Long-Term Ecophysiology

Moderator:

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SPECIAL SESSION: LONG-TERM ECOPHYSIOLOGY OF LOBLOLLY PINE

Session Coordinators: Eric J. Jokela, University of Florida and Phillip M. Dougherty, Westvaco Corporation

The natural range of loblolly pine is extensive, encompassing 15 southern and mid-Atlantic States from Florida to Delaware and west to eastern Texas and southeastern Oklahoma. Loblolly pine is the most important commercial species in this region, and it is found on more than 13 million ha and a wide variety of soil types. Throughout its natural range, intensive silvicultural practices have been used to enhance forest productivity and health. Considerable investments have been made over the last three decades in applied research programs emphasizing site preparation (mechanical, chemical), understory competition control, regeneration, fertilization, thinning, pest relationships, growth and yield, and genetic tree improvement as a basis for developing sound management strategies for this species.

Similarly, wide arrays of process-level research investigations have been conducted in the South to better understand the production ecology of loblolly pine. A special session of the 11th Biennial Southern Silvicultural Research Conference was organized to provide a forum for an exchange of ideas and a synthesis of knowledge on the ecophysiology of loblolly pine using long-term regional data sets. Five papers, summarizing the effects of intensive silvicultural practices on stand development, leaf area dynamics, productivity, wood quality and growth efficiency (aboveground production/leaf area), were presented. The session provided a unique opportunity to advance our understanding of how ecophysiological processes that control and limit loblolly pine productivity varied across climates, soils and management intensities. The presentations, based on long-term experiments conducted in North Carolina, Georgia, Florida, Louisiana and Oklahoma utilized a common variable format for examining key relationships. Abstracts of these presentations are presented in this volume and efforts are underway to publish the papers and an accompanying synthesis in the refereed literature.

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LONG-TERM TRENDS IN LOBLOLLY PINE SITE PRODUCTIVITY AND STAND CHARACTERISTICS OBSERVED AT THE IMPAC RESEARCH SITE IN ALACHUA COUNTY, FLORIDA

Timothy A. Martin, Eric J. Jokela[1]

While nutrient availability is a dominant factor controlling leaf area development and pine productivity in the southeastern USA, few studies have explored the long-term interactions among nutrient inputs, canopy foliage production, and aboveground biomass production. In order to address these questions, the Intensive Management Practices Assessment Center (IMPAC) southern pine "growth potential" experiment was established 6 miles northeast of Gainesville, Florida.

Soils at the experimental site are sandy, siliceous, hyperthermic Ultic Alaquods. In a typical profile, the spodic horizon occurs at 10-20 in, with an argillic horizon at 35-45 in. The experiment was planted in January, 1983, and consists of factorial combinations of species (loblolly and slash pine), fertilization (repeated or none) and understory weed control (complete or none), replicated three times. This resulted in four treatment combinations: control (C), fertilizer only (F), weed control only (W), and fertilizer combined with weed control (FW). Fertilization treatments were applied annually for ages 1-11 years, with cumulative rates of elemental application over the 11 year period as follows: N (321 lb/ac), P (128), K (283), Ca (96), Mg (64), Mn (2.7), Fe (2.7), Zn (2.7), Cu (0.4), B (0.4). The fertilization treatments were curtailed from ages 12-15 yr, then were re-initiated for ages 16-18 yr, with cumulative, three-year elemental application rates of: N (650 lb/ac), P (77), K (100), Mn (1.0), Cu (0.4), Fe (2.0), Zn (0.8), B (0.4), Mo (0.008). Biomass harvests at ages 4 and 13 yr were used to develop allometric relationships between diameter and aboveground biomass components, which were combined with annual inventories to estimate aboveground biomass production. Monthly litterfall collections starting at age 6 yr were used to estimate foliage biomass production and leaf area index (LAI). Although data were collected for both loblolly and slash pine, only loblolly pine results will be presented in this paper.

In general, growth responses due to silvicultural treatments were large over the entire study period. For example, at age 18 yr the FW treatment had an exhibited site index of 82 ft (base age 25 yr), compared to 58 ft in the untreated control. Age 18 yr total inside bark stem volume accumulation in the FW, F, W and C treatments were 3672, 3269, 2994 and 1394 ft^3/ac, respectively. Silvicultural treatments also tended to accelerate stand developmental processes. For example, at age 18 yr, 48 percent of stand stem volume in the FW treatment was in 9 in dbh or larger trees, compared to only 17 percent of the volume in the C treatment. Culmination of mean annual increment (i.e., "biological rotation age") occurred at approximately age 12 yr and 250 ft^3/ac/yr in the FW treatment, and age 18 yr and 78 ft^3 ac/yr in the C treatment. Density-related mortality was also accelerated in plots receiving silvicultural treatments. This density-related mortality became apparent at about age 16 yr in the F, W and FW treatments, but had not begun by age 18 yr in the C treatment. Self-thinning began at a Reineke stand density index (SDI) of about 360 (80 percent of maximum). Stand basal area of the F, W and FW treatments at the onset of self-thinning was 172, 159 and 192 ft^2/ac, respectively.

Leaf area development was also strongly impacted by silvicultural treatments, and was particularly responsive to nutrient additions. Projected LAI at age 11 yrs (just prior to the cessation of fertilization treatments) was approximately 3.3 in the F and FW treatments, compared to 2.7 and 1.2 in the W and C treatments, respectively. During the five years without fertilization (ages 11-16 yr), LAI in the F and FW treatments declined by approximately 15 percent, remained steady in the W treatment, and continued aggrading in the C treatment. LAI of the F and FW treatments responded dramatically to refertilization at age 16 yr, increasing from 3.1 to 3.5 and 2.9 to 3.3, respectively, in the year following the retreatment.

LAI across all treatments was strongly correlated with stand basal area, but the slope of this relationship declined with stand development (age 6 yr: LAI = 0.033 * stand BA, r^2 = 0.99; 16 yr LAI = 0.019 * stand BA, r^2 = 0.98). The relationship between stem volume production and LAI (i.e. stemwood growth efficiency) was strong, but also varied with stand development. At age 7-9 yr and 10-11 yr, average growth efficiency was 37.3 and 31.9 ft^3 ac/yr/LAI, but by age 14-16 had declined to 16.1 ft^3 ac/yr/LAI.

Wood quality parameters were impacted by tree age as well as cultural treatments. Tree ring earlywood / latewood ratios declined and ring specific gravity increased from age 4 yr to 10 yr. Ring specific gravity in the W treatment increased at a greater rate than in other treatments. The transition from juvenile to mature wood (defined as the age at which ring specific gravity > = 0.5) occurred at age 7 yr in the W treatment, and at age 8 yr in the F and FW treatments. Ring specific gravity reached 0.5 by age 8 yr in the C treatment, but fluctuated around the 0.5 point at age 9 and 10 yr, while specific gravity remained well above 0.5 after age 8 yr in the F, W and FW treatments.

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LONG-TERM TRENDS IN LOBLOLLY PINE PRODUCTIVITY AND STAND CHARACTERISTICS IN RESPONSE TO STAND DENSITY AND FERTILIZATION IN THE WESTERN GULF REGION

M.A. Sword, J.L. Chambers, Z. Tang, T.J. Dean, and J.C. Goelz[1]

Two levels each of fertilization and stand density were established to create four environments in a 7-year-old loblolly pine plantation on a N and P deficient western Gulf Coastal Plain site in Louisiana. Levels of fertilization were no fertilization and application of 120 lb N and 134 lb P/ac. Levels of stand density were the original stocking (1,210 trees/ac), and row thinning for a residual stocking of 303 trees/ac. Six years later (age 13), basal areas and relative stand densities on the non-thinned (NT) and thinned (T) plots were 176 and 79 ft^2/ac and 90 and 37 percent, respectively. At age 14, 178 lb N, 45 lb P and 45 lb K/ac were broadcast on the previously fertilized (F) plots and a second thinning was conducted on the previously thinned plots to a residual relative density of 31 percent of maximum, which corresponded to 67 ft^2/ac. Long-term measurements of climate, growth, leaf area dynamics and foliar nutrition were initiated at age 11. The objectives of this paper are to describe stand productivity between age 11 and 17 and offer ecophysiological explanations for these growth trends.

Fertilization increased basal area 8 and 9 percent, and stem volume 15 and 20 percent at age 11 and 17, respectively. At age 11, basal areas on the NT and T plots were 161 and 62 ft^2/ac, respectively. After removal of 12 ft^2/ac with the second thinning at age 14, basal areas increased on the NT and T plots, reaching 191 and 87 ft^2/ac and relative densities of 98 and 41 percent, respectively, by age 17. Similar stem volume responses to thinning were observed between age 11 and 17.

Interaction between light and water availability, and subsequent leaf area responses appeared to control mortality, current annual increment (CAI), growth efficiency (GE), and diameter class distribution. On the NT plots, for example, relative densities were within the self-thinning range of 60 to 100 percent of maximum stand density (81 to 98 percent) between age 11 and 17. During this period, peak leaf area index (LAI) increased between age 11 and 14, and began to decline at age 15 with the onset of water deficit and mortality. Specifically, annual soil water deficits at age 11 through 17 were 3.6, 7.3, 7.0, 4.7, 12.0, 10.6 and 15.9 in, respectively. Mortality for the entire period between age 11 and 15 was 5.5 percent; while mortality at age 16 alone was 7.0 percent. Water deficit at age 15 may have increased the rate of fascicle senescence, created a shortage of assimilate and increased self-thinning. Persistence of a high relative density and the simultaneous occurrence of water deficit and accelerated mortality after age 14 suggests that tree survival on the NT plots was dependent on a delicate balance between leaf area and assimilate supply.

In contrast to the NT plots, the T plots exhibited a positive curvilinear relationship between LAI and CAI (R^2 = 0.4549). This relationship improved with exclusion of data collected after age 14 when annual soil water deficits increased (R^2 = 0.7235). Variation associated with CAI on the T plots after age 14 may be attributed to the variable ability of individual plots to maintain normal levels of C fixation and growth when water deficit occurred. Below a LAI of approximately 3.25, this relationship was linear, but at LAI values greater than 3.25, a lower rate of CAI per unit LAI was observed both before and after the onset of water deficit. At our site, a LAI value of 3.25 may represent the point at which shading led to reduced lower crown light availability and less whole-crown C fixation, or the fraction of C allocated to sinks other than stem growth increased.

Growth efficiency (GE) between age 12 and 16 was expressed as the ratio of CAI and peak LAI. Year and stand density, but not fertilization affected GE. Average GE was 98 ft^3/ac/year at age 12. GE decreased to 30 and 86 ft^3/ac/year on the NT and T plots, respectively, at age 15, and increased to 78 and 91 ft^3/ac/year on the NT and T plots, respectively, at age 16. Declines in GE between age 12 and 15 may have been caused by temporary imbalances between CAI and peak LAI caused by self-thinning on the NT plots and operational thinning on the T plots. At age 16, the GE of the NT and T plots increased to 80 and 92 percent of that observed at age 12. It is likely that these gains in GE were caused by shoot and fascicle growth into canopy gaps created by self-thinning or operational thinning and subsequent increases in C fixation and volume growth.

In addition to volume increment, the diameter distribution of wood volume produced on the T plots changed over time in response to fertilization. Immediately before re-thinning at age 14, the majority of volume was in diameter classes less than 9 inches with the remaining 6 and 18 percent in the 9 to 12-inch diameter classes on the thinned, non-fertilized (TNF) and thinned, fertilized plots (TF), respectively. Three years later at age 17, 44 and 83 percent of the volume was in the 9 to 12-inch diameter classes on the TNF and TF plots, respectively. By age 17, fertilization on

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the T plots not only produced a 19 percent increase in volume but added 89 percent more volume to the 9 to 12-inch diameter classes than to the diameter classes less than 9 inches. Following re-thinning, LAI equilibrated to pre-treatment levels after two years on the TNF plots and one year on the TF plots. Thus, when thinning and fertilization were applied together, fertilization increased the rate at which LAI was re-established. In addition to an increase in LAI, rapid equilibration of LAI may have hastened movement of volume into the 9 to 12-inch diameter classes on the TF plots when compared to the TNF plots between age 14 and 17.

At age 14 through 16, nutrient use efficiencies were calculated as the ratio of CAI and foliar N and P content (N NUE and P NUE). Nutrient use efficiencies were affected by year but not stand density or fertilization and averaged 1.9 and 26.1 ft^3/lb of foliar N and P, respectively, at age 14 and 15. At age 16, N NUE and P NUE increased to 3.2 and 42.5 ft^3/lb, respectively. Increases in N NUE and P NUE at age 16 occurred simultaneously with increases in GE and may have been associated with re-establishment of leaf area in canopy gaps caused by self-thinning and operational thinning. Although foliar concentrations of N and P were increased, nutrient use efficiencies were unaffected by fertilization. Thus, positive effects of fertilization on stand growth were likely caused by changes in leaf area, rather than nutrition enhancement of physiological responses.

In summary, between age 11 and 17 the productivity of plantation loblolly pine in four environments created by thinning and fertilization in central Louisiana appeared to be controlled by interaction among light, water and leaf area. Mechanisms of control differed by stand density, and effects of fertilization were manifested through leaf area responses.

CONSORTIUM FOR ACCELERATED PINE PRODUCTION STUDIES (CAPPS): LONG-TERM TRENDS IN LOBLOLLY PINE STAND PRODUCTIVITY AND CHARACTERISTICS IN GEORGIA

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Beginning in 1987, a series of long-term study plots were installed to determine the effects of annual nitrogen fertilization and complete control of competing vegetation on loblolly pine (*Pinus taeda* L.) stand growth and development. The study had two locations, one at the Dixon State Forest (DSF) near Waycross, GA on the lower coastal plain and the other at the B.F.Grant Experimental Forest (BFG) near Eatonton, GA on the Piedmont. The Dixon State Forest is characterized by long, hot, humid summers, with an average maximum July temperature of 33°C, and winters that are cool and fairly short, with an average January low temperature of 2.6°C. Average annual precipitation is about 130 cm, with about 60 percent falling between April and September. Soils are spodosols or ultisols that are arenic or grossarenic with slopes < 1 percent. The B. F. Grant location is characterized by warm to hot summers, with average July high temperature of 33°C, and moderately cold but highly variable winters, with average January low temperature of 2.2°C. Average annual precipitation is about 120 cm, with a maximum in early spring, a minimum in fall, and fairly even distribution for the rest of the year. Soils are clayey ultisols with slopes < 15 percent. Within each location there were two study sites separated by less than 6 kilometers.

Loblolly pine stands were established at a density of 680 trees/ac in 1987, 1989, and 1993 at the DSF location and in 1988, 1990, and 1995 at the BFG location. Half-sib family 7-56 was planted (North Carolina State Tree Improvement Cooperative) at the DSF locations and half-sib family 10-25 (North Carolina State Tree Improvement Cooperative) was planted at the BFG location. Two treatment blocks of each stand age were established at each of the two sites within locations. The exception was only one block of the 1995 planting was established at each site at BFG location. Each treatment block comprised four 0.15 ha plots that were assigned one of four treatments. The plot-level treatments were a factorial combination of fertilization and interspecific competition control. The fertilizer treatment (F) was an annual fertilization regime, consisting of 280 kg/ha diammonium phosphate and 112 kg ha^{-1} potassium chloride in the spring and 56 kg/ha ammonium nitrate in the summer of the first two years after establishment, followed by a minimum of 168 kg/ha ammonium nitrate in the spring of subsequent years. The interspecific competition control treatment (H) was an herbicide treatment to eliminate all competing vegetation throughout stand development. The HF treatment was the combination of fertilization and competition control. The control treatment (C), received neither fertilization or competition control.

Response of tree growth to the treatments has been exceptional. In general, the effects of competition control were greatest during early stand development, causing an upward shift in the relationship between stand age and growth. In contrast, the fertilization treatment increased the slope of the relationship between stand age and growth. Overall, the response of competition control was greater at the BFG location than it was on the DSF location. Average tree height at the DSF location at age 14 was 52, 68, 56, and 69 ft for the C, F, H, and HF treatments respectively. At the BFG location at age 13, average tree heights were 45, 55, 54, and 60 feet for the C, F, H, and HF treatments respectively. Total standing volume for the DSF location was 2665, 5645, 3745, 6342 ft^3/ac at age 14 for the C, F, H, and HF treatments and was 2363, 3438, 3703, 4579 ft^3/ac for the same treatments at the BFG location at age 13. Basal area at the DSF location was 109, 183, 146, and 199 ft^2/ac for the C, F, H, and HF stands at age 14 and was 111, 142, 151, 172 ft^2/ac for the same plots at the BFG location at age 13. Mean annual increment of the fastest growing HF plots at the DSF location appeared to have peaked around age 13 at approximately 490 ft^3/ac yr. The HF stands at the BFG location were approximately 350 ft^3/ac yr at age 13, but had not yet reached their maximum. Current annual increment (CAI) of the F and the HF plots at the DSF location approached 800 ft^3/ac yr between ages 8 and 12, and then decreased. The CAI of the C and H plots have remained fairly stable, below 400 ft^3/ac yr, over the same age range. At the BFG location, CAI was greater for the H treatment than for the F treatment until age 9. After age 9, the opposite was true. Maximum CAI for the HF plots at the BFG location was approximately 600 ft^3/ac yr. At both locations, there was a positive and fairly linear relationship between LAI and basal area. Height to live crown and basal area also were linearly related. Although crown length increased with stand basal area, the increase was much smaller than that for the relationship between height to live crown and basal area. At both locations, the average number of branches per whorl increased with increasing height, reaching a maximum of about 3.5 at the DSF location and 4.0 at the BFG location.

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Fertilization and competition control had significant positive effects on litterfall-based estimates of stand leaf area index (LAI). All-sided LAI for the foliage cohort that developed in 1998 was 3.9, 5.3, 5.7 and 7.0 for the C, F, H, and HF treatment plots, respectively, at the BFG location and 5.3, 7.6, 6.1 and 8.2 for the corresponding DSF plots. The effect of fertilization on LAI was strongest in older stands at both locations (significant interaction between age and fertilization). Fertilization increased LAI at the BFG location by 3 percent, 34 percent, and 28 percent for stand ages 4, 9 and 11, respectively, and at the DSF location by 8 percent, 38 percent and 79 percent for stand ages 6, 10 and 12. Competition control influenced LAI most dramatically in the youngest BFG stands (significant interaction between age and competition control), where competition control resulted in more than four times greater LAI at age four compared with 23 and 29 percent greater LAI at ages 9 and 11. Treatment and age effects on foliar nitrogen concentration closely paralleled effects on LAI. Stemwood growth per unit of leaf area (GE) declined with stand age, with mean values of 480, 220 and 203 ft^3/ac yr proj LAI for stand ages 4, 9 and 11 at the BFG location, and 277 to 226 to 189 ft^3/ac yr proj LAI for stand ages 6, 10, and 12 at the DSF location. The response of nitrogen use efficiency (NUE) to fertilization and competition control was similar to that of GE.

At both locations, GE and NUE decreased linearly with tree size, indicating the decreases in GE and NUE were probably due to tree size rather than tree age. At the DSF location, but not the BFG location, fertilized stands had greater GE when compared to unfertilized stands with equal sized trees indicating that fertilization had a positive effect on GE throughout stand development. For instance, fertilization increased GE expressed on a biomass basis from 3.4 to 4.5 tons bolewood prod. per ton leaf biomass for trees 11 m tall and from 2.1 to 2.5 tons bolewood prod. per ton leaf biomass for trees 17 m tall. For NUE, the differences between the fertilized and unfertilized stands of equal size were less than those for GE due to greater nitrogen concentration in the foliage of the fertilized stands.

LONG-TERM TRENDS IN PRODUCTIVITY AND STAND CHARACTERISTICS FOLLOWING THINNING OF A LOBLOLLY PINE STAND IN S.E. OKLAHOMA

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EXTENDED ABSTRACT

A thinning levels study was initiated in Southeastern Oklahoma in the spring of 1984. The study was installed in a 9 year-old loblolly pine (Pinus taeda L.) plantation that contained 110 ft^2/ac of basal area. Thinning treatments consisted of (1) three control plots (BA-100) that were never thinned and contained an average of 860 trees/acre (tpa) at the beginning of the study (2) three plots that were thinned to approximately 25 percent of the original basal area (BA-25), basal area averaged 34 ft^2/ac after thinning and (3) three plots that were thinned to 50 percent (BA-50) of the original basal area, 54 ft^2/ac. In 1988 the BA-50 and BA-25 plots were rethinned to a basal area of 50 ft^2/ac. No other thinning has been done through age-24.

The control plots have attained a basal area of about 199 ft^2/ac and are now declining slightly. The BA-25 and BA-50 plots have basal areas between 140-150 ft^2/ac. Mortality has averaged about 34.7 tpa/year from age-10 through age-24 on the control plot, declining from 821 tpa to 335 tpa at age-24. Mortality losses in the BA-25 and BA-50 plots has been only 30-40 tpa over the entire study period. Standing inside bark volume in the control plots at age 24 is 47.9 cunits/ac, about 10 cunits/ac more than is present in the BA-25 and BA-50 treatments. About 5 cunits/ac were removed from the BA-50 treatment in the 1988 thinning. Average diameter at breast height (dbh) in the control plot is 9.8 inches and 33 percent of the trees in this treatment exceed 12 inches in dbh. Average tree size in the BA-25 and BA-50 is 15.9 inches with greater than 95 percent of the trees exceeding 12 inches in dbh. Mean annual increment (MAI) peaked at age 20 in the control plot at 225 cubic ft/ac/yr. MAI of the thinned plots have remained between 150 to 160 ft^3/ac/yr between ages 20 to 24 years but has not declined yet. Average ring width of the thinned plots exceeded 0.25 in/yr for four years following thinning, thus wood produced during this period would have less than four rings/inch. Average ring width of the control plot remained less than 0.25 in/yr since age 10 and has grown less than 1/8 in/yr since age-15. Ring specific gravity was not impacted by the thinning treatment and all treatments produced rings with similar latewood percentages. Year-to-year variation in ring specific gravity and latewood has been large and is related to the amount of late season rainfall. Periodic (3-year) annual increment (PAI) of the control plots have declined from a peak of 378 ft^3/ac/yr at age 14 to 36 ft^3/ac/yr at age 24. PAI of the BA-25 and BA-50 treatments peaked between 250 and 285 ft^3/ac/yr at age 17 but has remained at only slightly lower levels through age 24. This growth trend for thinned plots results in high stemwood production rates on large valuable trees. At age 22 the growth of trees in the control plots are supported by live crowns average 22 feet in length. Trees in the BA-25 and BA-50 plots have crown lengths that average 35 feet in length. Leaf area index (LAI) has remained between 3.0 to 4.8 in all treatments after basal area exceeded 130 ft^2/ac. Even the control plots that have attained basal areas of 199 ft^2/ac have retained LAI's in this range. However, growth efficiency (tons wood/acre/LAI) has declined with age. The decline in GE has been precipitous in the control plots since age 14. Growth efficiency of the thinned plots have declined only slightly from age 16 to age 24. This study concludes that early thinning on a site index 25 year 75 site has resulted in only minor reductions in total volume at age 24. The control plots contain 48.7 cunits that is distributed on 335 trees/acre. The BA-50 plots contains 39.1 cunits distributed on 117 trees/acre. This should have implications related to logging and processing cost. Average tree size is greatly influenced by thinning and thus product opportunities and stand value will be greatly influenced by early rotation thinning. Thinning does increase annual ring width, resulting in slightly less than four rings/inch for a period following the thin. Thus, lumber grade may be impacted. Thinning did not affect specific gravity so pulp yield per unit biomass would not be expected to differ across treatments.

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WATER AND NUTRIENT EFFECTS ON LOBLOLLY PINE PRODUCTION AND STAND DEVELOPMENT ON A SANDHILL SITE

H.L Allen, T.J. Albaugh, and K. Johnsen[1]

During the last decade, it has become apparent that production rates of pine plantations in the southeastern United States are far below levels that are biologically and economically optimal. By managing genetic and site resource effectively, production rates should exceed 350 ft^3/acre/year on most sites. In effort to better understand the ecophysiological constraints to production, the SETRES study was established in 1992 on a well-drained loamy sand site in Scotland County, NC. The experimental study consists of two levels of irrigation (none and optimum) and two levels of nutrient amendment (none and annual additions) replicated four times. Treatment plots measure 50 x 50 m with the internal 30 x 30 m as a measurement plot. Details of the experimental design, treatment regimes, and measurements are provided in Albaugh et al. 1998. Over the eight-year period since treatments were imposed, detailed assessments of individual tree and stand physiological, growth and development process have been examined.

Improved nutrition has had a very strong positive impact on production. Nitrogen, phosphorus, potassium, and boron were apparently the key limiting elements. Nutrient additions consistently increased peak leaf area by almost 100% over the eight years (figure 1).

Current annual volume increment was closely coupled with leaf area (figure 2). The combined gains in leaf area and growth efficiency (stemwood production per unit of leaf, GE) with nutrient additions resulted in a three-fold increase in annual stemwood production (80 to 240 ft^3/acre/year). After eight years of treatment, several water+nutrient plots had leaf area and current volume increment levels exceeding 3.5 and 350 ft^3/acre/year, respectively.

Over the eight years of study, GE varied from 55 to 70 ft^3/acre/year for control plots (figure 3). Water and nutrient additions increased GE but GE was not affected by stand age. GE reached 100 ft^3/acre/year on water+nutrient plots during the last two years of study.

Responses to water were much less than originally expected and there were no apparent interactions between water and nutrient additions. Although the soil has a very low water holding capacity, the rooting depth exceeded 10 feet apparently providing sufficient water for much of the growing season.

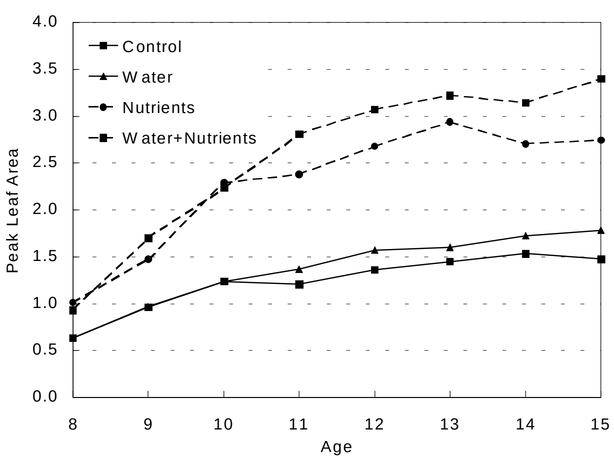

Figure 1— Peak leaf area with and without optimum water and nutrient additions in an eight- to 15-year old loblolly pine stand.
By age 13, peak leaf area had stabilized at a maximum value of 1.5 on control plots, whereas leaf area on plots receiving nutrient additions averaged 3.0. Clearly, native nutrient availability now constrains leaf area levels rather than stocking.

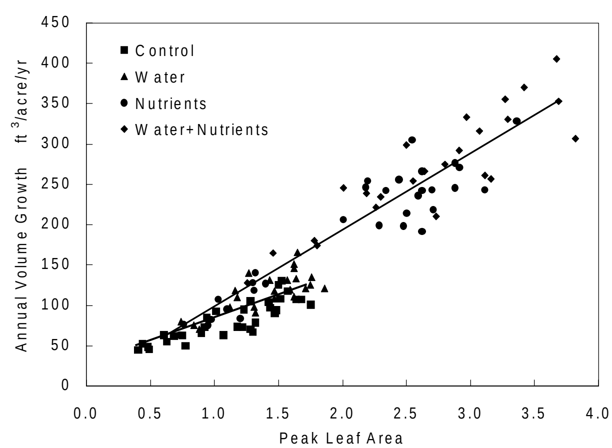

Figure 2—The relationship between current annual stemwood increment and peak leaf area across a range of water and nutrient availability conditions in an eight- to 15-year old loblolly pine stand.

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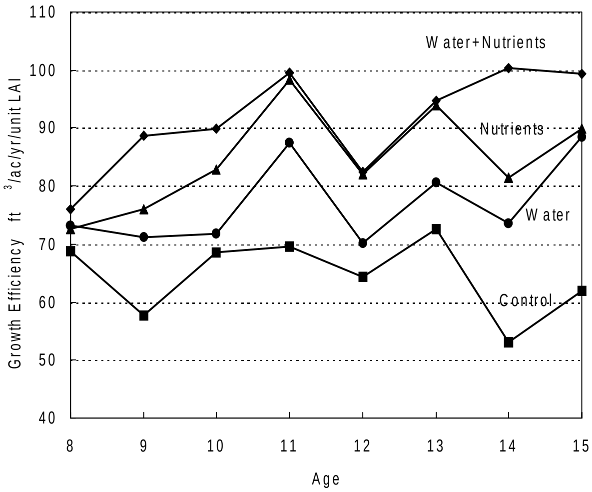

Figure 3— Growth efficiency (annual stemwood production per unit of peak leaf area) with and without water and nutrient additions in an eight- to 15-year old loblolly pine stand.

Interestingly, fine root production was not affected by the imposed treatments. However, aboveground production was dramatically increased with improved nutrition so a strong shift in biomass partitioning from roots to shoots was observed.

Estimates of nutrient use and soil nutrient uptake indicate that if the observed gains in production are to be sustained, soil nutrient availability will need to be maintained at a considerably higher level than naturally found on this site.

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