

# Effects of ontogeny and soil nutrient supply on production, allocation, and leaf area efficiency in loblolly and slash pine stands<sup>1</sup>

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**Abstract:** The effects of ontogeny and soil nutrient supply on aboveground biomass accumulation, allocation, and stemwood growth efficiency of loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm. var. *elliottii*) were investigated in north-central Florida over 16 years using a  $2 \times 2 \times 2$  factorial experiment (species, fertilization, weed control). Aboveground biomass growth responses to the combined fertilizer and weed control treatments (FW) averaged ~2- and 2.8-fold for slash and loblolly pine, respectively. In the same treatment, annual needlefall (NF) production for slash pine approached a “steady state” of  $6 \text{ Mg}\cdot\text{ha}^{-1}$  at ages 8–14 years, while loblolly pine NF production peaked at  $7 \text{ Mg}\cdot\text{ha}^{-1}$  at age 10 years, and then declined 17% following curtailment of the fertilizer treatment. Periodic stemwood biomass increment (PAI) for the FW treatment for both species culminated at about  $15 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$  at age 8 years and then declined rapidly (~275%) to  $<4 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$  at 15 years; reductions for the untreated control were considerably slower. The progressive decline in PAI following peak leaf area development was closely associated with a decrease in stemwood production per unit leaf area (growth efficiency). A unit increase in leaf area index in the 7- to 9-year-old stands produced about 3.0 and 3.1 times more stemwood biomass per year than in the 14- to 16-year-old stands for loblolly and slash pine, respectively.

**Résumé :** Les effets de l'ontogénèse et de l'apport de nutriments dans le sol sur l'accumulation de biomasse épigée, l'allocation et l'efficacité de croissance du bois de la tige chez le pin à encens (*Pinus taeda* L.) et le pin de Floride (*P. elliottii* Engelm. var. *elliottii*) ont été étudiés pendant 16 ans dans le centre-sud de la Floride à l'aide d'un dispositif expérimental factoriel comprenant trois facteurs (l'espèce, la fertilisation et le contrôle de la végétation) avec deux niveaux chacun. La fertilisation combinée au contrôle de la végétation (FW) a augmenté en moyenne la croissance de la biomasse épigée de respectivement ~2 et 2,8 fois chez le pin de Floride et le pin à encens. Dans le même traitement, la production annuelle de litière d'aiguilles chez le pin de Floride approchait le point d'équilibre de  $6 \text{ Mg}\cdot\text{ha}^{-1}$  entre l'âge de 8 à 14 ans, tandis que chez le pin à encens elle atteignait un maximum de  $7 \text{ Mg}\cdot\text{ha}^{-1}$  à l'âge de 10 ans et décroissait subséquemment de 17% suite à la réduction de la fertilisation. Avec le traitement FW, l'accroissement périodique de biomasse ligneuse dans la tige a culminé chez les deux espèces à environ  $15 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{a}^{-1}$  à l'âge de 8 ans et a ensuite diminué rapidement (~275%), à moins de  $4 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{a}^{-1}$  à l'âge de 15 ans. Dans le traitement témoin, la diminution était beaucoup plus lente. La diminution progressive de l'accroissement périodique de biomasse ligneuse dans la tige qui a suivi le développement maximum de la surface foliaire était étroitement associée à une diminution de la production de bois dans la tige par unité de surface foliaire (efficacité de croissance). Une augmentation d'une unité dans l'indice de surface foliaire des peuplements âgés de 7 à 9 ans a entraîné la production annuelle de 3,0 et 3,1 fois plus de biomasse ligneuse dans la tige dans les peuplements de pin à encens et de pin de Floride âgés de 14 à 16 ans.

[Traduit par la rédaction]

## Introduction

Over the past two decades, intensive management techniques have been increasingly applied to accelerate the growth of forests. These techniques, including chemical and mechanical site preparation, fertilization, and deployment of genetically improved planting stock, have the potential to increase tree productivity by several hundred percent com-

pared with less-intensively managed forests (Cromer and Williams 1982; Allen et al. 1990; Colbert et al. 1990). To more effectively predict the outcomes of these intensive silvicultural treatments and efficiently time their application, it is imperative that we understand the mechanisms underlying the associated growth increases. Growth responses resulting from intensive silvicultural treatments are commonly manifest through reductions in competition for soil nutrients and water between trees and understory plants and are associated with enhanced leaf area development and canopy light interception by the trees (Vose and Allen 1988; Dalla-Tea and Jokela 1991; Samuelson 1998). Numerous short-term investigations have documented the effects of nutrient amendments and competition control on leaf area development, net primary production, above- and below-ground biomass allocation patterns, growth efficiency, and nutrient cycling processes (Colbert et al. 1990; Gholz et al. 1991;

Received February 3, 2000. Accepted June 15, 2000.

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<sup>1</sup>Journal Series Paper No. R-07600 of the Florida Agriculture Experiment Station.

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**Table 1.** Selected chemical properties of air-dried bulk soils collected by treatment (0–5 cm) at age 6 years.

	Loblolly pine				Slash pine			
	C	W	F	FW	C	W	F	FW
Total C (g·kg <sup>-1</sup> )	10.6 (16.7)	16.9	13.6 (18.3)	15.0	10.8	15.0	11.5	15.9
Total N (mg·kg <sup>-1</sup> )	462	699	564	676	451	683	447	689
Total P (mg·kg <sup>-1</sup> )	25.8 (36.7)	35.4	36.7 (51.1)	37.8	26.9	34.1	25.9	37.4
C/N ratio	22.9	24.2	24.1	22.2	24.0	22.0	25.7	23.1
C/P ratio	411 (455)	477	371 (358)	397	401	440	444	425
pH	3.9 (3.9)	3.8	3.8 (3.8)	3.8	4.0	3.9	3.9	3.9

**Note:** The table is adapted from Polglase et al. (1992c); values in parentheses are data collected for loblolly pine at age 11 years as reported in Grierson et al. (1999). C, untreated control; W, sustained weed control; F, annual fertilization; FW, fertilization + weed control.

Heilman and Xie 1994; Albaugh et al. 1998; Grierson et al. 1999). Conversely, the long-term impacts of fertilizer and competition control treatments on stand development processes are still relatively poorly understood for most managed forest ecosystems (Jokela et al. 1988; Harding and Jokela 1994). Especially rare are comprehensive studies that span the range of stand development from establishment to maturity (e.g., pulpwood rotations) and compare species-level productivity under common growth environments.

Intensive silvicultural practices are especially important to commercial forest management in the southeastern United States. Throughout this region, stands of loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm. var. *elliottii*) occupy approximately 12 and  $5.3 \times 10^6$  ha, respectively, (Sheffield and Knight 1982; Sheffield et al. 1983). Although both species are well suited to the relatively infertile soils of this region, it has long been known that growth responses due to fertilizer additions, particularly nitrogen (N) and phosphorus (P), are biologically and economically justifiable (Pritchett and Llewellyn 1966; Bengtson 1979; Pritchett and Comerford 1982; Jokela and Stearns-Smith 1993). Recent estimates indicate that approximately  $2.35 \times 10^6$  ha of loblolly pine and  $0.89 \times 10^6$  ha of slash pine were fertilized between 1969 and 1998 (NCSFNC 1999). Similarly, woody and herbaceous weed control treatments applied at plantation establishment have become routine management practices for enhancing forest growth (Creighton et al. 1987; Shiver et al. 1990; Miller et al. 1991).

In 1983, the Intensive Management Practices Assessment Center (IMPAC), located at the University of Florida, designed and established a study to evaluate the biological growth potential of southern pines. An array of treatments (in factorial combination), including annual fertilizer applications and sustained elimination of understory competition was used to manipulate growth-limiting environmental factors by creating a soil nutritional gradient. Earlier reports demonstrated for this nutrient-impooverished site that above-ground biomass accumulation at 4 years was 17- and 5.5-fold greater in the combination treatment (fertilizer plus competition control) than the untreated control for loblolly and slash pine, respectively (Colbert et al. 1990). Because irrigation did not enhance pine growth (Swindel et al. 1988), nutrient availability represented the primary limiting factor (Neary et al. 1990).

The present study utilized the same IMPAC experiment to address the long-term effects of intensive silvicultural treatments on productivity and stand development processes in managed southern pine plantation ecosystems. To accom-

plish this objective, we examined and compared patterns of aboveground biomass accumulation and allocation, foliage development, stemwood production dynamics, and growth efficiency among treatments and between species over a period spanning 16 growing seasons.

## Materials and methods

### Study area description

The 4-ha site is approximately 10 km north of Gainesville, Fla. (29°30'N, 82°20'W), at an elevation of about 45 m. Mean annual precipitation is 1350 mm and mean annual temperature is 21°C (NOAA 1989). The soils are classified as sandy, siliceous, hyperthermic Ultic Alaquods (Pomona fine sands; Soil Survey Staff 1998). In a typical profile, the spodic horizon occurs at 20–50 cm with an argillic horizon at 90–120 cm. The soil nutrient reserves are inherently low (Table 1), as the A horizon is comprised predominantly of quartz sand that has both low organic matter content and cation exchange capacity (<5 cmol<sub>c</sub>·kg<sup>-1</sup>). Chemical characterization of the litter and surface soils for this site have been reported in Polglase et al. (1992b, 1992c, 1992d) and Grierson et al. (1999).

A wildfire destroyed the previous slash pine plantation in 1981. In January 1983, genetically improved (first generation, open-pollinated) 1-year-old loblolly and slash pine seedlings were hand planted at a 1.8 × 3.6 m spacing following roller-drum chopping and single-pass bedding. Understory plants were those common to lower Coastal Plain flatwoods sites, with gallberry (*Ilex glabra* (L.) Gray), sawtooth palmetto (*Serenoa repens* (B.) Small.), fetterbush (*Lyonia lucida* (Lam.) K. Koch), staggerbush (*Lyonia ferruginea* (Walt.) Nutt.), blueberries (*Vaccinium* spp.), St. John's-wort (*Hypericum fasciculatum* Lam.), and runner oak (*Quercus pumila* Walt.) the dominant woody species. Also commonly present, as herbaceous species were broomsedges (*Andropogon* spp.) and panic grasses (*Panicum* spp. and *Dicanthelium* spp.).

### Experimental design and treatments

The study consisted of three replicates of a 2 × 2 × 2 factorial of species, complete and sustained understory competition control, and annual fertilizer application arranged in a randomized split-plot (species) design (Swindel et al. 1988). Treatment plots were about 820 m<sup>2</sup> in size, with interior measurement plots being 260 m<sup>2</sup> (40 trees). An untreated, two-row planted buffer separated all plots. Understory vegetation was controlled annually from ages 1 to 10 years (1983–1993) using a combination of herbicides and mechanical rotary cutters (Neary et al. 1990). Thereafter, canopy closure reduced encroachment of the understory plants on treated plots. A balanced fertilizer regime was similarly applied annually from 1983 to 1993 as narrow bands (30-cm semicircle) around the base of each tree. Over the 10-year treatment period, total elemental application rates for those plots receiving fertilizer additions

were approximately ( $\text{kg}\cdot\text{ha}^{-1}$ ): N, 360; P, 143; K, 317; Ca, 108; Mg, 72; S, 72; Mn, 3; Fe, 3; Zn, 3; Cu, 0.5; and B, 0.5. The control plots did not receive either the fertilizer or understory competition control treatments.

## Procedures

Total tree and component aboveground biomass prediction equations were developed separately by species and treatment at age 4 and 13 years. Destructive sampling procedures used at age 4 years ( $n = 72$  trees) were reported in Colbert et al. (1990). At age 13 years, 80 trees ( $n = 10$  trees per species for each of 4 treatments) representative of the range of sizes encountered in each treatment plot were destructively harvested from treated buffer rows over a 3-week period during mid-September and early October. Trees were felled at groundline (stump height  $<15$  cm) and branches were cut flush from the stem. Needles were removed from all branches and both components, representing the entire crown, were weighed green in the field. Subsamples of needles and branches were bagged and brought back to the laboratory for determining moisture contents and dry masses. The stem was cut into 1.5-m sections and weighed green in the field. A 3 cm thick disk was cut from the butt section and the top of each bolt thereafter. The bark was separated from the disk, and both components were weighed green in the field. The disks and bark were transported back to the laboratory in sealed bags and dried to a constant mass at  $70^\circ\text{C}$ . Oven-dry masses of the stemwood and bark were calculated for each bolt from the field-determined green masses using subsample moisture contents and the bark/wood ratios from the disks. The dry mass of individual biomass components was summed for each tree.

The linear form of the allometric equation ( $\ln(\hat{Y}) = \beta_0 + \beta_1 \ln(X)$ ) was used to develop relationships between component dry mass and tree dimension (diameter and height at age 4 years, diameter at age 13 years). Analysis of covariance was used to test for equality in the regression coefficients among treatments (SAS Institute Inc. 1996). When no significant differences were found ( $P = 0.05$ ), the data were pooled and common regression equations were developed (Appendix).

Pine litter fall was collected monthly for each treatment and replication beginning at age 6 years and continuing through age 16 years. Six circular litter traps ( $0.7 \text{ m}^2$ ) were installed in each plot (Dalla-Tea and Jokela 1991). The collected litter was sorted into needles and other pine materials (branch, bark, twigs), dried at  $70^\circ\text{C}$ , and weighed to the nearest 0.1 g. In this report, data analyses and interpretations will consider only the needlefall (NF) component, as needles constituted  $>90\%$  of the annual pine litter-fall mass. Leaf area index (LAI) was calculated from NF and logistic models of foliage accretion as described by Kinerson et al. (1974) and Dougherty et al. (1995). Needlefall was used to estimate temporal patterns of canopy leaf area, because NF provides a more direct, dynamic record of canopy dynamics than do allometric estimates of leaf area developed at one point in time. Needlefall data were corrected for senescence-related biomass reductions (13 and 14% for slash and loblolly pine, respectively) and were converted to all-sided leaf area using specific leaf area for slash ( $0.0100 \text{ m}^2\cdot\text{g}^{-1}$ ) and loblolly pine ( $0.0115 \text{ m}^2\cdot\text{g}^{-1}$ ) (Dalla-Tea 1990; Dalla-Tea and Jokela 1991).

Foliage samples were collected from the upper third of the crown from four dominant and codominant trees per plot during the 1989 and 1996 growing seasons (March–September). Approximately 25 fascicles per tree (current-year needles) were composited from each treatment plot, dried to a constant mass at  $70^\circ\text{C}$ , and ground in a Wiley Mill to pass a 1-mm stainless steel sieve. Nitrogen was determined using a semi-micro-Kjeldahl method (Wilde et al. 1979). Tissue solution samples were analyzed for total P on a spectrophotometer using the ascorbic acid – antimony reduced phosphate method following a wet digestion procedure ( $\text{H}_2\text{SO}_4 - 30\% \text{ H}_2\text{O}_2$ ; Murphy and Riley 1962).

Diameter (1.3 m) of all living trees within the measurement plots were measured annually during the dormant season, except during years 8 and 12. The biomass prediction equations were applied to the inventory data to estimate dry matter accumulation ( $\text{Mg}\cdot\text{ha}^{-1}$ ), stemwood periodic annual increment (PAI;  $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ) and mean annual increment (MAI;  $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ) over time. The allometric equations developed at age 4 years were used to predict these variables for ages 4 and 6 years, while the equations from age 13 years were used at ages 9–16 years. These decisions were made considering both the range of tree size in each year compared with the range of tree size used to develop the allometric equations, as well as the developmental stage of the trees at each inventory. Corrections for logarithmic bias were made on all biomass estimates (Baskerville 1972). Component dry mass ratios (stemwood/foilage, stemwood/branches, branches/foilage) and a measure of growth efficiency (i.e., annual stemwood production/leaf area) were computed to examine ontogenetic and treatment effects on growth processes.

Analysis of variance for a split-plot design was used to test for species and treatment effects on growth parameters. A two-segment regression procedure described in Loo et al. (1985) and Martin et al. (1990) was used to quantify the relationship between foliage production and foliar phosphorus concentration. Coefficients of determination for no-intercept regressions were calculated as  $1 - \Sigma(y - \hat{y})^2 / \Sigma y^2$  ( $R^2$  version 7 in Kvalseth (1985)). All statistical analyses were conducted using the SAS statistical package (SAS Institute Inc. 1996).

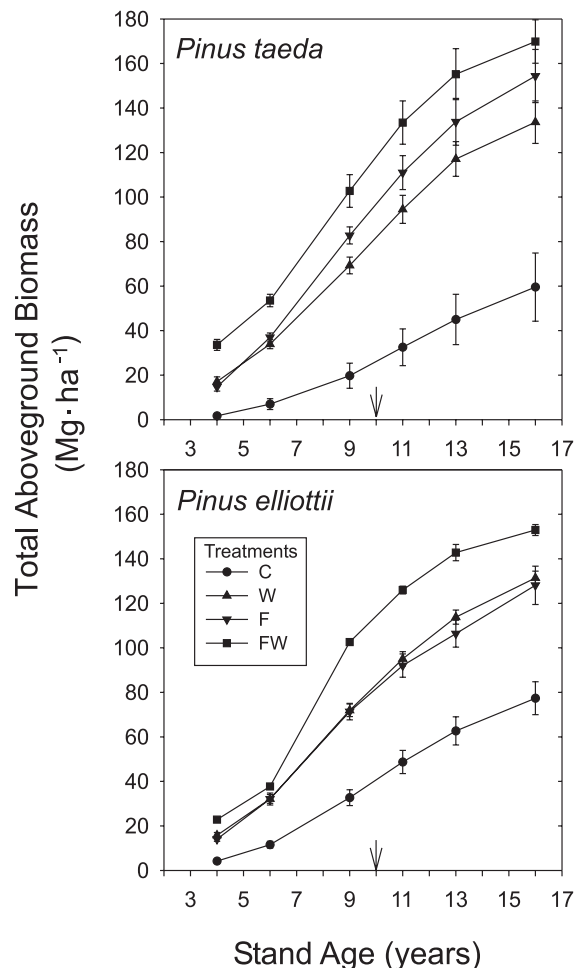
## Results

### Dry matter accumulation

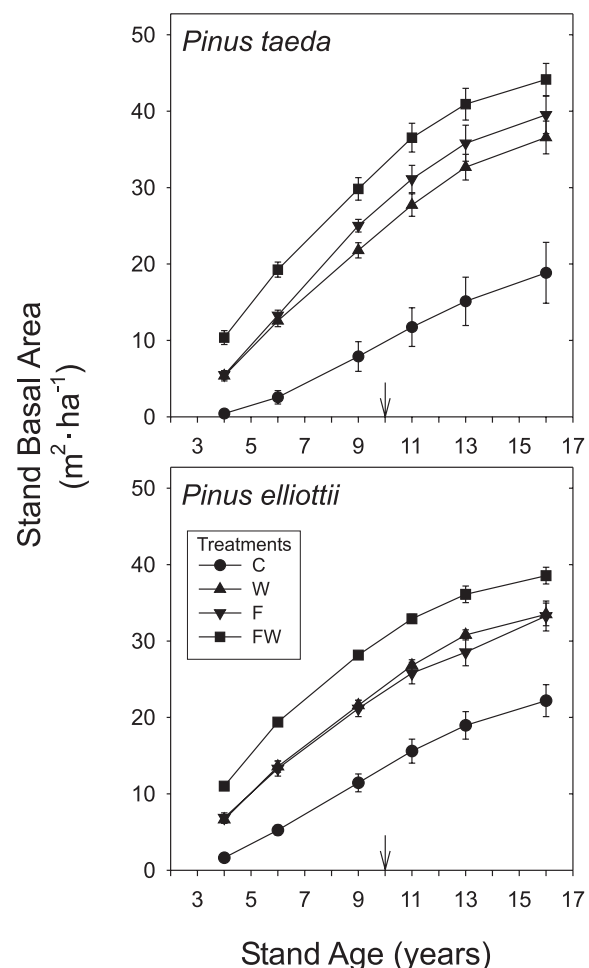
The effects of fertilizer and weed control treatments on aboveground dry matter accumulation were quantified periodically over the course of stand development (Fig. 1, Table 2). In general, growth responses due to silvicultural treatments were large over the entire study period. For example, at age 16 years the combined fertilizer plus weed control treatment (FW) for loblolly pine accumulated about  $170 \text{ Mg}\cdot\text{ha}^{-1}$  of biomass compared with  $60 \text{ Mg}\cdot\text{ha}^{-1}$  for the untreated control (C; 2.8-fold response; Fig. 1). Similar patterns were observed for slash pine, although relative growth responses tended to be smaller than for loblolly pine (e.g.,  $\sim 2.0$ -fold response; FW,  $153 \text{ Mg}\cdot\text{ha}^{-1}$ ; C,  $77 \text{ Mg}\cdot\text{ha}^{-1}$ ). Patterns of basal area accretion for each treatment closely paralleled that described for total aboveground biomass (Fig. 2).

Treatment main effects and interactions on dry matter accumulation and allocation patterns by tree component (e.g., stemwood, bark, branches, foliage) were examined using data from the last destructive harvest conducted at age 13 years (Tables 3 and 4). The main effects of fertilizer (F) and weed control (W) on total aboveground and tree component biomass accumulation were highly significant ( $P < 0.0001$ ). Species main effects were found for stem bark ( $P < 0.01$ ) and live branch ( $P < 0.05$ ) biomass accumulation. When averaged across all treatments, slash pine accumulated about 1.4 times more bark biomass than loblolly pine, whereas live branch biomass was 1.3 times greater for loblolly pine. The  $F \times W$  interaction (scale effect) was consistent and less than additive for stemwood, bark, live branches, foliage, and total biomass, suggesting a lack of independence between these two treatments, i.e., growth responses due to fertilizer additions were dependent on the associated level of weed control. In the case of total biomass, the nature and

**Fig. 1.** Total aboveground biomass accumulation (with standard error bars) for *P. taeda* and *P. elliottii* plantations grown under the following silvicultural treatments: control (C), complete and sustained understory competition control (W), annual fertilization with macro- and micro-nutrients from establishment through age 10 years (as indicated by arrow) (F), and combined competition control and fertilization treatments (FW)



**Fig. 2.** Stand basal area development (with standard error bars) for *P. taeda* and *P. elliottii* plantations grown under the following silvicultural treatments: control (C), complete and sustained understory competition control (W), annual fertilization with macro- and micro-nutrients from establishment through age 10 years (as indicated by arrow) (F), and combined competition control and fertilization treatments (FW).



interpretation of the  $F \times W$  interaction was also consistent (less than additive) among years (i.e., age 5–16 years; Table 2).

The significant  $S \times F$  interaction represented a species rank change (Tables 2 and 3B). At age 13 years, loblolly pine accumulated more stemwood (95.8 vs. 77.8  $\text{Mg}\cdot\text{ha}^{-1}$ ) and total biomass (144.5 vs. 124.6  $\text{Mg}\cdot\text{ha}^{-1}$ ) than slash pine on fertilized plots (Table 3A), while the opposite was true when no fertilizer additions were made (e.g., total biomass of 88.2 vs. 81.0  $\text{Mg}\cdot\text{ha}^{-1}$  for slash and loblolly pine, respectively).

#### Dry matter allocation patterns

The fertilizer and weed control treatments significantly altered aboveground biomass allocation patterns for both species (Table 4B). In most cases, the intensive silvicultural treatments accelerated stand development and thereby contributed to predictable changes in biomass allocation patterns. For example, allocations to live branches, especially

for slash pine, generally increased, while allocations to bark decreased as the level of silvicultural treatment increased beyond that of the untreated control (Table 4A). Regardless of treatment, biomass allocations were greater for loblolly pine than slash pine for stemwood (65.3 vs. 62.8%) and branches (18.5 vs. 15.3%), while the opposite was true for bark (9.1 vs. 13.0%) and foliage (7.4 vs. 9.2%).

Similar to that observed at age 4 years for this same site (Colbert et al. 1990), the magnitude of the interactions between silvicultural treatments were small but statistically significant for most biomass components. The significant  $F \times W$  interaction was less than additive for biomass allocations to stemwood, bark, live branches, and foliage; similar patterns were found for the stemwood/foliage, stemwood/branch, and branch/foliage biomass ratios (Table 4B). When averaged across species, stemwood and branch allocations were always lowest for the C treatment (e.g., C stemwood, 63.3%; C branch, 15.4%) and highest for the FW treatment (e.g., FW stemwood, 64.3%; FW branch, 17.8%); opposite

**Table 2.** Significance of analysis of variance for temporal levels of total aboveground biomass accumulation in slash and loblolly pine plantations as affected by fertilizer and weed control treatments.

Source of variation	df	Stand age (years)										
		3	4	5	6	9	10	11	13	14	15	16
<b>Whole plot</b>												
Block	2											
Species (S)	1		*	*	*							
Error	2											
<b>Split plot</b>												
Fertilization (F)	1	***	***	***	***	***	***	***	***	***	***	***
Weed control (W)	1	***	***	***	***	***	***	***	***	***	***	***
F × W	1			**	**	**	**	**	**	**	**	**
S × F	1		**	**	**	*	*	*	*	*	*	*
S × W	1	*	**	**	**							
S × F × W	1											
Error	12											

**Note:** For a given source of variation, main effects and interactions were significant at  $P < 0.05$  (\*),  $P < 0.01$  (\*\*), and  $P < 0.001$  (\*\*\*).

effects were found for bark (e.g., C, 12.3%; FW, 10.3%) and foliage (e.g., C, 8.8%; FW, 8.0%).

With the exception of bark, interactive effects between species and silvicultural treatments ( $S \times F$ ,  $S \times W$ ) were statistically significant for dry matter allocations to stemwood, live branches, and foliage (Table 4B). Stemwood allocations for loblolly pine increased on those plots receiving fertilizer and weed control treatments (C, 62.9%; FW, 66.3%), while slash pine demonstrated modest but opposite effects (C, 63.6%; FW, 62.2%). In contrast, foliage allocations for loblolly pine decreased as the intensity of silvicultural treatments increased (C, 8.7%; FW, 6.8%), while those for slash pine again showed a small but significant increase (C, 9.0%; FW, 9.2%).

Differential responses between species to the silvicultural treatments also contributed to the significant  $S \times F$ ,  $S \times W$ , and  $S \times F \times W$  interactions found for stemwood/foliage, stemwood/branches, and branch/foliage biomass ratios (Table 4B). For example, while loblolly pine had a higher overall stemwood/foliage biomass ratio than slash pine (8.94 vs. 6.87), each species responded uniquely to the imposed silvicultural treatments, i.e., the stemwood/foliage ratios for loblolly pine increased as the intensity of the silvicultural treatments increased (C, 7.23; FW, 9.76), while those for slash pine decreased (C, 7.04; FW, 6.74). Loblolly pine also tended to have higher branch/foliage biomass ratios than slash pine, especially on those plots receiving fertilizer additions (Table 4A).

### Canopy development

Eleven years of NF data were used to compare species and treatment effects on canopy development. Commensurate with results for total biomass accumulation, NF production rates were significantly increased by the fertilizer and weed control treatments (Fig. 3). Average annual NF production in slash pine stands that received maximum nutrient inputs and sustained competition control (FW) increased from about 4.25 Mg·ha<sup>-1</sup> at age 6 years to a “steady state” of 6.0 Mg·ha<sup>-1</sup> at ages 8–14 years. In contrast, loblolly pine NF production for the FW treatment increased from about 5.0 Mg·ha<sup>-1</sup> at age 6 years to a peak of 7.0 Mg·ha<sup>-1</sup> at age

10 years. Following curtailment of the fertilizer treatment at age 10 years, however, NF production for loblolly pine decreased by 17% to 6.0 Mg·ha<sup>-1</sup> at age 15 years. Canopy development associated with the C treatment for both species was considerably slower than the F and W treatments. At age 16 years, NF rates for the loblolly and slash pine C treatments averaged about 3.5 and 4.0 Mg·ha<sup>-1</sup>, respectively; comparable levels of NF production had already occurred on the F and W plots by ages 6 or 7 years (Fig. 3). The increases in NF production observed at age 16 years among all treatments, and especially pronounced for loblolly pine, were likely attributable to a major state-wide spring and summer drought. Average annual precipitation from April to August 1998 was about 38% below average (NOAA 1998).

Mean foliar P concentrations during the growing season were significantly related to annual foliage biomass production (Fig. 4). A single model was fitted to treatment and species data collected at ages 7 and 14 years, and it accounted for about 50% of the total variation in annual foliage biomass production. The upper level of production (~6 Mg·ha<sup>-1</sup>·year<sup>-1</sup>) corresponded to the approximate critical levels (0.10%) reported for these species for foliar P (Wells et al. 1973; Pritchett and Comerford 1982). No significant relationships were found between foliage production levels and foliar N concentrations (Fig. 4) or N/P ratios.

### Stemwood growth and stand development

The zone of rational action for setting a rotation length to maximize fiber production typically occurs when the MAI and PAI growth curves intersect (Nyland 1996). This stage of stand development is commonly referred to as “biological rotation age.” The intensive silvicultural treatments applied in this study accelerated stand development for both species (Fig. 5). Stemwood biomass MAI culminated (~8 Mg·ha<sup>-1</sup>·year<sup>-1</sup>) in the FW treatment at 11 years for slash pine and 13 years for loblolly pine. Culmination of MAI had not yet occurred in the C treatment for either species. By comparison, stemwood biomass PAI for the FW treatment for both loblolly and slash pine culminated at about 15 Mg·ha<sup>-1</sup>·year<sup>-1</sup> at age 8 years and then declined rapidly (~275%) to <4 Mg·ha<sup>-1</sup>·year<sup>-1</sup> at 15 years. A similarly timed peak and decline in PAI oc-

**Table 3.** (A) Mean component and total aboveground biomass accumulation ( $n = 3$ ) and (B) significance of ANOVA for 13-year-old loblolly and slash pine as affected by fertilizer and weed control treatments.

(A) Aboveground biomass accumulation.						
Treatment	Stemwood (Mg·ha <sup>-1</sup> )	Stem bark (Mg·ha <sup>-1</sup> )	Live branches (Mg·ha <sup>-1</sup> )	Foliage (Mg·ha <sup>-1</sup> )	Total aboveground (Mg·ha <sup>-1</sup> )	
<b>Loblolly pine</b>						
C	28.5 (12.8)	4.6 (1.7)	8.0 (3.6)	3.9 (1.4)	45.0 (19.6)	
W	76.9 (9.3)	10.3 (1.0)	21.8 (2.7)	8.4 (0.8)	117.1 (13.5)	
F	88.6 (12.5)	11.4 (1.4)	25.2 (3.6)	9.2 (1.1)	133.8 (18.2)	
FW	103.0 (14.1)	13.1 (1.3)	29.3 (4.1)	10.5 (0.9)	155.2 (19.8)	
<b>Slash pine</b>						
C	39.8 (6.9)	8.9 (1.5)	8.2 (1.6)	5.7 (1.0)	62.7 (10.9)	
W	71.4 (3.4)	14.7 (0.6)	17.4 (1.1)	10.4 (0.5)	113.8 (5.5)	
F	66.7 (6.6)	13.6 (1.5)	16.4 (1.5)	9.8 (0.9)	106.4 (10.5)	
FW	88.9 (4.0)	17.3 (0.9)	23.9 (0.9)	13.2 (0.6)	142.8 (6.3)	
(B) Significance of ANOVA.						
Source of variation	df	Stemwood	Stem bark	Live branches	Foliage	Total aboveground
<b>Whole plot</b>						
Block	2					
Species (S)	1		**	*		
Error	2					
<b>Split plot</b>						
Fertilization (F)	1	***	***	***	***	***
Weed control (W)	1	***	***	***	***	***
F × W	1		**	*	**	**
S × F	1	**		*		*
S × W	1					
S × F × W	1					
Error	12					

**Note:** Standard deviations are given in parentheses. Component biomass may not sum to total because equations were developed independently. For a given source of variation, main effects and interactions were significant at  $P < 0.05$  (\*),  $P < 0.01$  (\*\*), and  $P < 0.001$  (\*\*\*). C, untreated control; W, sustained weed control; F, annual fertilization; FW, fertilization + weed control.

curred on the C treatment for both species; however, growth reductions for the C treatment were considerably slower than the FW treatment for both slash pine (50%) and loblolly pine (33%). Although large differences in nutrient additions and competition control historically occurred between the FW and C treatments, no significant differences in PAI were found among treatments at age 15 years for either species (Fig. 5), despite the over twofold difference in total biomass accumulation previously noted (Fig. 1).

### Stemwood growth efficiency

Previous studies conducted with southern pines have documented the strong relationship between LAI and annual stemwood production (Vose and Allen 1988; Colbert et al. 1990; McCrady and Jokela 1998). Few studies, however, have quantified differences in the stemwood/LAI "growth efficiency" relationship as a function of stand development. While the overall association between stemwood biomass production and LAI was positive for both species ( $R^2 = 0.85$  and  $0.82$  for loblolly and slash pine, respectively,  $P < 0.0001$ ), the strength and nature of the function linking these variables changed as the stands aged (Fig. 6). Within each of the three age-classes examined, LAI explained >95% of the total variation ( $P < 0.0001$ ) in stemwood biomass production among all silvicultural treatments. A unit increase in LAI in

the 7- to 9-year-old stands produced about 3.0 and 3.1 times more stemwood biomass per year than in the 14- to 16-year-old stands for loblolly and slash pine, respectively.

Treatment differences in stemwood growth efficiency were generally small within each age-class (Table 5). Consistent with that found at age 4 years (Colbert et al. 1990), stemwood growth efficiency for slash pine was greater than loblolly pine at age 7–9 years. The significant  $S \times F \times W$  interaction suggested that, as the intensity of silvicultural treatments approached the maximum (FW), stemwood growth efficiency for slash pine increased, while opposite effects were found for loblolly pine. As stand development progressed, a consistent trend in the data suggested that the silviculturally treated plots tended to have lower levels of stemwood growth efficiency than the untreated controls. Similarly, at age 14–16 years, the weed control (W) main effect was significant, and those plots receiving understory competition control (i.e., W and FW treatments) had the lowest stemwood growth efficiency.

### Discussion

Understanding environmental constraints on development and productivity of forest ecosystems has remained a major focus of scientific interest for more than four decades

**Table 4.** (A) Mean aboveground biomass allocation (fraction of total) and dry matter ratios ( $n = 3$ ) and (B) significance of ANOVA for 13-year-old loblolly and slash pine as affected by fertilizer and weed control treatments.

(A) Biomass allocation and dry matter ratios.								
Treatment	Stemwood	Stem bark	Live branches	Foliage	Stemwood/ foliage	Stemwood/ branches	Branches/ foliage	
<b>Loblolly pine</b>								
C	0.629 (0.009)	0.103 (0.006)	0.177 (0.003)	0.087 (0.006)	7.23 (0.64)	3.57 (0.12)	2.03 (0.19)	
W	0.656 (0.004)	0.088 (0.002)	0.186 (0.002)	0.072 (0.002)	9.15 (0.33)	3.53 (0.01)	2.59 (0.10)	
F	0.662 (0.004)	0.086 (0.002)	0.188 (0.002)	0.069 (0.002)	9.60 (0.35)	3.52 (0.01)	2.73 (0.11)	
FW	0.663 (0.006)	0.085 (0.003)	0.189 (0.002)	0.068 (0.003)	9.76 (0.51)	3.52 (0.01)	2.78 (0.15)	
<b>Slash pine</b>								
C	0.636 (0.001)	0.143 (0.002)	0.131 (0.003)	0.090 (0.001)	7.04 (0.03)	4.86 (0.12)	1.45 (0.03)	
W	0.627 (0.001)	0.129 (0.001)	0.153 (0.003)	0.092 (0.001)	6.85 (0.02)	4.12 (0.07)	1.67 (0.03)	
F	0.627 (0.002)	0.128 (0.003)	0.155 (0.005)	0.092 (0.001)	6.84 (0.04)	4.05 (0.14)	1.69 (0.05)	
FW	0.622 (0.001)	0.121 (0.001)	0.168 (0.003)	0.092 (0.001)	6.74 (0.02)	3.71 (0.06)	1.82 (0.03)	
(B) Significance of ANOVA.								
Source of variation	df	Stemwood	Stem bark	Live branches	Foliage	Stemwood/ foliage	Stemwood/ branches	Branches/ foliage
<b>Whole plot</b>								
Block	2							
Species (S)	1	**	***	***	**	**	***	**
Error	2							
<b>Split plot</b>								
Fertilization (F)	1	**	***	***	***	***	***	***
Weed control (W)	1	*	***	***	**	**	***	***
F × W	1	**	***	**	**	**	**	***
S × F	1	***		***	***	***	***	**
S × W	1	***		***	***	***	***	
S × F × W	1	***			***	***	*	**
Error	12							

**Note:** Standard deviations are given in parentheses. Biomass component allocations may not sum to 1 because of rounding error. For a given source of variation, main effects and interactions were significant at  $P < 0.05$  (\*),  $P < 0.01$  (\*\*), and  $P < 0.001$  (\*\*\*). C, untreated control; W, sustained weed control; F, annual fertilization; FW, fertilization + weed control.

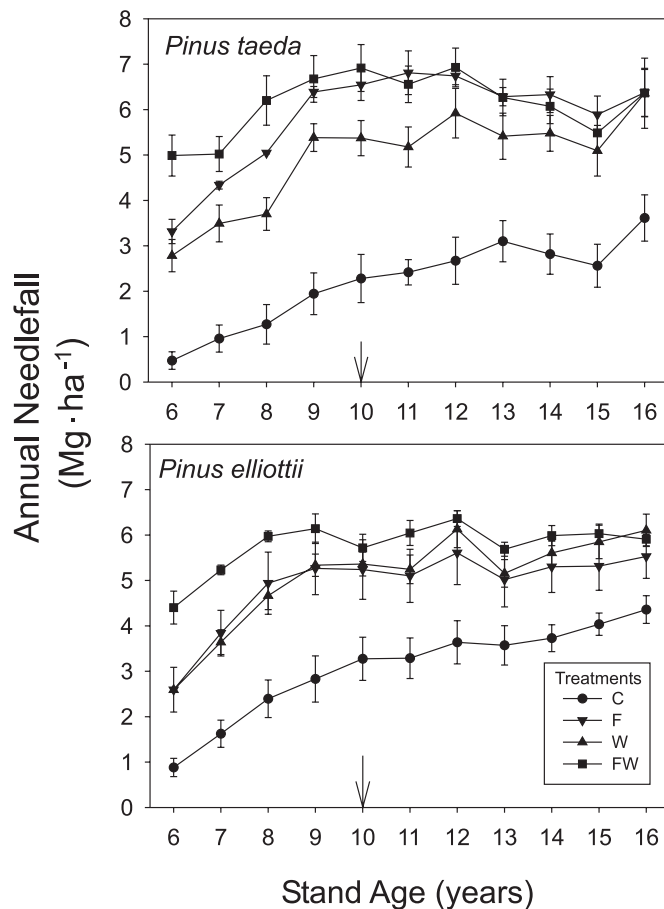
(Ovington 1957; Madgwick et al. 1970; Cannell 1982; Gower et al. 1994). Biomass accumulation and allocation can be influenced by a wide array of site and stand factors, including climate, soil fertility, genetics, stand age, and density (Møller 1947; Gholz and Fisher 1982; Beets and Pollock 1987; Beets and Whitehead 1996). In the current study, the strong nutritional gradient imposed by fertilizer additions and understory competition control provided a unique basis for comparing species and treatment effects on growth processes over a dynamic phase of stand development.

After 16 growing seasons, differences in total aboveground biomass accumulation for both slash and loblolly pine were large (~2- to 2.8-fold) and highly significant among silvicultural treatments (Tables 2 and 3B, Fig. 1). In a nutrient-limited environment such as this, sustained control of understory competition reduced nutrient deficiencies of pines, as did annual fertilizer applications. The significant and less than additive F × W interaction for total biomass accumulation (Table 2) supported the long-term importance of compensating treatment effects on meeting growth-limiting requirements for these species. The duration of growth responses to fertilizer and weed control treatments with southern pines is generally controlled by the short-term

benefits derived from nutrient inputs and the rates at which nutrients are recycled through organic residues discarded during stand development (Jorgensen et al. 1980; Polglase et al. 1992a, 1992b, 1992c, 1992d).

The distinctive species differences found in biomass accumulation for the range of imposed silvicultural treatments (e.g., S × F interaction) likely reflects differential nutrient demands. Loblolly pine, having higher nutrient requirements than slash pine (Fisher 1983), was most responsive to the fertilizer treatment. Similar but less long-lasting species differences were also apparent, as evident in the S × W interaction detected from ages 3 to 6 years (Table 2, Fig. 1). Although both the F and W treatments benefitted tree growth by reducing belowground competition for soil nutrients and water (Neary et al. 1990), the positive effects of the W treatment on loblolly pine growth was not as long lasting as the F treatment. In a related study conducted at this same site, Polglase et al. (1992b) reported a stimulatory effect of fertilizer additions on specific P mineralization rates. They noted that comparable effects were much less pronounced for the W treatment and concluded that the rapid recycling of P in fertilized stands had the potential to enhance long-term productivity beyond the immediate benefits derived by fertilizer uptake. Jokela et al. (2000) also reported similar results from

**Fig. 3.** Annual needlefall production (with standard error bars) for *P. taeda* and *P. elliotii* plantations grown under the following silvicultural treatments: control (C), complete and sustained understory competition control (W), annual fertilization with macro- and micro-nutrients from establishment through age 10 years (as indicated by arrow) (F), and combined competition control and fertilization treatments (FW).

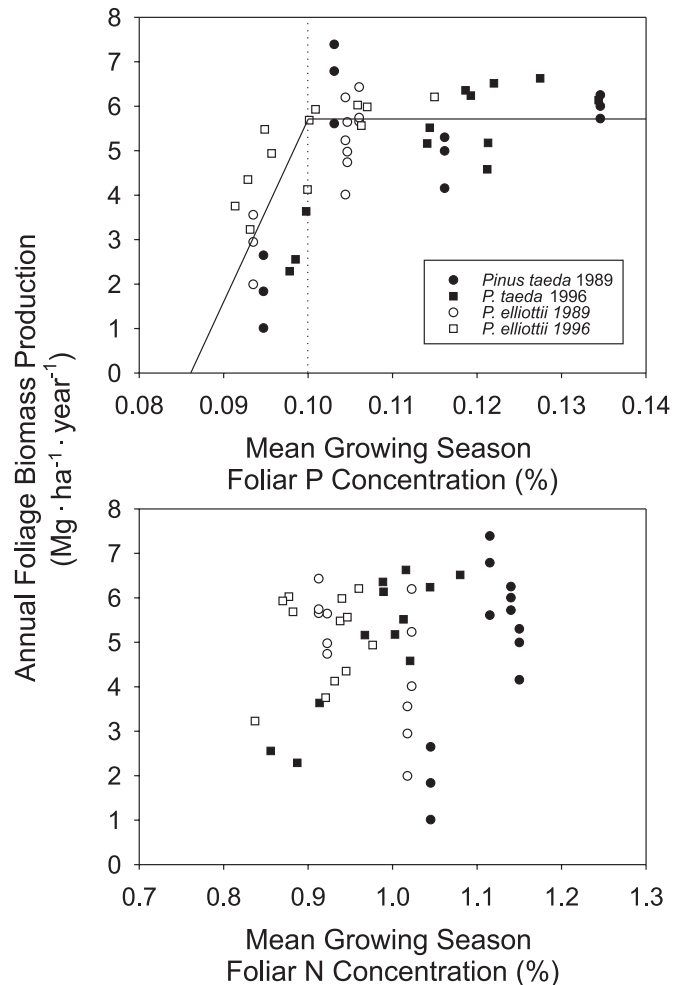


a region-wide study conducted in the southern United States. The duration of growth responses for 11 loblolly pine stands receiving herbaceous weed control treatments at establishment was not as long lasting as that from fertilizer additions. They too noted, as observed in this study, that comparable differences between treatments were less apparent for slash than loblolly pine.

Changes in aboveground biomass allocation patterns between ages 4 and 13 years followed expected trends associated with advancing stand development (Miller 1981), with the ratio of woody/total biomass increasing and foliage/total biomass decreasing for both species (Table 4A). For example, the ratio of stemwood/total biomass for loblolly pine on the FW treatment increased from 36% at age 4 years (Colbert et al. 1990) to 66% at age 13 years. Conversely, the comparative ranges in foliage/total biomass ratios for loblolly pine were 40 (C) to 26% (FW) at age 4 years and 8.7 (C) to 6.8% (FW) at age 13 years.

Results from this study have also demonstrated modest but significant differences in biomass allocation patterns between loblolly and slash pine and that each species re-

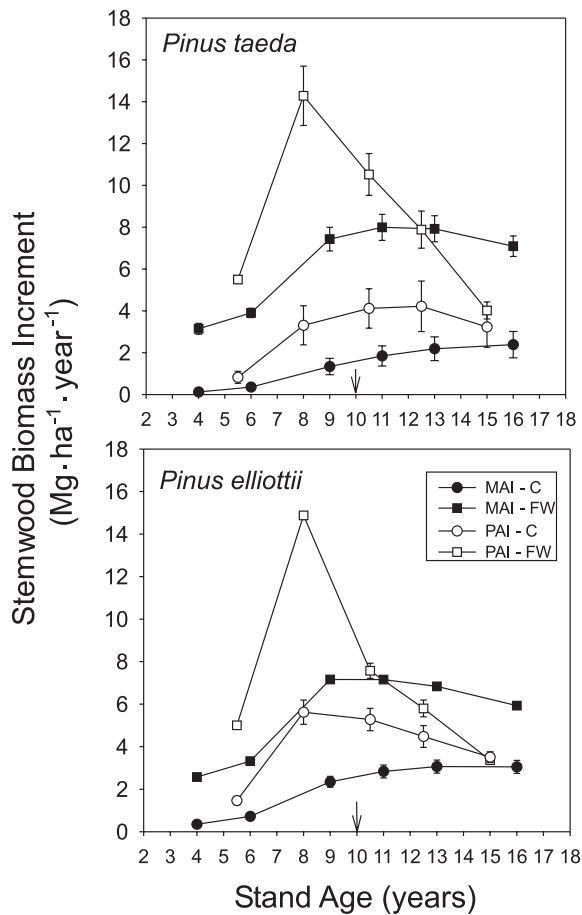
**Fig. 4.** Annual foliage biomass production as a function of mean growing season foliar phosphorus and nitrogen concentrations for *P. taeda* and *P. elliotii* plantations in 1989 (age 7 years) and 1996 (age 14 years). The broken line indicates the inflection point of a segmented regression through the data and also approximates the critical foliar P concentration for southern pines.



sponded differentially to the silvicultural treatments. From a growth strategy perspective, loblolly pine showed greater sensitivity to the fertilizer treatment than slash pine, especially in allocating carbon to stemwood and branches (Table 4). The crown structure of loblolly pine, typified by an extensive array of multiple-order branches (Dalla-Tea and Jokela 1991), also facilitated greater retention of leaf area than slash pine on plots receiving fertilizer additions. For example, although the general range in LAI (all sided) among treatments tended to become narrower for both species over time (Fig. 6), the maximum levels of LAI associated with the FW treatment for loblolly and slash pine were fairly constant at about 11 and 8.5, respectively, for each of the three growth periods examined. In addition, differences in specific leaf area contributed to species variation in LAI (Dalla-Tea and Jokela 1991).

Species differences in sensitivity to declines in soil nutrient supply were also apparent in the time-series NF data (Fig. 3). Although the fertilizer and weed control treatments

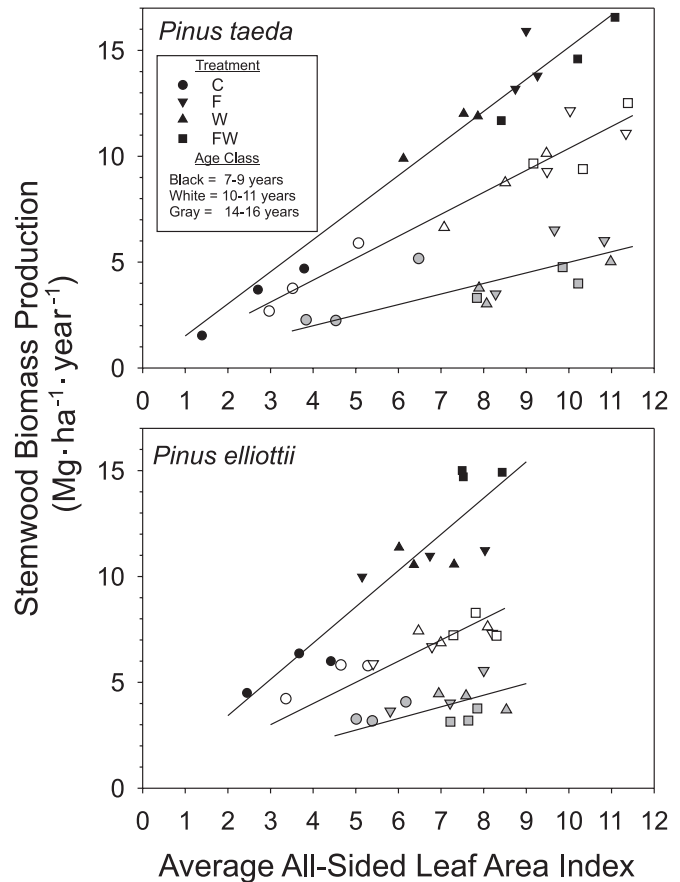
**Fig. 5.** Periodic and mean annual stemwood biomass increment for *P. taeda* and *P. elliotii* plantations grown under the control (C) and combined competition control and fertilization treatments (FW). Arrow indicates the last year fertilizer was applied.



accelerated peak NF production for both species, loblolly pine, unlike slash pine, showed a fairly steady decline in NF rates on fertilized plots from about age 10 to 15 years. Foliar N levels for loblolly pine also declined from about 1.14 to 1.01% over this same time period, well below the published critical levels of 1.2% for this species (Allen 1987). As stand nutrient demand is generally commensurate with growth rate, we hypothesize that declines in NF production for loblolly pine, especially on the fastest growing plots, occurred from a combination of higher nutrient demands associated with increased growth rates, and reductions in soil nutrient supply resulting from immobilization processes and curtailment of the fertilizer treatments at age 10 years. Similar but delayed effects would be expected on the W and C treatments over time. Gholz and Fisher (1982) also suggested that declines in foliage biomass in late-rotation slash pine plantations in the lower Coastal Plain, U.S.A., were due to the inherently infertile, sandy soils of this region. The continuing modest rates of NF accretion observed for the C treatment may reflect changes in understory species composition and their influences on soil nutrient supply processes (Table 1; Polglase et al. 1992b, 1992c, 1992d).

The patterns of aboveground PAI documented in this study were consistent with the generally accepted model of

**Fig. 6.** Stemwood biomass production as a function of average all-sided leaf area index for *P. taeda* and *P. elliotii* stands at three stages of stand development (a single relationship was fitted to all data points within an age period to document the overall relationship; however, individual treatments means for each species and age-class are found in Table 5). The slope and  $R^2$  for the no-intercept regression lines for *P. taeda* at age 7–9, 10–11, and 14–16 years are, respectively, 1.515 ( $R^2 = 0.994$ ), 1.037 ( $R^2 = 0.993$ ), and 0.499 ( $R^2 = 0.954$ ). The slope and  $R^2$  for the no-intercept regression lines for *P. elliotii* at age 7–9, 10–11, and 14–16 years are, respectively, 1.713 ( $R^2 = 0.984$ ), 1.002 ( $R^2 = 0.989$ ), and 0.549 ( $R^2 = 0.969$ ).



growth in even-aged forests. Biomass increment increased rapidly early in stand development, culminated at the approximate time of peak foliage development, and declined significantly thereafter (Fig. 5). Numerous chronosequence and growth and yield studies have confirmed this pattern (reviewed in Ryan et al. 1997), although the present study is the first to quantify this relationship for southern pines within a single site under different silvicultural regimes. While the PAI patterns observed in this study are qualitatively similar to others in the literature, there is considerable variation in the timing of the growth decline in other pine systems. In a chronosequence of slash pine plantations located within 20 km of the present study, total aboveground net primary production (PAI) peaked at age 15 years, in parallel with the peak in LAI (Gholz and Fisher 1982; Gholz 1986). Stemwood production in the Gholz and Fisher (1982) chronosequence peaked at approximately the same magni-

**Table 5.** (A) Variation in stemwood growth efficiency ( $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}/\text{LAI}$ ) and (B) significance of ANOVA for loblolly and slash pine as affected by fertilizer and weed control treatments.

(A) Stemwood growth efficiency.				
Treatment	Age (years)			
	7–9	10–11	14–16	
<b>Loblolly pine</b>				
C	1.24 (0.13)	1.05 (0.13)	0.63 (0.16)	
W	1.58 (0.05)	1.01 (0.07)	0.44 (0.05)	
F	1.59 (0.16)	1.06 (0.14)	0.55 (0.13)	
FW	1.44 (0.05)	1.02 (0.10)	0.43 (0.05)	
<b>Slash pine</b>				
C	1.64 (0.25)	1.20 (0.09)	0.63 (0.04)	
W	1.66 (0.22)	1.02 (0.11)	0.55 (0.11)	
F	1.66 (0.27)	0.99 (0.10)	0.63 (0.07)	
FW	1.91 (0.12)	0.97 (0.10)	0.44 (0.03)	

(B) Significance of ANOVA.				
Source of variation	df	Age (years)		
		7–9	10–11	14–16
<b>Whole plot</b>				
Block	2			
Species (S)	1	**		
Error	2			
<b>Split plot</b>				
Fertilization (F)	1			
Weed control (W)	1			**
F × W	1			
S × F	1			
S × W	1			
S × F × W	1	*		
Error	12			

**Note:** Standard deviations are given in parentheses. For a given source of variation, main effects and interactions were significant at  $P < 0.05$  (\*) and  $P < 0.01$  (\*\*). C, untreated control; W, sustained weed control; F, annual fertilization; FW, fertilization + weed control.

tude as the control plots in the present study. *Pinus radiata* D. Don plantations in Australia similarly peaked at a relatively young age (age 5–7 years; Forrest and Ovington 1970). In contrast, aboveground net primary production in a *Pinus contorta* Dougl. ex Loud. chronosequence in Wyoming peaked at age 30 years (Smith and Resh 1999) and between ages 40 and 60 years in naturally regenerated loblolly pine stands in Mississippi (Switzer et al. 1966). These variations in timing among studies are likely related to any number of factors, including differences in species characteristics, establishment and management practices, stand density, site quality, and the use of genetically improved growing stock in the present study.

While the increase in PAI early in stand development is often closely linked to leaf area accumulation, the biological causes of the growth decline subsequent to peak LAI development have not been firmly elucidated. Ryan et al. (1997) summarized the current hypotheses regarding the mechanisms of PAI decline. Briefly, these are (i) the respiration hypothesis (increases in the ratio of respiring to photosyn-

thesizing tissue in older, larger trees reduces carbon available for growth); (ii) the hydraulic resistance hypothesis (increased hydraulic resistance in taller trees with more complex crowns leads to greater stomatal limitation to photosynthesis during drought); (iii) the nutrient limitation hypothesis (soil nutrient supply decreases as stands age because of accumulation of nutrients in biomass and (or) decreases in N mineralization due to decreasing litter quality, leading to (individually or in combination) decreased photosynthesis rates, reduced stand leaf area, and increased allocation of carbon to fine root production); (iv) the crown abrasion hypothesis (crown abrasion increases as trees grow taller, resulting in reduced stand leaf area); (v) the tree mortality hypothesis (tree mortality increases in aging stands, resulting in decreases in stand-level biomass production rates); (vi) the reproduction cost hypothesis (allocation of carbon to reproduction increases in maturing stands); and (vii) the tissue maturation hypothesis (tissue maturation results in changes in gene expression and inherently slower growth in older tissue).

The data in our study allow us to directly address several of these hypotheses. Relatively few trees died over the course of the study, contrary to the mortality hypothesis. A minimal amount of cone material was found in the litter traps in this study (data not shown), suggesting that reproductive growth was not a major carbon sink, contrary to the reproduction cost hypothesis. Stand foliage biomass either remained constant after canopy closure (slash pine) or declined at a much slower rate than did PAI (loblolly pine), demonstrating that reductions in LAI alone were not the primary cause of growth declines. In contrast, the association between declining stemwood growth efficiency and PAI during stand development (Fig. 6, Table 5A) does not directly contradict the respiration, nutrient limitation, or hydraulic resistance hypotheses. Reductions in stemwood growth efficiency could result from decreased rates of canopy photosynthesis (hydraulic resistance and nutrient limitation hypotheses), increased respiratory costs (respiration hypothesis), shifts in carbon allocation from aboveground to belowground sinks (nutrient limitation hypothesis), or any combination of these factors.

It is not possible to eliminate any of the remaining hypotheses based on data collected in this study. Unfortunately, support for the various hypotheses in the literature is also equivocal. Contrary to the tissue maturation hypothesis, several studies suggest that the most pronounced maturational changes in conifers occur between ages 1 and 4 years (Greenwood 1995), well before most growth declines are observed. While the respiration hypothesis has been almost axiomatic for decades (Kira and Shidei 1967; Waring and Schlesinger 1985), recent reviews have discounted its importance (Gower et al. 1996; Ryan and Yoder 1997; Ryan et al. 1997), although published studies specifically testing this hypothesis with actual respiration measurements remain sparse (Ryan and Waring 1992). Several studies have recently demonstrated that reductions in xylem hydraulic conductance can occur with tree age (Mencuccini and Grace 1996; Hubbard et al. 1999). Although we have only indirect evidence to address this hypothesis, it follows that, if hydraulic limitations were important in the present study, reductions in growth efficiency would first be manifested in

the treated plots, where trees were taller, branches were longer, and crown architecture was more complex. Reductions in growth efficiency from age 10 years on were generally larger in treated plots; however, this was not consistent across all treatment combinations. For example, growth efficiency in the C and F treatments was identical (slash pine) or similar (loblolly pine) at age 14–16 years (Table 5), even though tree crown and stand structure varied considerably between these treatments (Figs. 1–3).

Recent experimental and modeling studies have also supported the role of decreased nutrient availability in declining growth rates in aging stands (Binkley et al. 1995; Murty et al. 1996). In the current study, silvicultural treatments that ameliorated soil nutrient supply resulted in increased stemwood growth efficiency during the early stages of stand development (e.g., age 4 years, Colbert et al. 1990; age 7–9 years, Table 5A). Albaugh et al. (1998) hypothesized that increases in total biomass production efficiency observed in fertilized and irrigated loblolly pine stands in North Carolina may have resulted from greater biomass allocation to photosynthesizing tissue (foliage) and reduced allocation to tissues with high maintenance respiration costs (fine roots). As stand development progressed, however, we found that stemwood growth efficiency decreased in all treatments, with the smallest reductions occurring in the untreated control plots (Table 5). At age 14–16 years, the strongest decline was apparent on plots that received the sustained understory competition control treatment, alone or in combination with fertilizer additions. This phenomenon may be attributable to reduced nutrient availability caused by variation in litter quality that influenced decomposition and mineralization rates among treatments. Polglase et al. (1992b, 1992c) found for this same site that phenol concentrations were highest in pine litter originating from plots receiving the weed control treatments. They also found that decomposition and nutrient turnover rates (P mineralization) were stimulated by fertilization but that the weed control treatment inhibited these processes, presumably because understory vegetation was a better supplier of P than was the more recalcitrant pine litter.

The weight of direct and indirect evidence suggests that the large reductions in stemwood growth observed on the FW treatment plots in this study likely resulted from higher nutrient demands and reduced nutrient supply, coupled with increased maintenance respiration costs and increased biomass allocation to fine roots following curtailment of the fertilizer treatment. It is clear, however, that manipulative experimental testing of these hypotheses will be necessary before a consensus emerges.

Understanding the cause of the peak LAI growth decline is clearly important from a biological sciences perspective, but there will also be compelling applied outlets for this knowledge. For example, the rapid declines in PAI observed for both species in the present study and the variation found among silvicultural treatments raises important questions on how available site resources affect stockability (maximum mean tree size–density relationships) and, ultimately, the physiological processes controlling stand productivity (DeBell et al. 1989; Harms et al. 1994; Harms et al. 2000). If respiratory processes primarily control the decline in PAI, then there are few management actions that can be taken to

modify the decline, short of genetic manipulation. However, if soil nutrient dynamics play a significant causal role, then the decline should be controllable to some extent through application of limiting nutrients. In the current study, annual macro- and micro-nutrient fertilizer additions have again been made since age 16 years, and the production ecology of these stands will continue to be monitored.

Finally, rates of stand production for many species have been closely correlated to levels of canopy leaf area, because it provides an important and active link between environmental factors and photosynthetic processes influencing the conversion of solar energy into dry matter production (Vose and Allen 1988; Heilman et al. 1996; Beadle 1997). Similar to other studies, results from this investigation demonstrated a significant linear relationship between stemwood biomass production and LAI (Fig. 6). Unlike most other studies, however, this relationship was best described over time using a series of linear models, the slopes of which provided an empirical index of stemwood “growth efficiency” for each species (see also Long and Smith 1992; Smith and Resh 1999). The threefold reduction in growth efficiency found between the youngest and oldest measurement periods was closely associated with comparable levels of reduction in stand productivity (PAI). Thus, although growth is closely correlated with levels of LAI, results from this study suggest that considering ontogenetic and species effects on leaf area efficiency would improve the accuracy for predicting stemwood biomass production.

## Acknowledgments

The Forest Biology Research Cooperative at the University of Florida is gratefully acknowledged for providing financial support for this research. Special thanks are extended to R.J. English, J.E. Smith, D.S. Wilson, W. Wood, and S. Brooker for technical field assistance.

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## Appendix

**Table A1.** Parameter estimates for allometric equations developed from a destructive harvest conducted at age 4 years to predict total biomass and component dry mass for *Pinus taeda* and *P. elliottii* stands grown under the control (C), fertilized (F), weed control (W), and combination (FW) treatments.

Species	Component ( $\hat{Y}$ )	Treatment	$\beta_0$	$\beta_1$	$X$	$R^2$	MSE	$n$
<i>P. taeda</i>	Total aboveground	C	-1.124	0.498	$D^2H$	0.982	0.012	6
<i>P. taeda</i>	Total aboveground	F,W,FW	-1.688	0.730	$D^2H$	0.930	0.042	27
<i>P. taeda</i>	Stemwood	C	-2.515	0.546	$D^2H$	0.974	0.022	6
<i>P. taeda</i>	Stemwood	F	-2.684	0.694	$D^2H$	0.960	0.011	6
<i>P. taeda</i>	Stemwood	W	-2.766	0.719	$D^2H$	0.992	0.008	9
<i>P. taeda</i>	Stemwood	FW	-3.196	0.825	$D^2H$	0.968	0.011	9
<i>P. elliottii</i>	Total aboveground	C,F,W	-2.264	0.802	$D^2H$	0.986	0.009	25
<i>P. elliottii</i>	Total aboveground	FW	-0.982	0.600	$D^2H$	0.770	0.007	9
<i>P. elliottii</i>	Stemwood	C,F,W,FW	-3.694	0.882	$D^2H$	0.992	0.006	34

**Note:** Equations are of the form  $\ln(\hat{Y}) = \beta_0 + \beta_1 \ln(X)$ .  $D$ , diameter at 1.3 m (cm);  $H$ , total tree height (m).

**Table A2.** Parameter estimates for allometric equations developed from a biomass harvest conducted at age 13 years to predict total biomass and component dry weight for *Pinus taeda* and *P. elliottii* stands grown under the control (C), fertilized (F), weed control (W), and combination (FW) treatments.

Species	Component ( $\hat{Y}$ )	Treatment	$\beta_0$	$\beta_1$	$X$	$R^2$	MSE	$n$
<i>P. taeda</i>	Total aboveground	C,F,W,FW	-2.886	1.284	$D^2$	0.969	0.015	40
<i>P. taeda</i>	Foliage	C,F,W,FW	-3.982	1.010	$D^2$	0.747	0.095	40
<i>P. taeda</i>	Branch	C,F,W,FW	-5.024	1.357	$D^2$	0.872	0.074	40
<i>P. taeda</i>	Stemwood	C,F,W,FW	-3.651	1.342	$D^2$	0.946	0.028	40
<i>P. taeda</i>	Bark	C,F,W,FW	-4.064	1.067	$D^2$	0.946	0.018	40
<i>P. elliottii</i>	Total aboveground	C,F,W,FW	-2.715	1.261	$D^2$	0.950	0.017	40
<i>P. elliottii</i>	Foliage	C,F,W,FW	-5.359	1.294	$D^2$	0.706	0.137	40
<i>P. elliottii</i>	Branch	C,F,W,FW	-6.740	1.629	$D^2$	0.884	0.0682	40
<i>P. elliottii</i>	Stemwood	C,F,W,FW	-3.009	1.231	$D^2$	0.935	0.020	40
<i>P. elliottii</i>	Bark	C,F,W,FW	-3.423	1.028	$D^2$	0.954	0.010	40

**Note:** Equations are of the form  $\ln(\hat{Y}) = \beta_0 + \beta_1 \ln(X)$ .  $D$ , diameter at 1.3 m (cm).