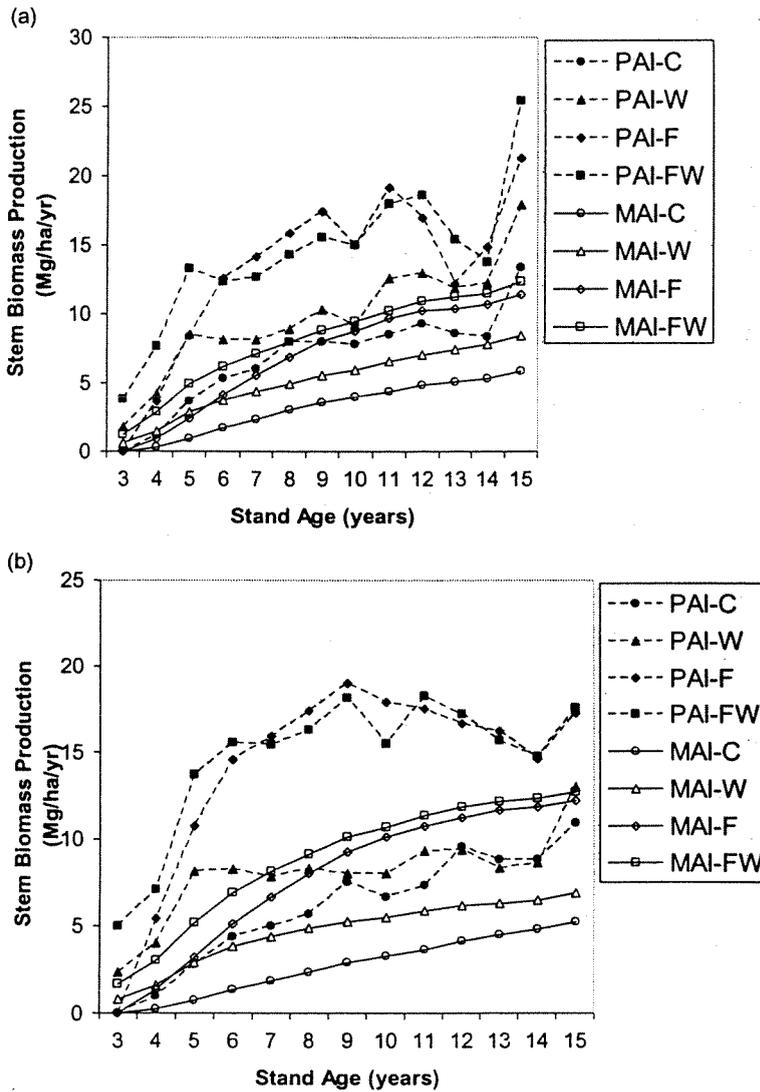


Fig. 7. (a) Mean and periodic (1 year) annual increment of stem biomass for plantations for loblolly pine on the lower coastal plain of Georgia for the dry site. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation. (b) Mean and periodic (1 year) annual increment of stem biomass for plantations for loblolly pine on the lower coastal plain of Georgia for the wet site. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation.

3.3. Canopy dynamics and functional relationships

Fertilization significantly increased foliar N concentration ($P < 0.01$) with the difference between fertilized and nonfertilized plots increasing with stand

age (age \times fertilization interaction $P < 0.01$) (Fig. 9). Without the annual fertilization treatment, foliar N decreased with stand age, indicating that competition control alone did not increase foliar N concentration and that stands may have become more nutrient

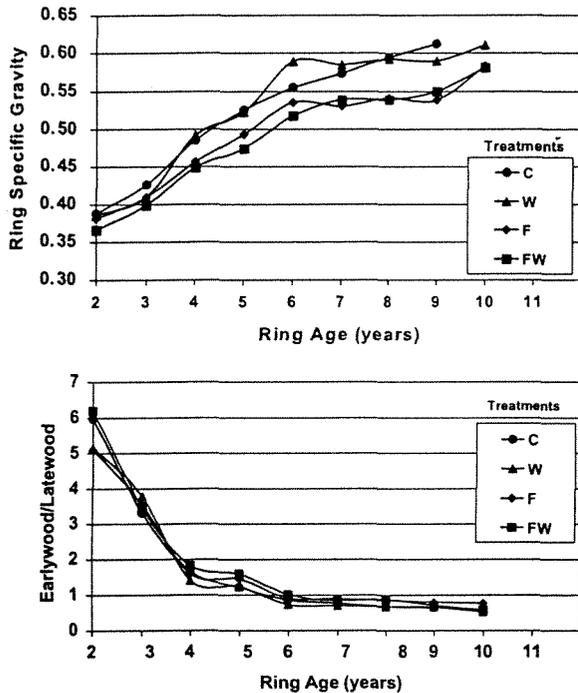


Fig. 8. Specific gravity and earlywood/latewood ratio by ring age for loblolly pine on the lower coastal plain. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation.

limited as available site nutrients were sequestered in living and dead biomass. Part of the increase in foliar N with increasing stand age in the fertilized plots may be associated with the increased N fertilization rate that took place on the 1987 time replicate starting at age 11 when the N application rate was doubled from approximately 56–112 kg ha⁻¹.

Total standing aboveground biomass at the end of the 1999 growing season increased with stand age ($P < 0.01$), with competition control ($P < 0.01$) and with fertilization ($P < 0.01$) (Fig. 10). In addition, the interaction between stand age and fertilization was significant because the positive impact of fertilization increased with age ($P < 0.01$). Increasing stand age as well as the fertilization treatment caused a proportional shift of standing biomass away from branch and leaf biomass to stem biomass ($P < 0.01$). Annual peak projected LAI decreased with stand age for the non-

fertilized treatments (C and W) while it increased with stand age for the fertilized treatments (F and FW) (fertilization effect $P < 0.01$, age \times fertilization interaction $P = 0.05$). Values for peak LAI of the 6-, 10-, and 12-year-old stands can be seen in Fig. 11, where within a treatment, the larger the basal area, the older the stand age.

Accordingly, the trends between basal area and LAI depended on fertilization regime, with a general downward trend in stands without fertilization and a general upward trend in stands with fertilization (Fig. 11). Annual increment (CAI) during the 1999 growing season for the three stand age ranged from approximately 8 Mg ha⁻¹ per year to about 16 Mg ha⁻¹ per year. Current annual increment decreased with increasing basal area for the unfertilized treatments while it remained fairly stable with increasing basal area for the fertilized treatments (Fig. 12).

The relationship between CAI and LAI depended on stand age (Fig. 13). In general, the amount of stem biomass produced per unit of LAI decreased as stand age increased from six to 12 (significantly different intercepts $P = 0.04$). Within a particular stand age, however, a good relationship existed between LAI and CAI. Growth efficiency (GE) defined as stemwood biomass production during the 1999 growing season per unit of peak LAI for the 1999 growing season tended to decrease with stand age ($P = 0.08$) (Fig. 14). Neither fertilization nor competition control had a significant effect on GE.

4. Discussion

Although both sites reported in this study are in close proximity to each other on the lower coastal plain of Georgia, slight elevation and soil differences create distinct sites characteristics. One site, referred to as the dry site is situated on a slight topographic rise and consists of soil with a sandy to sandy loam surface exceeding 100 cm. This site is well drained, has a low soil moisture storage capacity (8 cm of water equivalent in the upper 100 cm), and virtually never has standing water on site. Conversely, the second site, referred to as the wet site, is in a topographic depression adjacent to a swampland. This site is poorly drained, also has a low soil moisture storage capacity due to a sandy texture (12 cm of water equivalent in

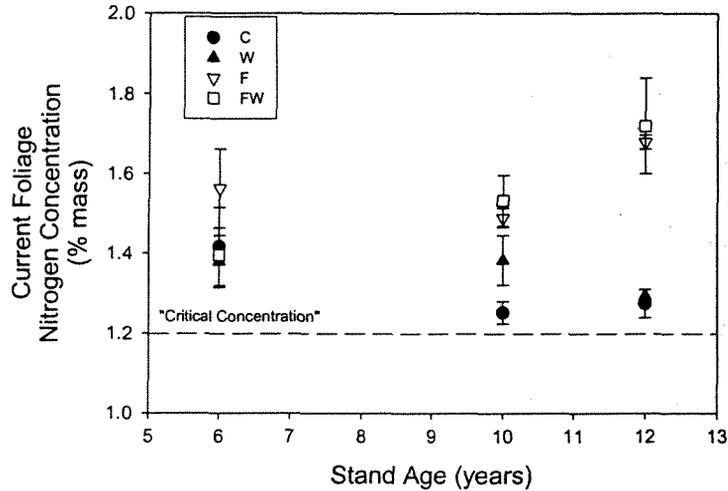


Fig. 9. Dormant season foliar nitrogen concentration of different aged loblolly pine stands growing on the lower coastal plain of Georgia. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation vertical bars represent standard errors.

the upper 100 cm), although in this case the water table is often <100 cm from the surface, and possesses standing water at the surface in as many as 6 of 10 years. Chemically the wet site is more acidic, possess more surface soil C, but less extractable P. The wet site

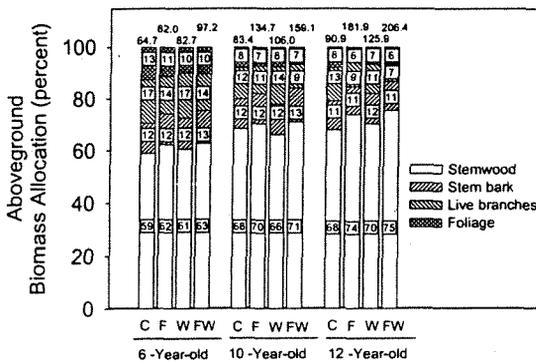


Fig. 10. Partitioning of standing aboveground biomass of different aged loblolly pine stands growing on the lower coastal plain of Georgia. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation estimates based on peak leaf biomass. Numbers above the bars represent total biomass (Mg ha⁻¹). Numbers within the boxes are percentage of total biomass in each component.

exhibited site index at base age 25 of approximately 23.5 m for the treatment that received no silvicultural inputs beyond mechanical site preparation (C) while the dry site exhibited base age 25 site index of approximately 24.8 m for the same treatment. The wet site was more responsive to the fertilizer amendments than the dry site demonstrating a greater biomass and height gain in the F and FW plots compared to C. The reduced moisture stress at the wet site, likely due both to slightly greater soil moisture storage capacity and greater proximity to the water table, appear to be contributing to greater growth at this site.

Stem biomass production at age 15 for the annually fertilized treatments (F and FW) was more than double the C treatment on both the dry and wet sites and more than 1.5 times than the W only treatment on the dry site and approximately double the W only treatment on the wet site. It is important to note that the F treatment is only slightly behind the FW treatment in terms of total stem biomass production on both sites, indicating that complete competition control is not nearly as important as annual fertilization in terms of total pine productivity on these sites, a similar finding has been reported by Jokela and Martin (2000). Mean annual increment for stem biomass has not yet reached a maximum for any of the treatments on either site. However, the F and FW treatments have MAI values

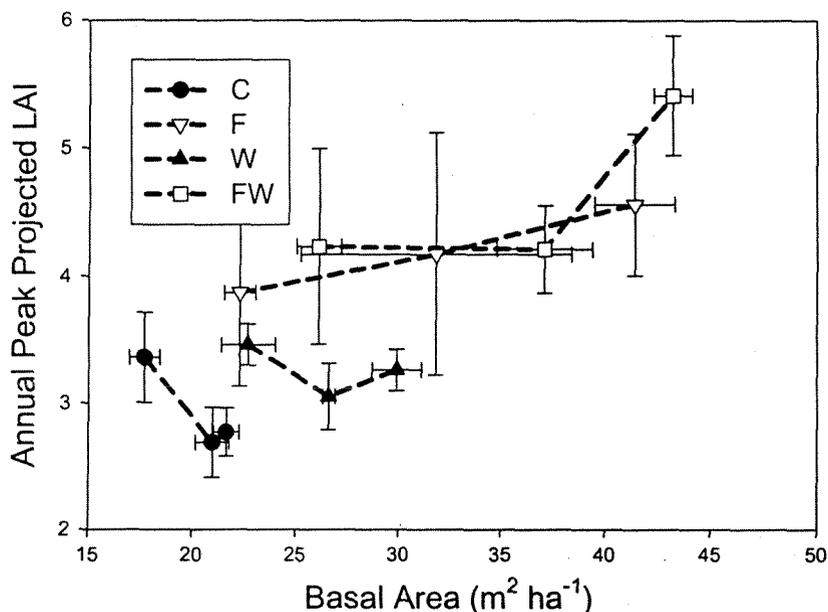


Fig. 11. Relationship between peak leaf area index (LAI) and basal area at the beginning of the growing season for loblolly pine stands on the lower coastal plain of Georgia. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation. Vertical bars represent standard errors.

that are more than double the C and W treatments and there is no indication that the C and W treatments will ever produce the level of stem biomass that is currently present on the F and FW treatment plots. Clearly, accelerated growth rates associated with competition control appear to be transitive while annual fertilization leads to continued acceleration in growth rates through age 15 years.

Results from a slash pine (*Pinus elliottii* Engelm.) site preparation study in the lower coastal plain of Georgia and north Florida indicate that complete vegetation control and a less intensive fertilization regime than used in this study show an inverse relationship between biomass gain associated with these treatments and underlying site index (within a range of 17 m to approximately 24 m base age 25 years) (Pienaar et al., 1998). The gain associated with the W treatment in our study is similar to the increases in growth for the slash pine study associated with competition control. Growth gains associated with the F and FW treatments are much larger than gains reported by Pienaar et al. (1998) even though the underlying base age 25 site index for our C treatments exceeds 23 m. This is not unexpected since the fertilization

regime used in our study is much more intensive than the one used by Pienaar et al. (1998) and, as Jokela and Martin (2000) point out, loblolly is more responsive to the addition of nutrients than slash. However, based on the inverse relationship between base age 25 site index and responsiveness to silvicultural inputs found for slash pine one may conclude that the expected response to silvicultural treatments on our sites would be less than observed. However, it appears that generalizations regarding pine growth responsiveness on a given site to vegetation control and/or fertilization is not straight forward and such generalizations must account for many factors including pine species, inherent nutrient status of the soil, availability of water during the growing season, type and amount of competing vegetation and possibly other factors.

Family 7–56 is known for its fast growth rates and responsiveness to resource addition. Compared to families with average growth rates, it was estimated that the response of 7–56 intensive management would be 28% higher (McKeand et al., 1997). Therefore, while our results are applicable for families such as 7–56, they may overestimate the positive effects of fertilization and competition control in some cases.

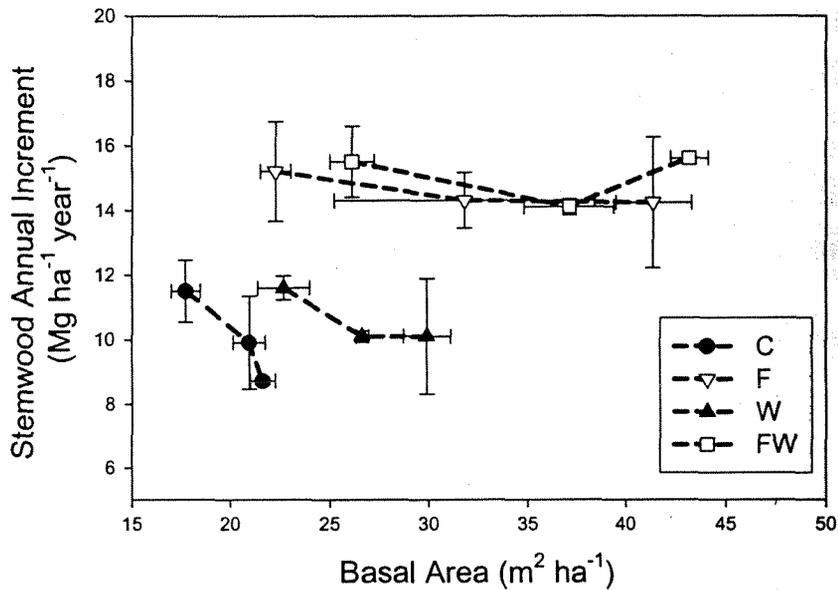


Fig. 12. Relationship between stemwood annual increment and basal area at the beginning of the growing season for loblolly pine stands on the lower coastal plain of Georgia. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation. Vertical bars represent standard errors.

The tremendous increase in stem growth for the F and FW treatments did have an impact on the stem wood characteristics. There was a slight decrease in

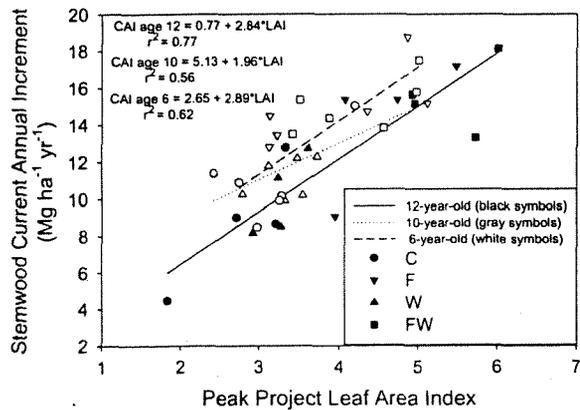


Fig. 13. Relationship between peak leaf area index and stemwood current annual increment for loblolly pine stands growing on the lower coastal plain of Georgia. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation.

specific gravity associated with the fertilization, but not competition associated with the fertilization, but not competition control. Transition from juvenile wood production to mature wood production occurred at about age 4 for the C and W treatments but did not occur until age 5 for the F and FW treatments. This difference is not meaningful from an operational point of view since transition to mature wood production at these early ages (4 or 5 years) is beneficial for the production of quality wood products later in the rotation. These transition ages are in fact earlier than transition ages that have been reported for loblolly pine grown under a similar set of conditions in the Piedmont of Georgia (Clarke et al., 2004).

Increased rates of stem growth in response to cultural treatments were largely mediated by increased leaf area. The benefits of fertilization and competition control on stem biomass growth and foliage development have been documented numerous times in loblolly pine (e.g. Zutter et al., 1986; Vose and Allen, 1988; Allen et al., 1990; Britt et al., 1990; Colbert et al., 1990; Jokela and Martin, 2000; Will et al., 2002; Burkes et al., 2003). In our study, the fertilization treatment resulted in the maintenance of high LAI with increasing stand age while stands that

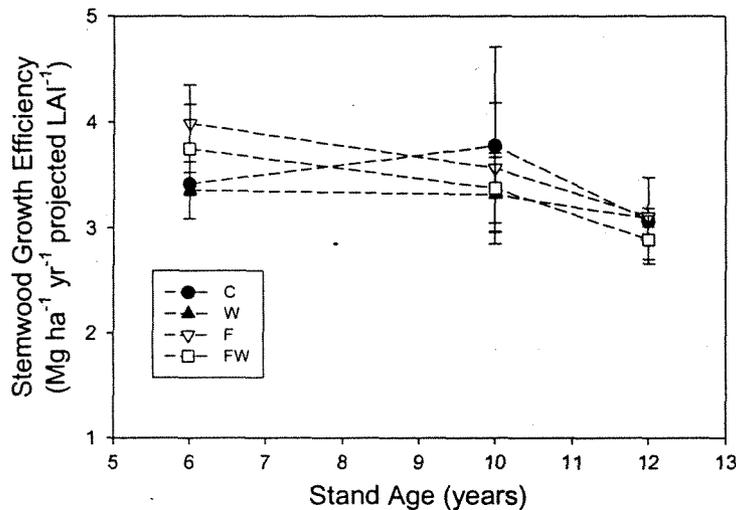


Fig. 14. Growth efficiency for different aged loblolly pine stands growing on the lower coastal plain of Georgia. C: stands receiving mechanical site preparation only, W: stands receiving complete control of interspecific vegetation in addition to mechanical site preparation, F: stands receiving annual fertilization in addition to mechanical site preparation, and FW: stands receiving both competition control and annual fertilization in addition to mechanical site preparation estimates based on peak leaf area. Vertical bars represent standard errors.

had not received fertilization exhibited a decrease in LAI with increasing stand age (Will et al., 2002), further emphasizing the importance of nutrient availability on LAI and ultimately stem growth. Although higher foliar N concentrations did not increase photosynthetic capacity (Munger et al., 2003), foliar N concentration may be related to stem growth if the additional nitrogen acquired by the foliage of the fertilized trees serves as a storage pool for subsequent foliage development.

The decrease in stem growth per unit LAI that occurred in response to increasing stand age indicated that changes related to tree size or tree age were decreasing carbon uptake or increasing carbon use for other functions besides stem growth. Changes in photosynthetic capacity did not cause the decline in growth efficiency with stand age since no effect of the treatments or stand age was measured on light-saturated net photosynthesis (Munger et al., 2003). Likewise, nutrient status did not cause the decrease in growth efficiency because growth efficiency decreased with stand age in fertilized plots as well as nonfertilized plots. Rather, increased stand respiration (Hunt et al., 1999) or increased biomass partitioning belowground (Grier et al., 1981; Kaufman and Ryan, 1986; Smith and Resh, 1999; Grulke and Retzlaff, 2001) may have occurred in our study as

tree size or age increased and probably contributed to the decreases in growth efficiency.

The decreases in proportion of standing biomass in branch and leaf and increases in the proportion of standing stem biomass that occurred with both the stand age and fertilization were related to increased tree size. As stands grow larger, stem biomass increases while leaf biomass either stabilizes or decreases once crown closure is reached (Ryan et al., 1997). Similarly, branch biomass stabilizes as senescence of lower branches roughly corresponds to growth of new branches. To confirm that the effect of fertilization was size mediated and not caused by a shift of biomass partitioning related to resource availability, we compared the relationship between tree size and proportional allocation of the different tree components for fertilized and nonfertilized plots. The relationships for fertilized and nonfertilized stands fell along the same curve indicating the fertilization effects were due to increased size, not shifts in partitioning.

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References

- Allen, H.L., 1987. Forest fertilizers: nutrient amendment, stand productivity, and environmental impact. *J. For.* 85 (2), 37–46.
- Allen, H.L., Dougherty, P.M., Campbell, R.G., 1990. Manipulation of water and nutrients—practice and opportunity in southern US pine forests. *For. Ecol. Manage.* 30, 437–453.
- Borders, B.E., Bailey, R.L., 2001. Loblolly pine—pushing the limits of growth. *S. J. Appl. For.* 25 (2), 69–74.
- Britt, J.R., Zutter, B.R., Mitchell, R.J., Gjerstad, D.H., Dickson, J.F., 1990. Influence of herbaceous interference on growth and biomass partitioning in planted loblolly pine (*Pinus taeda*). *Weed Sci.* 38, 497–503.
- Burkes, E.C., Will, R.E., Barron-Gafford, G.A., Teskey, R.O., Shiver, B.D., 2003. Biomass partitioning and growth efficiency of intensively managed *Pinus taeda* and *Pinus elliotii* stands of different planting densities. *For. Sci.* 49, 224–234.
- Clarke III, A., Borders, B.E., Daniels, R.F., 2004. Impact of vegetation control and annual fertilization on wood properties of loblolly pine at age 12. *For. Prod. J. Rev.*
- Colbert, S.R., Jokela, E.J., Neary, D.G., 1990. Effects of annual fertilization and sustained weed control on dry matter partitioning, leaf area, and growth efficiency of juvenile loblolly and slash pine. *For. Sci.* 36, 995–1014.
- Gent Jr., J.A., Allen, H.L., Campbell, R.G., 1986. Phosphorus and nitrogen plus phosphorus fertilization in loblolly pine stands at establishment. *S. J. Appl. For.* 10 (2), 114–117.
- Georgia Automated Environmental Monitoring Network, 2001. Climatological data. Available at <http://www.griffin.peachnet.edu/bae/> (Verified 21 June 2001).
- Goetzl, A., 1998. AF&PA Southern Forest Management Intensity Survey: Data Summary And Survey Results. Unpublished Report. American Forest and Paper Association, Washington, DC.
- Grier, C.C., Vogt, K.A., Keyes, M.R., Edmonds, R.L., 1981. Biomass distribution and above-and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Can. J. For. Res.* 11, 155–167.
- Grulke, N.E., Retzlaff, W.A., 2001. Changes in physiological attributes of Ponderosa pine from seedlings to mature tree. *Tree Physiol.* 21, 275–286.
- Harrison, W.M., Borders, B.E., 1996. Yield prediction and growth projection for site-prepared loblolly pine plantations in the Carolinas, Georgia, Alabama, and Florida. PMRC Tech. Rep. 1, p. 49.
- Hunt Jr., E.R., Lavigne, M.B., Franklin, S.E., 1999. Factors controlling the decline of net primary production with stand age for balsam fir in newfoundland assessed using an ecosystem simulation model. *Ecol. Model.* 122, 151–164.
- Jokela, E.J., Martin, T.A., 2000. Effects of ontogeny and soil nutrient supply on production, allocation, and leaf area efficiency in loblolly and slash pine stands. *Can. J. For. Res.* 30, 1511–1524.
- Kaufman, M.R., Ryan, M.G., 1986. Physiographic, stand, and environmental effects on individual tree growth and growth efficiency in subalpine forests. *Tree Physiol.* 2, 47–59.
- McKeand, S.E., Crook, R.P., Allen, H.L., 1997. Genotypic stability effects on predicted family responses to silvicultural treatments in loblolly pine. *S. J. Appl. For.* 21, 84–89.
- Miller, J.H., Zutter B.R., Zedaker, S.M., Edwards, M.B., Newbold, R.A., 1995. A regional framework of early growth responses for loblolly pine relative to herbaceous, woody, and complete competition control: the COMProject. Gen. Tech. Rep. SO-117, USDA Forest Service, Southern Forest Experiment Station, New Orleans, LA, p. 48.
- Moffat, S., Cabbage, F., Cascio, A., Sheffield, R., 1998. Estimation of future forest management intensity on NIPF lands in the south: results of the southern state foresters' survey. Working Paper Series, SOFAC Report 14, Research Triangle Park, NC.
- Munger, G.T., Will, R.E., Borders, B.E., 2003. Effects of competition control and annual nitrogen fertilization on gas exchange of different aged *Pinus taeda*. *Can. J. For. Res.* 33, 1076–1083.
- Pienaar, L.V., Shiver, B.D., 1993. Early results from an old-field loblolly pine spacing study in the Georgia Piedmont with competition control. *S. J. Appl. For.* 17 (4), 193–196.
- Pienaar, L.V., Shiver, B.D., Harrison, W.M., 1998. Slash pine site preparation study: age 17 results. PMRC. Tech. Rep. 1998-4. D.B. Warnell School of Forest Resources. The University of Georgia, Athens, GA. P. 46.
- Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age-related decline in forest productivity: pattern and process. *Adv. Ecol. Res.* 27, 213–262.
- Smith, F.W., Resh, S.C., 1999. Age-related changes in production and below-ground carbon allocation of *Pinus contorta* forests. *For. Sci.* 45, 333–341.
- Thortwaite, C.W., Mather, J.R., 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Publications in Climatology, vol. 10. Centerton Laboratory of Climatology, NJ, p. 3.
- Vose, J.M., Allen, H.L., 1988. Leaf area, stemwood growth, and nutrition relationships in loblolly pine. *For. Sci.* 34, 547–563.
- Will, R.E., Munger, G.T., Zhang, Y., Borders, B.E., 2002. Effects of annual fertilization and complete competition control on current annual increment canopy development and growth efficiency of different aged *Pinus taeda* stands. *Can. J. For. Res.* 32, 1728–1740.
- Zhang, Y., Borders, B.E., Bailey, R.L., 2002. Derivation, fitting, and implication of a compatible stem taper–volume–weight system for intensively managed fast growing loblolly pine. *For. Sci.* 48 (3), 595–607.
- Zutter, B.R., Gjerstad, D.H., Glover, G.R., 1986. Effects of herbaceous weed control using herbicides on a young loblolly pine plantation. *For. Sci.* 32, 882–899.