ABSTRACT

ROJAS, JULIO CESAR. Factors influencing responses of loblolly pine stands to fertilization (Under the direction of Dr. H. Lee Allen).

Fertilization of pine plantations has increased dramatically in the last decade. Over 600,000 hectares are being fertilized annually to overcome chronic widespread nitrogen (N) and phosphorus (P) limitations. However, responses to fertilization vary widely since specific responses after fertilization for any particular stand will be the result of complex interactions of nutrients and rates applied, stand and site conditions at time of application, years since application, and climatic conditions after application.

Stand, soil and forest floor (FF) responses to fertilizations were assessed at three different sites located in the "flatwoods" area of southeast Georgia and northeast Florida after five years of repeated fertilizer additions. Significant leaf area index (LAI), stemwood growth and FF responses were found at all three sites. Leaf area index was double for some treated plots as compared to control plots (from 1.4 to 3.0), five year cumulative growth on treated plots almost tripled that of the control plots (32 to 89 m^3 ha^{-1}). Soil N availability increased dramatically soon after fertilization however, it decreased few months after application. Several nutrients affected growth at these three sites, N and P at all three sites and potassium (K) and manganese (Mn) at the Georgia study sites.

Factors affecting growth efficiency (GE) of loblolly pine plantations across the southeast were examined using 86 studies sites with different climatic, edaphic and stand conditions. Two modeling approaches were developed, one where GE would change with levels of LAI (non-linear using Gompertz model) and a second where GE was independent of the level of LAI (linear model), in both cases significant reduction in RMSE (>200%) was achieved when parameters in the models were allowed to be

functions of edaphic, climatic and stand characteristics. In conclusion, GE is a dynamic rather than static stand parameter; it changes with stand age, drainage, soil texture and climate. Current year climatic variables were better predictors of GE than long term climatic averages, indicating that the inter-annual variation on temperature and rainfall exerts great influence on GE.

Further modeling efforts were undertaken to determine factors affecting the variation in growth responses to N+P fertilization in loblolly pine stands. By utilizing a standardization procedure on the original data, 66% of the variation in the standard response was explained by LAI, Foliar N, and growth efficiency. These variables are ecophysiological variables proposed as drivers of stand response to fertilizer application(s). Two other variables, quadratic mean diameter ($\overline{D_q}$), and stand age were also significant predictors in the model.

Factors influencing responses of loblolly pine stands to fertilization

by

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To my parents Marcos and Ana, my brothers Luis and Marco, my wife Maria Venecia and my sons Cesar Eduardo and Sebastian Alejandro.
"*Source of inspiration and endurance*"

In memory of Maria Hortencia Davila
"*I will always keep you in my heart Grandma*"

BIOGRAPHY

Julio Rojas was born on September the 23rd of 1968. From his parents, Ana and Marcos, he got the inspiration and strength to pursue his goals. Since he was young one of his dreams was to be able to attend and graduate from a university, coming from a low-income family the opportunities were few. He received his high school diploma in July 1985 and started university studies in January 1986. After several semesters lost due to university strikes, he obtained his degree in July 1993 at the Los Andes University in Merida-Venezuela, graduating with Magna Cum Laude Honors, he was awarded the "Gran Mariscal de Ayacucho" national academic award, and the Estate of Merida academic award. He started working in 1994 as research forester for Smurfit Carton de Venezuela, a forestry company that grows eucalypts and caribbean pine plantations in western Venezuela. He married Maria Venecia in May 1996. In 1997, he earned a scholarship from Smurfit to pursue a masters degree in Forestry. He started his masters in January 1998 and completed it with a GPA of 4.0 in March of 2000. He returned to Venezuela and continued working for Smurfit. One of the happiest and wonderful days of his life was May 27, 2000, the day that Cesar Eduardo, his first son, was born. In April 2002 Julio decided to return to school and pursue a Doctoral degree in Forestry under Dr. H. Lee Allen. Dr. Allen has been one of Julio's great friends as well as being his academic mentor. Another day of great joy for Julio was June 19, 2002 when Sebastian Alejandro, his second son, was born. In June 2005 Julio and his family started a new life in Columbus, Mississippi working for Weyerhaeuser Co. as a Research Scientist, his job and his family has always been his passions.

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I thank god for the life, health and guidance through all this time. My parents Ana and Marcos and my brothers Marco and Luis who always believed in me and encouraged me to pursue my dreams, thanks so much. I am so grateful to my wife Maria Venecia, she was always there for me to help me pick up the pieces and put them together for the next day. Thanks to my sons, Cesar Eduardo and Sebastian Alejandro, for making me smile everyday. Thanks to my friend Rafael Arrieche for your help and support when things got difficult.

Lee Allen, my academic mentor, my friend, my great friend, thanks for the opportunity to be here again, thanks for believing in me, for seeing the potential others could not. Under your shade my scientific expertise, critical and objective thinking grew exponentially. To you Lee all my blessings.

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CHAPTER 1

Effects of repeated fertilization in young loblolly pine plantations

Abstract

Forest floor, litterfall, soil, leaf area and growth were measured after repeated applications with different dosages of nitrogen (N), phosphorus (P), and other nutrients in balance with N on three loblolly pine plantations in the wet "flatwoods" of southeast Georgia and northeast Florida. Applied N varied from 0 to 269 kg ha^{-1} in frequencies of every 2, 4 and 6 years in an incomplete factorial design. After five years, the cumulative N ranged from 0 to 606 kg ha^{-1}. Treatments significantly increased forest floor mass accumulation and nutrient contents, while Carbon (C) to N ratio (C/N) decreased with cumulative applied fertilizer. Changes in the quality of the forest floor could have important implications in organic matter decomposition and nutrient release for the rest of the rotation and subsequent rotations. Soil N availability during the growing season was significantly enhanced on fertilized plots. Soil N availability peaked soon after fertilizer application and was proportional to the rate of N applied; however at the end of the growing season available N decreased to pretreatment levels.

Leaf area display was in some cases doubled with fertilization (from 1.4 to 3.0) and its cumulative effects. Linear and quadratic cumulative dose effects were significant at all three sites; however the Florida site growing on a more clayey soil had a significantly higher intercept indicating a more fertile soil than the two sites in Georgia. Leaf area had an asymptotic relationship with average growing season available N. Leaf area increased sharply before 5 ppm of available N and then level off at a leaf area maximum of 5. Growth efficiency remained unaffected across sites and treatments with an overall average of 8.14 m^3 ha^{-1} yr^{-1} per unit of leaf area. Five year cumulative growth had a quadratic relationship with cumulative applied dose.

1. Introduction

Economic factors coupled with the biological responsiveness of loblolly pine have made fertilization an attractive investment in the southeast United States. Fertilization of pine plantations has increased dramatically in the last decade so that now over 600,000 hectares are being fertilized annually to overcome chronic widespread nitrogen (N) and phosphorus (P) limitations (Allen et al. 2005). Although N and P have been identified as the nutrients most limiting to the growth of southern pine plantations, other nutrients such as potassium (K), boron (B) and manganese (Mn) have also been identified as limiting (Pritchett and Smith 1972, Valentine and Allen 1990, Jokela et al. 1991, Martin and Jokela 2004). As leaf area develops and stand growth accelerates, the potential use of nutrients increases rapidly (Wells and Jorgensen 1975). In contrast, soil N availability typically decreases throughout the life of a stand (Allen et al. 1990, Richter et al. 2000, Piatek and Allen 2000, Piatek and Allen 2001). Several reasons have been hypothesized for the observed declines in soil N availability as a stand develops including sequestration of nutrients within the accumulating tree biomass and forest floor (FF) (Miller 1981), and changes in soil temperature, soil moisture, and labile carbon resulting in changes in microbial mineralization and immobilization of N (Hart et al. 1994, Bradley et al. 2000, Li et al. 2003).

Nitrogen fertilization typically results in high N availability immediately after fertilization; however, the magnitude and duration depend on the amount of N applied (Mundano 1986, Maimone et al. 1991). Because the N rates used are normally low as compared with the original N capital of the site, growth responses to N fertilization are often short term (Miller 1981, Amateis et al. 2000, Hynynen et al. 1998, Martin and

Jokela 2004). Consequently, multiple applications will be needed for a plantation to achieve optimum productivity (Allen et al. 2005). Application rates and frequencies for N are perhaps more critical than for other fertilizer materials because most N sources are highly soluble, are subject to losses (volatilization and leaching), and may promote growth of competing vegetation. The effect of multiple applications of fertilizer on soil nutrient availability, stand growth, and nutrient cycling needs to be understood to optimize the nutritional management of the stand.

Strong links have been established among wood production, leaf area and resources availability for loblolly pine and other species (Linder 1987, Cannell 1989, Albaugh et al. 1998, Albaugh et al. 2004, Martin and Jokela 2004). Improving resource availability in pine plantations has resulted in large increases in foliage production, leaf area and stand productivity as leaf area is typically well below levels for optimum light interception and consequently production (Vose and Allen 1988, Colbert et al. 1990, Sampson and Allen 1999, Albaugh et al. 2004, Martin and Jokela 2004, Jokela et al. 2004). Fertilization also results in a higher proportion of fixed carbon being partitioned to above ground biomass (Albaugh et al. 1998).

The increase in foliage production with fertilization in responsive stands leads to an increase in litterfall soon after fertilization. The improved nutrition in the foliage and therefore in the litterfall can change litter quality and consequently decomposition rates and nutrient availability (Hart and Stark 1997, Grant and Binkley 1987, Sanchez 2001, Li et al. 2003, Gurlevik et al. 2003, Gurlevik et al. 2004, Allen and Schlesinger 2004). Needles with higher initial nutrient concentrations release nutrient more rapidly (Berg and Staaf 1981, Berg 1988, Prescott et al. 1993, Polglase et al. 1992). The FF may be either source or sink of nutrients during the life of a stand (Polglase et al. 1992, Piatek and Allen 2001) and may also contribute to inter-rotational retention of nutrients (Li et al. 2003, Piatek and Allen 1999).

The objectives of this study were to assess the effects of repeated fertilization on several important properties and processes of the soil, forest floor, and stand.

2. Methodology

2.1. Experimental Design.

This study was undertaken on three trials established in the "flatwoods" of southeast Georgia (Brantley Co.) and northeast Florida (Nassau Co.) in young loblolly pine plantations. The topography at all three sites was nearly flat. The two Georgia sites (GA1 and GA2) were on moderately well drained Seagate soils (sandy over loamy, siliceous, active, thermic typic Haplohumods) (Soil Survey Staff 1998), while the Florida site (FL1) was on a poorly drained Meggett soil (fine, mixed, active, thermic, typic Albaqualf) (Soil Survey Staff 1998). These three sites were located within 50 km of one another and had very similar climates with annual precipitation averaging 1310 mm and daily mean temperature averaging 20 ^{o}C (Table 1). Site index (25 years) for the Florida and Georgia sites were 21 m and 17 m, respectively. Site preparation for the current rotations consisted of piling and bedding with a spring application of Arsenal™ during the first growing season.

All three stands were initially selected to ensure as uniform soil and stand conditions as possible. Treatments consisted of an incomplete factorial of dose and frequency of N application (Table 2). Phosphorus was applied at a fixed ratio (0.10) with N at all sites, and K, Mg, S, Mn, and B were added at the Georgia sites (Tables 2 and 3) when foliar analyses indicated a need. Treatments were applied as a completely randomized block design with two blocks at each site. Treatment plots varied between 1538 and 1821 m^2 with internal measurement plots between 315 and 445 m^2. Individual plot estimates of dominant height and stand density were used for blocking purposes to minimize within block pretreatment variation. Analysis of variance (ANOVA) indicated no significant pretreatment differences in these two variables.

The GA1 and GA2 trials were established in February 1998 while FL1 was established one year later (February 1999, Table 1). Much of the detailed soil, litter, and FF sampling was conducted during 2003, the fifth growing season since initiation of treatments at FL1 and the sixth growing season at GA1 and GA2. The last fertilizer application occurred at the beginning of the fifth growing season, April 2002 at GA1 and GA2 and April 2003 at FL1 (Tables 2 and 3). Therefore, cumulative nutrient doses were greater on all treatments for the fifth growing season assessments as compared with the fourth growing season assessments (Table 3).

2.2. Soil Sampling and Laboratory Analysis

The soil was sampled several times in 2003 (March 12, May 23, July 7, August 11, September 6 and October 18) (Table 4). At each date, a composite sample of A horizon soil was collected from each plot. This sample was composited from 10 samples within each measurement plot (five from beds and five from inter-bed areas). All samples were kept cool until they were processed in the laboratory (usually within two days).

Extractions were made on duplicate 10 g sub-samples of fresh soil for field extractions (FE). Fresh soils were then incubated and extracted for samples collected in March 2003. Duplicate 10 g sub-samples of fresh soil were incubated at field moisture content at 25 ^{o}C. After 30 days, these incubated samples were extracted (IE). Moisture content of the incubated samples was monitored and deionized water added when moisture content dropped 5% below initial levels. Extractions were undertaken by adding 35 ml of 2M KCl solution to the 10 g soil samples (fresh and incubated), shaking at high speed for 30 minutes, and centrifuging for 15 minutes at 4,000 rpm. The supernatant solution was then filtered using a G8 glass fiber filter and analyzed for both ammonium-N (NH_4^+-N) and nitrate-N (NO_3^--N) concentrations using a Lachat Autoanalyzer (Quick-Chem 8000, Zellweger Analytics, Inc., Milwaukee, WI). Two indexes of N availability were calculated from these data. An index of N availability using fresh soils extractions (FEN) was calculated as the average of extractable N (NH_4^+-N + NO_3^--N) from the six 2003 sampling dates. A mineralizable N index (MEN) was calculated by subtracting FE from IE values for the March 2003 sampling date.

Total carbon (C), total N, and extractable P, Mn and copper (Cu) were also determined on soil samples collected in March 2003 for all three sites. Total C and N were determined on 50 mg air-dried sub-samples using dry combustion on a CHN Elemental Analyzer (CE Instruments – NC 2100, CE Elantech Inc.). Extractable P, Mn, and Cu were determined by adding 20ml of Mehlich-3 extracting solution (Reed and Martens 1996) to 2 g of air dry soil, shaking at high speed for 5 minutes, filtering using Whatman No. 40 filter paper, and finally analyzing for P, Mn and Cu using an inductively coupled plasma – emission spectrometer (ICP-AES, Varian ICP, Liberty series 2, Varian Analytical Instruments, Walnut Creek, CA). All analyses were duplicated for quality purposes.

2.3. Forest Floor, Litterfall, Foliage, and Leaf Area Sampling

The FF was sampled in March 2003 using a 30x30 cm square frame. Samples were collected in two layers, the undecomposed, recognizable material of the litter layer (L or O_i) and the fermentation plus humus layers (F+H or O_e+O_a). Litter and F+H layers were sampled at six randomly selected locations within each measurement plot and composited.

Litterfall was collected monthly from March 2003 through February 2004 representing foliage produced during 2002 (Vose and Allen 1988). Five square traps (1 m^2) were randomly placed in each measurement plot at all three sites. Only pine needles were collected. Total litterfall for the 2002 needle cohort was calculated for each plot by summing the monthly litterfall weights. Litterfall nutrient concentrations were determined for the two months with the most litterfall (October and November) and these concentrations were then averaged using litterfall weight as the weighting factor.

Green foliage was sampled during the dormant season prior to and during each successive dormant season through the fifth year following the first fertilization on each plot for the three sites (Table 4). Twenty fascicles from each of five selected dominant and codominant trees were collected and composited. Fascicles were taken from the first flush on a primary lateral branch in the upper one-third of the live crown. Weight of the 100 fascicles was recorded.

Leaf area assessments were made during the fifth growing season at all the sites (2002 for GA sites and 2003 for FL1 site) on each plot (Table 4). Measurements were made during the period of peak leaf area display, corresponding to end of August and the beginning of September using a Li-COR LAI-2000 plant canopy analyzer. Twenty measurements were obtained from each plot and averaged.

2.4. Tissue Nutrient Analyses.

Nutrient concentrations were determined for FF, foliage, and litterfall. Samples were oven dried soon after collection to a constant weight at 70 ^{o}C, weighed, ground in a rotary mill and sieved to a 1mm mesh prior to chemical analysis. Analysis included N concentration for all tissues and C concentrations for FF only using a CHN elemental analyzer (CE Instruments –NC 2100, CE Elantech Inc.). Phosphorus, K, Ca, Mg, S, Mn, B, Cu and Zn were analyzed by digesting 800 mg of ground material with nitric acid (Zarcinas et al. 1987) followed by analysis using inductively coupled plasma – emission spectrometer (ICP-AES, Varian ICP, Liberty series 2, Varian Analytical Instruments, Walnut Creek, CA). Ash content of FF samples was determined by loss-on-ignition and all nutrients and weights were expressed on an ash-free basis (Lee et. al 1983).

2.5. Pine Stem Growth.

Planted pines were measured in the dormant season (December to February) prior to the first fertilization and in each successive dormant season through five years following the first fertilization (Table 4). Assessments of tree height (ht) and diameter at breast height (dbh) were completed on all measurement trees. Individual total tree volumes were calculated using equation [1] (NCSFNC 2003) and summed to obtain stand volume estimates.

$$V_{ob} = 0.71173\ (dbh^2\ ht) \qquad [1]$$

Where:

V_{ob}= Volume outside bark, cubic meters
dbh= diameter at breast height, meter
ht= total height, meter.

Several growth and response measures were calculated from the inventory data. Current annual increment (CAI) for each year was calculated as the difference between two successive dormant season volume estimates. For example, the CAI for 1999 was calculated by subtracting the January 1999 volume estimate from Jan 2000 volume estimate. Annual growth response to fertilizer was calculated for each year by subtracting control plot volume growth from treatment plot growth values. Finally, five year cumulative growth since treatments were initiated was calculated by subtracting the initial (pretreatment) volume estimate from the volume estimate at the end of the fifth year.

2.6. Nutrient Retranslocation, Litterfall Nutrients, and FF Decomposition

The linear relationship between 2003 CAI and 2003 litterfall was used to estimate the litterfall in previous years given the CAI measured for those years. The Litterfall-CAI relationship was determined separately for the Georgia and Florida sites. Relative retranslocation for each nutrient from 2002 foliage cohort (2003 litterfall) was calculated using equation [2]:

$$\text{Retranslocation}_i = (\text{Folc}_i - \text{Litc}_i)/\text{Folc}_i \qquad [2]$$

Where: Retranslocation= Retranslocation for the i^{th} nutrient
Folc= foliar concentration for the i^{th} nutrient
Litc= average litterfall nutrient concentration for the i^{th} nutrient

Nutrient concentrations in litterfall for each year and each nutrient were estimated by multiplying (1-Retranslocation$_i$) by the foliar concentration for that year and plot combination. Estimates of litterfall weight and nutrient concentrations were then used to calculate nutrient inputs coming from litterfall for each plot. Nutrients included in this analysis were N, P, K, S, and B. The ratios between litterfall and FF (LL/FF) for weight and nutrient content were calculated to provide an index of FF decomposition.

2.7. Statistical Analysis.

Although several nutrients were applied (Table 2), the cumulative N dose (Table 3) was used to represent the nutrient dose effect. To test for dose and frequency effects, analyses of variance (ANOVA) for individual studies were performed on soil, forest floor and litterfall variables (Table 4) using the following model.

$$Y_{ijk} = \mu + \delta_i + \gamma_j + \tau(\gamma)_{k(j)} + e_{ijk} \quad [3]$$

Where: μ= the overall mean

δ_i=deviation from the overall mean due to the effect of i^{th} block,

γ_j= deviation from the overall mean due to the effect of j^{th} cumulative N dose,

$\tau(\gamma)_{k(j)}$= deviation from the overall mean due to the effect of the k^{th} treatment nested within the j^{th} cumulative N dose (timing effect),

e_{ijk} = the random residual term.

Because FE was assessed at six dates during 2003 and foliar nutrient concentrations were determined every year, repeated measures analyses of variance were performed to determine treatment effects as well as year effects by using the SAS GLM procedure with a REPEATED statement. Single degree of freedom contrasts using a PROFILE statement were used to test for differences between adjacent years.

For LAI and 5-year growth (both measured 5 years since the first fertilization), regression analyses were performed to test for linear and/or quadratic cumulative dose effects and whether the dose response differed across sites. For these analyses, SAS MIXED procedure with a REPEATED statement was used to fit the regression models. To account for the correlation expected among plots within the same block and blocks within the same site, compound symmetry was used to model the variance-covariance matrix. This approach proved especially useful when comparisons across sites were important, i.e. to test if cumulative dose effect (either as a linear and/or quadratic effect) differed across sites. Contrast tests for detecting differences in parameter estimates across sites were performed. Models used were as followed.

$$Y_{ijk} = \begin{cases} \beta_1 + \beta_2 X_{ij1} + \beta_3 X_{ij1}^2 + e_{ij1} & \text{for FL1 site} \\ \beta_4 + \beta_5 X_{ij2} + \beta_6 X_{ij2}^2 + e_{ij2} & \text{for GA1 site} \\ \beta_7 + \beta_8 X_{ij3} + \beta_9 X_{ij3}^2 + e_{ij3} & \text{for GA2 site} \end{cases} \qquad [4]$$

Where:

Y_{ijk}= Response variable from the ith block and jth plot within block for the kth site
β_k= Parameter to be estimated.
X_{ij}= Cumulative dosage from the ith block and jth plot within block.
e_{ijk}= random plot effect within a block
$Var(e_{ijk})=\sigma^2_k$

$$Cov(e_{ijk}, e_{i'j'k'}) = \begin{cases} 0 & \text{if k=k' (two different sites)} \\ 0 & \text{if i=i' (two different blocks)} \\ \sigma_{b_k}^2 & \text{if j=j' (two plots within the same block in the k}^{th} \text{ site)} \end{cases}$$

Two independent productivity estimates (five year cumulative growth and fifth year LAI) were correlated with the measured soil, FF, litterfall, and foliage variables using data from all plots from all three sites. For all analyses, differences were accepted as being significantly different at the 0.10 alpha level.

3. Results

All three stands were very responsive to the various fertilizer treatments. Nutrient dose effects were very strong for most of the properties and processes assessed; however, frequency effects were rarely statistically significant. As a result, the presentation of results focuses on nutrient dose effects.

3.1. Soil

Soil responses to nutrient doses were the most variable and least affected of all the characteristics assessed. Total C and total N were significantly increased with increasing dose at FL1 and GA2 but not the GA1 site (Tables 5 and 6, Figure 1). Total C was 19.6 and 20.3 Mg ha^{-1} for FL1 and GA2, respectively on the control plot and ranged upward to 36.1 and 44.4 Mg ha^{-1} respectively, on the fertilized plots. Total N was 757 and 838 kg ha^{-1} on the control plots for FL1 and GA2, respectively and ranged upward up to 1348 and 1410 kg ha^{-1} respectively, on the fertilized plots. Extractable P was significantly increased with increasing P dose only at FL1, the site with the lowest P values (Tables 5 and 6, Figure 1). Interestingly, extractable Mn was significantly increased with increasing dose at GA1 but not GA2, although Mn as added to both GA sites (Tables 5 and 6, Figure 2). Mn values at GA1 ranged from 0.8 kg ha^{-1} for control plots up to 76.9 kg ha^{-1} on fertilized plots. Several indexes of availability were examined; however, only FEN values (average extractable N from 6 growing season samples) were significantly increased with increasing dose treatments (Tables 5, Figure 3). FEN values were 2.5 to 3.3 mg kg^{-1} on control plots and ranged upward for the fertilized plots to 23.7 mg kg^{-1} at FL1 (where N had just been reapplied) and 4.2 to 5.5 mg kg^{-1} at the GA sites (Figure 3). The 2003 fertilization at FL1 had a strong significant impact on the patterns of soil N availability during the 2003 growing season with proportionately higher FE levels (up to 74.2 mg kg^{-1}) found with the higher doses (Figure 4A). These strong seasonal dynamics were not as apparent for the GA sites where fertilizer was applied at the beginning of the previous growing season (April 2002) (Figure 4B). Treatment differences were however significant at GA1 and FL1 (Table 5).

3.2. *Forest Floor*

Forest floor mass accumulations (total, L layer, and F+H layers) were significantly increased with increasing dose at the GA sites but not at FL1 site (Tables 7 and 8). Accumulations in the L layer ranged from 1659 up to 7538 kg ha^{-1} across sites and treatments (Table 7). Accumulations in the F+H layer were typically greater than in the L layer and ranged from 2781 up to 11,813 kg ha^{-1} (Table 7).

Nitrogen, P, and S concentrations were significantly increased with increasing dose for both FF layers at all three sites (Tables 7 and 8, Figure 5). Nitrogen concentrations in the layers ranged from 0.46 to 0.53% on control plots and from 0.69 to 0.89% on higher dose plots. N concentrations were higher in the F+H layers and ranged from 0.64 to 0.82% on control plots and from 1.05 to 1.35 on higher dose plots (Table 7). C/N ratios for both layers were significantly decreased with increasing nutrient dose apparently due to the increases in N concentrations. K concentrations were also increased with increasing dose in the L layers at all three sites and in the F+H layer at GA1. Although B and Mn were added at the GA sites, FF concentrations of these elements were not affected by treatment except that B concentrations were significantly increased in the L layer at GA1 (Tables 7 and 8). Calcium concentrations were significantly decreased in both FF layers at GA2.

Because of increases in both FF mass and FF nutrient concentrations at the GA sites, N, P, K, and S accumulations in the forest floor were dramatically increased (300% or more) at the higher doses (Tables 9 and 10). For example, N accumulations in the FF were 34 and 38 kg ha^{-1} for control plots and 170 and 162 kg ha^{-1} for the highest fertilization dose at GA1 and GA2, respectively. FF nutrient contents at FL1 were not significantly increased due to the lack of increase in FF mass even though concentrations of several nutrients were increased (Tables 9 and 10). The FF was none existent at study establishment, so these accumulations occurred in the last four (FL1) or five (GA sites) years.

3.3. Litterfall and Litterfall Nutrients

Litterfall amounts were significantly increased with increasing dose at all three sites (Tables 11 and 12, Figure 6). Litterfall amounts on control plots were less and fertilizer responses much greater on the GA sites as compared with FL1. Litterfall averaged 4257, 2837, and 2774 kg ha^{-1} on control plots and 6493, 5903, and 6799 kg ha^{-1} on the highest fertilization dose plots for FL1, GA1, and GA2, respectively (Table 11).

The effects of increasing dose on litterfall nutrient concentration were more variable (Tables 11 and 12). Nitrogen and S concentrations were increased at FL1 and GA2. Phosphorus and Cu concentrations were increased only at FL1. Potasium concentrations were increased at all sites and B concentrations were increased at both GA sites. Calcium and Zn concentrations were reduced at the GA sites

Because of increases in both litterfall mass and litterfall nutrient concentrations, litterfall N, P, K, and S contents were significantly increased with increasing dose at all sites (Tables 12 and 13, Figure 7). Litterfall nutrient inputs on treated plots were increased by over 200% for several nutrients. Annual litterfall N inputs were 19.5, 10.7, and 10.5 kg ha^{-1} for control plots and 45.2, 27.7, and 45.9 kg ha^{-1} on the highest fertilization dose plots for FL1, GA1, and GA2 sites, respectively. Similarly, annual P inputs were 0.8, 1.4, and 1.3 kg ha^{-1} for control plots and 3.4, 2.9, and 3.9 kg ha^{-1} for the highest fertilization dose plots, respectively. Boron content also increased with increasing fertilizer dose at the GA sites where B was applied (Tables 12 and 13). Annual B inputs were 44.5 and 44.1 g ha^{-1} for control plots and 145 and 150 g ha^{-1} for the highest dose plots at GA1 and GA2, respectively. Similar to litterfall N inputs, B inputs for control plots were almost double at FL1 as compared to GA sites, however, this difference was reduced with fertilization.

3.4. Foliage Nutrient Concentrations

An overall treatment effect over five years was found for foliar N, Ca and S concentrations for FL1, and foliar N and K at the GA sites. However, the influence of dose on all nutrient concentrations varied by year as indicated by the significant year and in most cases year x treatment interaction effects (Repeated measures ANOVA, Greenhouse-Geisser F-test, Tables 14 and 15). Foliar P concentrations were generally less affected than N concentrations by nutrient dose but exhibited strong year to year variations as indicated by significant year (all sites) and year x treatment interaction (FL1 and GA1) effects (Table 15). Potassium and B concentrations exhibited similar effects as N concentrations at the GA sites where K and B were added. Not surprisingly, dose effects on foliar nutrient concentrations were most pronounced in foliage collected the dormant season immediately following fertilizer application.

Fascicle weight and foliar N, P, and S nutrient concentrations from the 2002-2003 dormant season (after the fourth and fifth growing season respectively for FL1 and the GA sites) were significantly increased with increasing doses at all three sites (Tables 14 and 16). Foliar K and B concentrations were significantly increased at both GA sites where K and B were added (Tables 14 and 16). Foliar Ca concentrations were significantly reduced with increasing dose at GA1. Foliar N concentrations averaged about 1.15% for control plots and ranged upward to 1.50 to 1.75% for higher dose plots across the three sites. Foliar P concentrations were lower at FL1 for both control (0.09%) and treated (0.12%) plots as compared with the GA sites (0.13 and 0.14% on control plots and 0.15% on treated plots) (Table 14). In contrast, foliar K concentrations were lower on control plots for the GA sites (0.30 versus 0.44%). Potassium additions at the GA sites increased foliar K concentrations to 0.50% or greater on the higher dose plots (Table 14).

3.5. Leaf Area and Stand Growth

Peak LAI values during the fifth growing (2002 for GA sites and 2003 for FL1) increased with increasing dose at all sites (Tables 17 and 18, Figure 8, Equations [4], [5] and [6]). Both linear and quadratic dose effects were significant and explained between 76 and 86% of the variation in LAI. Peak LAI values were generally higher at the FL1 than the GA sites for all dose levels. Peak LAI averaged 3.3, 1.4, and 1.6 on control plots and 5.3, 2.9, and 3.1 for the highest fertilization dose plots, for FL1, GA1, and GA2, respectively (Table 17). These site differences were evident in the regressions where the intercepts differed by site but not the linear and quadratic parameter estimates (Table 18).

Five-year stemwood volume growth increased dramatically with increasing dose at all sites (Table 17 and 18, Figure 9). Both linear and quadratic dose effects were significant and explained between 85 and 97% of the variation in estimated volume growth. Similar to LAI, growth rates were generally higher at the FL1 than the GA sites for all dose levels and again only intercepts differed for the growth – dose regressions (Table 18). Five year growth averaged 85.4, 40.1 and 32.4 m^3 ha^{-1} on control plots and 141, 92, and 89 m^3 ha^{-1} for the highest fertilization dose plots, for FL1, GA1, and GA2, respectively. These growth rates represent responses of 65 to 175%.

No differences were observed for cumulative volume versus age relationships on the 606 kg N ha^{-1} plots indicating similar growth trajectories for all three sites (Figure 10A). In contrast, growth trajectories for the control plots differed, with FL1 clearly having higher inherent growth rates than the GA sites (Figure 10B).

Growth responses peaked in the third year for both the two and four-year application frequencies at all three sites (Figure 11). Incremental responses declined in the fourth year but increased again in the fifth year following refertilization of all treatments.

3.6. Nutrient retranslocation

Retranslocation percentages for N, P, and K from the 2002 foliage cohort averaged 63, 65, and 85% respectively, and generally decreased with increasing dose (Tables 19 and 20, Figure 12). Significant reductions in retranslocation were observed for N at FL1 and GA2, for P at FL1, and for K at all three sites. Nitrogen retranslocation average 62, 67, and 67% for control plots and 53, 68, and 58 for the highest fertilization dose plots for FL1, GA1, and GA2 respectively. Interestingly, N retranslocation values for FL1 (fertilized in 2003 – the year of litterfall) were consistently lower than those found at the GA sites for any given nutrient dose. Even though K was applied only at the GA sites, K retranslocation was significantly reduced with higher dose on all three sites (Tables 19 and 20, Figure 12). Sulfur (34%) and B (22%) retranslocation values were always lower than those found N, P, and K (Table 19). Unlike N, P, and K retranslocation values, B retranslocation percentages were significantly increased with increasing dose at GA1.

3.7. Estimated FF Inputs and Decomposition

Estimated mass and nutrient inputs from litterfall through 2002 were significantly increased with increasing dose at all sites (Tables 21 and 22). Estimated litterfall inputs ranged from 7835 to 19392 kg ha^{-1} for mass, 35 to 113 kg ha^{-1} for N, 3.5 to 9.6 kg ha^{-1} for P, 3.2 to 16.9 kg ha^{-1} for K, 4.9 to 13.9 kg ha^{-1} for S and 114 to 419 g ha^{-1} for B.

The ratios of litterfall mass to FF mass (or nutrient content) were greater than unity (one) indicating mass loss (decomposition) or nutrient release (Table 23). The exception was N where some treatments had LL/FF ratios lower than 1 indicating immobilization of additional N from sources other than litterfall. The relative rates of nutrient release across sites and treatments were K=B>P>S>N. These ratios were only affected by treatment at GA1 where the N, P, K, and S LL/FF ratios were decreased with increasing dose suggesting slower decomposition on this site with treatment.

3.8. Relationship among Variables

As expected, measures of productivity (cumulative 5-year growth and 5th year LAI) were highly correlated with one another (r=0.94) and also with several of the soil, litter, FF, and foliage variables (Tables 24). The two productivity measures were positive significantly correlated with soil FEN, litter mass, litter N, K Ca, and Mn concentrations, L layer K, Ca, S, and Mn concentrations, F+H layer N, P, Ca, and Mn concentrations, fascicle weight, and foliar K, Ca, Mg, and Mn concentrations. Significant negative correlations were found between the productivity measures and L layer C concentrations and C/N, F+H layer C concentrations and C/N, and foliar P and Cu concentrations.

Of particular note were the strong positive relationships between LAI and FEN with an asymptotic LAI value of 5 above a FEN value of 5 mg kg^{-1} (Figure 13), LAI and litter N (Figure 14A), LAI and litter Mn (Figure 14B), LAI and foliar Ca (Figure 15A), and LAI and foliar Mn (Figure 15B); and the strong negative relationships between LAI and L layer C (Figure 16A) concentration, and LAI and foliar Cu (Figure 16B).

Current annual increment and peak LAI during the fifth growing season were also highly correlated ($r = 0.94$) (Figure 17), with all three sites falling on the same line. Growth efficiency (the slope of the CAI-LAI relationship) was 8.14 m^3 ha^{-1} yr^{-1} per unit of leaf area.

4. Discussion

Fertilization increased soil nutrient availability (Figure 1, 2, and 3) resulting in greater leaf area production (Figure 13) and stand growth (Figure 17) at all three sites. These three trials were extremely responsive both in terms of absolute and relative volume as compared to the majority of studies in the southeast US (Chapter 3). Pine stands in the flatwoods of southeast Georgia and northeast Florida are known to be responsive to fertilization (Martin and Jokela 2004) so it was no surprise that these stands were responsive; however, what was surprising was the magnitude of response and that such young stands (2 to 5 years old) would be so responsive.

Even at the highest rates of N used (202 kg ha^{-1} every two years and 270 kg ha^{-1} every four years), it appears that the stands could have responded more because for all three sites there was a noticeable reduction in response in the fourth year following the first treatment (Figure 11). The same trend was found for periodic annual increment responses in midrotation fertilization trials where growth response peaked during the years 3-4 after application of 224 and 56 kg ha^{-1} of N and P respectively (Hynynen et al. 1998).

Soil N availability during the growing season was tremendously enhanced by fertilization (Figures 4A). This was expected at the Florida site since it received a new application of fertilizer in March 2003. The same set of treatments was applied the year before (March 2002) for those sites located in Georgia and although N availability was significantly higher on fertilized treatments, the differences between control and fertilized treatments were not as large as the one found in FL1. Other studies have also shown rapid increases in available N with strong differentiation by rate followed by equally rapid decreases in available N within a few months of application (Johnson et al. 1980, Mudano 1986, Sven et al. 1996). The higher soil N availability at all three sites clearly provided for short term increases in N uptake as indicated by foliar N concentrations (Table 14) and increases in LAI (Figure 13). In addition, there was strong evidence of a longer term increase in N uptake as indicated by the significance of the overall treatment effect on foliar N at all three sites (Table 15), the large increases in estimated litterfall N (Tables 21 and 22) and significant increase in N accumulations in the FF (Table 9 and 10). Modeling analyses completed by Ducey and Allen (2001) also suggested greater uptake of applied N from the soil than could be accounted for by uptake during the first year following fertilization. Tree growth ultimately depends on nutrient availability and N has been identified to be an important nutrient across the southeast US (Allen et al. 2005). We found that peak of leaf area increases sharply with average growing season available N (Figure 13). Although this relationship was measured after several application of fertilizer (Table 2), the rates of fertilizer application and its cumulative effect on soil N availability seems to play an important factor on leaf area display (Table 24, Figure 13) and also tree growth response (Table 24, Figure 17).

Although the three sites were very responsive, they apparently have different nutrient limitations. For instance, N and P seemed to be the two main nutrients limiting growth at FL1 as indicated by low soil and foliar P and strong responses in foliar N and P to nutrient dose, while the GA sites appear to be limited by N and K as indicated by the low foliar N and K concentrations on controls and the strong relative response in foliar N and K soon after these nutrients were added (Table 14).

A strong positive correlation was found between productivity and foliar Ca and Mn over the three sites (Table 24, Figure 15A). This could be a result of the FL1 stand being located on an Alfisol soil with normally high Ca content. Since FL1 was more productive, a positive correlation was found across site. This may not indicate a cause and effect however, more testing needs to be done in order to determine if Ca would be limiting growth at the GA sites. Interestingly, for GA1 litterfall Ca concentration in 2003 decreased significantly with increasing nutrient dose (Table 12) which happens to be the faster growing plots. Because foliar Mn concentrations dropped to undetectable levels for treated plots after the third growing season (Table 14), Mn was applied at both GA sites during the fourth and fifth growing season (Table 2). After these applications, foliar Mn values raised up to similar or higher values of those measured prior to treatment initiation (Table 14) indicating probably that this nutrient would have limited growth if not applied. Fertilization response to Mn additions has been reported on a somewhat poorly drained Spodosols in northern Florida (Jokela et al. 1991). Manganese values at the control plots have been continuously declining through time probably indicating that this nutrient could become deficient at some stage of stand development when growing on Spodosols soils. Manganese deficiencies are common on poorly drained, sandy-textured soils in the

Atlantic Costal Plain, and in soils that often fluctuate between waterlogged and well drained conditions (Moraghan and Mascagni 1991).

Productivity was negatively correlated with foliar Cu concentration across sites. Again this could be due to the higher growth rates found at FL1 which were lower in foliar Cu concentration. Another reason for this could be that the two GA sites with higher Cu concentration are located in Spodosols soil where Cu tends to accumulate in the organic-rich illuvial horizon typical of these soils. Critical concentrations for foliar Cu have not been yet defined for loblolly pine, however, foliar Cu critical level for conifers around the world has been postulated to be between 1.5-5.0 (Turvey and Grant 1990), certainly foliar Cu concentrations at the FL1 site are close to the lower end of this range and may become problematic in the future if it continues to fall.

Strong negative correlation was also found between productivity and FF L-layer C concentration. This could be due to the positive cumulative nutrient dose effects found on other FF nutrient concentrations (Tables 8 and 9). The typically higher nutrient concentrations found in both FF layers with increasing nutrient dose will reduce C in relative terms.

The enhanced nutrient availability not only resulted in better foliar nutrition but also higher foliage production (Figure 13). The strong relationship between volume growth and leaf area (Figure 17) and the lack of a strong treatment or site effect on GE (the slope of this relationship) clearly indicates that increased foliage was the key mechanism of response to nutrient additions as has been found by many others (Albaugh et al. 2004, Martin and Jokela 2004, Jokela et al. 2004, Sampson and Allen 1999).

Nutrient rather than water has been shown to limit growth in loblolly pine plantations in the southeast (Albaugh et al. 2004), and this was clearly the case at all three sites.

These three plantations were located in an area suggested the Sampson and Allen's (1999) modeling efforts and empirical data (Chapter 2) to have a high GE. Certainly, the high growth efficiency, averaging 8.14 m^3 ha^{-1} yr^{-1} per unit of leaf area across sites, agrees with Sampson and Allen's (1999) findings. Consequently a very strong volume growth response would be expected on sites such as these when leaf area is increased. This may be in part why these stands exhibited such large volume growth responses.

Forest floor accumulation has developed over the years since plantation establishment. This represents storage of nutrients that play an important role in forest nutrient cycling. Fertilization and its cumulative effect resulted in a large range of stemwood production and FF accumulation. Some treatment plots accumulated up to 227% more FF mass than control plots. The significantly higher leaf area developed on treatments with higher nutrient dose (Table 17, Figure 8) significantly increased litterfall (Table 12) and FF accumulation (Tables 9 and 10). Although treatment differences in FF accumulation were not statistically significant at the Florida site, the trend was to increase accumulation of FF with increasing fertilizer dose. The Florida site responded to fertilization relatively slower than the other two sites at Georgia (NCSFNC 2003) and treatment differentiation in terms of volume were not significant until the third growing season after the second application of fertilizer. This slow start at the Florida site may have prevented the FF from accumulating as fast as in the Georgia sites for the treated plots since leaf area may have not initially improve significantly either. We can expect that changes in FF accumulation would develop with more, time since litterfall in 2003 showed a significant positive relationship with growth and fertilizer dose (Tables 12 and 23, Figure 6).

As a consequence of the improved foliar nutrient concentrations (Tables 14 and 15) and greater foliage production (Figure 8), litterfall mass and nutrient concentrations were also increased. This change in the amount and quality of litter inputs also carried over into lower C/N in the FF. Nitrogen inputs through litterfall increased with increasing dose of applied fertilizer due to both higher amounts of litterfall with higher N concentrations (Tables 11, 12 and 13) allowing higher amounts of N to accumulate in the FF layer and lower C/N ratios.

Litterfall/Forest floor ratios indicated that the release of these nutrients from the FF is higher for K and B followed by P, S and N. Similar results were found by Sanchez (2001) in an intensively managed stand. The stability of the LL/FF ratios does indicates that fertilizer has had little to no effect on FF decomposition and nutrient release for two of the three sites. Even though higher nutrient content (and concentrations) with lower C/N were associated to increasing nutrient dose, FF decomposition does not seem to be affected by these two factors at this moment. This could be due to two things; first it is still too early to detect differences in decomposition rates and/or second imperfection on the estimation of litterfall inputs. More work needs to be done to follow FF changes over time in these plantations. It can be hypothesized that the higher nutrient concentrations as well as lower C/N ratios found in the FF from fertilized treatments may promote higher rates of microbial activity and decomposition of FF. This may have some implications on the dynamics of the decomposition of the FF and nutrient release in the future. Sanchez

(2001) found that quality of the incorporated litter affected rate of nutrient release. Nutrient availability can place very substantial constraints on the decomposition rate of organic matter by its associated microflora. During the process of organic matter decomposition microorganisms must obtain their necessary supplies of inorganic nutrients, this would promote immobilization under high C/N ratios which certainly reduce nutrient availability for plant growth (Schmidt et al. 1999, Lars 1998). The incorporation of nutrients by means of a fertilizer can help microbes in the decomposition process and release of nutrients (Schmidt et al. 1999). The observed changes on FF composition (quality) with treatment application may play an important role in nutrient availability in the future. Better understanding of these changes through time needs to be developed as stands are being more intensively managed. Certainly, these three sites represent an opportunity to study FF decomposition through time, as affected by intensive silviculture, and its role on nutrient release or sink as has been found in midrotation stands (Piatek and Allen 2001).

Leaf area measured at five years since establishment was significantly different across sites (Table 18). Leaf area indexes were similar between the GA sites, but they were significantly lower as compared to LAI measures at FL1 (Table 18; Figure 8). The Georgia studies were established on stands with similar stand densities and soil conditions and differed in age by 1 year, while Florida's site was two years older (Table 1), so the difference may be due to the lack of time at the Georgia sites to fully develop leaf area display. Cumulative stemwood volume for the highest fertilizer dose (606 kg N ha^{-1}), at all three sites had similar trajectories (Figure 10A), indicating that when comparison are done at the same age, site differences would disappear on the most intensive treatments. This could also be true for LAI for sites under similar GE. Another factor playing an important roll in the observed difference in LAI between Florida and Georgia sites is stand density. Stand density was higher at Florida site, this could affect leaf area display initially in the stand life especially when canopy closure has not yet been achieved. The same explanation could be also true for the observed differences in cumulative growth with increasing nutrient dose across sites. At the FL1 site, stand density was higher with an average of 2206 trees.ha^{-1}, while GA1 and GA2 averaged 1742 and 1720 trees ha^{-1}, respectively, the almost 450 tree difference plays an important role in the early life of the stand.

Year to year changes in foliar nutrient concentration were very strong for all nutrients (Table 15). This was expected to happen for those applied nutrients since nutrient uptake and hence foliar nutrient concentration were strongly enhanced soon after each fertilization application (Table 14, Figure 13) for both 2-year and 4-year frequencies. Micronutrients uptake is metabolically controlled and strongly influenced by the effect of environmental factors (precipitation and temperature) on plant and soil processes (transpiration, root growth, mineralization organic matter decomposition, etc.). An overall treatment effect was found for N, the only nutrient that was significantly changed over the whole 5-years period following fertilization initiation across all three sites (Table 15). Treatment effects were not found for foliar P concentrations over the 5-year period even though it was added at all three sites. However, foliar P concentration as well as other nutrients were typically higher the year after each fertilization period (Table 14) but decreased again in the following years.

5. Conclusions

Soil N availability during the growing season was substantially enhanced soon after fertilizer application. Enhanced values of soil available N were still detectable a year after fertilizer was applied. The higher availability of nutrients in the soil due to fertilizer application improved foliar nutrient status, needle biomass, leaf area index, and tree growth at all three sites.

Repeated fertilizer application increased leaf area and tree growth, helping to realize site potential of flatwoods sites. Leaf area and tree growth increased with rates of application (treatment effects) but also LAI was highly correlated with cumulative fertilizer dose, certainly suggesting the necessity for repeated application of fertilizer during the life of the stand. The enhancement of LAI and foliar nutrient status with fertilization in all three sites also increased litterfall inputs increasing FF accumulation.

Changes in the forest floor accumulation and composition were substantial across sites. The higher accumulation of forest floor, lower C/N and higher nutrient concentrations and contents in the fertilized plots could have important implications in the decomposition process and nutrient release for tree growth either in this rotation and/or future rotations. At this moment no substantial differences were detected in FF decomposition and/or nutrient release across treatments.

Since GE was relatively constant across the sites, the high stemwood volume response was attributable to LAI changes due to enhanced nutrient availability.

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Table 1. Site characteristics and initial stand conditions of three trials established to study the effect of rates and frequency of fertilization on loblolly pine plantation growth in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

	Sites		
Characteristic	**FL1**	**GA1**	**GA2**
State, County	FL, Nassau	GA, Brantley	GA, Brantley
Establishment year	1999	1998	1998
Plantation age at time of establishment.	5	3	2
Soil series	Meggett	Seagate	Seagate
Soil order	Alfisol	Spodosol	Spodosol
Drainage	Poorly	Moderately well	Moderately well
Subsoil texture	Clay	Sandy loam	Sandy loam
Long term mean annual precipitation (mm)	1301	1320	1320
Long term daily mean annual temperature (^oC)	20	19	19
Average Height (m)	5.1	3.2	2.1
Stand density (trees ha^{-1})	2246	1782	1754

Table 2. Timing of nutrient applications at three different loblolly pine plantations[1] in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1).

Code	Treatment description	Beginning of growing season since treatment						
		N	P	K	Mg	S	B	Mn
206	67 kg N ha^{-1} every other year	1,3,5	1,3,5	1,3,5	5	1,3,4,5	1,3,5	4,5
212	135 kg N ha^{-1} every other year	1,3,5	1,3,5	1,3,5	5	1,3,4,5	1,3,5	4,5
218	202 kg N ha^{-1} every other year	1,3,5	1,3,5	1,3,5	5	1,3,4,5	1,3,5	4,5
412	135 kg N ha^{-1} every four years	1,5	1,5	1,5	5	1,4,5	1,5	4,5
418	202 kg N ha^{-1} every four years	1,5	1,5	1,5	5	1,4,5	1,5	4,5
424	270 kg N ha^{-1} every four years	1,5	1,5	1,5	5	1,4,5	1,5	4,5
624	270 kg N ha^{-1} every six years	1	1	1,5	5	1,4,5	1,5	4,5

[1] Only N and P were added at the Florida site.

Table 3. Cumulative dose of applied nutrients after the fourth (4) and fifth (5) years since treatments were first applied[1] at three different loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

Code	**Treatment description**	**Cumulative rate after 4/5 years since establishment (kg^{-1} ha)**						
		N	P	K	Mg	S	B	Mn
000	Control non-treated	0/0	0/0	0/0	0/0	0/0	0/0	0/0
206	67 kg N ha^{-1} every other year	135/202	13/20	47/52	0/1.4	15	0.4/0.4	7/10
212	135 kg N ha^{-1} every other year	270/404	27/41	53/58	0/2.8	31	0.7/0.8	13/20
218	202 kg N ha^{-1} every other year	404/606	41/61	79/87	0/4.2	46	1.1/1.8	20/30
412	135 kg N ha^{-1} every four years	135/270	14/27	26/31	0/2.8	15	0.4/0.4	7/13
418	202 kg N ha^{-1} every four years	202/404	20/41	40/47	0/4.2	23	0.5/0.6	10/20
424	270 kg N ha^{-1} every four years	270/538	27/54	53/62	0/5.7	31	0.7/0.9	13/27
624	270 kg N ha^{-1} every six years	270/270	27/27	53/62	0/5.7	31	0.7/0.9	13/27

[1] Florida site only received N and P.

Table 4. Timing (year since treatment) for soil, forest floor, leaf area index and pine growth variables measured at three different loblolly pine plantations in the flatwoods area of southeast Georgia and Florida

	Year since treatment[1]	
Variables	Florida	Georgia
Fresh and Incubated soil extractions (N)	4	5
Total soil C and N, Extractable P, Mn, Cu	4	5
Average growing season field extraction (N)	5[2]	6[2]
LAI	5	5
Foliar weight and nutrients	0,1,2,3,4,5	0,1,2,3,4,5
Litterfall weight and nutrients	4[3]	5[3]
Forest floor weight and nutrients	4	5
Pine growth	0,1,2,3,4,5	0,1,2,3,4,5

[1] After growing season
[2] During growing season
[3] collected cohort belongs to this particular growing season

Table 5. Summary of significance of 2003 cumulative N dose effects on total C and N, extractable P, Mn and Cu (Pr>F) at three different loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1). Model [3].

	Pr>F[1]		
Variables	**FL1**	**GA1**	**GA2**
Soil			
Total C	***0.055***	0.877	***0.011***
Total N	***0.024***	0.616	***0.007***
Extractable P	***0.060***	0.417	0.459
Extractable Mn	0.188	***0.001***	0.484
Extractable Cu	0.518	0.631	0.398
Mineralizable N (MEN)	0.755	0.320	0.311
Growing season average field extraction N (FEN)	***0.001***	***0.001***	0.225

[1] Shaded cell with bold-italic numbers indicates significance with alpha=0.10

Table 6. Nutrient content in the soil after repeated fertilization at three loblolly pine plantations in southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

Variable	Cumulative N dose (kg ha^{-1})							
	0	135	202	270	404	538	606	MSE
				FL1				
Number of plots (n)	2	4	2	6	2			
Mineralizeable N (kg ha^{-1})	7.7	3.6	2.8	6.2	5.8			21.93
Total C (Mg ha^{-1})	19.6	17.8	36.1	25.3	27.7			0.33
Total N (kg ha^{-1})	757	724	1348	1013	1177			0.0003
Extractable P (kg ha^{-1})	8	11	11	16	31			45.39
Extractable Mn (kg ha^{-1})	1.2	5.6	8.7	7.2	8.3			9.56
Extractable Cu (kg ha^{-1})	0.22	0.18	0.01	0.16	0.24			0.019
				GA1				
Number of plots (n)	2		2	4	4	2	2	
Mineralizeable N (kg ha^{-1})	6.4		6.3	10.0	14.8	34.7	21.3	104.36
Total C (Mg ha^{-1})	31.0		28.1	32.3	36.5	36.0	40.0	1.22
Total N (kg ha^{-1})	528		521	646	764	711	985	0.0010
Extractable P (kg ha^{-1})	18		29	27	23	24	35	34.21
Extractable Mn (kg ha^{-1})	0.8		8.7	13.0	5.9	22.7	76.9	65.93
Extractable Cu (kg ha^{-1})	0.28		0.10	0.19	0.25	0.17	0.18	0.01
				GA2				
Mineralizeable N (kg ha^{-1})	8.0		8.7	20.9	17.5	20.9	22.6	22.32
Total C (Mg ha^{-1})	20.3		20.8	33.3	31.6	44.5	34.1	0.24
Total N (kg ha^{-1})	838		883	1204	1213	1410	1249	0.0001
Extractable P (kg ha^{-1})	33		25	57	98	104	66	871.46
Extractable Mn (kg ha^{-1})	ND		4.1	4.3	7.1	17.7	2.9	27.96
Extractable Cu (kg ha^{-1})	0.15		0.23	0.29	0.18	0.27	0.20	0.002

ND: not detectable. Standard errors = $(MSE/n)^{1/2}$.

Table 7. Forest floor mass and nutrient concentrations at three sites in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

Variable	Cumulative N dose (kg ha^{-1})																
	FL1					GA1						GA2					
	0	135	202	270	404	0	202	270	404	538	606	0	202	270	404	538	606
Total FF mass (kg ha^{-1})	6806	7683	9681	7743	8231	5594	8825	11369	12494	18288	15138	6478	8909	12541	10650	11253	16119
Litter (L) layer																	
Weight (kg ha^{-1})	2550	2755	3222	3250	3288	2813	4325	5194	5750	7538	6213	1659	2844	3025	3266	4422	4306
C (%)	48	48	48	48	48	51	50	50	51	50	51	50	51	50	50	50	50
N (%)	0.533	0.576	0.561	0.620	0.687	0.499	0.550	0.543	0.681	0.788	0.779	0.458	0.526	0.575	0.770	0.808	0.886
C/N	91.07	83.64	86.45	77.99	69.99	101.75	90.47	92.92	74.83	65.17	66.31	109.35	97.48	87.05	66.67	61.70	56.18
P (%)	0.023	0.031	0.029	0.041	0.043	0.042	0.045	0.045	0.055	0.046	0.055	0.041	0.047	0.053	0.057	0.074	0.062
K (%)	0.035	0.042	0.047	0.045	0.052	0.026	0.037	0.039	0.052	0.044	0.061	0.028	0.041	0.044	0.053	0.072	0.079
Ca (%)	0.582	0.587	0.511	0.559	0.539	0.376	0.365	0.225	0.252	0.307	0.241	0.468	0.425	0.336	0.268	0.380	0.199
Mg (%)	0.118	0.110	0.114	0.102	0.118	0.114	0.106	0.101	0.117	0.179	0.112	0.111	0.119	0.111	0.110	0.107	0.121
S (%)	0.064	0.063	0.062	0.067	0.076	0.057	0.061	0.057	0.067	0.068	0.069	0.055	0.057	0.062	0.070	0.074	0.080
B (mg kg^{-1})	12.45	12.28	12.54	11.40	13.48	11.33	13.12	12.78	15.37	13.92	15.89	11.90	13.53	13.99	14.18	15.20	15.27
Cu (mg kg^{-1})	3.49	3.59	3.09	3.07	3.22	4.96	2.42	3.54	3.15	2.74	3.70	2.34	2.07	2.35	2.82	3.54	2.42
Zn (mg kg^{-1})	19.94	16.01	15.08	14.32	13.32	11.93	10.27	8.39	8.95	7.42	8.50	25.54	12.95	11.83	12.37	15.56	8.03
Mn (mg kg^{-1})	508	523	457	421	763	59	74	48	85	294	90	76	70	81	65	73	41
Fermentation + Humus (F+H) layer																	
Weight (kg ha^{-1})	4256	4928	6459	4493	4944	2781	4500	6175	6744	10750	8925	4819	6066	9516	7384	6831	11813
C (%)	46	43	45	44	45	46	44	47	45	45	48	49	49	45	49	49	45
N (%)	0.824	0.880	0.935	0.955	1.154	0.721	0.802	0.872	1.044	1.156	1.354	0.635	0.638	0.774	1.048	0.981	1.052
C/N	55.52	50.47	47.61	45.91	38.67	63.48	54.60	55.46	43.90	39.72	35.75	77.44	77.47	59.55	47.89	50.63	42.25
P (%)	0.037	0.048	0.057	0.061	0.069	0.039	0.046	0.044	0.054	0.049	0.052	0.043	0.047	0.060	0.067	0.051	0.079
K (%)	0.042	0.047	0.058	0.052	0.054	0.032	0.037	0.039	0.045	0.045	0.046	0.038	0.049	0.054	0.058	0.048	0.090
Ca (%)	0.635	0.627	0.557	0.536	0.513	0.302	0.321	0.267	0.244	0.273	0.221	0.566	0.353	0.292	0.314	0.337	0.240
Mg (%)	0.110	0.104	0.097	0.088	0.087	0.066	0.064	0.076	0.074	0.169	0.109	0.108	0.084	0.090	0.111	0.112	0.107
S (%)	0.079	0.082	0.088	0.089	0.105	0.081	0.084	0.089	0.100	0.102	0.086	0.074	0.072	0.086	0.097	0.074	0.119
B (mg kg^{-1})	9.36	8.12	7.48	8.23	8.58	5.02	7.89	18.69	10.19	10.11	9.57	8.41	10.76	9.41	11.03	11.56	12.27
Cu (mg kg^{-1})	4.87	4.71	5.38	5.11	4.78	6.01	6.29	4.85	5.46	5.23	3.85	3.70	2.92	3.86	4.54	3.22	4.09
Zn (mg kg^{-1})	26.95	18.29	19.04	17.78	17.85	16.80	15.74	16.46	13.23	19.20	10.90	46.15	13.40	14.73	38.89	14.91	13.62
Mn (mg kg^{-1})	506	545	445	470	988	47	89	171	280	1581	535	110	62	371	223	148	716

Table 8. Summary of significance of 2003 cumulative N dose effects (Pr>F) on forest floor layers mass and nutrient concentrations at three sites in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

	Pr>F[1]		
Variable	**FL1**	**GA1**	**GA2**
Total FF mass	0.599	***< 0.001***	***0.011***
		Litter (L) layer	
Mass	0.653	***0.016***	***< 0.001***
C	0.931	0.753	0.319
N	***0.080***	***0.045***	***0.013***
C/N	***0.051***	***0.016***	***0.010***
P	***0.002***	***0.093***	***0.023***
K	***0.099***	***0.014***	***0.009***
Ca	0.372	0.130	***0.090***
Mg	0.458	0.252	0.869
S	***0.002***	***0.008***	***0.004***
B	0.108	***0.002***	0.154
Cu	0.728	0.724	0.521
Zn	0.114	0.134	***0.063***
Mn	0.482	0.481	0.312
		Fermentation + Humus (F+H) layer	
Mass	0.514	***0.005***	***0.039***
C	0.613	0.495	0.540
N	***0.038***	***0.016***	***0.061***
C/N	***0.013***	***0.013***	***0.002***
P	***0.021***	***0.097***	***0.082***
K	0.318	***0.065***	0.203
Ca	0.270	0.448	***0.098***
Mg	0.484	0.317	0.803
S	***0.083***	***0.046***	***0.041***
B	0.680	0.827	0.244
Cu	0.811	0.260	0.862
Zn	0.142	0.632	0.546
Mn	0.147	0.349	0.448

[1] Shaded cell with bold-italic numbers are significant with alpha=0.10

Table 9. Nutrient accumulation in the forest floor as affected by cumulative N dose at three sites in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

	Cumulative Cumulative N dose (kg ha^{-1})							
Variable	**0**	**135**	**202**	**270**	**404**	**538**	**606**	**MSE**
				FL1				
Number of plots (n)	**2**	**4**	**2**	**6**	**2**			
C (kg ha^{-1})	3191	3480	4442	3525	3779			789666
N (kg ha^{-1})	49	61	79	63	80			382.4
C/N	65	59	56	56	48			18.3
P (kg ha^{-1})	2.1	3.3	4.7	4.1	4.8			1.41
K (kg ha^{-1})	2.6	3.5	5.3	3.8	4.3			1.37
Ca (kg ha^{-1})	41.6	47.1	52.4	42.8	42.4			116.6
Mg (kg ha^{-1})	7.8	8.1	10.1	7.4	8.1			6.51
S (kg ha^{-1})	5.0	5.9	7.8	6.1	7.7			3.28
B (g ha^{-1})	71.8	73.6	88.8	75.0	85.9			397.3
Cu (g ha^{-1})	28.8	33.2	45.2	32.7	33.7			54.3
Zn (g ha^{-1})	162.6	135.2	173.1	125.5	129.4			1019
Mn (kg ha^{-1})	3.2	4.1	4.5	3.5	7.2			2.11
				GA1				
Number of plots (n)	**2**		**2**	**4**	**4**	**2**	**2**	
C (kg ha^{-1})	2699		4107	5543	5976	8622	7435	182819
N (kg ha^{-1})	34		61	82	109	185	170	661
C/N	79		68	68	55	48	45	60.42
P (kg ha^{-1})	2.3		4.0	5.0	6.7	8.7	8.0	0.459
K (kg ha^{-1})	1.6		3.2	4.5	6.1	8.2	7.9	0.491
Ca (kg ha^{-1})	19.0		29.2	27.9	30.9	52.9	34.4	49.9
Mg (kg ha^{-1})	5.0		7.3	9.9	11.9	32.3	16.4	61.3
S (kg ha^{-1})	3.8		6.4	8.4	10.5	16.1	11.9	0.375
B (g ha^{-1})	45.7		91.9	181.9	152.2	216.1	180.7	6836.8
Cu (g ha^{-1})	30.7		38.5	48.5	54.9	76.4	56.9	110.5
Zn (g ha^{-1})	80.3		115.9	146.1	141.4	257.5	148.8	1685
Mn (kg ha^{-1})	0.3		0.7	1.3	2.7	20.2	5.2	81.7
				GA2				
C (kg.ha^{-1})	3195		4435	5869	5236	5493	7389	933541
N (kg.ha^{-1})	38		54	92	103	85	162	396.0
C/N	83		83	65	52	69	46	37.15
P (kg.ha^{-1})	2.8		4.2	7.5	6.8	7.3	12.0	3.96
K (kg.ha^{-1})	2.3		4.2	6.6	6.0	6.9	14.0	5.07
Ca (kg.ha^{-1})	34.6		33.2	39.2	31.7	40.0	37.1	155.4
Mg (kg.ha^{-1})	7.1		8.4	12.3	11.9	11.9	17.7	12.85
S (kg.ha^{-1})	4.5		6.0	10.1	9.5	8.8	17.4	4.71
B (g.ha^{-1})	60.5		103.9	134.0	127.9	146.2	210.6	1006
Cu (g.ha^{-1})	21.8		24.0	42.7	42.8	43.6	58.6	200.5
Zn (g.ha^{-1})	268.8		117.8	178.3	314.2	186.8	195.4	34963
Mn (kg.ha^{-1})	0.7		0.6	4.2	1.9	1.5	8.7	14.87

Standard errors = $(MSE/n)^{1/2}$.

Table 10. Summary of significance of 2003 cumulative N dose effect (Pr>F) on total forest floor weight and nutrient content at three sites in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

	Pr>F[1]		
Variable	**FL1**	**GA1**	**GA2**
Total FF weight	0.599	***< 0.001***	***0.011***
C	0.673	***< 0.001***	***0.040***
N	0.497	***0.003***	***0.005***
C/N	***0.038***	***0.014***	***0.001***
P	0.205	***< 0.001***	***0.026***
K	0.296	***< 0.001***	***0.016***
Ca	0.795	***0.026***	0.943
Mg	0.779	***0.076***	0.171
S	0.490	***< 0.001***	***0.007***
B	0.836	0.374	***0.030***
Cu	0.312	***0.034***	0.204
Zn	0.400	***0.044***	0.829
Mn	0.118	0.303	0.334

[1] Shaded cell with bold-italic numbers are significant with alpha=0.10

Table 11. Litterfall mass and nutrient concentrations in 2003 at three sites in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1) after receiving repeated doses of fertilizer

	Cumulative N dose (kg.ha^{-1})																
	FL1					**GA1**						**GA2**					
Variable	**0**	**135**	**202**	**270**	**404**	**0**	**202**	**270**	**404**	**538**	**606**	**0**	**202**	**270**	**404**	**538**	**606**
Litterfall (Kg ha^{-1})	4257	4759	4877	4851	6493	2837	4884	4811	5546	5136	5903	2774	5197	5624	5301	5985	6799
N (%)	0.46	0.55	0.71	0.61	0.70	0.38	0.39	0.41	0.46	0.49	0.47	0.38	0.41	0.46	0.57	0.62	0.67
P (%)	0.019	0.038	0.057	0.050	0.051	0.050	0.043	0.042	0.042	0.038	0.049	0.047	0.049	0.048	0.048	0.065	0.057
K (%)	0.053	0.072	0.104	0.093	0.113	0.015	0.024	0.034	0.060	0.045	0.114	0.013	0.033	0.043	0.068	0.117	0.163
Ca (%)	0.49	0.48	0.45	0.46	0.44	0.33	0.27	0.29	0.30	0.28	0.24	0.54	0.37	0.34	0.27	0.35	0.24
Mg (%)	0.12	0.12	0.13	0.13	0.11	0.15	0.13	0.12	0.12	0.13	0.10	0.15	0.12	0.13	0.11	0.12	0.10
S (%)	0.058	0.062	0.072	0.069	0.073	0.057	0.053	0.062	0.063	0.063	0.068	0.072	0.073	0.079	0.079	0.091	0.089
B (mg kg^{-1})	21	17	19	16	18	16	20	18	19	18	25	15	17	20	19	21	22
Zn (mg kg^{-1})	16	13	16	15	11	17	7	9	7	6	7	28	15	15	11	10	8
Cu (mg kg^{-1})	9.7	7.3	6.6	6.2	6.6	5.7	5.8	7.0	5.0	6.6	3.8	2.0	2.3	4.5	5.6	3.9	13.9
Mn (mg kg^{-1})	419	561	574	512	849	101	129	157	180	184	100	113	174	275	219	356	175

Table 12. Summary of significance of 2003 cumulative N dose effect (Pr>F) on 2003 litterfall, nutrient concentrations and nutrient contents at three sites in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

Variable	Pr>F[1]		
	FL1	**GA1**	**GA2**
Nutrient concentration			
N	***0.004***	0.167	***<0.001***
P	***0.016***	0.532	0.147
K	***0.022***	***<0.001***	***0.009***
Ca	0.643	0.425	***0.026***
Mg	0.583	0.101	0.331
S	***0.014***	0.122	***0.061***
B	0.190	***0.008***	***0.030***
Zn	0.257	***0.020***	0.118
Cu	***0.086***	0.819	0.184
Mn	0.314	0.393	0.213
Nutrient content			
N	***0.003***	***0.002***	***0.003***
P	***0.013***	***0.011***	***0.024***
K	***0.003***	***<0.001***	***0.007***
Ca	***0.083***	***0.009***	0.190
Mg	0.287	***0.036***	0.353
S	***0.001***	***<0.001***	***0.017***
B	0.122	***0.001***	***0.007***
Zn	0.633	0.564	0.753
Cu	0.217	0.700	0.169
Mn	***0.024***	***0.066***	0.110
Litterfall weight	***0.005***	***0.004***	***0.007***

[1] Shaded cells with bold-italic numbers are significant with alpha=0.10.

Table 13. Summary of nutrient contents in 2003 litterfall at three sites in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

	Cumulative N dose (kg ha^{-1})																
	FL1					**GA1**						**GA2**					
Variable	**0**	**135**	**202**	**270**	**404**	**0**	**202**	**270**	**404**	**538**	**606**	**0**	**202**	**270**	**404**	**538**	**606**
N (kg ha^{-1})	19.5	26.0	34.7	30.1	45.2	10.7	19.0	19.7	25.3	25.4	27.7	10.5	21.1	25.9	30.3	37.2	45.9
P (kg ha^{-1})	0.8	1.8	2.8	2.4	3.4	1.4	2.1	2.0	2.3	2.0	2.9	1.3	2.6	2.7	2.6	3.9	3.9
K (kg ha^{-1})	2.2	3.5	5.1	4.6	7.3	0.4	1.1	1.6	3.4	2.3	6.7	0.4	1.7	2.5	3.6	7.2	11.1
Ca (kg ha^{-1})	21.1	22.4	22.0	22.3	28.4	9.4	13.0	13.8	15.9	14.6	14.1	14.6	19.6	19.2	14.2	21.1	16.4
Mg (kg ha^{-1})	5.2	5.7	6.3	6.4	7.3	4.3	6.5	5.8	6.4	6.7	5.6	4.1	6.2	7.4	6.0	6.9	6.7
S (kg ha^{-1})	2.5	3.0	3.5	3.4	4.8	1.6	2.6	3.0	3.4	3.2	4.0	2.0	3.8	4.4	4.2	5.5	6.1
B (g ha^{-1})	89.6	79.7	93.5	79.0	118.3	44.5	97.0	85.6	105.7	94.6	145.5	41.1	87.3	112.7	100.1	125.8	150.2
Zn (g ha^{-1})	68.5	61.6	78.5	72.9	69.1	49.8	33.5	44.9	39.2	32.3	37.2	79.7	82.0	84.3	57.9	59.9	51.5
Cu (g ha^{-1})	41.5	34.5	32.2	31.0	42.5	16.3	27.7	33.6	27.3	33.5	21.4	5.5	11.6	25.9	29.8	22.8	97.3
Mn (kg ha^{-1})	1.8	2.7	2.8	2.4	5.4	0.3	0.6	0.8	1.0	0.9	0.6	0.3	0.9	1.6	1.2	2.1	1.2

Table 14. Summary of foliar nutrient concentration by year at three loblolly pine plantations in southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

Treatment*	Year since initiation of treatments**																	
	FL1						GA1						GA2					
	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5
	Nitrogen concentration (%)																	
Control	1.10	0.99	1.16	1.23	1.19	1.27	0.99	1.21	1.04	1.13	1.19	1.13	1.01	1.35	1.14	1.06	1.25	1.15
206	1.12	1.09	1.11	1.40	1.27	1.34	1.11	1.36	1.06	1.27	1.31	1.31	1.06	1.53	1.15	1.36	1.41	1.40
212	1.23	1.26	1.19	1.51	1.34	1.34	1.02	1.68	1.01	1.58	1.41	1.48	1.00	1.56	1.16	1.71	1.58	1.44
218	1.21	1.29	1.22	1.49	1.47	1.57	1.13	1.74	1.16	1.92	1.56	1.48	1.03	1.53	1.22	1.70	1.65	1.59
412	1.15	1.26	1.16	1.34	1.27	1.37	1.02	1.73	1.10	1.20	1.32	1.48	1.01	1.48	1.29	1.22	1.31	1.40
418	1.19	1.42	1.22	1.29	1.23	1.48	1.13	1.79	1.17	1.26	1.27	1.53	1.01	1.73	1.12	1.27	1.41	1.70
424	1.26	1.45	1.37	1.44	1.44	1.56	0.93	1.84	1.13	1.29	1.35	1.56	1.17	1.72	1.21	1.37	1.49	1.75
624	1.14	1.34	1.20	1.31	1.23	1.30	1.11	2.13	1.12	1.19	1.20	1.29	1.10	1.82	1.25	1.37	1.49	1.41
	Phosphorous concentration (%)																	
Control	0.10	0.10	0.11	0.11	0.09	0.08	0.13	0.14	0.12	0.14	0.13	0.13	0.12	0.13	0.11	0.13	0.14	0.14
206	0.11	0.10	0.10	0.13	0.11	0.11	0.13	0.13	0.11	0.14	0.13	0.13	0.12	0.14	0.11	0.13	0.13	0.14
212	0.12	0.11	0.11	0.14	0.12	0.11	0.13	0.15	0.11	0.14	0.14	0.14	0.13	0.14	0.11	0.15	0.14	0.13
218	0.11	0.11	0.12	0.13	0.13	0.13	0.13	0.15	0.10	0.16	0.14	0.14	0.12	0.14	0.11	0.15	0.14	0.15
412	0.11	0.10	0.11	0.12	0.11	0.11	0.13	0.15	0.10	0.13	0.14	0.14	0.13	0.14	0.11	0.12	0.12	0.13
418	0.11	0.11	0.11	0.12	0.11	0.12	0.13	0.15	0.10	0.13	0.13	0.14	0.12	0.14	0.11	0.13	0.13	0.15
424	0.11	0.12	0.12	0.13	0.12	0.13	0.13	0.15	0.11	0.13	0.13	0.15	0.14	0.15	0.11	0.14	0.14	0.16
624	0.11	0.12	0.12	0.13	0.12	0.12	0.14	0.16	0.10	0.12	0.12	0.12	0.13	0.15	0.11	0.14	0.13	0.14
	Potassium concentration (%)																	
Control	0.42	0.45	0.41	0.48	0.44	0.36	0.32	0.34	0.32	0.31	0.31	0.31	0.27	0.31	0.27	0.25	0.29	0.27
206	0.37	0.47	0.38	0.53	0.44	0.49	0.25	0.44	0.33	0.54	0.45	0.43	0.28	0.47	0.36	0.45	0.45	0.39
212	0.39	0.51	0.44	0.56	0.47	0.48	0.30	0.57	0.38	0.62	0.59	0.53	0.27	0.59	0.39	0.58	0.61	0.47
218	0.41	0.48	0.48	0.53	0.47	0.49	0.33	0.60	0.45	0.70	0.68	0.57	0.26	0.67	0.44	0.65	0.72	0.55
412	0.36	0.44	0.40	0.43	0.42	0.49	0.30	0.54	0.42	0.40	0.40	0.43	0.27	0.64	0.40	0.35	0.37	0.37
418	0.36	0.50	0.43	0.46	0.45	0.48	0.27	0.63	0.40	0.41	0.41	0.40	0.22	0.74	0.42	0.38	0.38	0.43
424	0.41	0.45	0.45	0.48	0.44	0.52	0.24	0.61	0.47	0.50	0.41	0.45	0.43	0.85	0.52	0.54	0.57	0.59
624	0.40	0.45	0.44	0.43	0.41	0.49	0.27	0.61	0.45	0.52	0.43	0.41	0.29	0.73	0.49	0.48	0.48	0.44

* For description of treatments see Table 2. ** 0 indicates establishment year, all other numbers indicate year since initiation of treatments.

Table 14. Continued.

Treatment*	Year since initiation of treatments**																	
	FL1						GA1						GA2					
	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5
	Calcium concentration (%)																	
Control	0.27	0.25	0.19	0.23	0.22	0.22	0.12	0.17	0.13	0.10	0.09	0.10	0.33	0.25	0.22	0.13	0.12	0.15
206	0.29	0.26	0.20	0.24	0.22	0.27	0.21	0.13	0.13	0.05	0.06	0.09	0.31	0.23	0.16	0.05	0.07	0.12
212	0.33	0.25	0.17	0.23	0.21	0.26	0.14	0.17	0.14	0.05	0.05	0.10	0.30	0.19	0.15	0.03	0.05	0.10
218	0.33	0.21	0.14	0.22	0.19	0.27	0.16	0.20	0.09	0.03	0.04	0.08	0.30	0.14	0.15	0.05	0.06	0.12
412	0.31	0.28	0.23	0.27	0.27	0.29	0.16	0.17	0.12	0.05	0.10	0.13	0.28	0.18	0.13	0.06	0.10	0.13
418	0.29	0.20	0.16	0.20	0.21	0.29	0.19	0.18	0.13	0.07	0.08	0.13	0.34	0.12	0.13	0.07	0.09	0.11
424	0.34	0.27	0.15	0.19	0.23	0.26	0.20	0.15	0.10	0.07	0.11	0.13	0.32	0.18	0.19	0.11	0.09	0.15
624	0.31	0.24	0.15	0.21	0.24	0.25	0.20	0.16	0.11	0.04	0.08	0.11	0.31	0.12	0.14	0.08	0.12	0.14
	Magnesium concentration (%)																	
Control	0.15	0.12	0.13	0.13	0.11	0.11	0.09	0.16	0.13	0.12	0.11	0.12	0.15	0.17	0.12	0.09	0.09	0.11
206	0.16	0.12	0.13	0.13	0.11	0.12	0.12	0.11	0.11	0.07	0.09	0.09	0.15	0.13	0.11	0.06	0.08	0.11
212	0.16	0.12	0.12	0.14	0.12	0.12	0.11	0.12	0.11	0.07	0.07	0.10	0.14	0.11	0.10	0.05	0.06	0.09
218	0.15	0.11	0.10	0.12	0.11	0.13	0.10	0.13	0.08	0.06	0.06	0.08	0.13	0.09	0.10	0.05	0.07	0.10
412	0.15	0.12	0.14	0.16	0.14	0.13	0.11	0.12	0.10	0.08	0.10	0.12	0.13	0.11	0.10	0.08	0.09	0.11
418	0.15	0.11	0.11	0.12	0.11	0.12	0.12	0.12	0.10	0.09	0.09	0.12	0.14	0.09	0.09	0.08	0.09	0.10
424	0.16	0.13	0.11	0.12	0.13	0.13	0.12	0.12	0.09	0.09	0.11	0.13	0.12	0.08	0.10	0.08	0.07	0.10
624	0.15	0.11	0.11	0.13	0.12	0.13	0.12	0.10	0.08	0.07	0.08	0.11	0.13	0.08	0.09	0.08	0.08	0.10
	Sulfur concentration (%)																	
Control	0.09	0.09	0.10	0.11	0.09	0.08	0.08	0.09	0.10	0.09	0.09	0.10	0.10	0.11	0.08	0.09	0.10	0.11
206	0.10	0.10	0.10	0.12	0.09	0.10	0.09	0.09	0.09	0.09	0.10	0.10	0.09	0.11	0.08	0.10	0.11	0.12
212	0.11	0.10	0.10	0.14	0.10	0.10	0.08	0.10	0.09	0.10	0.10	0.11	0.09	0.11	0.08	0.12	0.12	0.12
218	0.10	0.10	0.11	0.13	0.10	0.11	0.09	0.11	0.07	0.12	0.13	0.11	0.09	0.10	0.08	0.12	0.11	0.11
412	0.10	0.11	0.10	0.12	0.09	0.10	0.09	0.11	0.08	0.09	0.10	0.11	0.09	0.10	0.08	0.09	0.10	0.10
418	0.10	0.11	0.11	0.11	0.09	0.10	0.09	0.12	0.08	0.10	0.13	0.11	0.09	0.12	0.08	0.10	0.10	0.11
424	0.10	0.12	0.11	0.12	0.11	0.11	0.09	0.12	0.08	0.10	0.10	0.12	0.09	0.12	0.09	0.10	0.10	0.12
624	0.09	0.11	0.11	0.12	0.10	0.10	0.09	0.13	0.08	0.09	0.09	0.10	0.09	0.12	0.09	0.10	0.11	0.10

* For description of treatments see Table 2.
** 0 indicates establishment year, all other numbers indicate year since initiation of treatments

Table 14. Continued.

Treatment*	Year since initiation of treatments**																	
	FL1						GA1						GA2					
	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5
	Boron concentration (mg kg^{-1})																	
Control	18	15	15	18	17	14	11	16	16	18	21	17	18	24	20	18	15	18
206	19	16	17	20	18	15	11	15	20	18	20	24	15	21	29	21	23	29
212	17	17	17	26	19	18	11	18	24	26	27	34	16	22	30	26	25	31
218	18	18	17	23	22	22	12	23	24	29	31	39	16	23	30	31	32	43
412	19	15	14	20	17	16	10	18	19	20	19	25	19	27	32	26	22	27
418	18	16	15	19	17	19	14	24	24	22	21	25	18	31	34	28	23	28
424	21	18	17	19	20	20	13	23	24	26	27	29	13	30	42	31	24	33
624	21	15	16	21	18	18	13	26	31	25	24	28	17	30	34	32	26	28
	Zinc concentration (mg kg^{-1})																	
Control	31	35	29	34	30	23	26	31	23	18	18	22	46	42	28	19	19	27
206	30	38	27	34	28	25	25	29	17	13	18	22	36	39	22	15	18	26
212	40	31	24	33	27	21	29	32	20	14	18	22	35	40	21	17	18	25
218	37	34	26	31	30	25	30	32	15	17	17	21	34	29	20	18	19	23
412	33	30	23	30	29	22	35	33	16	14	18	22	36	38	19	14	17	20
418	32	33	25	31	30	25	32	28	18	14	18	26	36	36	16	16	19	21
424	39	28	27	29	31	25	31	27	16	16	20	23	47	39	27	24	23	27
624	38	28	23	32	30	27	29	23	15	15	17	22	38	30	19	18	21	24
	Copper concentration (mg kg^{-1})																	
Control	2.6	3.0	3.1	3.9	3.8	1.9	2.4	3.1	2.5	2.5	2.5	3.1	2.3	3.3	2.4	2.2	2.3	3.9
206	2.6	2.8	2.8	3.0	3.7	1.7	2.2	2.7	2.1	2.3	2.3	3.3	2.6	3.3	2.5	2.3	2.7	3.4
212	3.0	2.5	2.8	2.5	3.1	1.3	2.3	3.2	2.1	2.3	2.2	3.7	2.0	2.9	2.5	2.1	2.1	3.3
218	5.7	2.5	2.1	2.5	3.2	1.5	2.1	2.5	1.9	2.4	2.2	3.3	2.3	2.4	2.5	2.0	2.1	2.9
412	2.8	2.6	2.6	3.1	3.8	1.6	2.4	2.8	2.1	2.5	2.7	3.3	2.6	2.8	2.7	2.3	2.6	3.0
418	2.7	2.8	2.3	3.0	3.6	1.9	2.7	2.6	1.8	2.1	2.7	3.5	2.2	2.5	2.4	2.6	2.8	3.4
424	3.2	2.6	2.6	3.1	3.6	1.8	1.7	2.0	1.5	2.2	3.1	3.0	2.6	2.5	2.5	2.6	2.9	4.3
624	3.9	2.4	2.4	3.2	3.7	1.7	2.4	1.9	1.6	1.8	2.5	3.6	2.4	2.3	2.5	2.6	2.7	3.2

* For description of treatments see Table 2.
** 0 indicates establishment year, all other numbers indicate year since initiation of treatments

Table 14. Continued.

Treatment*	Year since initiation of treatments**																	
	FL1						GA1						GA2					
	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5
	Manganese concentration (mg kg-1)																	
Control	364	236	221	314	273	269	108	120	80	47	49	55	150	133	55	21	36	50
206	341	303	394	422	457	479	112	59	38	1	29	63	137	88	54	ND	27	89
212	463	210	146	217	261	323	99	61	29	ND	24	99	163	60	38	ND	17	66
218	421	292	354	527	504	591	100	66	19	ND	11	72	145	36	35	3	12	123
412	460	357	211	239	299	368	100	67	25	5	39	100	148	52	35	7	41	194
418	405	257	202	301	389	499	129	46	19	12	34	116	166	29	18	8	32	99
424	338	233	189	213	296	387	91	34	3	4	31	116	90	40	22	5	22	135
624	342	241	273	392	620	578	117	37	7	1	32	100	179	40	19	14	44	125

* For description of treatments see Table 2.
** 0 indicates establishment year, all other numbers indicate year since initiation of treatments
ND not detectable

Table 15. Significance[+] of treatment and year effects (Pr>F) on foliar nutrient concentrations at three different loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1).

Source of variation	**Pr>F[1]**									
	N	P	K	Ca	Mg	S	B	Zn	Cu	Mn
FL1										
TRT	***0.085***	0.250	0.597	***0.051***	0.141	***0.001***	0.247	0.976	0.589	0.731
YST	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***
YST*TRT	***0.05***	***0.029***	0.152	0.109	*0.559*	***0.050***	0.618	0.653	0.370	0.137
GA1										
TRT	***0.004***	0.596	***0.002***	0.120	0.179	0.254	0.110	0.918	***0.036***	***0.033***
YST	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***
YST*TRT	***<0.001***	***0.005***	***<0.001***	***0.080***	***<0.001***	***0.039***	***0.008***	0.519	0.593	***0.003***
GA2										
TRT	***0.014***	0.327	***0.017***	0.587	***0.038***	0.135	***0.003***	0.567	0.238	0.590
YST	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***
YST*TRT	***0.016***	0.174	***<0.001***	0.263	***0.028***	***0.094***	***<0.001***	0.604	***0.014***	***0.012***

TRT: Treatments; YST: Years since initiation of treatments

[1] Shaded cells with bold-italic numbers are significant with alpha=0.10.

[+] From repeated measures model with unstructured covariance matrix.

Table 16. Significance of cumulative N dose (Pr>F) for 2002-2003 dormant season foliage mass and nutrient concentrations at three loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

	Pr>F[1]		
Variable	**FL1**	**GA1**	**GA2**
Foliage weight (g)	0.177	***0.033***	***0.056***
N (%)	***0.007***	***0.001***	***0.001***
P (%)	***0.031***	0.125	***0.044***
K (%)	0.107	***0.003***	***0.004***
Ca (%)	0.452	***0.045***	0.465
Mg (%)	0.158	0.168	0.676
S (%)	***0.025***	***0.008***	0.168
B ($g.kg^{-1}$)	0.174	***0.001***	***0.002***
Zn ($g.kg^{-1}$)	0.891	0.979	0.567
Cu ($g.kg^{-1}$)	0.962	0.704	***0.011***
Mn ($g.kg^{-1}$)	0.369	***0.042***	0.211

[1] Shaded cell with bold-italic numbers are significant with alpha=0.10.

Table 17. Average peak leaf area index at the 5th growing season and 5-year volume growth period at three loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

	Cumulative N dose (kg ha^{-1})						
Sites	**0**	**202**	**270**	**404**	**538**	**606**	**MSE+**
			5th growing season LAI				
Number of plots (n)	**2**	**2**	**4**	**4**	**2**	**2**	
FL1	3.3	4.2	4.5	4.5	4.3	5.3	0.182
GA1	1.4	2.5	2.2	3.0	2.7	2.9	0.124
GA2	1.6	2.8	2.5	2.8	2.8	3.1	0.056
			5-year volume growth (m^3 ha^{-1})				
Number of plots (n)	**2**	**2**	**4**	**4**	**2**	**2**	
FL1	85	117	121	125	128	141	60.24
GA1	40	69	76	89	87	92	87.21
GA2	32	76	74	79	84	89	107.05

+ Mean square error from model [4]. Standard errors = $(MSE/n)^{1/2}$.

Table 18. Comparison among linear and quadratic cumulative N dose effects across sites on peak leaf area index at the fifth growing season and 5-year cumulative growth at three loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

Parameter[*]	**Sites**[**]		
	FL1	**GA1**	**GA2**
(LAI at 5th growing season)			
R^{2}[+]	0.76	0.86	0.86
Intercept	3.43a	1.55b	1.64b
Slope	0.0040a	0.0052a	0.0041a
Quadratic	-0.00000277a	-0.00000459a	-0.00000343a
(5-year growth)			
R^{2}[+]	0.87	0.97	0.85
Intercept	87.99a	39.63b	35.47b
Linear	0.144a	0.183a	0.191a
Quadratic	-0.00011a	-0.00016a	-0.00018a

[*] All parameter estimates (Equations [4], [5], and [6]) were significant at 0.10.
[**] Same letter indicates no statistical difference for the parameter estimate among site at an alpha level of 0.10.
[+] For the purpose of computing R^2 an individual model was fit to each site.

Table 19. Summary of nutrient retranslocation after receiving repeated dosages of fertilizer at three loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

Cumulative N dose (kg ha^{-1})	Nutrient retranslocation (%)				
	N	**P**	**K**	**S**	**B**
FL1					
0	62	79	88	34	-24
202	59	66	82	34	1
270	60	64	84	34	10
404	47	52	77	25	-5
538	48	55	76	30	21
606	53	60	77	29	16
GA1					
0	67	63	95	39	10
202	71	68	95	45	18
270	71	69	92	43	32
404	69	70	87	44	34
538	69	74	90	47	36
606	68	64	80	36	37
GA2					
0	67	66	95	32	16
202	71	64	92	37	43
270	68	65	90	22	28
404	64	65	85	31	36
538	65	59	81	24	36
606	58	61	70	21	49
Overall mean	63	65	85	34	22

Table 20. Significance of cumulative N dose effect (Pr>F) on nutrient retranslocation at three loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

Nutrient	(Pr>F)[1]		
	FL1	GA1	GA2
N	***0.012***	0.526	***0.005***
P	***0.017***	0.241	0.638
K	***0.017***	***0.013***	***0.003***
S	0.439	0.371	0.302
B	0.322	***0.044***	0.336

[1] Shaded cell with bold-italic numbers are significant with alpha=0.10

Table 21. Summary of estimated litterfall and nutrient inputs after repeated doses of fertilizer at three loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

Cumulative N dose ($kg\ ha^{-1}$) up to end of 2002 growing season	**Litterfall and nutrient inputs**					
	Litterfall ($kg\ ha^{-1}$)	**N ($kg\ ha^{-1}$)**	**P ($kg\ ha^{-1}$)**	**K ($kg\ ha^{-1}$)**	**S ($kg\ ha^{-1}$)**	**B ($g\ ha^{-1}$)**
FL1						
0	9201	40	3.5	6.1	6.10	118
135	12283	57	4.9	7.9	8.60	164
202	12511	62	5.2	8.5	9.10	163
270	13172	66	5.6	9.0	9.87	193
404	14177	71	6.1	10.3	10.55	211
GA1						
0	9635	42	4.5	4.6	5.95	130
202	15347	72	7.1	9.8	9.50	214
270	16774	85	7.7	11.3	10.50	310
404	18859	96	8.9	13.3	12.60	332
538	18772	95	8.8	13.1	12.35	347
606	19392	113	9.6	16.9	13.90	386
GA2						
0	7835	35	3.6	3.2	4.90	114
202	16205	81	7.4	10.1	10.40	298
270	15986	83	7.2	11.0	10.40	345
404	16846	89	7.8	12.0	11.30	349
538	17678	94	8.4	15.5	11.85	419
606	18360	102	8.7	15.8	12.30	408

Table 22. Significance of cumulative dose N effect (Pr>F) on estimated litterfall mass and nutrients inputs (up to end of 2002) and Litterfall/Forest floor ratios at three loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

Variable	**(Pr>F)[1]**		
	FL1	**GA1**	**GA2**
Inputs through litterfall			
Weight	***<0.001***	***0.013***	***0.005***
N	***<0.001***	***0.007***	***0.003***
P	***<0.001***	***0.018***	***0.011***
K	***0.010***	***0.002***	***0.015***
S	***0.001***	***0.011***	***0.013***
B	***0.010***	***0.073***	***<0.001***
Litterfall/ Forest Floor ratios			
Weight	0.580	***0.036***	0.457
N	0.690	***0.023***	0.337
P	0.614	***0.009***	0.412
K	0.769	***0.011***	0.625
S	0.662	***0.030***	0.386
B	0.446	0.168	0.751

[1] Shaded cell with bold-italic numbers are significant with alpha=0.10

Table 23. Summary of litterfall/Forest floor ratios for weight and nutrients after repeated dosages of fertilizer at three loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1)

Cumulative N dose (kg ha^{-1}) up to end of 2002 growing season	Litterfall/Forest floor ratios					
	Weight	**N**	**P**	**K**	**S**	**B**
Florida FL1						
0	1.37	0.83	1.67	2.30	1.25	1.69
135	1.68	1.04	1.66	2.45	1.60	2.35
202	1.32	0.80	1.17	1.70	1.21	1.87
270	1.73	1.08	1.42	2.43	1.64	2.67
404	1.74	0.91	1.28	2.40	1.40	2.46
Mean	**1.57**	**0.93**	**1.44**	**2.26**	**1.42**	**2.21**
Georgia GA1						
0	1.72	1.21	1.99	2.80	1.54	2.82
202	1.75	1.20	1.76	3.10	1.49	2.34
270	1.48	1.04	1.53	2.58	1.25	2.85
404	1.56	0.91	1.34	2.38	1.24	2.20
538	1.03	0.53	1.01	1.60	0.77	1.63
606	1.29	0.69	1.21	2.15	1.17	2.15
Mean	**1.47**	**0.93**	**1.47**	**2.43**	**1.24**	**2.33**
Georgia GA2						
0	1.23	0.93	1.31	1.45	1.10	2.02
202	1.83	1.52	1.80	2.50	1.74	2.90
270	1.30	0.94	1.05	1.80	1.07	2.79
404	1.58	0.88	1.14	2.05	1.19	2.76
538	1.71	1.32	1.33	2.55	1.61	3.03
606	1.14	0.63	0.73	1.20	0.72	1.94
Mean	**1.46**	**1.04**	**1.22**	**1.93**	**1.24**	**2.57**

Table 24. Pearson correlation coefficients[1] between two independent measures of productivity (5-year growth and LAI) and soil, 2003 litterfall, forest floors and foliage characteristics across three loblolly pine stands in the flatwoods area of southeast Georgia and northeast Florida

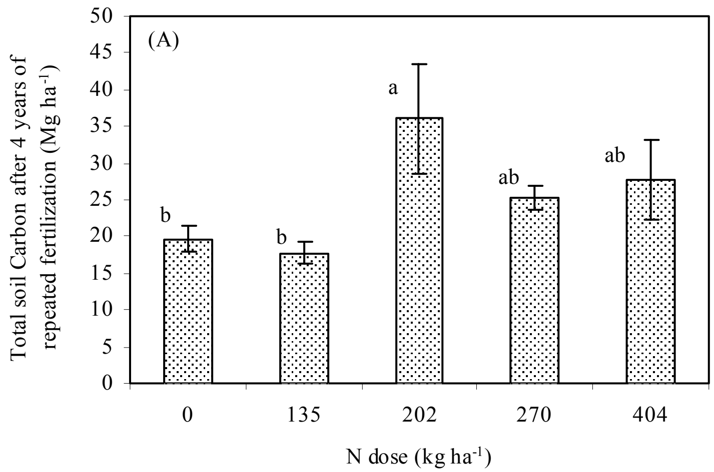
Variable	5-years	LAI5yst
LAI 5th growing season	***0.938***	
	Soil	
MEN	-0.165	-0.181
FEN	***0.649***	***0.647***
Total C	-0.133	-0.198
Total N	0.210	0.242
Extractable P	-0.104	-0.173
Extractable Cu	0.092	0.077
Extractable Mn	0.104	0.027
	Littefall	
Mass	***0.416***	***0.318***
N	***0.653***	***0.643***
P	0.105	0.015
K	***0.605***	***0.541***
Ca	***0.334***	***0.474***
Mg	-0.171	-0.114
S	0.050	0.025
B	-0.013	-0.068
Mn	***0.634***	***0.714***
Cu	0.165	0.187
Zn	-0.176	-0.066
	Forest Floor	
Total FF	-0.099	-0.217
	FF	L-layer
Mass	0.003	-0.162
C	***-0.691***	***-0.728***
N	0.202	0.123
C/N	***-0.395***	***-0.316***
P	-0.208	-0.323
K	***0.290***	***0.182***
Mg	-0.014	-0.024
Ca	***0.481***	***0.626***
S	***0.418***	***0.381***
Mn	***0.674***	***0.734***
Cu	0.019	-0.026
B	-0.097	-0.155
Zn	-0.006	0.151

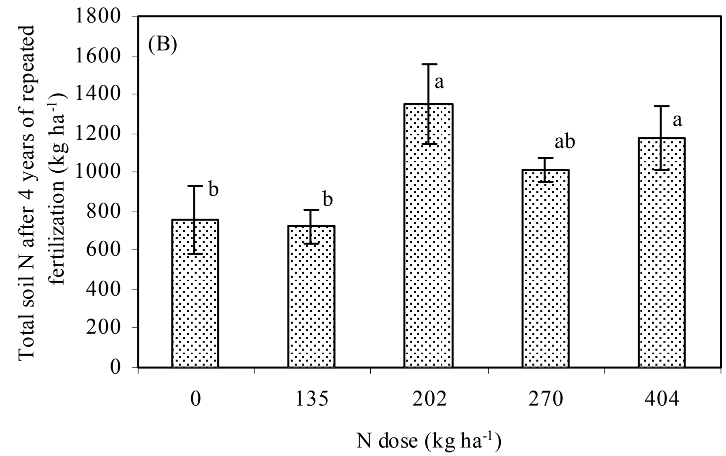
[1] Shaded cell with bold-italic numbers indicatessignificant correlation at an alpha level of 0.10.

Table 24. Continued

Variable	5-years	LAI5yst
	FF	F+H-layer
Mass	-0.135	-0.196
C	***-0.474***	***-0.442***
N	***0.426***	***0.322***
C/N	***-0.613***	***-0.501***
P	***0.327***	***0.321***
K	0.221	0.239
Mg	0.093	0.060
Ca	***0.463***	***0.607***
S	0.231	0.189
Mn	***0.409***	***0.331***
Cu	0.100	0.106
B	-0.083	-0.150
Zn	-0.238	-0.120
	Foliage	
Needle mass	***0.464***	***0.431***
N	***0.291***	0.190
P	***-0.334***	***-0.410***
K	***0.561***	***0.470***
Ca	***0.729***	***0.806***
Mg	***0.388***	***0.405***
S	-0.055	-0.118
B	-0.187	***-0.316***
Zn	0.099	0.097
Cu	***-0.738***	***-0.792***
Mn	***0.762***	***0.833***

[1] Shaded cell with bold-italic numbers indicatessignificant correlation at an alpha level of 0.10.





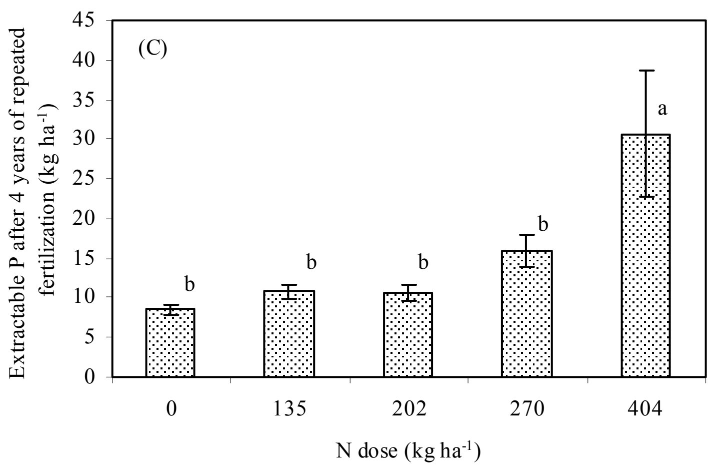


Figure 1. Total soil C, N and extractable P after four years of receiving repeated fertilization with different dosages of N and P at a loblolly pine plantation located in the Flatwoods area of northeast Florida (FL1). Lines represent standard errors.

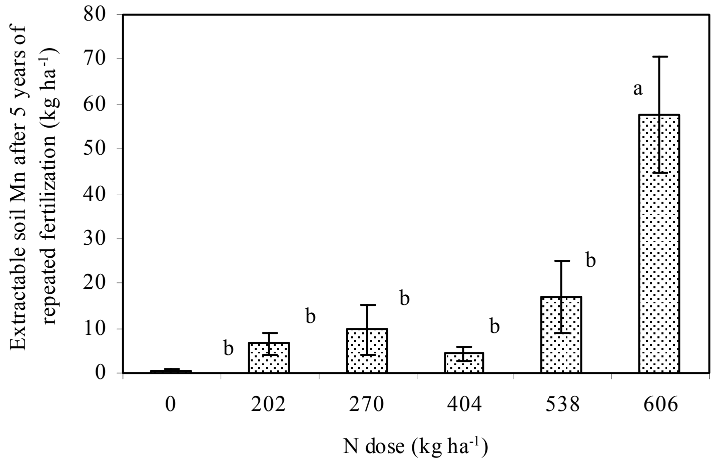
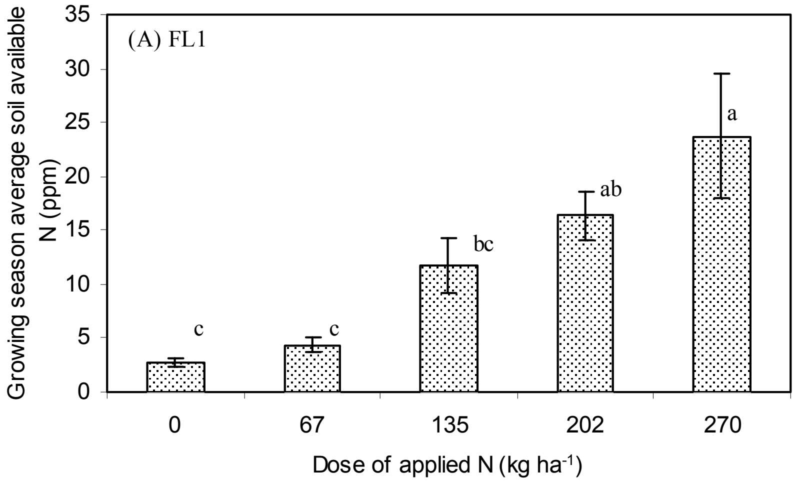
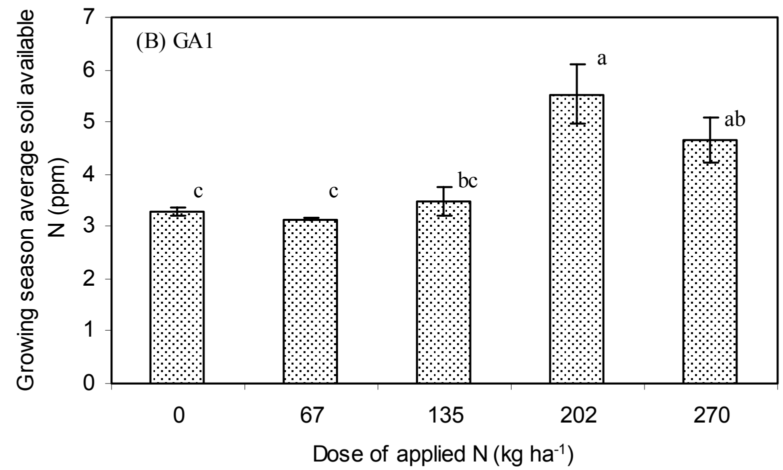


Figure 2. Extractable soil Mn after five years of repeated fertilization at a loblolly pine plantation located in the Flatwoods area of Southeast Georgia (GA1). Lines represent standard errors.





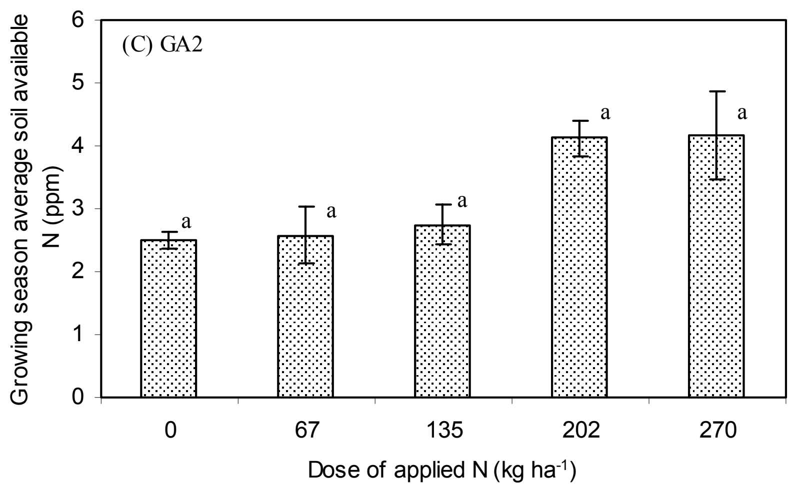


Figure 3. Growing season average N availability following N application at a Florida (FL1) site (A) and a year after N application at two Georgia sites (GA1 (B) and GA2 (C)). Lines represent standard errors.

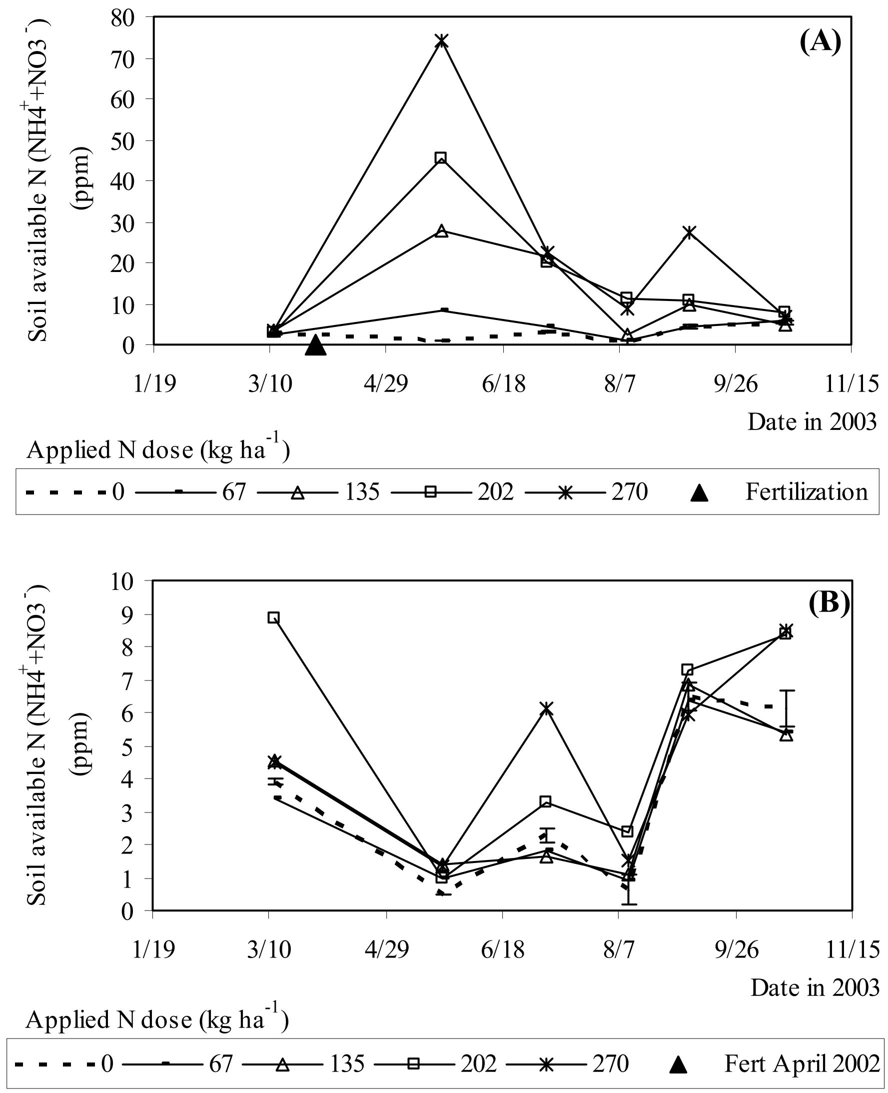


Figure 4. Changes in soil available N during the growing season after application of different doses of N soon after fertilization at FL1 site (A) and a year after at GA1 (B). Lines indicate standard errors.

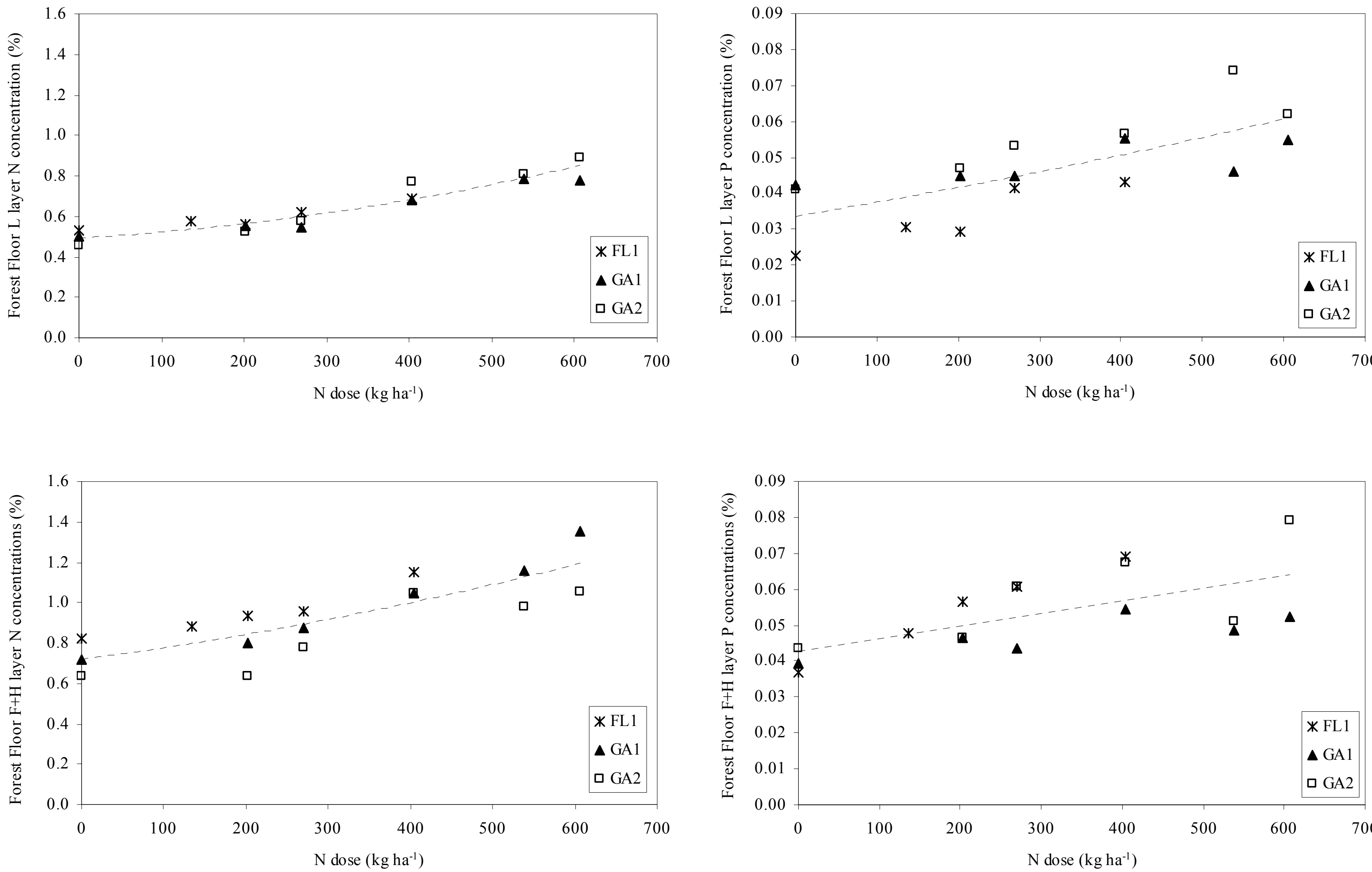


Figure 5. Nitrogen and P concentration in two different forest floor layers at three loblolly pine plantation in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1) after repeated applications of fertilizer.

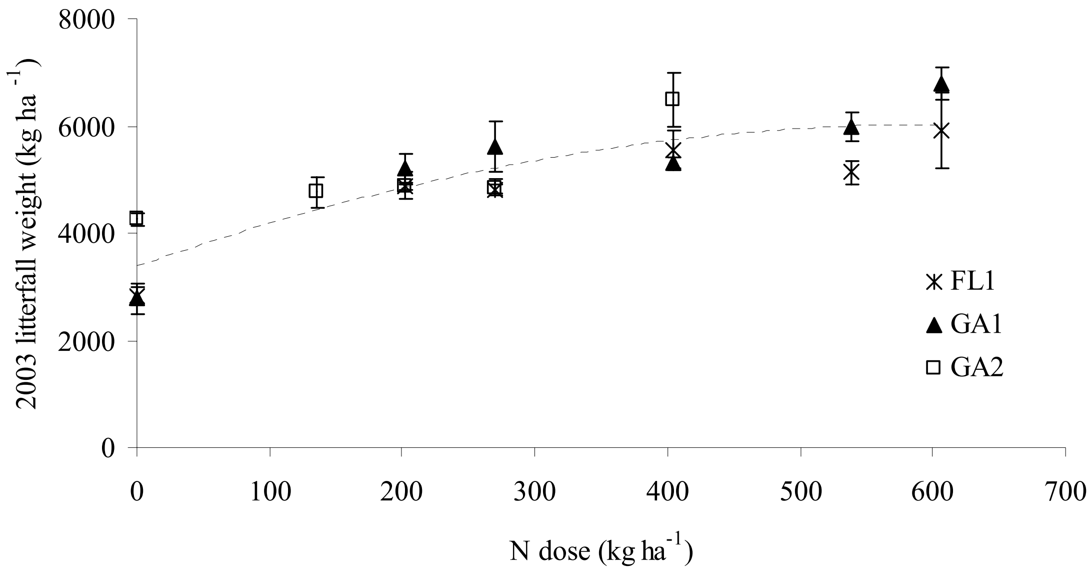


Figure 6. Litterfall weight vs. cumulative N dose at three loblolly pine plantations located in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1). Vertical lines represent standard errors.

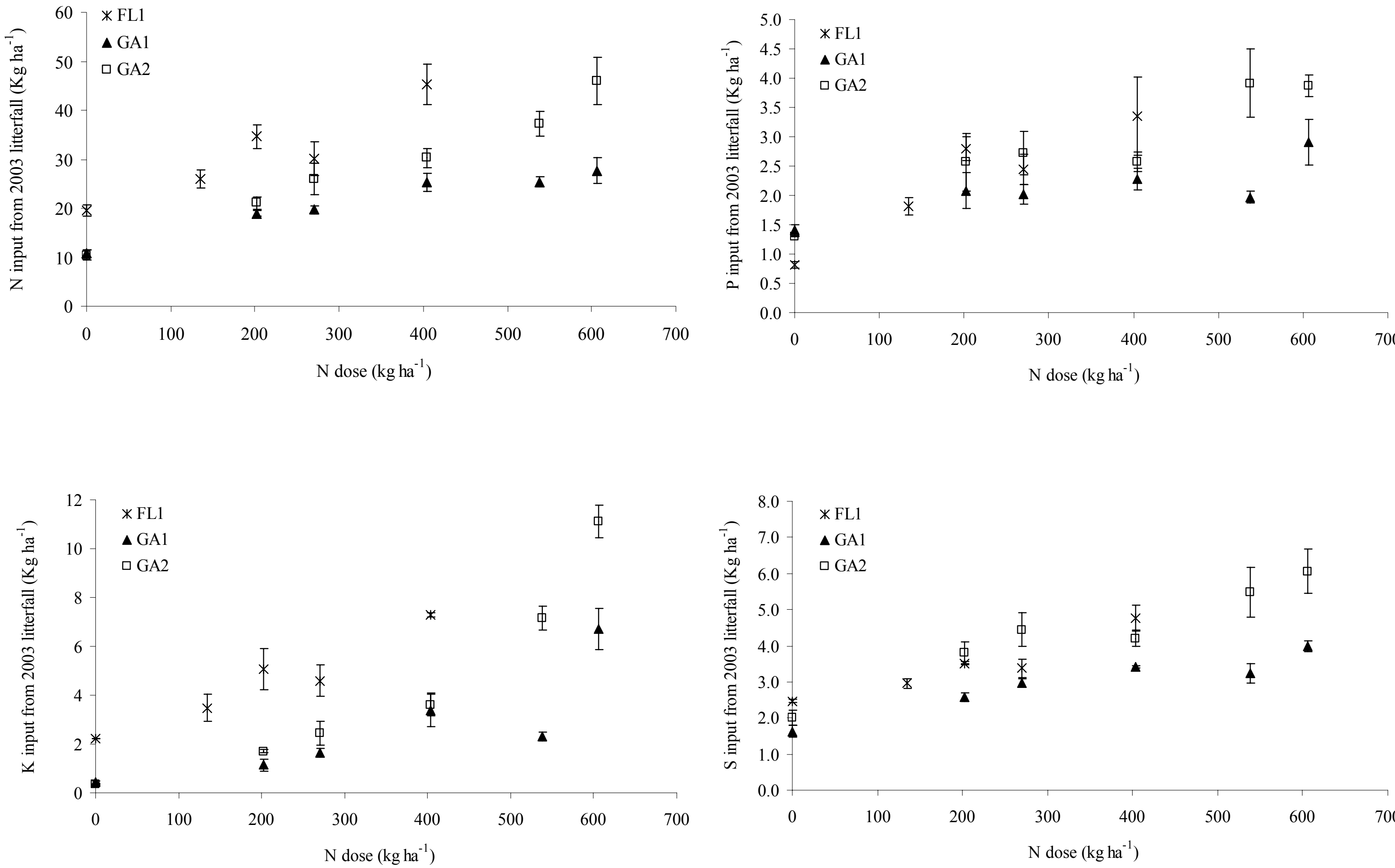


Figure 7. Nutrient inputs through 2003 litterfall as affected by cumulative N dose at three loblolly pine plantations located in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1). Lines represent standard errors.

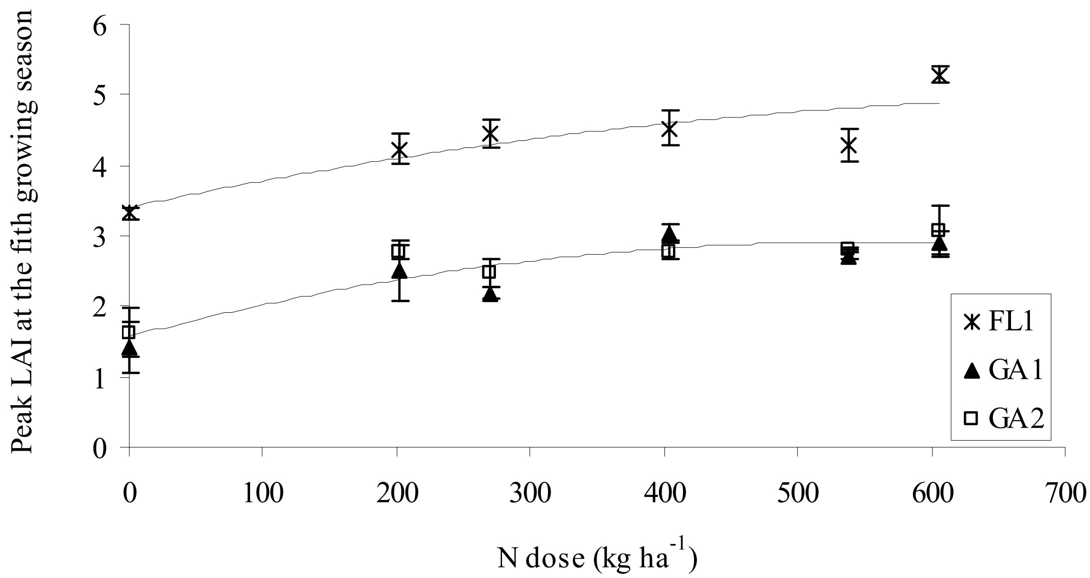


Figure 8. Peak leaf area index at the fifth growing season after treatment initiation with repeated dose of fertilizer vs cumulative N dose at three loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1). Vertical lines represent standard errors.

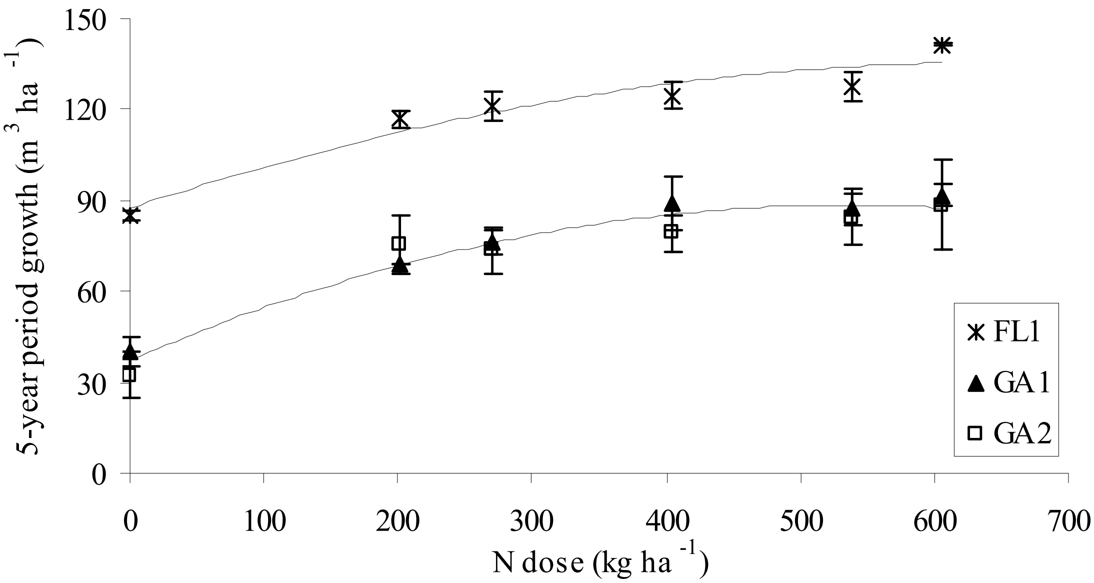
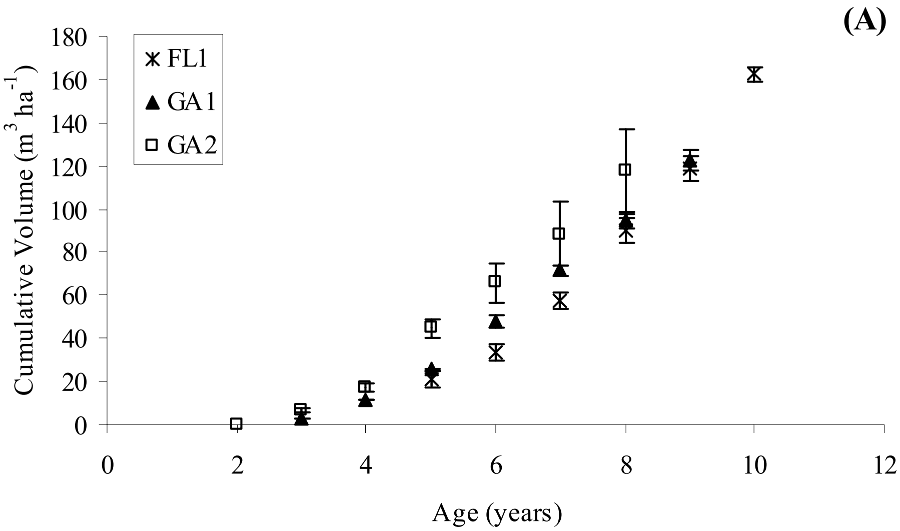


Figure 9. Five year period growth after repeated dosage of fertilizer vs. cumulative N dose for three loblolly pine plantation in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1). Vertical lines represent standard errors.



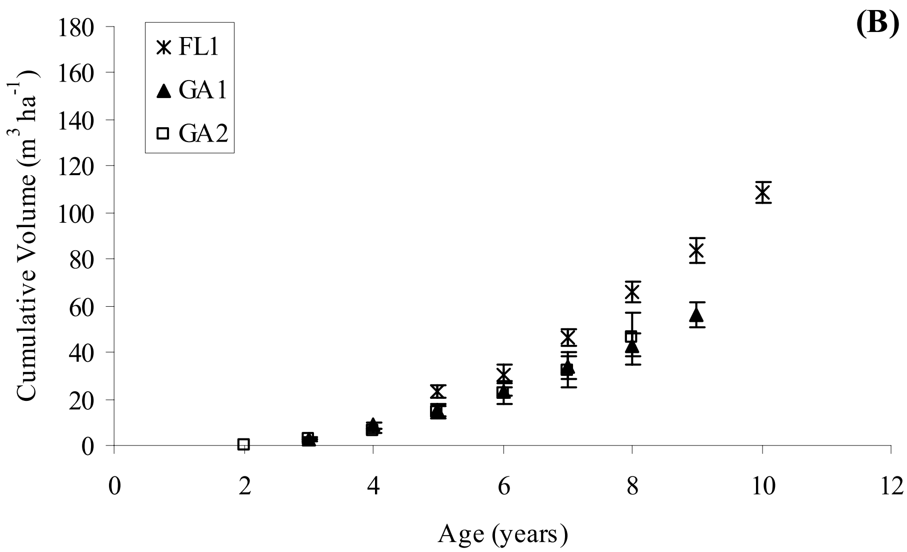


Figure 10. Comparison between average standing volume vs age for 606 kg ha^{-1} cumulative N dose plot (A) and control plot (B) at three loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1). Lines represent standard errors.

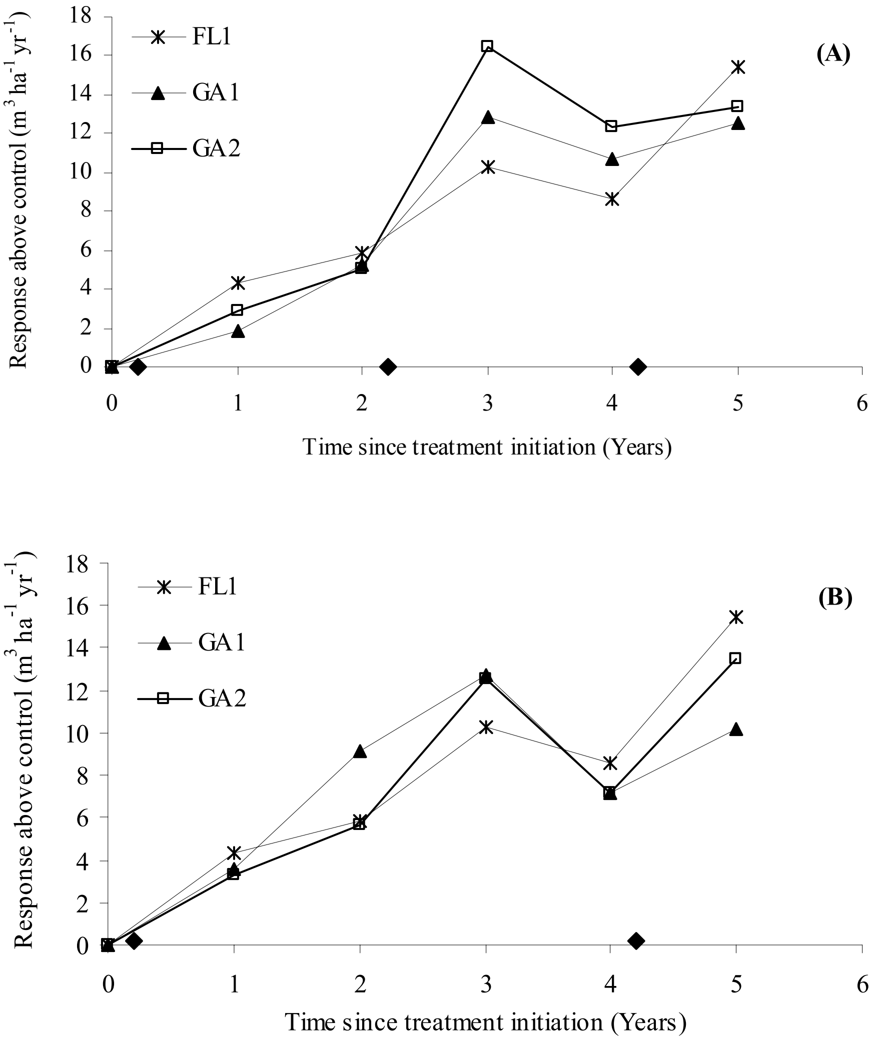
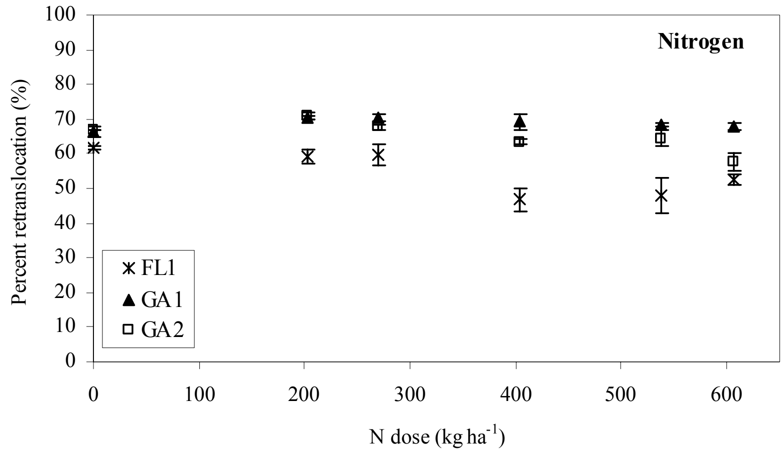
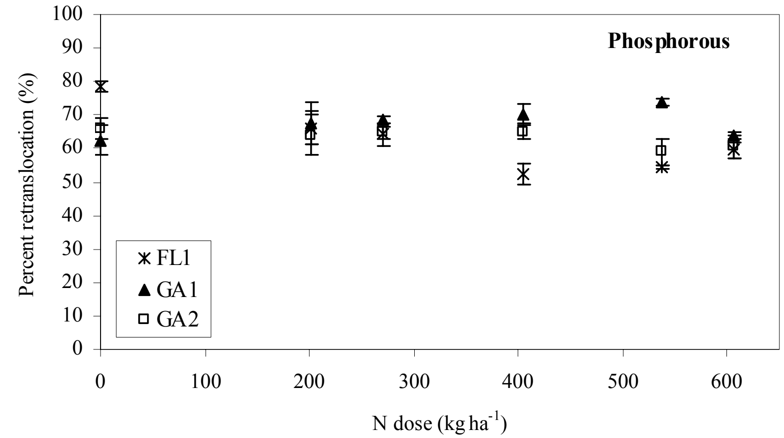


Figure 11. Average growth response above control for every other year (A) and every four year (B) frequencies of fertilizer application at three loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2), northeast Florida (FL1).

♦ = fertilization date.





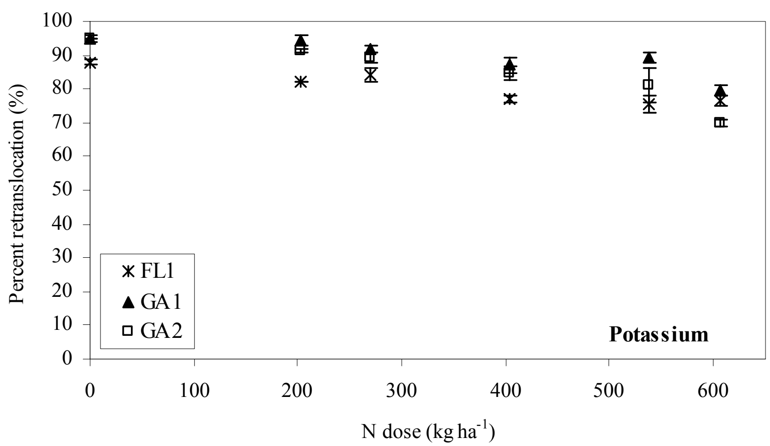


Figure 12. Relative retranslocation for N, P and K after repeated application of fertilizer at three different loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1). Lines represent standard errors.

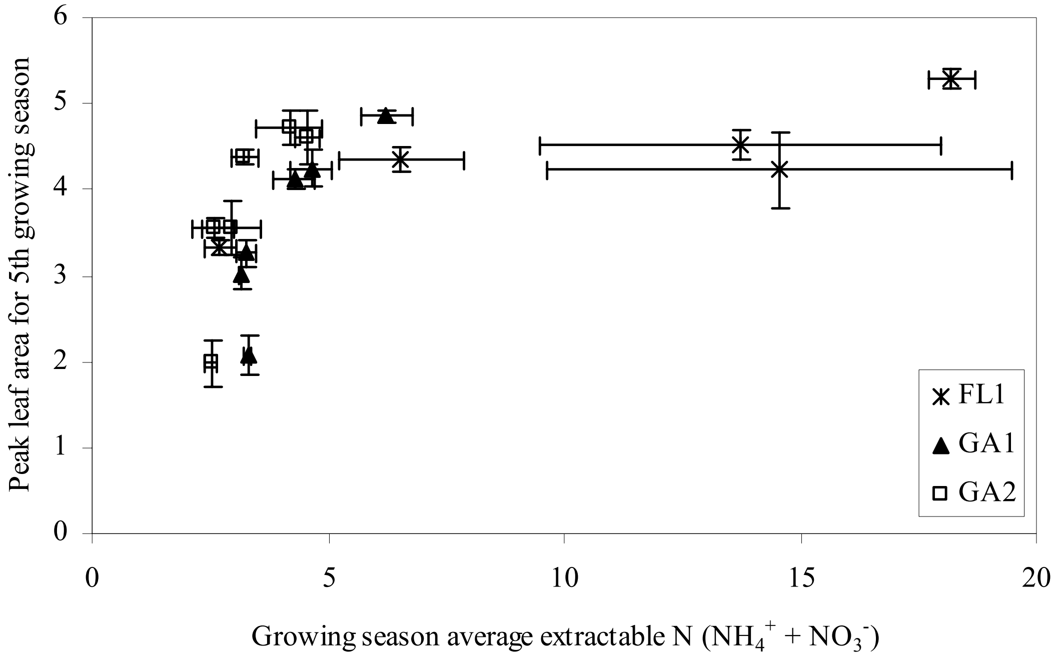
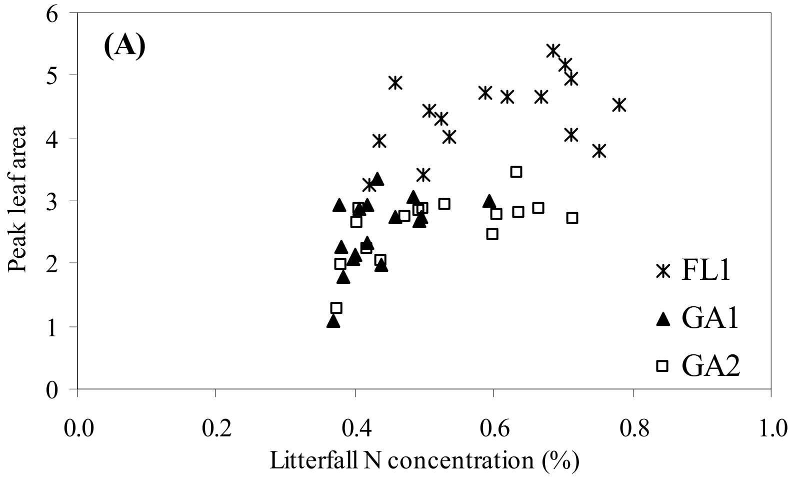


Figure 13. Peak leaf area index at the fifth growing season vs. growing season average extractable N (FEN) at three different loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1). Lines represent standard errors.



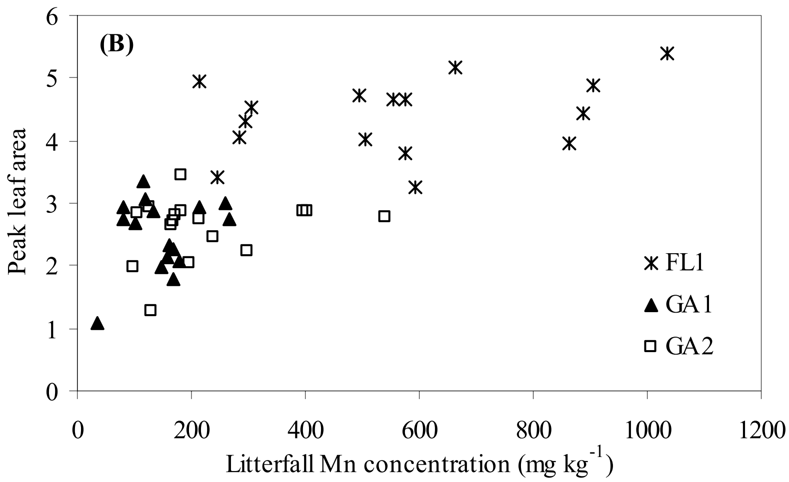


Figure 14. Relationship between peak leaf area and litterfall N (A) and Mn (B) concentrations at three different loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1).

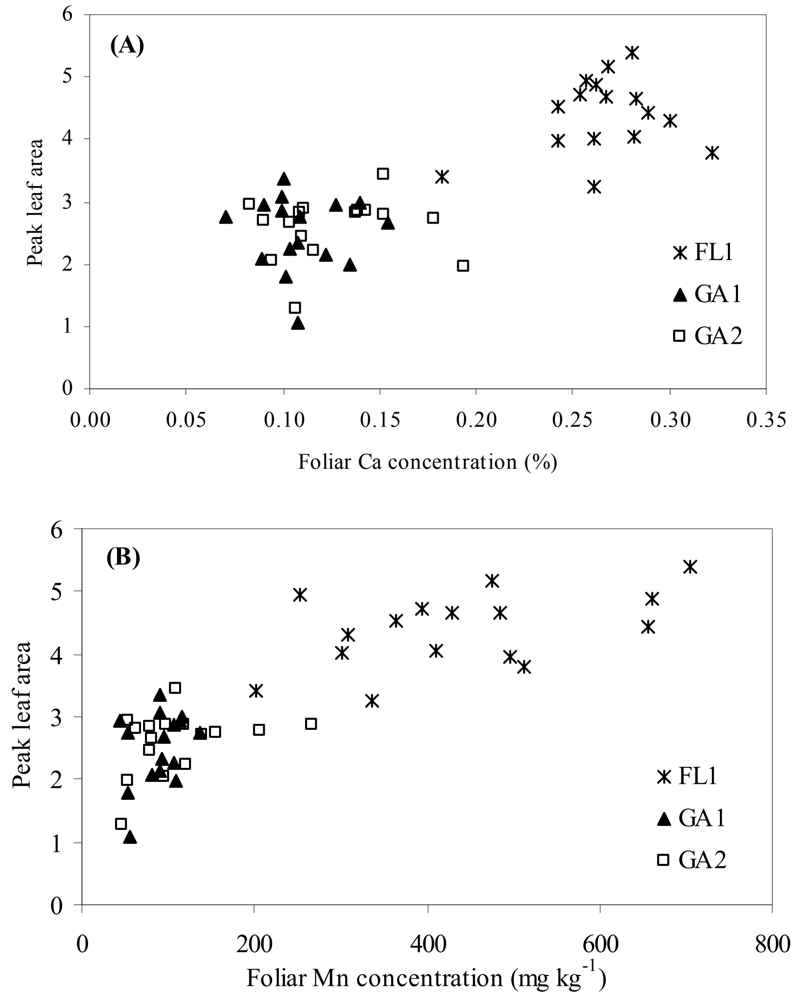


Figure 15. Relationship between peak leaf area and foliar Ca (A) and Mn (B) concentrations at three different loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1).

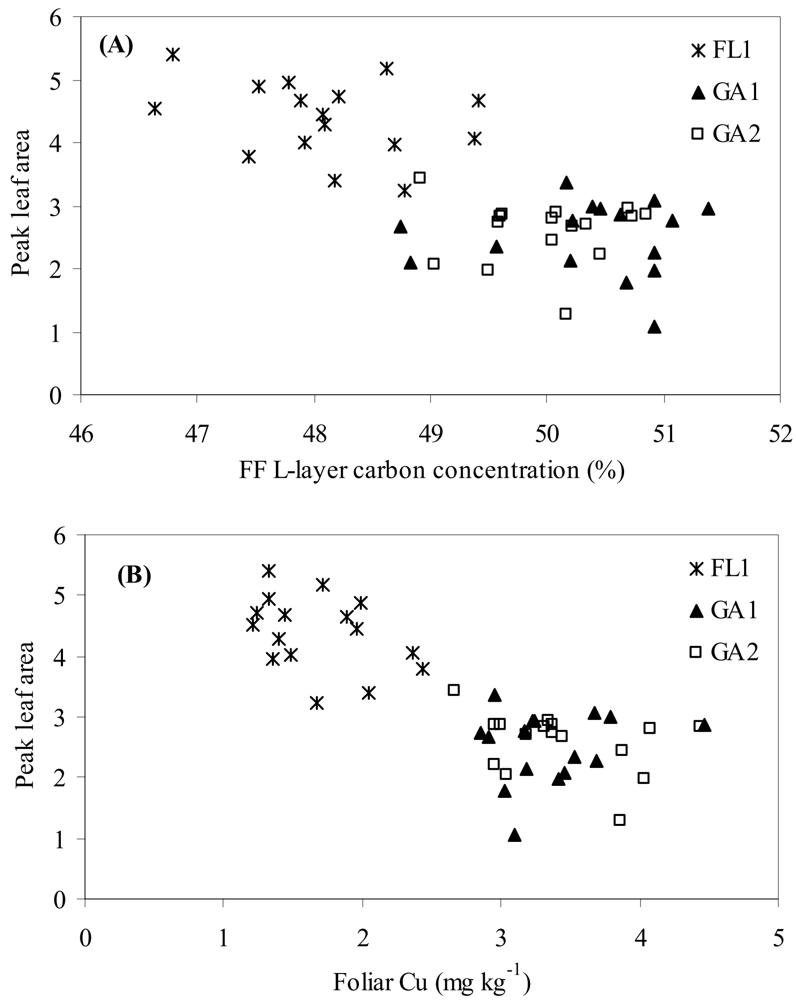


Figure 16. Relationship between peak leaf area and FF L-layer carbon concentration (A) and foliar Cu concentration (B) at three different loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1).

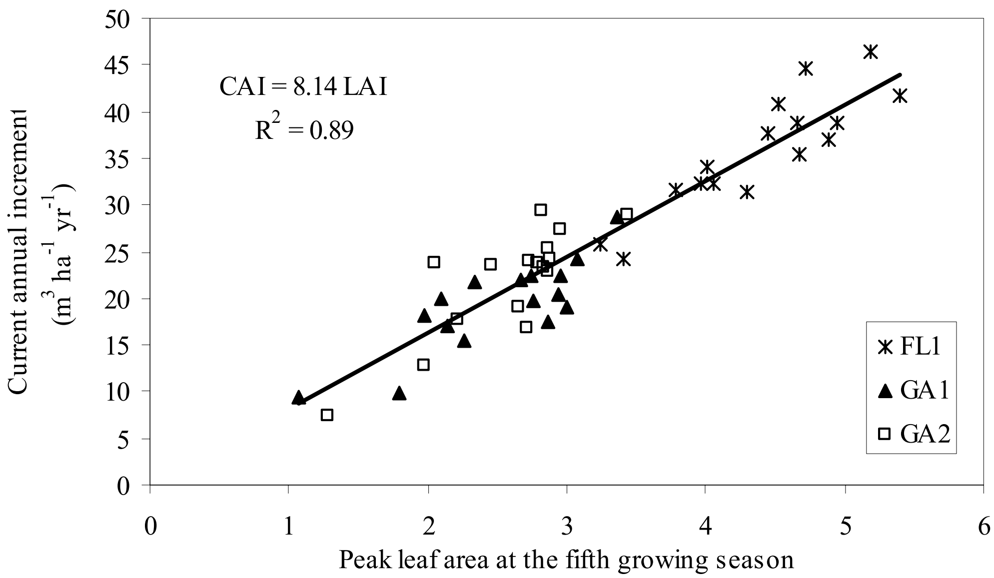


Figure 17. Current annual increment vs. peak leaf area index at the fifth growing season after repeated nutrient application at three different loblolly pine plantations in the flatwoods area of southeast Georgia (GA1 and GA2) and northeast Florida (FL1).

CHAPTER 2

Factors affecting growth efficiency in loblolly pine plantations across the southeast of US: A modeling effort

Abstract

Growth efficiency (GE) is the amount of stemwood produced per unit of leaf area. It is an index that accounts for the influences of both photosynthetic efficiency and carbon allocation on stemwood production. Factors affecting GE of loblolly pine plantations across southeast were examined using 86 different studies with different climatic, edaphic and stand conditions. Two modeling approaches were developed, one where GE would change with levels of LAI (non-linear using Gompertz model) and a second where GE was independent of the level of LAI (linear model). In both cases significant reduction in RMSE (>200%) was achieved when parameters in the models were allowed to be functions of edaphic, climatic and stand characteristics. Drainage class, subsoil texture, plantation age, precipitation and maximum temperature were significant predictors on both models. Current year climatic variables were better predictors of GE for that given year than long term climatic averages, indicating that the inter-annual variation in temperature and rainfall exerts great influence on GE. In both models, GE decreased with plantation age, however fine textured soils and fair drainage class (somewhat poor and poorly drained soils) increased GE. A Non-linear model is a more reasonable representation of what is known about the biology of the volume growth-LAI relationship.

1. Introduction

Forest productivity depends in part on resource availability and the efficiency that these resources are used to produce biomass. Stemwood production depends on how the biomass is partitioned or allocated into tree components (stem, branches, foliage, and roots). Since variation in wood production can be accounted for by the amount of light intercepted, which is principally a function of leaf area display (Cannell 1989, Landsberg and Gower 1997), stemwood growth efficiency (GE) is then normally defined as the amount of wood produced per unit of leaf area (Waring 1983). This measurement of growth efficiency is of particular interest to forest land management since stemwood is the principal product in forest harvest operations and stemwood growth is in essence the target when silvicultural treatments are applied. Recently, results from different long-term studies in the southern United States for loblolly pine (*Pinus taeda*) suggested that GE varies widely (Jokela and Dougherty 2004). Several factors may cause differences in GE, Albaugh et al. (2004) found that after 10 years of repeated nutrient and water additions in a loblolly pine plantation, 20% of the increment in GE was due to nutrient addition, while only 8% was attributable to water addition, both of the effects were additive. The change in GE was further attributed to a shift in the allocation pattern from highly respiratory tissues (e.g. fine roots) to photosynthesizing tissue (i.e. foliage). Other research (Samuelson et al. 2001) reported no effect of fertilization on GE in a 4-year old loblolly pine plantation. In studies focusing on other species, such as eucalypts, stem growth and GE were increased by water addition rather than nutrients (Linder et al. 1987).

Few attempts have been made to understand how GE changes on a more regional scale for loblolly pine. Sampson and Allen (1999) found that simulated production response increased from 30 to 60% when peak projected leaf area index (LAI) was raised from 2 to 4. The modeling effects found by Sampson and Allen (1999) suggests dramatic changes in GE across the southern US since different production responses were achieved by the same level of LAI.

Stemwood growth efficiency can be influenced by several factors including soil, nutrients, climate, stand development and genetics. From a practical stand point, climate ultimately determines the production potential for any forest species. Since a broad variability in climate is found where loblolly pine is grown, it is expected that climate has strong control over productivity (Sampson et al. 1996) and GE for this species. Leaf area index has been shown to change with climate (Hennessey et al. 1992) as well as tree growth and GE (Hennessey et al. 2004). These changes in growth and LAI as a consequence of climatic differences have an effect on GE locally but also across sites depending on other factors such as soil water retention and stand conditions. For eucalyptus plantations in tropical climates, it was found that stands with high resource use and high efficiency where located on sites that had lower mean vapor pressure deficits, less soil water stress, and smaller coarse root to above-ground biomass ratios (Stape et al. 2004). Stape et al. (2004) further concluded that productivity of fertilized tropical plantations of eucalyptus was most likely constrained by water supply, and that water supply substantially affected the efficiency of resource use as well as biomass allocation to roots, stems, and leaves, clearly indicating changes in GE for eucalyptus plantation with water supply.

Stand development has also been reported to affect GE. Burkes et al. (2003) found that GE increased with higher stand densities in young stands. Aging has also been shown to affect GE, Jokela et al. (2004) found that GE decreased with stand age in intensively managed loblolly pine stands in the lower coastal plain of Georgia. Similarly another study in north-central Florida showed declines of GE with age (Martin and Jokela 2004), in both cases stem growth and GE increased after re-fertilization suggesting that the decline was partially due to nutrient limitations. Thinning may also affect GE in loblolly pine plantations. Thinning in young loblolly pine plantations in southeastern Oklahoma reduced GE after the thinning operation; however GE was similar to unthinned plots after three years (Hennessey et al. 2004). Similar results were reported by Sword Sayer et al. (2004) where significant changes in GE were found three years after thinning when compared to values found a year after the treatment was imposed. Although GE values were not available on the year previous to the thinning treatment at Sword et al. (2004), values of GE two years prior to thinning were substantially higher than those a year after, indicating a negative thinning effect on GE soon after thinning but positive effect over a longer period of time. Since thinning often selectively removes the slower growing (and possible less efficient) trees, GE could be then highly improved after thinning operations. Similar results have been found for eucalyptus plantation (Stoneman and Whitford 1995).

Tree genetic make-up has been shown to impact stemwood production when growing under similar soil and climatic conditions. Strong fertilizer, genetic and genetic x fertilizer effects have been found in young loblolly pine plantations growing under intensive culture (FBRC 2005, McKeand et al. 2000). Changes in biomass allocation patterns with different families has also been reported in a controlled greenhouse environment (Li et al. 1991) and in the field (McKeand et al. 2000).

Results from the aforementioned studies indicate that GE may not be a static value but changes with site characteristics such as soil and climate as well as stand conditions, including genetics. It is unlikely that any single characteristics will explain most of the regional variation in GE due to important interactions among soil-climate-stand factors. For example, higher temperatures would increase transpiration rate, during this process the stomata opens allowing CO_2 to enter the leaves and get fixed, but CO_2 fixation also depends on an adequate water and nutrient supply. The capacity of the soil to supply water depends on soil physical characteristics such as texture, depth and drainage and the amount and distribution of precipitation. Soil nutrient supply on the other hand, depends greatly on the chemical characteristics and soil biology. These complex relationships make it challenging to develop models that explain regional differences in GE for loblolly pine.

The objective of the current study is to model the relationship between stem volume growth and LAI (or GE) and to identify what factors explain the variation in this relationship across the range of loblolly pine by utilizing observed data from studies across the Southeast US.

2. Methodology

2.1. Site Description

A set of 86 Forest nutrition Cooperative studies were selected for exploring the regional variation in volume growth and leaf area relationships (growth efficiency). The studies considered deal with silvicultural treatments such as fertilization, vegetation control and various treatment combinations. The basic criterion for study selection was that the study had to have at least four years of data since treatment. The studies selected included midrotation fertilization studies; Regionwide (RW) 13 (NCSFNC, 1989) and RW15 (NCSFNC, 1996), fertilization and vegetation control in midrotation stands or RW 17 (NCSFNC, 2001) and frequency and dose of fertilizer application in young loblolly pine plantations, or RW 18 (NCSFNC, 2004).

Studies included in this research were established from 1984 to 2000 across 10 states (Figure 1) in loblolly pine plantations covering different soil textural and drainage classes, climate, age, and stocking levels (Table 1). All studies were established after rigorous guidelines for site selection were met, providing minimization of within plot stand variation as well as soil variation within the study. Treated plots varied between 0.284 and 0.744 acres, with internal measurement plots varying from 0.021 to 0.234 acres. All studies were established using a randomized complete block design with two to four blocks.

Sites were grouped for analysis purposes into three drainage classes and two subsoil texture classes. Excessively well, well, and moderately well drained sites were grouped into one drainage class called “well drained” soils. Somewhat poorly and poorly drained soils were grouped into another drainage class termed “fair” and very poorly drained soils into a third class termed “poorly”. Similarly, sites were grouped into two subsoil textures classes. Clay, silty clay, silty clay loam, clay loam, and sandy clay loam were grouped into one textural class termed “fine” and all the other textures into a second class called "coarse texture". This grouping was performed after exploring the relationship between GE and these two edaphic variables (see Section 2.4).

2.2. Stand Data

Planted pines were measured in the dormant season (December to February) prior to study establishment. Some studies were measured annually and some were measured every other year following establishment, all studies had pretreatment and four year since treatment data. Assessments of total stem height (Ht) and diameter at breast height (dbh) were collected on all trees in the measurement plots. Individual total tree volumes were calculated using the following combined variable equation (NCSFNC 2004):

$$Volume_{ob} = 0.002\ (dbh^2\ Ht) \qquad [1]$$

Where $Volume_{ob}$ = Stem volume outside bark, cubic feet
dbh= diameter at breast height, inches
Ht=stem height, feet.

Total volumes were summed to obtain stand level volume estimates.

For this analysis, data from control (nontreated) plots were used from each study. These studies were all established in operational plantation so they were comparable in terms of their management history. Initial stand values for dbh, Ht, stand density in trees per acre (TPA), standing volume (Vol) and basal area (BA) were obtained. Initial volume growth (VG_i) was calculated as follows: on those sites with every other year measurement frequency, the periodic annual increment was calculated from the first 2-year period after establishment; for those sites with annual measurements, the current annual increment of the first year following establishment was used.

2.3. Climatic Data

Climatic data were obtained from the National Climatic Data Center (NCDC). Daily values from January 1960 to December 2004 for minimum temperature (Tmin), maximum temperature (Tmax) and precipitation (PPT) were obtained from the NCDC. The total number of weather stations available across the southeast was 5906. Vapor pressure deficit (VPD) was calculated from daily Tmax and Tmin values using the equation given by Allen et al. (1998).

To obtain a local estimate of these climatic variables for each study site, weather stations within a 31 mile radius from each study were selected (Figure 2). The selection was obtained by creating two geographic layers, one for studies and another for weather stations, each having latitude and longitude coordinates. Using Arc-GIS software, 877 weather stations were selected and assigned to individual sites. Depending on the proximity of the weather station to each site, several stations were assigned to one or more sites. The number of weather stations assigned to each site varied from 7 to 29, depending on the density of weather stations.

Climatic data were summarized in several stages. First the averages for each year from each weather station were calculated. Values for each study site were then obtained by averaging across all weather stations within a 31 mile radius of the site. For each climatic variable, two types of annual averages were obtained; whole year averages (WY) and growing season averages (GS). For the latter, only values from March through October were included. Since inter annual changes in the weather variables could potentially affect pine plantation growth, weather variables utilized in the modeling efforts included long term (LT) averages (25 years). The averages were calculated for the first-year after treatment (FIY) and for the four-year following treatment (FY).

2.4. Leaf Area Index Data

Peak of leaf area index, defined as the leaf area display of two needle cohorts, was measured on a set of 18 studies utilizing a Li-Cor LAI2000 plant canopy analyzer. This measurement of LAI varied in time for each site. Measurements were obtained between 1 and 4 years after establishment of the studies.

Peak of leaf area index was calculated for the other set of 24 sites using a litterfall vs LAI regression equation developed with unpublished data from a long term study located in Scotland county, NC (Appendix 1). At each study installation, between 5 and 12 littertraps (7.5-ft^2 each) were placed randomly within each measurement plot soon after establishment of the studies. The number of littertraps varied according to plot size. Litterfall was collected on a monthly basis for a minimum of two years. Samples were dried at 160 ^oF until a constant weight was obtained. A cohort was defined as the litterfall collected between March of one year and February of the following year. At least two cohorts were collected from each of the 24 study sites. Peak of LAI was then predicted from the litterfall vs LAI equation (Appendix 1) using the 2-year foliage cohort weight. This procedure allowed for comparable LAI estimates across all sites.

A total of 42 studies had measurements of LAI (complete data set). Since most of the LAI measurements were obtained during the first growing season except for few studies, initial values of leaf area index (LAI_i) were estimated for the sites with LAI values taken after the first growing season. First, actual growth efficiency (GE_a) was calculated by dividing volume growth from the same period that the LAI was measured over the value of LAI, then the following formula was used to obtained LAI_i:

$$LAI_i = VG_i / GE_a \qquad [2]$$

Equation [2] assumes that GE is constant within a site and that LAI and volume growth are linearly related. This may be a reasonable assumption given that: 1) only control plots were used, 2) Changes in volume growth from year to year for control plots were not significant and 3) LAI and stemwood volume growth are highly correlated (Allen et al. 2005).

Leaf area index was imputed for the remaining study sites (44 different sites). A set of variables were selected for the imputation process. Initially, 67 variables were included in the exploratory analysis. Factor analysis using principal components was used for grouping related variables (Appendix 2). Variables that accounted for most of the variation were then selected from these groups. This permitted a supervised selection of a set of plausible variables to be further explored. The general model used for variable selections at this stage of the analysis was as follow:

$$\mathrm{Ln}\,(VG_i/LAI_i) = f\,(\text{site, stand, weather, and foliar variables}) \qquad [3]$$

Variables kept in the model were those that were statistically related to and gave meaningful explanation about changes in GE (VG_i/LAI_i). Indicator variables (0-1) were used to describe characteristics such as soil drainage and texture classes. The set of variables selected in equation [3] was then utilized to generate multiple imputations of LAI values for the 44 sites without LAI measurements. Multivariate normality among all these variables was assumed. Utilizing SAS MI procedure (SAS Help and Documentation 2004), at each site 300 imputations were obtained using Markov Chain Monte Carlo

(MCMC) option. Variables included in the imputation procedure were: VG_i, subsoil texture class, drainage class, annual precipitation, average annual maximum temperature, stand age, foliar N concentration, Foliar P concentration, and needle weight. The multiple imputation technique has been utilized for research in other areas with high degree of success (Rubin 1987, Rubin 1996, Allison 2000 and 2001). As described by Rubin (1996) the goal of multiple imputations is to provide statistically valid inference of parameter estimates. This technique provides a useful strategy for dealing with data sets with missing values, where instead of filing in a single value for each missing value, the multiple imputation procedure replaces each missing value with a set of plausible values that represent the uncertainty about the correct value to impute (Rubin 1987, Allison 2001). These imputed data sets are then analyzed by using standard procedures such as analysis of variance and then combining the results from these analyses, valid statistical inferences can be achieved.

In our analysis, the multiple imputed data were then average by site to obtain an estimate of mean for LAI_i at each of the 44 sites with missing values. As described by Allison (2001), when using multiple imputed data, the parameter estimates allow for valid statistical inferences that properly reflect the uncertainty due to missing values.

2.5. Modeling Volume Growth Relationship with LAI

Two approaches were selected for modeling volume growth-LAI relationships, one a linear model where GE was not allowed to be function of the values of LAI, and the second approach where GE was allowed to change with levels of LAI in a non-linear model. In the first approach, volume growth was modeled utilizing the following equation.

$$VG_i = GE_p*LAI_i + e \qquad [4]$$

Where: VG_i= initial stemwood volume growth ($ft^3\ ac^{-1}\ yr^{-1}$)
GE_p= growth efficiency parameter (slope)
LAI_i= initial values of LAI
e= error term.

For the second approach, the nonlinear Gompertz model was used. After exploring different models such as, the Exponential saturation, Logistic, Von Bertalanffy and Richards, the Gompertz model fit the data better and had the desirable population growth characteristics such as: 1) The first derivative of the model (slope) increases with LAI to a peak and then decreases; 2) and inflexion point and 3) an asymptotic value. The general form for the Gompertz model is given by:

$$VG_i = Me^{-Ae^{-SLAI_i}} + e \qquad [5]$$

Where VG_i = stemwood volume growth ($ft^3\ ac^{-1}\ yr^{-1}$)
M= maximum value where Y is asymptotic, to be estimated
S= shape of the curve, to be estimated
A= parameter to be estimated
e= error term

For comparison purpose, Equation [4] was fitted using the average of the LAI_i and on each individual data sets (300 data sets) generated during the imputation process. In both cases SAS REG procedure was used and the parameter estimates from each individual data set was outputted. SAS MIANALYZE procedure was then used to combine the results and obtained the average of the parameter estimate (GE_p) and the standard error associated with the estimation of this parameter. All other Equations were fitted using the average LAI_i.

In an attempt to describe the variation found across all sites, Equations [4] and [5] were initially fitted and estimates for GE_p, M, and S obtained (mean models). The models were then modified (full models) so that GE_p parameter in Equation [3] and the M and S parameters in Equation [4] allowed to be linear functions of edaphic, stand, foliar and climatic variables (Table 2).

$$GE_p, M, S = f(\text{edaphic, stand, foliar and climate}) \quad [6]$$

Variable inclusion in the model was done interactively running SAS NLIN procedure (SAS Institute, 1992) to determine if each additional variable significantly reduced the variation found in initial volume growth in Equations [4] and [5]. That is if the parameter estimate for the included variable was significantly different from zero. Only variables with biologically meaningful interpretations were included in the model and only additive effects were accounted for in the Equation [6]. An alpha level of 0.10 was used to determine if parameter and/or models were significant.

3. Results

The location of the 86 studies provides a good range of loblolly pine plantations (Figure 1) and climatic conditions (Table 1). Long term average annual precipitation varied from 43.4 to 65.1 inches. Average daily minimum and maximum temperatures ranged from 44.5 to 59.3 ^{o}F and from 68.3 to 79.9 ^{o}F respectively.

Stands included in this study ranged from 2 to 25 years of age with a wide range of stocking levels from 131 to 938 trees per acre and basal area from 0 to 137 $ft^2\ ac^{-1}$. Sites also varied in soil characteristics with pH and base saturation ranging from 3.8 to 7.3 and 3.5% to 96.7%, respectively (Table 1). Levels of leaf area index and volume growth also varied greatly. Measured LAI ranged from 0.35 to 3.78 while the inclusion of imputed values of LAI made it varied from 0.18 to 3.78 (Table 1). Initial volume growth across the 86 studies was highly variable, ranging from 9 to 386 ft^3 ac^{-1} yr^{-1}. Foliar nutrient concentrations ranged from 0.82 to 1.37% for N, 0.06 to 0.15% for P and 0.20 to 0.73% for K. These values of foliar nutrients show a wide range of conditions, including stands with and without nutrient deficiencies (Allen, 1987).

Average volume growth across sites followed the expected trajectory when graphed against age (Figure 3). Volume growth peaked at an approximate age of 9 years, declining after this age. This is typical for annual growth curves for plantation loblolly pine and the data from these studies followed this trend.

3.1. Growth Efficiency and LAI Imputation

Growth efficiency was significantly higher for sites with a fair drainage class with 120 ft^3 ac^{-1} yr^{-1} per unit of leaf area, followed by poorly drained sites with 89 ft^3 ac^{-1} yr^{-1} per unit of leaf area and well drained sites with 88 ft^3 ac^{-1} yr^{-1} per unit of leaf area (Figure 4A). Similarly, subsoil texture classes showed significant differences, with higher GE value for fine textures (Figure 4B).

Drainage classes, subsoil texture class, current annual precipitation, mean annual maximum temperature and plantation age, explained 60% of the variation in GE for the complete data set (42 studies). No other variables included in the analysis made significant improvement to this relationship. As judged by the Mallows C(p) value, the model did not significantly increase the variation explained after 6 to 7 parameters were included in the model (Figure 5). The final form of the Equation [2] is as follow:

$$Ln(VG_i/LAI_i) = b_0 + b_1\, DC_2 + b_2\, STC + b_3\, Age + b_4\, FIY\_WY\_PPT + b_5\, FIY\_WY\_Tmax + \varepsilon \qquad [7]$$

Where: $Ln(VG_i/LAI_i)$= Natural logarithm of VG_i/LAI_i
DC_2= dummy variable for drainage class 2 (Fair),
STC= dummy variable for subsoil texture class 1 (fine texture soils),
Age= Plantation age (years),
FIY_WY_PPT= Current year annual precipitation (inches),
FIY_WY_Tmax= Current year mean annual maximum temperature (^oF),
b_0, b_1, b_2, b_3, b_4, b_5, b_6= Parameters to be estimated
ε= error term

The root mean square error (RMSE) for this model was 0.165 ft^3 ac^{-1} yr^{-1} per unit of leaf area.

All the variables in Equation [7] were included in the imputation procedure. The average of the LAI including imputed values was 1.94 which was slightly lower than the complete data set which averaged 2.03 (Table 1). The standard deviation of the imputed LAI values and of the LAI values from the observed data was 0.71 and 0.70 respectively. Figure 6 showed that the relationship between LAI and VG was maintained.

3.2. Stemwood Volume Growth vs. LAI Model

Only edaphic, climate and stand characteristics were significant in both the linear and non-linear models. No foliar variable introduced in the models significantly improved the model performance. Both mean and full linear models were highly significant ($p<0.001$). The parameter estimate for the mean linear model (GE_p=94.422) was slightly higher when using the average of the 300 imputed values of LAI as compared to the combined parameter estimate (GE_p=93.560) from MIANALYZE. In contrast, the standard error (3.008) was slightly higher for the combined parameter estimate from MIANALIZE as compared to the standard error (2.1296) for the parameter estimate from the model fitted with the average LAI values.

The RMSE for the mean linear model was 40.8, but significant reduction (16.2) was achieved when GE was modeled as linear functions of edaphic, climate and stand characteristics (Table 3). The linear function for GE_p parameter was:

$$Ln(GE_p)= \beta_0 + \beta_1 {*}DC_2 + \beta_2 {*}STC + \beta_3 {*}FYI\_WY\_Tmax + \beta_4 {*}FIY\_WY\_PPT + \beta_5 {*}(Age) + \varepsilon \qquad [8]$$

Where: $Ln(GE_p)$= the natural logarithm of GE, and

b_i = parameters to be estimated, and all other variables were as previously defined.

When Equation [8] was applied to individual sites, predicted values of GE_p varied from 67 to 135 $ft^3\ ac^{-1}\ yr^{-1}$ per unit of leaf area with a mean value of 96 $ft^3\ ac^{-1}\ yr^{-1}$ per unit of leaf area (Table 4)

Similarly, non-linear models were highly significant ($p<0.001$). The RMSE decrease from 39.5 $ft^3\ ac^{-1}\ yr^{-1}$ per unit of leaf area for the nonlinear mean model to 13.0 $ft^3\ ac^{-1}\ yr^{-1}$ per unit of leaf area for the full model when the S and M parameters were modeled as linear functions of edaphic, climate and stand characteristics (Table 3). The shape parameter S, was affected only by drainage, texture and mean annual precipitation. In addition to them, the maximum asymptotic parameter, M, was also affected by mean annual maximum temperature of the current year and the age of the plantation. The linear functions for these two parameters are given by:

$$M= \alpha_0 + \alpha_1 {*}DC_2 + \alpha_2 {*}STC + \alpha_3 {*}FYI\_WY\_Tmax + \alpha_4 {*}FIY\_WY\_PPT + \alpha_5 {*}(1/Age) \qquad [9]$$

$$S= \alpha_0 + \alpha_1 {*}DC_2 + \alpha_2 {*}STC + \alpha_4 {*} FIY\_WY\_PPT \qquad [10]$$

Since all parameter estimates were positive (Table 3), steeper curves with higher maximum asymptotic values would be achieved on those sites with fine textured subsoil, fair drainage and higher annual average precipitation. Additionally, the asymptotic maximum value (M) would be higher in young plantation growing in places with higher temperatures.

When Equations [9] and [10] were applied to individual sites, estimated of M parameter varied from 356 to 615 with a mean of 409, while the estimated S parameter ranged from 0.769 to 1.516 with a mean value of 1.143 (Table 4).

In both cases, the linear and non-linear full models accounted for more variation in the data than the mean models. The standardized residuals also had more constant variance in the full model when compared to the mean models (Figure 7).

4. Discussion and Model Performance

The relationship between LAI and stemwood growth, as suggested by the results presented here, changed with over the various site conditions and stand characteristics such as plantation age (Table 3). The natural distribution of loblolly pine encompasses a wide range of site and climate conditions that ultimately influences stand development and growth (Sampson and Allen 1999). While some of these variables can be easily manipulated others can not. The understanding of how much these variables affect tree growth is important in order to have a better understanding of the regional spatial growth pattern and responses to silvicultural treatments.

Depending on the assumed VG-LAI relationship, GE will also change with leaf area values (Figure 8). GE has been reported to have non-linear (Martin and Jokela 2004, Sword et al. 2004, Dean and Baldwin 1996) and linear (Albaugh et al. 2004) trend on intensively managed loblolly pine stands. Even though Albaugh et al. (2004) reported linear relationships between volume growth and LAI, these relationships changed with treatments which influenced LAI levels. Looking at the whole range of LAI reported by Albaugh et al. (2004), it is clear that GE changed with levels of LAI; however, the asymptotic behavior of the VG-LAI relationship described here and by others has not been reached. Values of LAI reported by Albaugh et al. (2004) were not larger than 3.5, range at which both linear and non-linear models reported here behaved relatively linear with little difference in GE (Figure 8b). From a biological stand point, it is expected that GE would decrease at higher LAI values, this is because of the increase in respiration cost and water use associated with larger LAI value since foliage is the highest maintenance respiration cost tissue of loblolly pine (Vose and Allen 1988, Maier et al., 2004),

Plantation age was a significant predictor in both the linear and nonlinear models (Table 3). In both cases, GE decreased with age but reductions in GE were more pronounced with the nonlinear model (Figure 9). With the non-linear model, GE declined sharply in young plantations and became practically asymptotic after age 12. This agrees with published results from intensively managed loblolly pine plantations reported by Martin and Jokela (2004) as well as with other species. Several hypotheses have been proposed for the decline in volume growth and GE with the age of a plantation, including 1) increases in the ratio of respiring to photosynthesizing tissue in aging trees, 2) increase in xylem hydraulic resistance resulting in higher stomatal limitations to carbon gain in taller trees, 3) decline in soil nutrient supply, 4) increased mortality in aging stands, 5) allocation of carbon to reproduction at the expense of growth in maturing stands, and 6) age-related changes in gene expression and inherently slower growth in older tissue (Ryan et al. 1997).

Results presented here suggest that climatic variables exert strong influence on the VG-LAI (GE) relationship. Maximum temperature and precipitation were significant predictors in both models (Table 3). When selecting variables for these models, the current year averages of the climatic variables were better predictors than four year average or long term average. This would imply that the variation from year to year is important in defining the VG (and GE) for any particular site. Year to year variation in climatic variables has been reported to affect stand growth and leaf area in loblolly pine plantations (Sword et al. 2004, Jokela et al. 2004, Hennessey et al. 1992, Hennessey et al. 2004, Dougherty et al. 1995) as well as other species (Raison and Myers 1992, Snowdon et al. 1999, Snowdon 2001). Stemwood growth efficiency increased with increasing values of annual precipitation and temperature (Figure 10). Changes in GE with precipitation were higher for the linear model than for the nonlinear. In the nonlinear model, the more dramatic changes in GE were attributed to LAI (Figure 10), GE decreased by approximately 40% when changing LAI from 2 to 4. Major changes in VG and GE has been shown previously when with LAI changes (Vose and Allen 1988, Sampson and Allen 1999, Jokela and Martin 2004, Sword et al. 2004, Hennessey et al. 2004)

Edaphic variables were also important predictors in the VG-LAI models. The drainage class fair and soil texture class fine were significant in both of the full models (Table 3). Both variables affected the GE_p parameter in the linear model and the asymptotic maximum M and shape S parameters in the nonlinear model. For the nonlinear model, the major effect of these two edaphic variables was reflected on the shape parameter (Equation [9]), i.e. how VG approaches the maximum asymptotic value. Growth efficiency was higher on sites with fair drainage and/or fine textured soils, however the difference decreased with an increase in LAI values in the nonlinear model (Figure 11 and 12).

Stemwood growth efficiency was higher at lower LAI (Figures 11 and 12). This behavior may help to explain growth response patterns to silvicultural treatments observed in young plantations where canopy closure has not been achieved. For example, bedding improves drainage and so higher growth rates are observed due to better conditions for tree growth (soil aeration) and improvement in GE with better drainage. The typically faster growth rates found in soil with fine texture as compared to coarse soil texture due better water retention and nutrient availability but also higher GE, e.g. higher volume growth per unit of leaf area.

None of the foliar and soil nutrient variables were good predictors in any of the models considered. One reason for this could be that LAI is already an integrated parameter acting as a surrogate for nutrient availability. Research across the region where loblolly pine is cultivated demonstrates that the most important variable impacting VG is LAI, which is a reflection of nutrient availability (Vose and Allen 1988, Sampson and Allen 1999, Jokela and Martin 2004, Sword et al. 2004, Hennessey et al. 2004, Samuelson et al. 2004). It has been also demonstrated, that fertilization altered GE (Jokela and Martin, 2004 Albaugh, et. al., 2004) and it is hypothesized here that the increase in nutrient availability due to fertilizer application could potentially impact the maximum (M) and the shape (S) of the curve since well fed trees could be more efficient in capturing light at comparable LAI levels. Since this factor could not be included in the model, it could not be tested.

5. Conclusion

Results presented here and by other researchers invariable imply that GE is a dynamic rather than static stand parameter. Changes in GE were due to stand aging, drainage, soil texture and climate. Long term climatic data should give a rough estimate of GE for any given site, but users must be aware that inter annual variation of climate affects the VG-LAI relationship.

Edaphic characteristics also exert changes in GE. Fine soils with good hydrological conditions increased GE under any given LAI level as compared to coarse soils with less favorable hydrological conditions (excessively drained and very poorly drained).

Depending on the assumed VG-LAI relationship, the GE may or may not fluctuate with levels of LAI. Since the nonlinear model gives a more realistic representation of the biology of the relationship, it is preferred over the linear model. The resulting variation in GE represented in both linear and nonlinear models demonstrates that the stand developmental stage as well as climatic and edaphic factors must be considered whenever the relationship between productivity and LAI is assessed.

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Table 1. Descriptive statistics for the 86 studies used in this research.

Characteristics	Mean	Minimum	Maximum
Establishment year		1984	2000
Initial stand values			
Age (years)	12	2	25
Diameter (in)	5.2	0.0	8.8
Height (ft)	33.2	4.8	57.2
Volume (ft^3 ac^{-1})	1075	0	2203
Basal area (ft^2 ac^{-1})	77	0	137
Trees per acre	526	131	928
LAI	2.03	0.35	3.77
LAI imputed	1.94	0.18	3.77
Growth (ft^3 ac^{-1} yr^{-1})	185.8	9.0	386.2
Foliar characteristics			
N (%)	1.10	0.82	1.37
P (%)	0.10	0.06	0.15
K (%)	0.41	0.20	0.73
Soil characterstics			
pH	4.8	3.8	7.3
Total N (%)	0.09	0.02	0.27
Base Saturation (%)	41.9	3.5	96.5
Weather variables (Long term annual averages)			
Precipitation (in)	52.8	43.4	65.1
Max. Temperature (^oF)	75.0	68.3	79.9
Min. Temperature (^oF)	51.6	44.5	59.3
Vapor pressure deficit (mbar)	8.7	7.0	9.9

Table 2. Independent variables used in the modeling process, organized by edaphic, climate, foliar and stand type categories.

Group	Variables
Edaphic	Total soil C and N, extractable nutrients (P, K, Ca, Mg, K, Mn, Zn, Cu), soil nutrient ratios, subsoil texture, surface texture, pH, Cation exchange capacity, base saturation, soil acidity
Climatic	Whole-year and growing-season rainfall, temperature (mean, maximum and minimum), VPD for current-year and long-term averages.
Stand	Initial values for diameter at breast height, height, stand density, volume, volume growth, mean annual increment for volume and basal area, leaf area index.
Foliar	Needle weight, Foliar nutrients (N, P, K, Ca, Mg).

Table 3. Parameters estimates and standard errors for mean and full models.

Parameter (definition)	Parameter Estimate	Standard Error	RMSE ($ft^3\ ac^{-1}\ yr^{-1}$ per unit of leaf area)
Linear models			
GE_p[@]	93.560	3.0081	
GE_p[@@]	94.422	2.1296	
Mean model[+]			**40.8**
β_0	2.6422	0.3882	
β_1	0.2208	0.0279	
β_2	0.2531	0.0390	
β_3	0.0176	0.0049	
β_4	0.00824	0.0017	
β_5	-0.0088	0.0033	
Full model[++]			**16.2**
Nonlinear models			
M	321.5	37.4326	
A	2.9994	0.5492	
S	0.9156	0.2079	
Mean model[*]			**39.5**
α_0 (Intercept)	0.3315	0.1044	
α_1 (Drain class, Fair)	0.2267	0.035	
α_2 (Subsoil texture class, Fine)	0.2056	0.0401	
α_3 (Current mean annual temperature)	4.7629	0.3123	
α_4 (Current annual precipitation)	0.0114	0.002	
α_5 (inverse of plantation age)	462.8	123.3	
A	3.2282	0.1708	
Full model[**]			**13.0**

[+] Equation [4]
[++] Equation [8]
[*] Equation [5]
[**] Equations [9] and [10]
[@] Parameter estimate and standard error obtained by combining the output from fitting the mean linear model [4] 300 times (300 imputed data sets) and combining the output using Proc MIANALYZE.
[@@] Parameter estimate and standard error obtained by fitting the mean linear model [4] with the average LAI from 300 imputations.

Table 4. Summary of the variation in the values of the parameters when Equation [7], [8] and [9] were applied using individual sites characteristics.

Equation #	Parameters	Mean	Standard deviation	Min	Max
			Linear[+]		
7	$\mathbf{GE_p}$	96.0	16.632	67	135
			Non-Linear[*]		
8	**M**	409	39.25	356	615
9	**S**	1.143	0.164	1.516	0.769

[+] Equation [4]
[*] Equation [5]

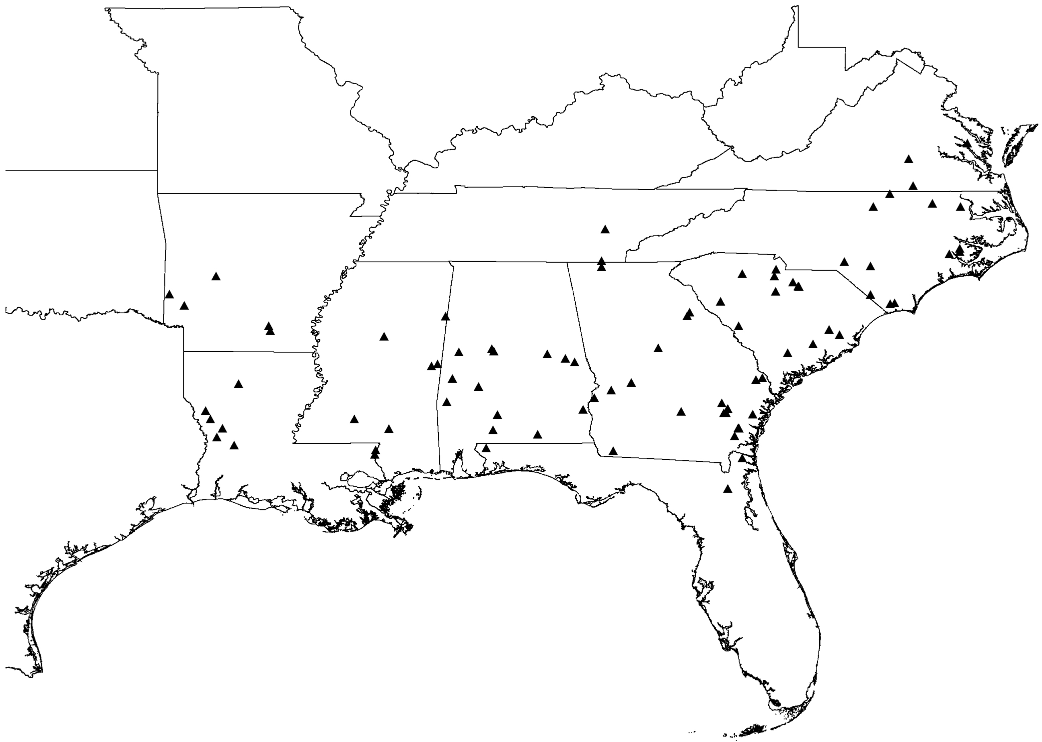


Figure 1. Distribution of 86 studies across the southeast US.

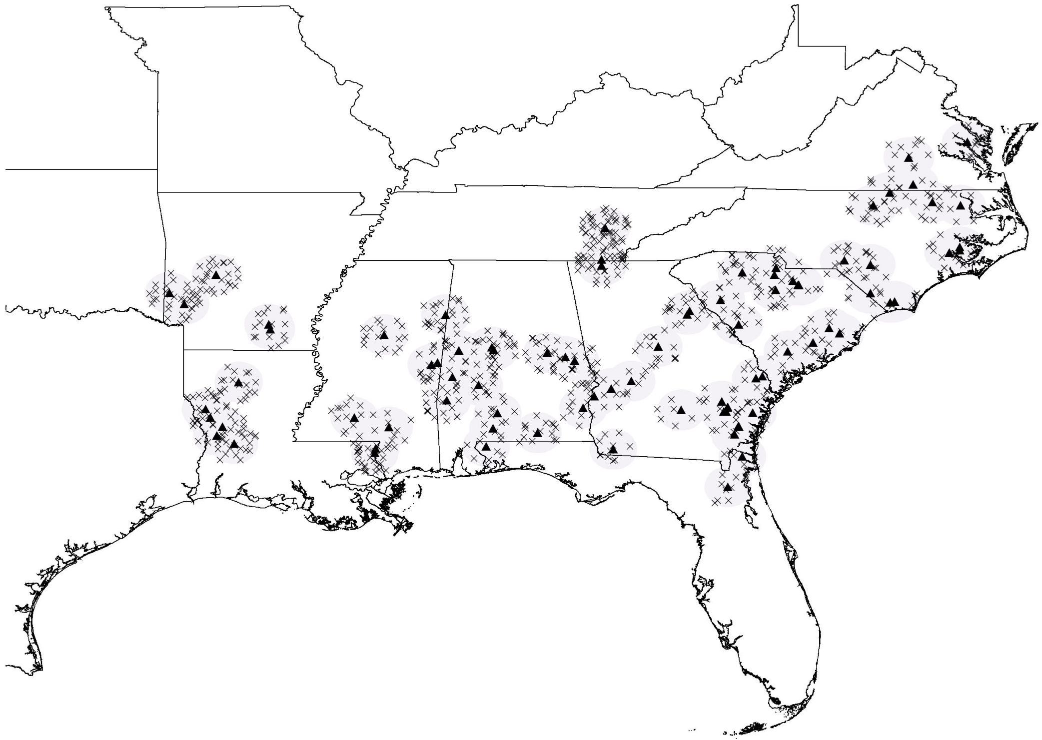


Figure 2. Spatial selection of weather stations within 31 mile radius of each study site.

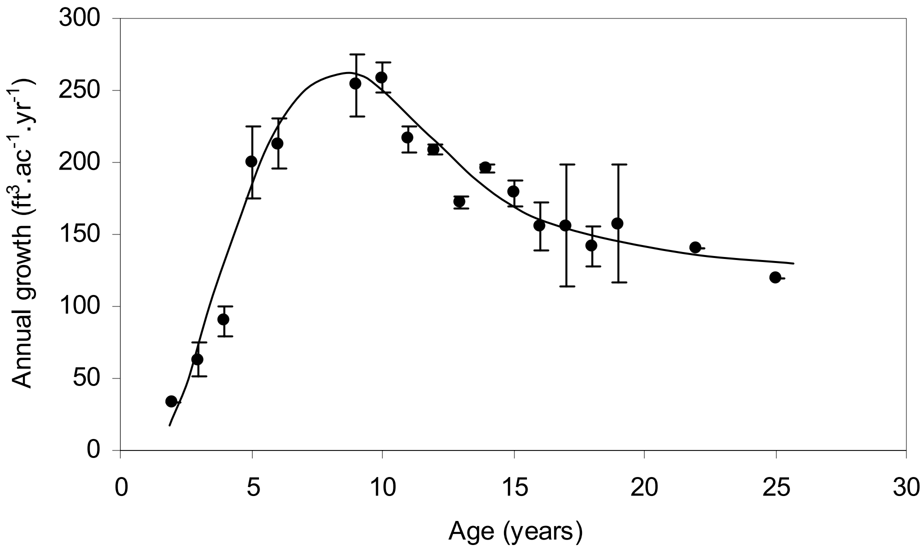


Figure 3. Averages of the annual volume growth vs. age for 86 different loblolly pine plantations across Southeast of US. Line indicates standard errors.

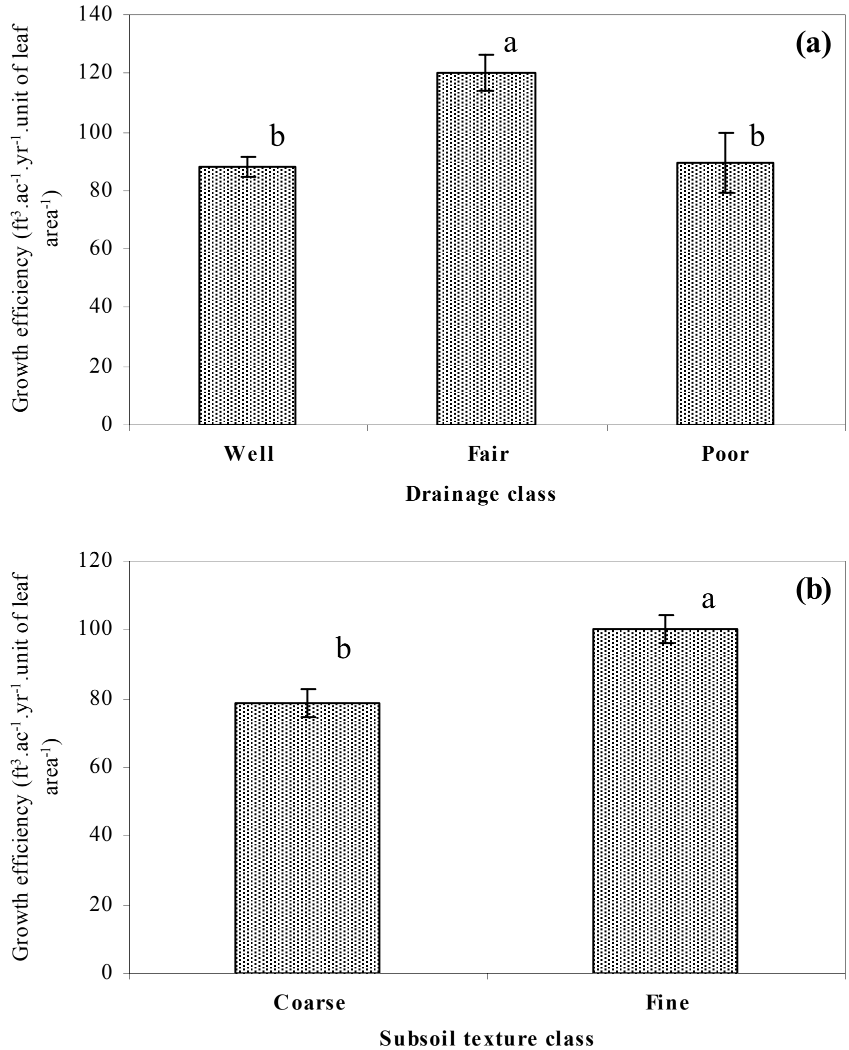


Figure 4. Effect of grouping soil drainage (a) and textures (b) on growth efficiency. Line indicates standard errors.

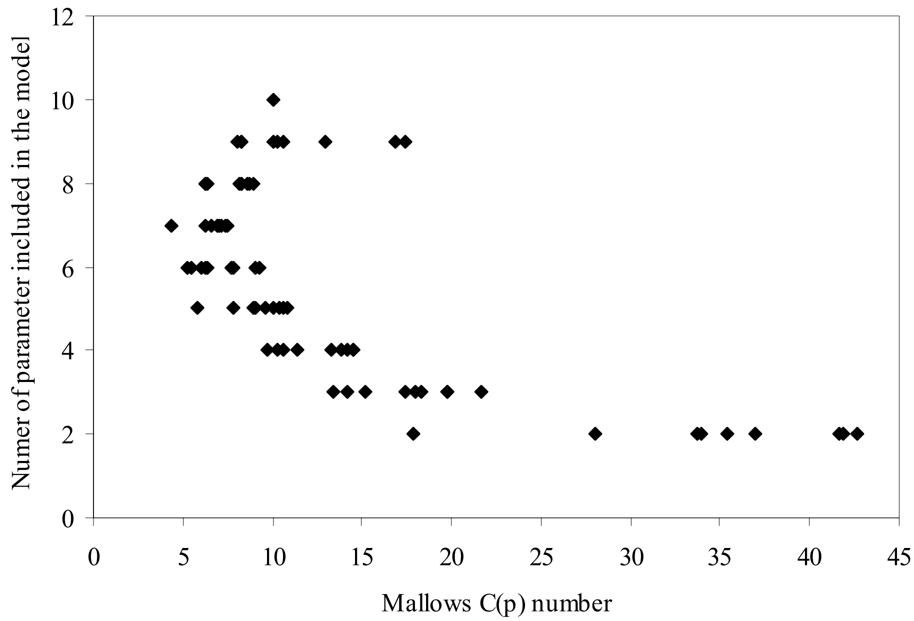


Figure 5. Mallows C(p) value vs. number of parameters to be included in Equation [3]

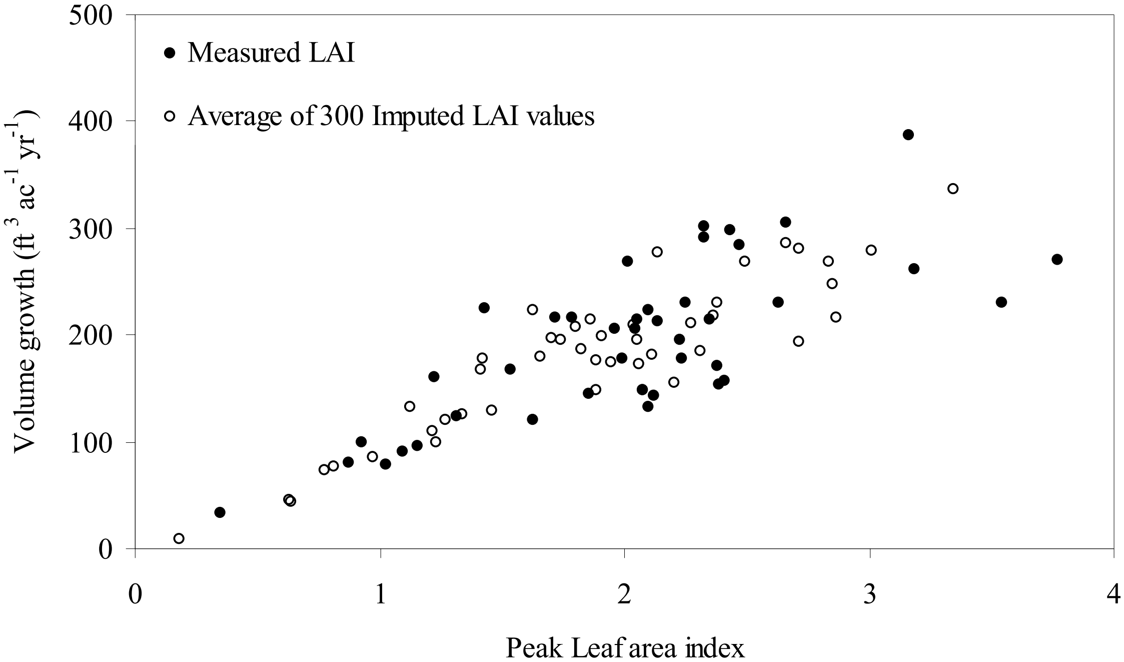


Figure 6. Comparison between observed and imputed values of LAI when associated with stem volume growth for each individual sites.

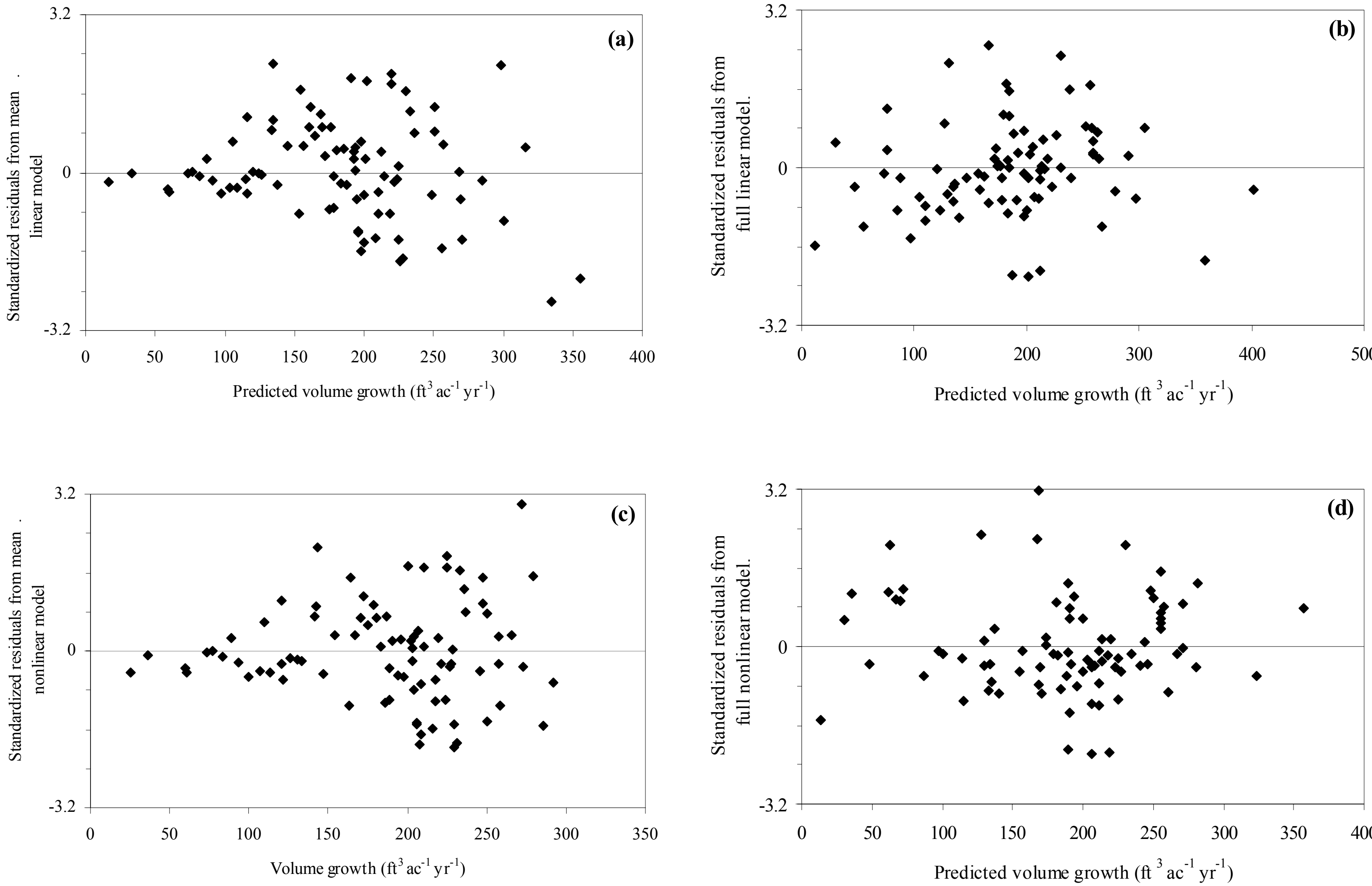


Figure 7. Standardized residuals for the mean models (a and c) and the full models (b and d) vs. predicted volume growth

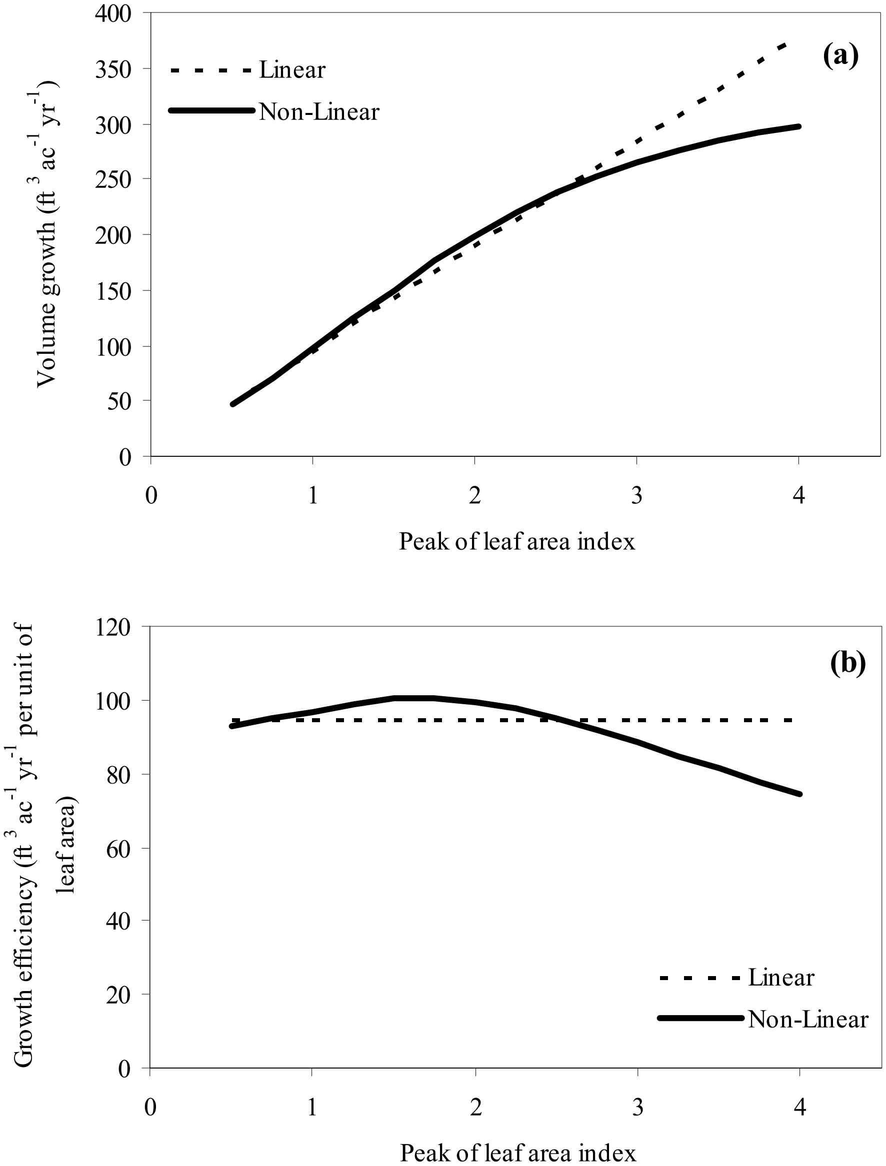


Figure 8. Changes in predicted volume growth (a) and predicted stemwood growth efficiency (b) with leaf area index for the mean linear and nonlinear models, Equations [4] and [5], respectively.

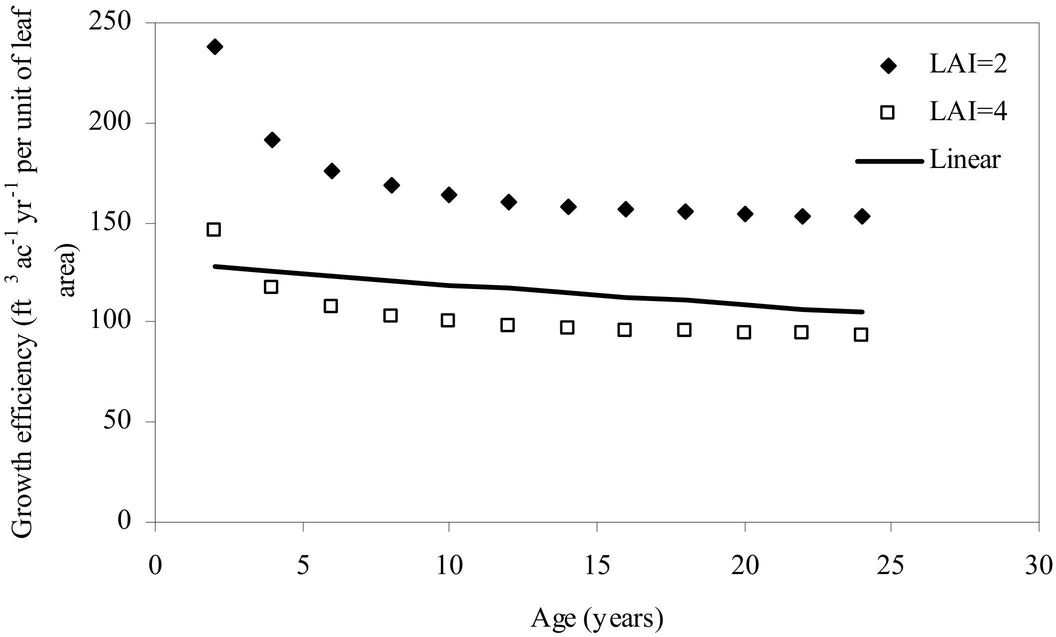


Figure 9. Changes in predicted stemwood growth efficiency with plantation age for a linear model and for two levels of leaf area index in a non-linear model. Growth efficiency values were calculated using fair drainage class, fine textured soil and the across site average precipitation and maximum temperature (Table 1). Equations [8], [9] and [10]

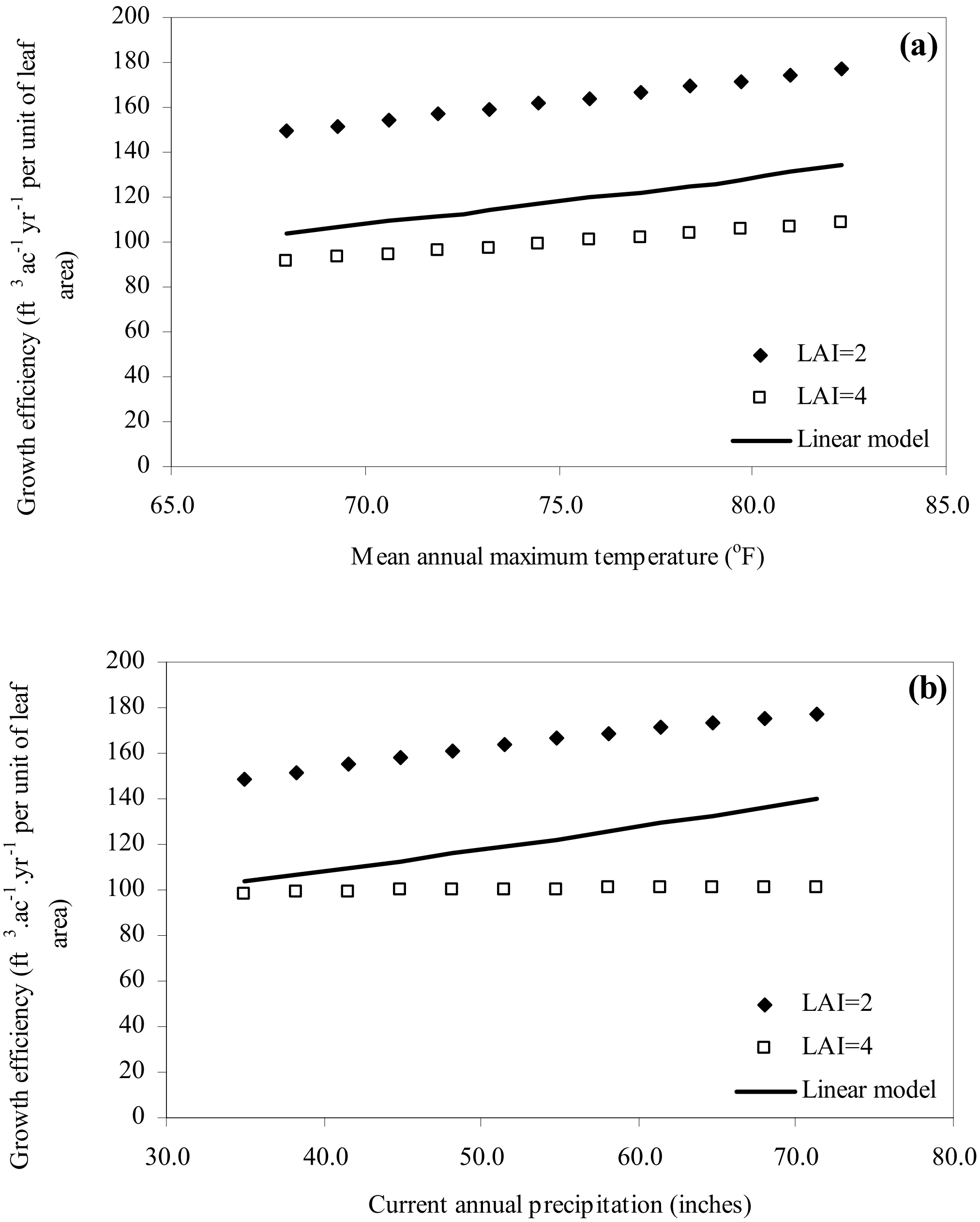
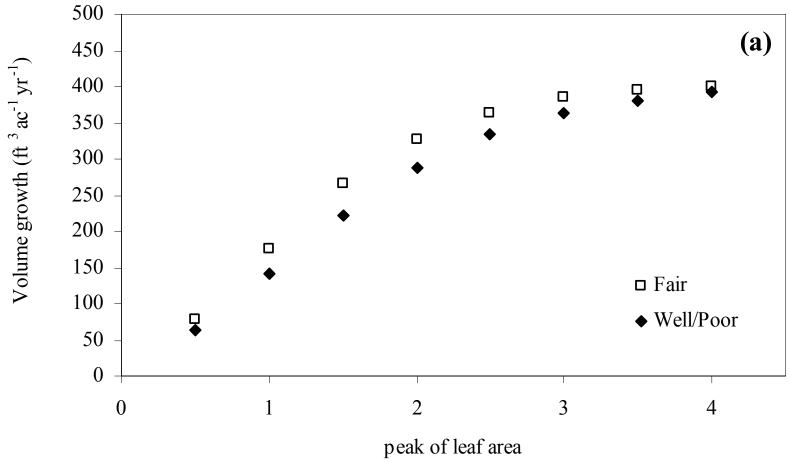
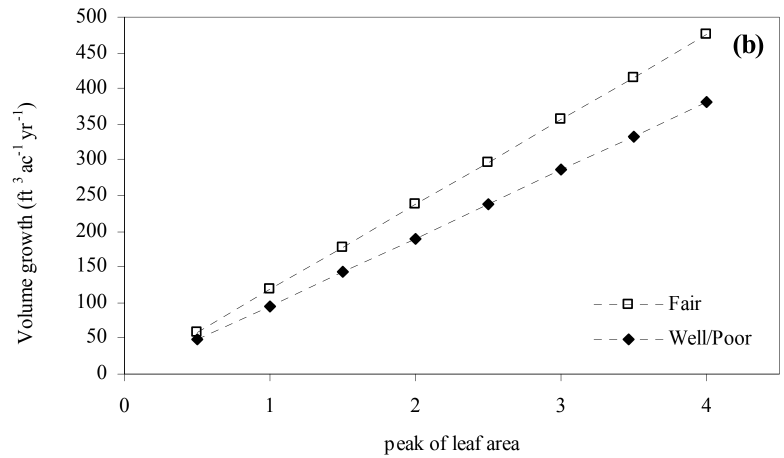


Figure 10. Changes in predicted stemwood growth efficiency with temperature (a) and precipitation (b) for a linear model and two levels of LAI in a non-linear model. Growth efficiency values were calculated for a 10-year old stand with fair drainage class, fine textured soil with average annual precipitation (a, Table 1) and average maximum temperature (b, Table 1). Equations [8], [9] and [10]





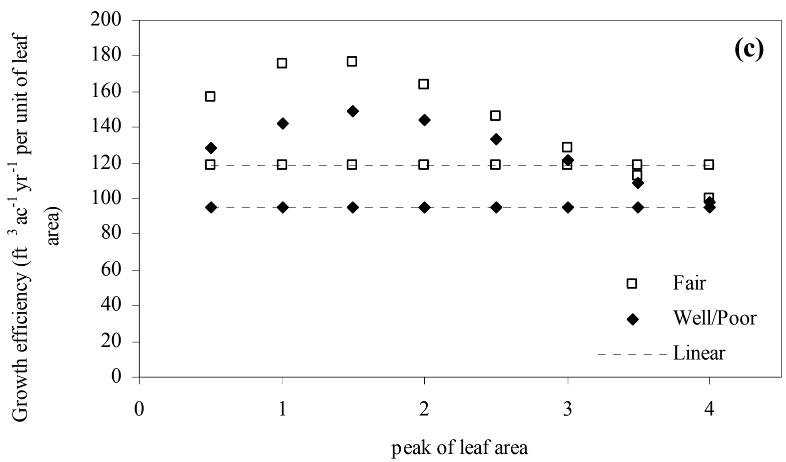
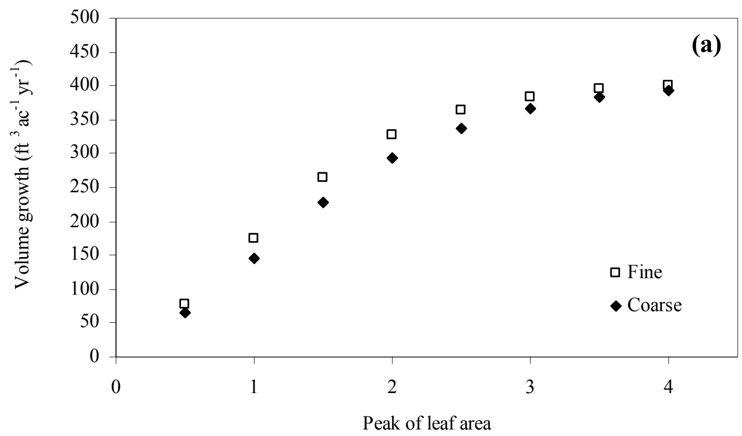
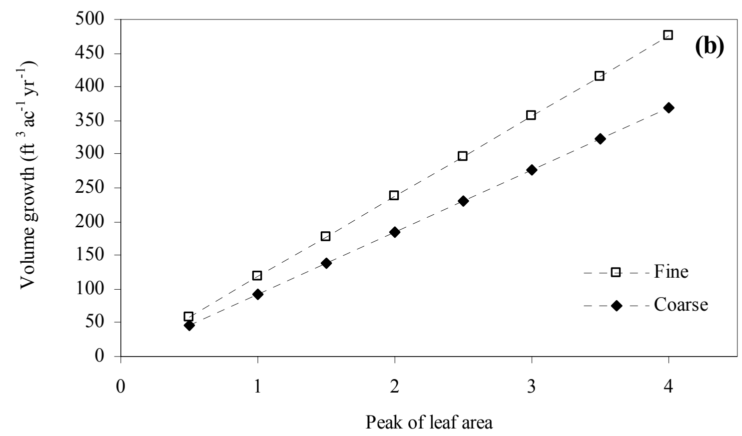


Figure 11. Changes in predicted values of stemwood growth efficiency (c) and volume growth (a) with leaf area index for a non-linear model and a linear model (b) as affected by drainage class. Predicted values were calculated for a 10-year old stand with, fine textured soil and the across site average precipitation and maximum temperature (Table 1). Equations [4], [5], [8], [9], and [10].





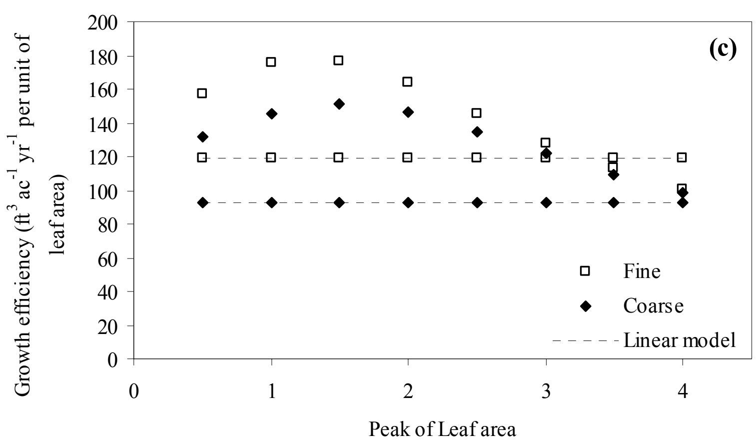
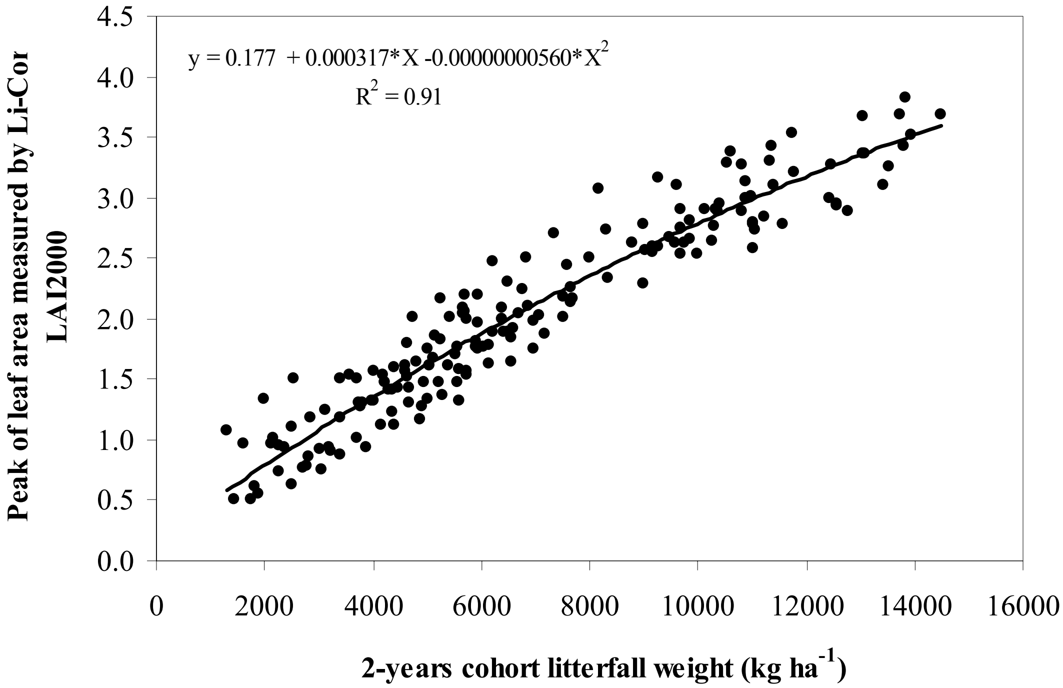


Figure 12. Changes in predicted values of stemwood growth efficiency (c) and volume growth (a) with leaf area index for a non-linear model and a linear model (b) as affected by subsoil texture class. Predicted values were calculated for a 10-years old plantation on fair drainage class and the across site average precipitation and maximum temperature (Table 1). Equations [4], [5], [8], [9], and [10].

7. Appendices

Appendix 1. Relationship between needle cohorts and peak of leaf area index as measured by Li-Cor LAI 2000, at a site in Scotland Co, NC with loblolly pine plantation.



Appendix 2. Results from factor analysis performed on the initial 67 variables used for modeling growth efficiency.

Group	Number of Factors	Variation explained[1]	Factors (variables or contrasts)
Edaphic	4	77	(Ca, Mg, BS); (C, N, P, CEC, acidity); (Mn, Cu, Mn) and (drainage)
Climatic	4	93	(Temperature); (VPD); (PPT) and (current vs long term data)
Stand	3	90	(LAI, initial growth); (Initial Volume, Initial basal area, MAI for volume) and (age, dbh, ht, TPA)
Foliar	2	75	(N, P, K) and (Ca, Mg)

[1]*Percent variation from total explained by factors within each group of variables.*

CHAPTER 3

Modeling responses to fertilization in loblolly pine plantations

Abstract

The operational objective of every forest company is to maximize wood yield/value per acre per year at the lowest possible cost. This can only be achieved by managing efficiently the resources available and/or added. With the increasing move to intensive silviculture across the southeastern United States, better tools that integrate current knowledge on plantation production are needed in order to efficiently allocate the inputs where and when they are most needed. A growth response to fertilizer application was developed utilizing data from 82 different loblolly pine plantations across the southeastern United States. Data included a wide range of edaphic, environmental and stand conditions. Control and treatment plots were used to calculate response to N+P fertilization after four years. By utilizing a standardization procedure on response values, 66% of the variation was explained by LAI, Foliar N concentration, and growth efficiency; these are ecophysiological variables that have been proposed as drivers of stand response to fertilizer application(s). Two other variables related to tree size ($\overline{D_q}^{\,2}$) and average tree growth ($\overline{D_q}^{\,2}$/age) were also significant predictors of standardized stand response to fertilization. None of the variables and their interactions included in the model helped to explain more than 20% of the variation in absolute values of response. Correlation coefficients of the two measurements of growth response and all the other variables showed substantial improvements with the standardized response. The final model presented here will help in discriminating between responsive stands and those that would be less responsive to N+P fertilization.

1. Introduction

The operational objective of every forest company is to maximize wood yield/value per acre per year at the lowest possible cost. This only can be achieved by efficiently managing the resources available and/or added. Historically, forest management has been focused on minimizing per acre costs associated with plantation establishment and tending which has resulted in underperforming plantations with higher wood costs (Allen et al. 2005). Intensive silviculture provides for higher inputs with greater cost per acre but with normally lower wood costs. This is because most stands where loblolly pine is grown are nutrient limited during some stage of the stand development (Valentine and Allen 1990). Responses to fertilization have been observed across the southeastern United States (Hynynen et al. 1998, Jokela, et al. 2004). Currently, over 1.5 million acres of pine plantations are being fertilized on an annual basis in the southeastern United States (Allen et al. 2005). However, fertilization prescriptions have been done with a varying degree of success. This is because specific responses after fertilization for any particular stand will be the result of complex interactions of nutrients/rates applied, stand and site conditions at time of application, years since application and climatic conditions soon after application and on the following years (Amateis et al. 2000). According to Allen et al. (1990), by the age of 5 a plantation's potential to use N and P generally surplus the available soil supply, resulting in restricted leaf area development and growth. By mid-rotation age, loblolly pine plantation has been already under severe nutrient limitation and response to N+P addition are normally high (Allen et al. 2005).

Although in loblolly pine plantation nutrients limit growth more strongly than water availability (Albaugh et al. 2004), the uncertainty regarding the potential for response, i.e. what drives the response to fertilization application, has been a concern to forest managers. This is because responses to fertilization has been documented to vary widely (NCSFNC 1989), ranging from almost 200% above non-fertilized stands (NCSFNC 2004) to none. Several approaches have been taken in order to predict when and where plantations would be responsive to fertilization and what variables drive such response. Foliar nutrient concentrations, soil nutrient status, stand characteristics such as basal area, site index among others (Duzan and Allen 1981, Duzan et al. 1982, Wells et al. 1986, McNeil et al. 1988, Valentine and Allen 1990, Hynynen et al. 1998, Amateis et al. 2000) have been historically used to predict responses to nutrient addition. For instance, foliar and litterfall nutrient status have been used to detect nutrient limitations. Foliar critical values and vector analysis, first developed by Timmer and Stone (1978) and later applied to loblolly pine (Valentine and Allen 1990) have been used with mixed results. The vector analysis is applied to stands already fertilized, so to be able to predict if a stand responds to fertilizer additions, one must fertilize it first. This clearly is a disadvantage since forest managers would like to know before hand if the stand would be responsive to the addition of fertilizer. Nonetheless, vector analysis has the advantage of detecting if another nutrient could become a problem (deficient, antagonism) later on after fertilizer has been applied. Critical values are a good predictor of responses normally when plantations are already in a chronic deficit of nutrients and losses in productivity have been large.

Today's plantation growth and yield models use site index as an important predictor of wood production (Allen et al. 2005). Thus equations have been modified to incorporate growth increase from fertilizer treatments (Hynynen et al. 1998, Amateis et al. 2000). These response models have been developed under the assumption that resources availability is fixed, so the applicability of these types of models for intensively managed plantations is limited (Allen et al. 2005). Wood productivity of a given stand partially depends on the resource supply, which can be manipulated (fertilization). Wood productivity also depends on the proportion of the resources captured by trees and the efficiency with which trees use resources to fix carbon dioxide (Binkley et al. 2004). The efficiency of carbon fixation has been reported to change depending on climatic conditions (Sampson and Allen 1999) and models for other species such as radiate pine have been developed to reflect this (Snowdon et al. 1999, Snowdon 2001).

Given the strong relationship between stemwood growth (SWG) and leaf area index (LAI), it has been suggested that this relationship can be potentially used for predicting responses to fertilization (Vose and Allen 1988, Flores 2003). Since LAI is a good indicator of current nutrient deficiencies and growth (Albaugh et al. 2004, Jokela et al. 2004), plantations growing under low nutrient supply conditions attain lower LAI (and lower SWG). These stands would have higher potential for increasing productivity with nutrient additions. Under this perspective, it is expected that by maximizing the LAI displayed in all stages of stand development, stemwood production would be also be maximized. As mentioned by Allen et al. (2005), it is particularly striking in the case of intensively managed plantations, where large investments provide a strong incentive to use better information for decision-making, that LAI has not been incorporated into prediction models on a broad scale as an aid for silvicultural decision-making. Clearly, models that integrate LAI into the prediction system would have the advantage to more accurately reflect changes in stand growth patterns since this is a trait that can be easily monitored on a regional scale (Flores, 2003). In the tropics with eucalyptus plantations significant improvements in regional empirical site index based yield models have been achieved by incorporating rainfall and/or LAI variables into the prediction equation system (Stape et al. 2004).

The issue remains on what nutrients are deficient and/or if the plantation would be capable to utilize the added resources efficiently to make it economically feasible to invest in fertilization. There is no perfect system available that would predict where/when a plantation would be responsive to nutrient additions. Tree growth and responses to nutrient additions are complex to model and require the use of integrated systems. However, an integrated technology/model that helps to better quantify and/or discriminate, with a high degree of success, responsive from non-responsive sites would be highly valuable to forest managers. These models would assist forest managers in targeting those sites where large responses would be attained and where economic maximization of the investment would be achieved.

The purposes of this study were: 1) quantify variation in response to fertilization across southeast of US, 2) determine factors causing that variation, and 3) model the volume growth response to fertilization as function of these factors.

2. Methodology

2.1. Stand Characteristics

A set of 82 Forest Nutrition Cooperative (FNC) studies were selected to explore the regional variation in growth response to N+P fertilization. The studies included in this analysis were established from 1984 to 2000, across 10 states (Figure 1) in loblolly pine plantations ranging from 2 to 25 years old, covering different soil textural, drainage classes and physiographic provinces. Climate between sites was also variable with long term annual precipitation ranging from 53 to 65 inches Minimum and maximum temperatures ranged from 44 to 59 ^{o}F and 68 to 80 ^{o}F, respectively. Stand conditions also varied among sites. Height ranged from 4.8 ft for the youngest plantations to 57.2 ft for the oldest. Stand density varied from 131 to 928 trees per acre. However, all studies shared a common objective of evaluating response to nutrient addition.

Sites were established after rigorous guidelines for site selection were met; providing minimization of within plot stand variation as well as minimizing soil variation within a study. Treated plots varied between 0.284 to 0.744 acres, with internal measurement plots from 0.021 to 0.234 acres. The experimental design used was a randomized complete block with two to four blocks.

Two selection criteria were used for selecting this set of studies. First, each site had to have control (non-fertilized) and fertilized treatments. Only comparable rates of nitrogen plus phosphorous (N+P) were chosen from each study. Secondly, all sites had to have at least four years of data since treatment. The studies selected included mid-rotation fertilization studies; Regionwide (RW) 13 (NCSFNC 1989) and RW15

(NCSFNC 1996), fertilization and vegetation control in mid-rotation stands or RW 17 (NCSFNC 2001) and frequency and dose of fertilizer application in young loblolly pine plantations, or RW 18 (NCSFNC 2004). From RW13, two treatments were selected, 200 lb of N per acre (200N) in combination with 25 and 50 lb of P per acre (25P and 50P, respectively). From RW15 and RW17, one treatment corresponding to 200N and 50P was chosen, and a treatment with 180N and 18P was selected from RW18. All these treatments were regarded simply as the N+P treatment.

2.2. Stand Data

Measurements taken on control and N+P treatments plots prior to establishment and four years after treatments were selected for this analysis. Planted trees within the measurement plot were measured in the dormant season (December to February) at each site. Assessments of pine tree total height in feet (Ht) and diameter at breast height in inches (dbh) were completed and individual tree volumes were calculated using the following equation (NCSFNC 2004):

$$\text{Volume}_{ob} = 0.002\ \text{dbh}^2\ \text{Ht} \qquad [1]$$

Where: Volume_{ob}= volume outside bark, and all other terms has been previously defined.

Total volumes were summed to obtain stand level volume estimates. The squared of the quadratic mean diameter was calculated as (183.34*basal area)/stand density.

Initial stand values by site for Ht, dbh, stand density (TPA) standing volume (VOL) and basal area (BA) were obtained by averaging the pre-treatment measurements of all selected plots. Annualized 4-year periodic growth (or periodic annual increment, PAI) on a plot basis was calculated by subtracting pre-treatment measurements from 4-years since treatment measurements and then dividing by four years. Since the variation in stand conditions and initial values were high, and given that these conditions influence the volume response differentially depending on site characteristics (Amateis et al. 2000), a standardization of the data was performed by utilizing the following formula:

$$Y_{ij} = \left(\frac{X_{ij} - \overline{X_i}}{s_i} \right) * CV_i + 100 = \frac{X_{ij}}{\overline{X_i}} * 100 \qquad [2]$$

Where Y_{ij}: Standardized growth value of the j^{th} plot from the i^{th} site.
X_{ij}: Periodic annual increment of the j^{th} plot from the i^{th} site.
$\overline{X}_i$: Mean of periodic annual increment for site i^{th}.
σ_i: Standard deviation of the periodic annual increment at site i^{th}.
CV_i: Coefficient of variation of the periodic annual increment at site i^{th}.

This standardization eliminated the across site variation in the data by setting the overall means at each site to 100, while preserving the relative variation (ranking) within site of each plot. On both original data and the transformed data, treatment means were then calculated per site for both control and fertilized treatments. Stem wood volume growth response for absolute values (AR) and standardized values (SR) was calculated on a site basis by subtracting the non-fertilized treatment growth mean from the fertilized treatment mean. The relative growth response over the non-fertilized treatment was the same using either the standardized or original data.

2.3. Foliar and Soil Characteristics

Prior to establishment foliage data for macro and micro-nutrients were available at each site on an individual plot basis (Chapter 2). Initial values of foliar nutrient concentration for N, P, K, Ca, Mg, B, Zn, Cu, Mn and Fe were calculated on a site basis by averaging values from all selected plots.

2.4. *Leaf Area Index Measured and Estimation*

In our interest to explore the relationship between LAI at time of treatment and the growth response after it, initial leaf area index was estimated at each site for control plots (see Chapter 2). Peak of leaf area index, defined as leaf area display of two needle cohorts (Vose and Allen, 1988), was used. Growth efficiency (GE) was calculated by dividing PAI over LAI on the control plots and averaging on a site basis.

2.5. *Climatic Variables*

Climatic data used in the modeling efforts are described in Chapter 2. Briefly, climatic data included minimum and maximum temperature, precipitation and vapor pressure deficit (VPD). Different levels of summarization were utilized; e.g. current year, four years since fertilization and long term averages.

2.6. *Statistical Analyses*

Multiple regression analysis with stepwise procedures in SAS were used to investigate the influence of climatic, stand, canopy and stand variables on both measures of growth response (AR and SR). Variables and interactions among them were used as predictor variables. Single correlation analysis between response variables and predictor variables were performed initially due to the large number of variables (68). This allowed a supervised selection of predictor variables to be introduced into the model. Those predictor variables with high correlation values between them were avoided. Variables kept in the model were only those that showed to be statistically related and gave meaningful explanations about changes in growth responses. Both AR and SR values were utilized as dependent variables. Residual analysis was used to check for normality and constancy of error variance.

3. Results

Values of AR ranged from 3 to 124 $ft^3\ ac^{-1}\ yr^{-1}$, this corresponded to 1 to 152% response over control plot. The frequency distribution for AR was bell-shaped suggesting a normal distribution for this variable (Figure 2); the mean and standard deviations were 55 $ft^3\ ac^{-1}\ yr^{-1}$, and 26 $ft^3\ ac^{-1}\ yr^{-1}$ respectively. The SR varied from 1 to 74 with a mean of 25.

Correlation analysis of AR and the different stand, edaphic and climatic variables were always lower than with SR (Table 1). Absolute response was poorly correlated with most of the stand variables except for the inverse of age (r=0.26), stand density (r=0.28), the square of the quadratic mean diameter ($\overline{D_q}^2$; r=0.36), and tree growth as ($\overline{D_q}^2$/age)^2 (r=-0.36) where correlations were significant. Similarly AR was also poorly correlated with canopy variables except for foliar B (r=0.21) and none of the climatic variables introduced in the analysis showed significant correlation. However, substantial improvements were obtained in the correlation coefficients when SR was used (Table 1). Besides those stand variables significantly correlated with AR, SR was significantly correlated with other variables such as initial TPA, BA, BA/age and GE (Table 1). The biggest impact in correlation coefficients was obtained on the canopy variables. Correlation coefficient values changed from -0.18 to -0.59 when AR and SR respectively were correlated to LAI and even higher values (r=-0.69) were obtained with the ln(LAI)

(Table 1, Figure 3). Correlation coefficients also improved when the log transformation of foliar N was used.

None of the variables and interaction terms introduced in the regression analysis helped to explain more than 20% of the variation in AR. The final equation presented here (Equation [3]) explained 66% of the variation in the SR (Table 2).

$$SR= \alpha_0 + \alpha_1 \, Ln(LAI) + \alpha_2 \, GE + \alpha_3 \, (\overline{D_q}^{\,2}/age)^2 + \alpha_4 \, \overline{D_q}^{\,2} + \alpha_5 \, Ln(fol\ N) \qquad [3]$$

Where: SR= standardized response
Ln(LAI)= Natural logarithm of LAI
GE= growth efficiency, in $ft^3\ ac^{-1}\ yr^{-1}$ unit of leaf area^{-1}.
$\overline{D_q}$ = Quadratic mean diameter, in inches
Age= stand age, in years,
α_i= parameters to be estimated.

Leaf area index, foliar N, growth efficiency, age and D_q were significant predictor variables in the model (Table 2). Standardized response decreased with increasing values of LAI and foliar N, however the relationship was not linear. Logarithm of LAI and foliar N were better predictors (Table 2), implying an asymptotic value on the SR with these two variables. The standardized growth response decreased with increasing values of GE. Basal area and TPA were significant predictor variables, represented in the model by D_q^2 (Table 2). A measure of the average individual tree growth over time was important as a predictor variable since the term $(D_q^2/age)^2$ was a significant predictor in the model (Table 2). Normal probability plots of the residuals showed no deviation from normality and the residual vs. predictor variables plots showed constant variances (Figures 4 and 5).

4. Discussion

The lack of relationship between explanatory variables and the AR was probably due to the high variation in stand conditions. In this case, modeling response with such a variable data set, coming from 82 stands with such a diverse soil and climatic conditions, the standardization provided for a more effective way to discriminate among variables. During the standardization process, the site to site variation was “eliminated” allowing to focus on the within site variation to compare how stand-canopy conditions influence response to fertilization. This is the case, as in most single site studies, where response to fertilizer application is explained by changes in the stand-canopy conditions since the age, edaphic, and climatic conditions are similar across all plots. Through the standardization process, variables that have been proposed as ecophysiological drivers of fertilizer response (Waring 1983, Vose and Allen 1988, Allen et al. 1990, Stoneman and Whitford 1995, Landsberg and Waring 1997, Flores 2003, Stape et al. 2004, Allen et al. 2005, Samuelson et al. 2004) were highly related to a measure of response (SR) on a regional scale.

In relative terms, stands with lower leaf area would give higher responses to N+P application; this response would decrease asymptotically with increasing levels of LAI. Similarly, stand response to N+P application would decrease asymptotically with increasing levels of foliar N. These two parameters behaved as expected for a response model. The interpretation of the GE parameter is counterintuitive though. One may expect to have higher growth response on sites with a higher efficiency of light interception, but the standardized response model compares sites in relative terms. So when two sites, one with high GE and the other with low GE are compared using this model, the site with higher GE would give a relatively lower response to fertilization since the growth rate of the stand is already higher than the one with low GE for comparable values of initial LAI. Growth efficiency is a measure of the amount of wood produced per unit of leaf area, it is an index that integrates all variables influencing carbon gain (Stoneman and Whitford, 1995) and its use is common among foresters and researchers The incorporation of this variable into the response model would then act as a surrogate for other variables, such as climatic and edaphic factors, that have been shown to affect GE (Chapter 2).

Since $\overline{D_q}^2$ and $(\overline{D_q}^2/\text{age})^2$ were significant predictor terms in the model, the interpretation has to account for the combined effect of these two terms. For stands with similar values of $\overline{D_q}^2$, response would be relatively larger on the stand that took more time to get to that $\overline{D_q}^2$ value. Stands growing under nutrient limitations will take a longer time to achieve a given size ($\overline{D_q}^2$). Intuitively, these stands would be relatively more responsive to fertilization than those with lower nutrient limitation that allowed them to get to a given size in less time.

The response model presented here, would not give absolute values of response, although both AR and SR are highly correlated (r=0.80). The response model gives a way to prioritize where input should be given when different stands are to be evaluated for fertilization application, allowing more informative decisions on resources use.

5. Conclusion

In this study, growth response to N+P fertilization was analyzed using 82 different loblolly pine stands with a wide variety of soil, climatic and stand conditions. The annualized 4-years period growth ranged from 3 to 124 $ft^3\ ac^{-1}\ yr^{-1}$. None of the stands, soil and climatic variables and their combinations explained more than 20% of the variation in absolute response to fertilizer. A standardization procedure (Equation [2]) performed over response values helped to relate response to leaf area index, foliar N and growth efficiency which are the ecophysiological variables that have been proposed as drivers of stand response to fertilization. Other variables related to stand characteristics, tree size ($\overline{D_q}^2$) and growth ($\overline{D_q}^2$/age)^2 were also important predictors in the response model. The final model presented here explained 66% of the variation in standardized response. This model will help to discriminate responsive stands from those that would give little or no response to fertilization.

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Table 1. Correlation coefficient[1] between absolute response and standardized response for some selected predictor variables.

Variable	Absolute response	Standardized response
Stand factor		
Tree Volume	-0.17	-0.16
Initial stand volume	-0.10	***-0.30***
Initial Basal Area	-0.06	***-0.35***
Stand age	-0.09	-0.07
Stand age inverse	***0.26***	***0.38***
Basal area/stand age	-0.05	***-0.47***
Initial stand density	***0.28***	0.12
Growth Efficiency*	-0.14	***-0.35***
Square of quadratic mean diameter (D_q^2)*	***-0.22***	***-0.35***
$(D_q^2/\text{age})^2$*	***-0.36***	***-0.45***
Canopy factor		
Peak of leaf area (LAI)	-0.18	***-0.59***
Ln (LAI) *	-0.22	***-0.69***
Foliar N	-0.16	***-0.30***
Ln (foliar N)*	-0.16	***-0.33***
Foliar P	0.01	-0.12
Foliar K	-0.15	***-0.34***
Foliar Ca	0.15	0.15
Foliar Mg	0.14	0.09
Foliar B	***0.21***	***0.25***
Climatic factor		
Current year annual precipitation	-0.10	-0.10
Current year average minimum temperature	0.05	0.13
Current year average maximum temperature	0.08	***0.20***
Current year average vapor pressure deficit	0.03	***0.19***
Long term average annual precipitation	0.00	0.03
Long term average annual minimum temperature	0.06	0.14
Long term average annual maximum temperature	0.07	0.17
Long term average annual vapor pressure deficit	0.03	0.15

[1] *Shaded cell with bold-italic numbers indicates significance with alpha=0.10.*
* *Variables selected on the final model.*

Table 2. Parameter estimates, model sequential R^2 and significance of parameter estimates for variables selected in the final model with standardized response.

Variable	Parameter estimates	Model sequential R-Square	Pr>F
Intercept	57.08		<0.001
Ln (LAI)	-18.70	0.48	<0.001
Growth efficiency (GE)	-0.170	0.58	<0.001
$(D_q^2/\text{age})^2$	-1.501	0.62	0.006
Square quadratic mean diameter (D_q^2)	0.245	0.64	0.034
Ln (foliar N)	-16.14	0.66	0.082

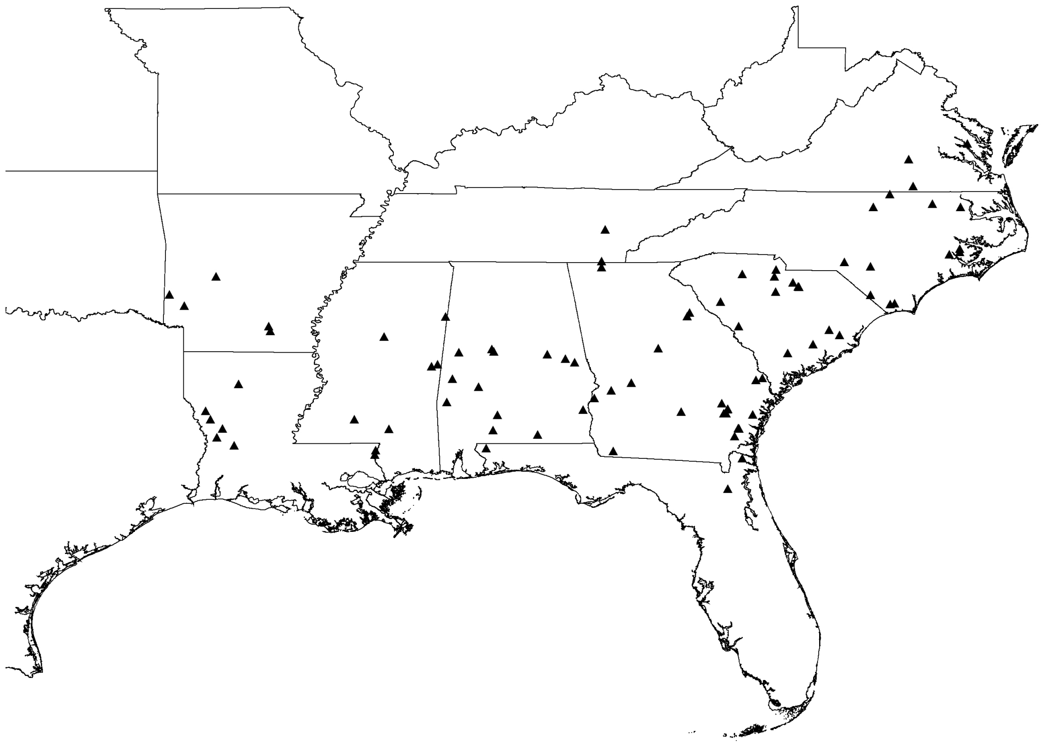


Figure 1. Distribution of 82 studies across the southeast U.S.

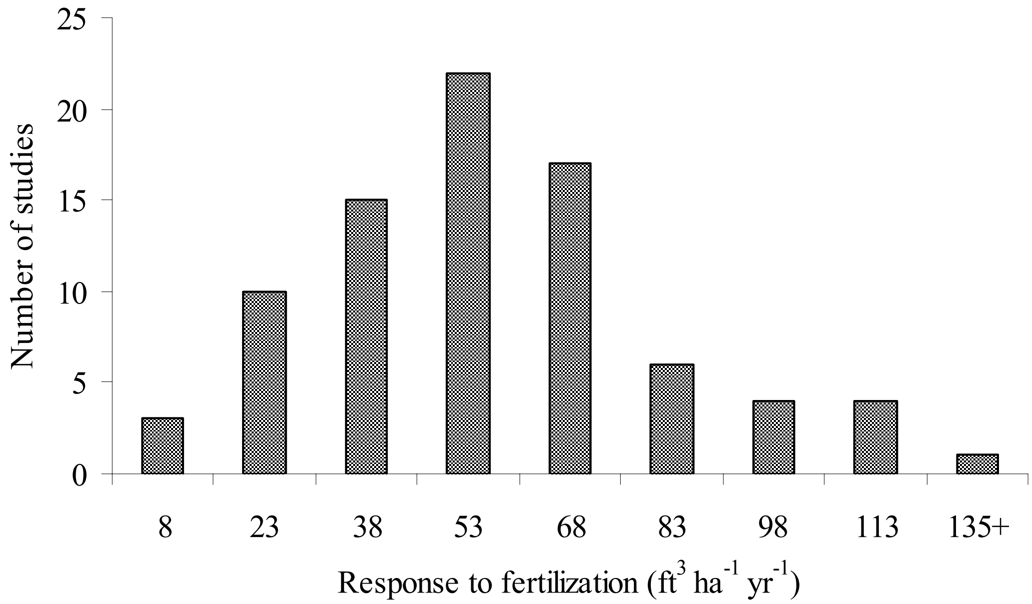


Figure 2. Distribution of growth response to N+P fertilization for 82 different loblolly pine plantations across southeast of U.S..

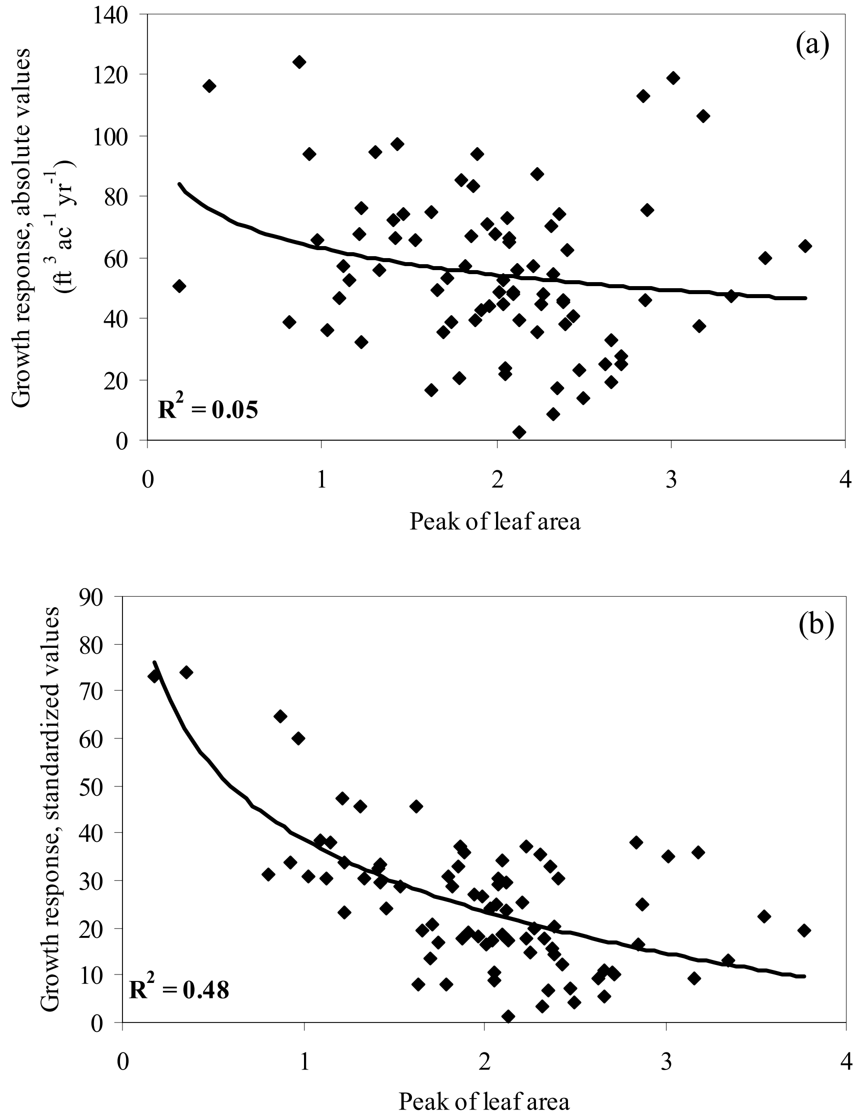


Figure 3. Relationship between two measures of growth response to N+P fertilization and peak of leaf area. Absolute growth response values (a), and standardized growth response values (b), for 82 different loblolly pine plantations across southeast of U.S.

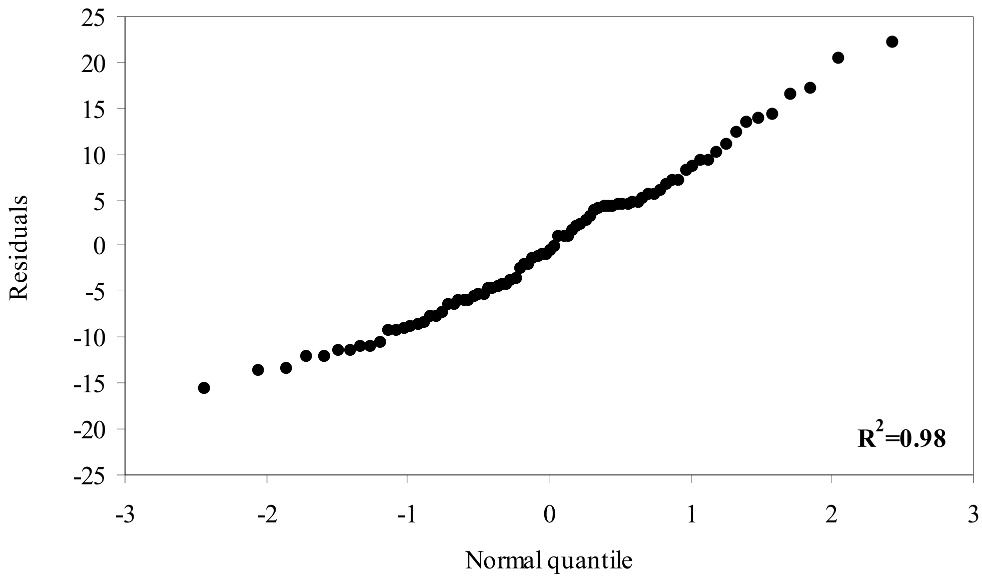
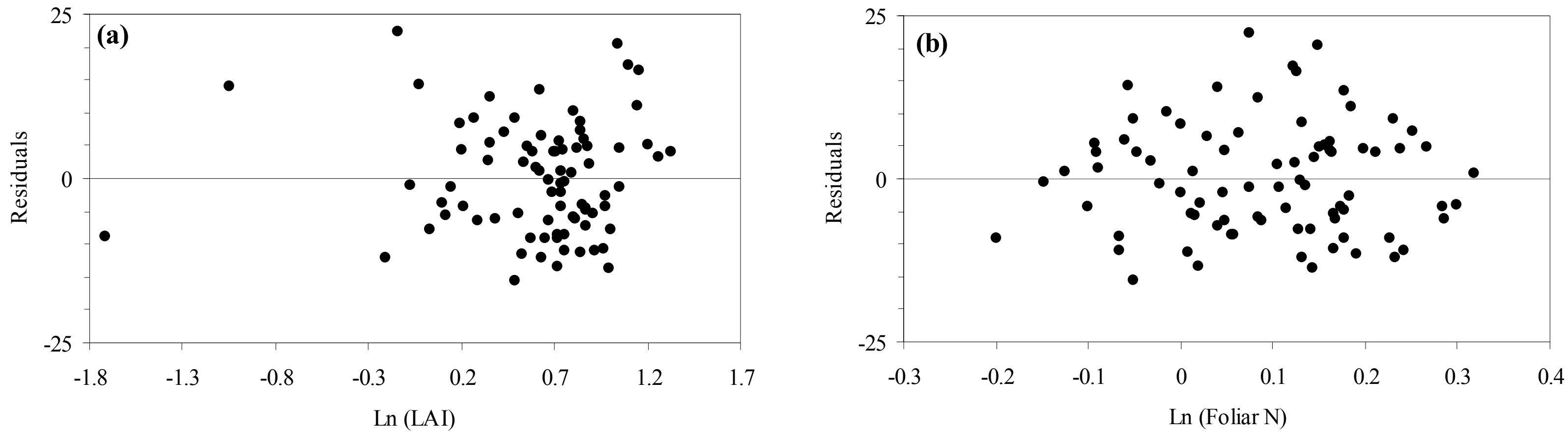


Figure 4. Normal probability plot for residual from the standardized model.



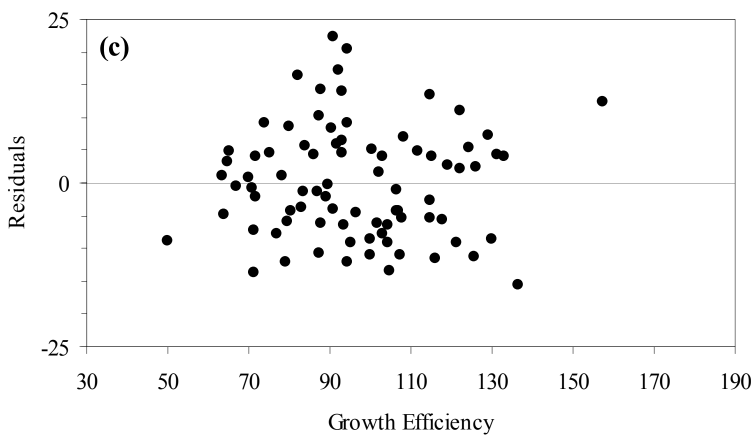


Figure 5. Scatter plots of residuals vs. independence variables for the standardized model.