Factors influencing production efficiency of intensively managed loblolly pine plantations in a 1- to 4-year-old chronosequence

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Abstract

Changes in biomass, nutrient accumulation and production efficiency (PE—total biomass increment per unit leaf area) were investigated in intensively managed plantations of loblolly pine (Pinus taeda L.) using an age sequence of replicated 1-, 2-, 3-, and 4-year-old stands (n = 13). All stands, located on sandy Spodosols in the Coastal Plain of southern Georgia, were managed using a similar prescription that included a common genetic source, fertilization (years 1 and 3) and understory competition control. Total biomass accumulation (above- and below-ground) ranged from about 13 Mg ha⁻¹ at age 2 years to 49.7 Mg ha⁻¹ at age 4 years. Dry matter distributions averaged 30%, 34%, 18%, 6%, 15%, 12% and 3% for foliage, stemwood, branches, bark, taproots, coarse roots and fine roots, respectively, at age 4 years. Intensive management and rapid growth rates markedly increased soil nutrient demands, being about 15-fold higher than that documented in extensively managed stands of comparable age. Nutrient accumulations in tree biomass at age 4 years averaged 195, 22, 86, 72 and 28 kg ha⁻¹ for N, P, K, Ca and Mg, respectively. Large declines (~50%) in PE (2.6 Mg ha⁻¹ year⁻¹/unit LAI versus 1.3 Mg ha⁻¹ year⁻¹/unit LAI) were apparent among all sites between the second and third years, with a noted recovery occurring at age 4 years. Changes in branch and taproot PE were most apparent, whereas stemwood PE did not change appreciably between ages 2 and 3 years. Correlation analyses suggested that larger declines in PE were associated with decreasing foliar nutrient levels (dilution), although changes in growth dynamics (carbon allocation) associated with advancing stand development may have also contributed. Collectively, these results suggest that intensive management may induce multiple nutrient limitations on sandy Spodosols, and that a better understanding of nutrient requirements, including macro- and micronutrient supply, will be necessary to maintain and enhance soil quality and long-term site productivity on these soils.

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Keywords: Biomass production; Allocation patterns; Nutrient accumulation; Nutrient distribution; Pinus taeda L.; Sandy Spodosols

1. Introduction

A dynamic period of forest stand development occurs between seedling establishment and canopy
closure. During that stand initiation phase, annual biomass production is preferentially allocated to foliage and fine roots, followed by increasing proportions to stemwood over time (Forrest and Ovington, 1970; Gholz and Fisher, 1982; Beets and Pollock, 1987; Miller, 1995; Oliver and Larson, 1996; Adegbidi et al., 2002). These changes in production have been used to assess functional relationships among tree components (King et al., 1999), estimate nutrient budgets (Gholz et al., 1985; Van Lear and Kapeluck, 1995; Wang et al., 1996, 2000), compare inter- and intra-specific growth strategies (Pope, 1979; Colbert et al., 1990) and contrast silvicultural treatments and developmental stages (Ledig et al., 1970; Naidu et al., 1998). The overwhelming majority of studies conducted in forest ecosystems have only documented above-ground dynamics, often due to the difficulty of sampling and estimating coarse and fine root biomass (Santantonio et al., 1977; Kapeluck and Van Lear, 1995).

Many previous studies, spanning a range of species, have reported a strong correlation between leaf area and annual stemwood biomass (volume) production (Waring, 1983; Vose and Allen, 1988; Long and Smith, 1992). This relationship, referred to as leaf area efficiency or growth efficiency (GE), has been used as an index for assessing differences in growth performance among species (Colbert et al., 1990; Xiao et al., 2003a), genotypes (McCrady and Jokela, 1998), silvicultural treatments (Colbert et al., 1990) and stand developmental stages (Jokela and Martin, 2000). The concept of growth efficiency has been further extended to the relationship between above-ground net primary production (ANPP) and leaf area index (LAI) and is referred to as production efficiency (PE) (McCrady and Jokela, 1998; Samuelson et al., 2001).

Age-related declines in growth and PE (mainly after canopy closure) have been observed in a variety of forest types (Long and Smith, 1992; Binkley et al., 1995; Ryan et al., 2004). Jokela and Martin (2000) reported that stemwood PE was three times higher at age 7–9 years than at 14–16 years in a Florida loblolly pine (Pinus taeda L.) stand, and suggested that nutrient limitations may be partially responsible. In subalpine fir (Abies lasiocarpa (Hook.) Nutt.) and lodgepole pine (Pinus contorta Doug. ex Loud.) stands, Roberts and Long (1992) and Roberts et al. (1993) hypothesized that as trees grew older, crown abrasion, an unfavorable light environment due to minimal height increases, and an increasing ratio of non-photosynthetic to photosynthetic tissues (i.e., respiration/photosynthesis ratio) caused net carbon accretion and PE to decline. Other hypotheses related to hydraulic resistance, reproduction and below-ground carbon costs, and tissue maturation have been proposed as factors contributing to temporal declines in net primary production (NPP) and PE (Schoettle, 1994; Yoder et al., 1994; Gower et al., 1996; Ryan et al., 1997; Smith and Resh, 1999).

Reliance on intensively managed plantations has been advocated as a means to supply societal wood needs by concentrating timber production on sites capable of high yields (Sedjo and Botkin, 1997). In the southeastern United States, where soils are inherently poor, nitrogen and phosphorus fertilization of loblolly and slash pine (P. elliottii Engelm.) plantations has been practiced with success since the 1960’s (Pritchett and Llewellyn, 1966; Pritchett and Comerford, 1982; Jokela et al., 1988; Allen et al., 1990). Micronutrient responses (Mn) have also been documented in rapidly growing stands fertilized with N, P and K (Jokela et al., 1991). Yet, growth dynamics and nutrient demands of fast-growing loblolly pine stands are still poorly understood (Fox, 2000).

The current study was designed to examine early growth (age 1–4 years) dynamics of intensively managed loblolly pine stands growing on lower Coastal Plain Spodosols in the southeastern USA. Thirteen stands, arranged as a chronosequence, were used to: (1) quantify above- and below-ground biomass production and nutrient accumulation and (2) examine how PE changed with respect to stand age, plant nutrient status and biomass distribution patterns.

2. Materials and methods

2.1. Study sites and procedures

The study was conducted in 13 fast-growing loblolly pine stands that ranged in age from 1 to 4 years in the lower Coastal Plain region of southern Georgia (Adegbidi et al., 2002). Ages 1 and 2 years were represented by three spatially unique replicate plantations sampled at age 1 in fall 1999 and
resampled at age 2 years in fall 2000. Age 3 years was represented by three additional spatially unique plantations (sampled in fall 2000); similarly, age 4 years data originated from four more spatially unique forest plantations (sampled in fall 1999). The sample plantations were established on sandy Spodosols (sandy siliceous, thermic Ultic Alaquods and Oxyaquic Alorthods) derived from marine sediments and underlain by an argillic horizon. The soil nutrient reserves are inherently low, as topsoil horizons are comprised predominantly of quartz sand that have both low organic matter content and cation exchange capacity (<5 cmol, kg⁻¹; Table 1). Although these soils belong to different series, they have similar levels of nutrient availability and inherent site quality, and they support similar levels of response from fertilizer additions (Fisher and Garbett, 1980; Comerford, 1986; Jokela et al., 1991). Mean annual precipitation for the study sites ranged from 1250 to 1275 mm. During the 2-year study period, droughty conditions persisted. Annual precipitation levels were 8% (1999) and 33% (2000) below the long-term recorded averages.

Pre- and post-establishment procedures were similar at all sites. Prior to planting, all sites received mechanical site preparation (chopped, burned, disked and bedded). Genetically improved 1-year-old loblolly pine seedlings from the same family were planted at a 1.8 m × 3.7 m spacing (1495 trees ha⁻¹). Actual densities measured in sampled plots were 1360–1443 stems ha⁻¹ (1- and 2-year-old), 1284–1385 stems ha⁻¹ (3-year-old) and 1321–1510 stems ha⁻¹ (4-year-old). Understory vegetation was chemically controlled during the first two growing seasons using directed spray applications of herbicides applied at labeled rates (i.e., hexazinone, sulfometuron, imazapyr, glyphosate). Nitrogen and P fertilizers

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Mean soil properties for experimental sites established in fast-growing loblolly pine plantations on sandy Spodosols in the lower Coastal Plain of Georgia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Texture*</td>
<td>1-year 85-12-3 82-17-1 85-13-2</td>
</tr>
<tr>
<td>Bulk density (g cm⁻³)</td>
<td>1-year 1.10 0.97 1.11</td>
</tr>
<tr>
<td>Organic matter (%)</td>
<td>1-year 3.80 3.60 3.95</td>
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<tr>
<td>TKNb (mg g⁻¹)</td>
<td>1-year 0.70 0.91 0.83</td>
</tr>
<tr>
<td>Basec cations (cmol + /kg)</td>
<td>1-year 0.13 0.54 0.17</td>
</tr>
<tr>
<td>pH (H₂O)</td>
<td>1-year 4.00 4.09 4.25</td>
</tr>
</tbody>
</table>

Each value represents a mean based on three soil pits per stand in three stands.

* Values represent percent of sand–silt–clay.

b Total Kjeldahl nitrogen.

c Summation of exchangeable base cations.
were applied during the first growing season at elemental rates of 30 and 33 kg ha\(^{-1}\), respectively. Additional applications of N, P, K and B were applied during the third growing season at elemental rates approximating 90, 25, 40 and 1.5 kg ha\(^{-1}\), respectively.

At each of the 13 selected plantation sites, three inventory plots (261 m\(^2\)) were established within fully stocked areas. Above- and below-ground biomass sampling procedures were previously described by Adegbidi et al. (2002). Briefly, plot inventory (for all stocked areas. Above- and below-ground biomass counting (\(n = 60, 100 \text{ cm}^2 \text{ cells/soil pit}\)) and soil core subsamples (\(n = 6 \text{ or } 7, 1000 \text{ cm}^3 \text{ cores/soil pit}\)), and regression relationships based on root number and root length (Böhm, 1979; Escamilla et al., 1991; Adegbidi et al., 2002). Total fresh weights were determined in the field and all tissues were subsampled for determining moisture contents and dry weights (70 °C) in the laboratory. Regression and covariance analyses indicated that two separate regression equations could be used to predict above-ground or total tree biomass across all sites: one for the 1- and 2-year-old stands (with height as predictor variable) and a second for 3- and 4-year-old stands (with diameter at breast height (dbh) as predictor variable; Adegbidi et al., 2002). These biomass equations were applied to data (heights, dbh) collected on the three inventory plots (261 m\(^2\) per site/plantation) to estimate dry matter accumulation and increment. Corrections for logarithmic bias were made on all biomass estimates (Baskerville, 1972).

Subsamples of fresh needles were collected from each sample tree and specific needle area (SNA; all-sided) was determined using a volume displacement procedure (Johnson, 1984). Total all-sided leaf area index (LAI) was estimated for each site as the product of total needle biomass and average SNA. Production efficiency (i.e., annual dry matter increment/leaf area) was computed by tree component to examine ontogenetic and treatment effects on growth processes. Litterfall estimates were also made in the 3- and 4-year-old stands. Collections in all 3-year-old stands were made on December from four random locations (0.7 m\(^2\) quadrats) in each plot. Peak litterfall occurs during October and November and does not become significant until the third year because loblolly pine retains its needles for two growing seasons (Dalla Tea and Jokela, 1991). Monthly litter collection was accomplished with six litter traps per plot (0.7 m\(^2\); \(n = 18\)), randomly installed in both the bed and interbed areas, at one 4-year-old site. Net primary production was approximated as the sum of the annual biomass increment (excluding herbivory) and needlefall mass.

Plant tissues were kept on ice until oven-dried to a constant weight at 70 °C. All tissues were ground in a Wiley Mill to pass a 2 mm mesh stainless steel screen. Nitrogen was determined using a semi-micro Kjeldahl method (Thomas et al., 1967). All other nutrients were measured by dry ashing in a muffle furnace at 500 °C for 3 h, then digesting at 180 °C in 8 cm\(^3\) of 4.8 M HCl until dry, followed by digesting in 5 cm\(^3\) of 12.1 M HCl until dry. Digested samples were then taken up in 0.1 M HCl and analyzed on an inductively coupled argon plasma emission spectrometer. Soils samples were collected by horizon from three soil pits at each of the 1-, 3- and 4-year-old sites, and characterized for pH, effective cation exchange capacity by summation of exchangeable bases and 1 M KCl extractable Al, soil particle size by hydrometer, Mehlich I extractable P and organic matter by loss on ignition (Table 1). Plant nutrient content (kg ha\(^{-1}\)) was estimated for each stand as the product of tree component dry weights and average tissue nutrient concentrations.

Inventory data (numbers of trees, their heights and dbh) and foliar nutrient data were obtained from four additional sites (hereafter, referred to as independent sites and named IP #1–4) established on Spodosols of the same soil group in the same general locale by International Paper Co. All sites received comparable management inputs (site preparation, genetic stock, fertilization, competition control) as the studied age
sequence stands, and they were inventoried annually (1–4 years). Estimates of biomass were made for these four additional sites using the same allometric equations described above. Foliage samples were annually collected from the upper third of the crown during the dormant season (December–January). All tissues were analyzed using a wet digestion procedure (H$_2$SO$_4$; H$_2$O$_2$; Jones et al., 1991), with N determinations made using an Aipkem Flow Solution IV analyzer, and concentrations of other nutrients using an inductively coupled argon plasma emission spectrometer.

Correlation analyses were used to examine relationships between production efficiency (PE) and foliar nutrient concentrations (SAS Institute Inc., 1996). All significance tests were made at $\alpha = 0.05$.

3. Results and discussion

3.1. Tree biomass production and distributions

Total tree biomass accumulation (above- and below-ground) and leaf area development were described in a previous paper (Adegbidi et al., 2002). Total biomass accumulation increased rapidly through age 4 years (49.7 t ha$^{-1}$ year$^{-1}$; Fig. 1) and was about 20-fold higher compared to extensively managed stands of similar age growing on Spodosols (Colbert et al., 1990). All sided leaf area index was 1.1 at age 1 year, rapidly increased to 7.1 at age 2 years, reached a maximum of 10.5 at age 3 years and was 9.8 at age 4 years (Adegbidi et al., 2002).

When total biomass was separated into component parts, the distributions of above- and below-ground biomass by tree component were variable over time. Foliage accounted for about 30% of total tree biomass (standing crop) at age 2 years and then declined to 14% by age 4 years. Stemwood continued to increase over time, ranging from about 10% at age 1 year to 34% at age 4 years. Bark showed a modest increase (from 3 to 6%) over the same period. In contrast, after peaking at 25% during the second growing season, live branches accounted for a decreasing percentage of total tree biomass by age 4 years (18%). With the exception of fine roots, that also accounted for a decreasing percentage of total biomass over time (age 1 year = 30%, age 4 years = 3%), coarse root and tap roots remained fairly constant (i.e., about 11–15% for stump + tap root and 7–12% for coarse roots). Overall, roots (tap, coarse, fine) accounted for about 30% of total tree biomass in these 4-year-old stands.

The partitioning of NPP among components changed significantly from ages 1 to 4 years (Table 2). Proportions of annual production allocated to stemwood and bark followed similar trends, initially increasing and then reaching a plateau from age 3 to 4 years (i.e., 10–35% of NPP for stemwood and 3–7% of NPP for bark). Partitioning of NPP to fine roots followed a trend opposite that of stemwood, decreasing from a maximum of 30% at age 1 year to a minimum of 1% at age 4 years. Allocation of NPP to foliage increased from age 1 (26%) to 3 years (33%) when maximum LAI was attained, and then decreased to 14% by age 4 years. The percentage of NPP
partitioned to taproot was stable throughout the study period (≈12–13%).

These biomass allocation patterns highlight the dynamic nature of growth during the early stages of stand development. As loblolly pine retains its needles for only 2 years, significant carbon construction costs are associated with foliage and branch production during this rapid leaf area accretion phase (Chung and Barnes, 1977). Once canopy closure and intraspecific competition becomes more significant, foliage loss and branch recession from the lower crown occurs in response to self-shading. This appeared to begin at age 4 years, as previously shown for intensively managed loblolly pine in South Carolina (McCrady and Jokela, 1996). Management practices like forest fertilization accelerate tree growth and stand structural changes (Miller, 1981; Colbert et al., 1990), with the ratio of woody/total biomass increasing and foliage/total biomass decreasing over time (Albaugh et al., 1998; Jokela and Martin, 2000). Close correspondence between studies highlight the predominant role that ontogeny plays in affecting the above-ground dry matter allocation patterns for this species.

### 3.2. Nutrient accumulations and distributions

Rapidly growing southern pine stands place high nutrient demands on the soil, especially during the canopy development phase. Yet, few estimates of nutrient accumulation and uptake exist for fast growing southern pine plantations. Such data are critical for quantifying plant nutrient demands and for developing fertilizer prescriptions based on soil nutrient supply. Especially rare are studies quantifying below-ground nutrient contents (Van Lear et al., 1984; Gholz et al., 1985).

In the current study, nutrient content increased with biomass accumulation (Table 3), with the 4-year-old stands accumulating about 195 kg N ha⁻¹ and 22 kg P ha⁻¹ in the total tree. The crown represented the dominant pools for both N and P at age 4 years, with 36% of the total P content and 42% of the total N content in the foliage; roots accumulated about 23% of the N and 30% of the P. Needlefall N and P returns at age 4 years averaged 28 and 2.9 kg ha⁻¹ year⁻¹, respectively, which closely matches the values of 24.8 and 3.3 kg ha⁻¹ year⁻¹ reported by Dalla Tea and Jokela (1994) in north-central Florida for a 7-year-old loblolly pine stand growing on similar soils and managed using comparable silvicultural treatments.

Cation (K, Ca, Mg) accumulations in the tree biomass were also highest in the above-ground components (Table 3). By age 4 years, K, Ca and Mg accumulations in the total tree were approximately 86, 72 and 28 kg ha⁻¹, respectively. Foliage accumulations were about 34% for K, 21% for Ca and 26% for
Mg in the total tree nutrient content. Calcium accumulations were also significant in litterfall, accounting for about 16 kg ha\(^{-1}\) or 18% of Ca in the total biomass (total tree + litterfall). Cation distributions in roots became a more significant pool over time and ranged from about 28% for Ca to 31% for Mg at age 4 years. Overall, the fine root standing crop at time of sampling represented a small nutrient pool, accounting for less than 5% of the stand total nutrient content.

When expressed on an annual basis, differences in net nutrient accumulation (including litterfall) among years ranged from about 60 to 73 kg ha\(^{-1}\) year\(^{-1}\) for N and 6 to 8 kg ha\(^{-1}\) year\(^{-1}\) for P (Table 3). Annual cation accumulation rates were about 24–31 kg ha\(^{-1}\) year\(^{-1}\) for K, 24–33 kg ha\(^{-1}\) year\(^{-1}\) for Ca, and 9–11 kg ha\(^{-1}\) year\(^{-1}\) for Mg. Although these estimates include fine root biomass and litterfall inputs (age 3 and 4 years), they do not account for seasonal fine root turnover, exudation and canopy leaching. Gholz et al. (1985) reported that canopy leaching for N and P was negligible in developing slash pine plantations, and because fine roots represented such a small nutrient pool for these stands, the estimates of N and P annual accumulation likely represent reasonable approximations of annual soil uptake. In contrast, cation leaching can be more significant in developing pine plantations (Gholz et al., 1985) and annual soil uptake rates for K, Ca and Mg would likely need to be elevated by another 5–15% based on the estimates reported above.

The nutrient accumulation levels for the intensively managed stands sampled in this study were about 15-fold greater than those in extensively managed stands on other Spodosols (Colbert, 1988). These results clearly demonstrate that sustaining high levels of productivity places correspondingly high levels of demand on soil nutrient pools. The nutrient uptake estimates reported here are reflective of what would be expected in a non-competitive (inter-specific) environment, as understory vegetation was largely absent in these stands.

### 3.3. Production efficiency

Previous studies with southern pines have documented a strong relationship between annual biomass production and LAI (Vose and Allen, 1988; Colbert...
et al., 1990; McCrady and Jokela, 1998; Samuelson et al., 2001). Production efficiency (PE), expressed here as total biomass (above- and below-ground) increment per unit leaf area, incorporates both the effects of carbon allocation and photosynthetic efficiency (Waring, 1983). A variety of factors influence PE, including genetics, environmental and physiological stresses (nutrition) and age-related changes due to stand development (Waring and Running, 1998). A common finding with shade intolerant species is that stemwood PE generally increases until maximum LAI is attained. Then, as crown size increases, stemwood PE tends to decrease as an increasing proportion of the leaf area is displayed on large, older branches in the lower crown that are sustained physiologically at the expense of stemwood production (Long and Smith, 1989; Jack and Long, 1992).

In the current study, large differences in PE were apparent over time (Fig. 2A). Between the second and third growing seasons, PE declined by 50% (2.6 Mg ha\(^{-1}\) year\(^{-1}\)/unit versus 1.3 Mg ha\(^{-1}\) year\(^{-1}\)/unit LAI), but recovered to earlier levels (3.0 Mg ha\(^{-1}\) year\(^{-1}\)/unit LAI) by the fourth year. Additional data from the four independent sites (IP #1–4) confirmed these findings, particularly the change occurring between the second and third years (Fig. 2A). The low standard errors of PE provide additional confidence for accepting these interpretations (Fig. 2).

Our estimates of total tree PE at age 4 years are higher than those observed by Albaugh et al. (1998) for 9- and 12-year-old loblolly pine stands (3.0 Mg ha\(^{-1}\) year\(^{-1}\)/unit versus 1.9 Mg ha\(^{-1}\) year\(^{-1}\)/unit LAI). In closely spaced 4-year-old loblolly pine stands, McCrady and Jokela (1998) observed a range of 2.7–

Fig. 2. Temporal dynamics in production efficiency (PE; with standard error bars) by tree component (Panel A, total tree; Panel B, stemwood; Panel C, branchwood; Panel D, stump + tap root) for intensively managed loblolly pine stands growing on sandy Spodosols in the lower Coastal Plain of Georgia. The figure was based on data from the 13 sampled sites (our sites) and four independent IP sites (IP #1–4).
4.2 Mg ha\(^{-1}\) year\(^{-1}\)/unit LAI for above-ground PE compared to 2.1 Mg ha\(^{-1}\) year\(^{-1}\)/unit LAI in the current study. Other 4-year-old intensively managed loblolly pine stands had lower values of PE than our estimates: 0.6 Mg ha\(^{-1}\) year\(^{-1}\)/unit LAI (Colbert et al., 1990) and 1.0 Mg ha\(^{-1}\) year\(^{-1}\)/unit LAI (Samuelson et al., 2001) for stemwood PE and stem + branch PE, respectively, compared to 1.2 and 1.7 Mg ha\(^{-1}\) year\(^{-1}\)/unit LAI in the current study.

Total tree destructive sampling conducted in the current study provided a unique opportunity to examine which biomass components contributed to the PE declines between years 2 and 3. Stemwood PE (Fig. 2B) increased over time for all sampled stands and was not involved with the observed declines in total tree PE. This likely reflects changing carbon allocation patterns in developing stands, as stemwood dry matter distributions doubled (16% versus 34%) between years 2 and 4. In contrast, branch and taproot PE both exhibited large declines between the second and third years (Fig. 2C and D), and these results closely mirrored the declines previously described for total tree PE. Consistency in these trends was generally observed among all of the stands sampled (e.g., chronosequence \(n = 13\)), including the four independent sites.

Explanations for the temporal declines in PE include: (i) drought effects, as the study period included several drought years, (ii) carbon allocation responses to the silvicultural treatment and concomitant changes in stand structure, (iii) growth and maintenance respiration associated with increasing tree size or (iv) nutrient deficiencies and antagonisms induced through rapid tree growth. The drought hypothesis is unlikely since sampling of the 2- and 3-year-old stands were conducted in the same year, and declines were only observed at age 3 years. Similarly, results from the four independent stands showed the same trend from age 2 to 3 years, yet this age sequence at the independent sites occurred in 1995–1998, which had varying levels of precipitation.

With respect to the carbon allocation hypothesis, significant changes in carbon allocation patterns do occur over time, and silvicultural treatment has affected these processes in conifers (Cropper and Gholz, 1994; Haynes and Gower, 1995; Beets and Whitehead, 1996). Albaugh et al. (1998) hypothesized that fertilization and irrigation influenced total biomass production efficiency in loblolly pine because of greater carbon allocation to foliage and less to fine roots. Also, Haynes and Gower (1995) reported that both fine and coarse root production in red pine (Pinus resinosa Soland.) plantations in northern Wisconsin were lower in fertilized than in unfertilized plots. Although data from this study do not allow rigorous testing of this hypothesis, fertilizer induced reductions in carbon allocation to fine roots, especially during the early stages of stand development, could have led to reduced fine root numbers, and concentrated their distribution in the surface horizons (i.e., A and E).

The respiration hypothesis is based on the idea that larger trees have greater respiration demands (Yoda et al., 1965; Chung and Barnes, 1977), and this use of carbon causes the shift in PE. In this study, reductions in PE were associated with increasing tree size (Fig. 3). However, it seems unlikely that...
increased growth and maintenance respiration were responsible for the change in PE because: (i) PE recovered in year 4 and (ii) respiration was not a large enough component of the carbon budget to elicit this large of an efficiency change. In support of this, Cropper and Gholz (1993) concluded that growth respiration of slash pine on similar sites in Florida was a small portion of the total carbon budget.

The last hypothesis invokes temporal declines in PE due to nutrient deficiencies and antagonisms induced through rapid tree growth (Stone, 1990). Nutritional disorders can be short-lived and diminish as root systems exploit greater soil volumes, or they

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**Fig. 4.** Mean annual foliar nutrient concentrations from age 1 to age 4 years for intensively managed loblolly pine stands growing on sandy Spodosols in the lower Coastal Plain of Georgia. The figure was based on data from the four independent IP sites (IP #1–4).
Correlations were based on data from the four independent IP sites (IP #1–4) documented cause of growth reductions in the southeastern U.S., Albaugh et al. (1998) and Xiao et al. (2003b) reported low foliar Mg levels in intensively managed loblolly pine stands. Similarly, acute Cu deficiency symptoms have been observed in 2- and 3-year-old intensively managed loblolly pine plantations growing on Spodosols (E.J. Jokela, unpublished data). In accordance with the conclusion drawn by Stone (1990), these observations suggest the rapid growth resulting from N, P, K and B additions through fertilization may have induced Mg, Zn and Cu deficiencies in these stands.

### Table 4

<table>
<thead>
<tr>
<th></th>
<th>Branchwood PE</th>
<th>Taproot PE</th>
<th>Total Tree PE</th>
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<tbody>
<tr>
<td>N</td>
<td>-0.53</td>
<td>-0.14</td>
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<tr>
<td>P</td>
<td>-0.50</td>
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<td>K</td>
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<td>Mg</td>
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<tr>
<td>Zn</td>
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</table>

Correlations were based on data from the four independent IP sites (IP #1–4) (n = 18 plots).

* Values in bold represent correlation coefficients with *p*-values <0.05.

Intensive management systems that include deployment of genetically improved seedling stock, mechanical and chemical site preparation and fertilization are commonly used to increase productivity of loblolly and slash pine plantations in the southern U.S. Spodosols are a dominant soil type used for intensive management in the lower Coastal Plain region and are mapped on approximately 5.7 × 10^6 ha (Adegbidi et al., 2002). Surprisingly, limited information is available on the developmental and nutrient dynamics of rapidly growing loblolly pine stands on these soils. Results from this study have demonstrated that high levels of biomass accumulation are possible on these soils. Although this result alone is not too surprising, the magnitude of the nutrient accumulation and the demands being placed on these soils is impressive and until now largely undocumented for this period of stand development.

Another useful outcome of these data was the opportunity to evaluate PE at this young age. These data showed a trend for reduced PE between ages 2 and 3 years. These results were based on a number of unique sites that were whole tree sampled, as well as four additional longer term studies established on similar soils. The low error terms within an age class argues strongly for the integrity of this chronosequence. Corroboration of these results, using four intensively sampled and independent sites, also argues for acceptance of these PE trends, which may be indicative of impending stand developmental problems, including nutrient disorders.

The data suggested four working hypotheses to explain the decrease in PE between ages 2 and 3 years.
Drought, along with growth and maintenance respiration were considered but not supported as the primary causes of these PE decreases. Multiple nutrient deficiencies induced through rapid growth or ontogenetic changes in carbon allocation patterns were the two competing hypotheses that appeared most plausible. This study did not address the ontogenetic issue, but did provide empirical evidence of multiple nutrient limitations, particularly between ages 2 and 3 years.

Rapidly growing loblolly pine can produce a range of concerns, from pest and disease issues to basic growth patterns that are still poorly understood. It is clear that a better understanding of carbon allocation processes, nutrient requirements and critical nutrient levels of fast growing southern pines will be required to maintain the sustainability of biomass production, given this level of silvicultural treatment intensity in the southeastern U.S. This study highlights the need to focus on multiple nutrient deficiencies and the complex interactions in plant growth that can result from soils having low levels of inherent fertility.

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