

## DEVELOPMENTAL PATTERNS AND NUTRITION IMPACT RADIATION USE EFFICIENCY COMPONENTS IN SOUTHERN PINE STANDS

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**Abstract.** A number of contemporary forest productivity models use some variation of a growth efficiency ( $\varepsilon$ ) approach. Typically, these models predict production (aboveground net primary production, ANPP, in units of dry mass biomass per unit of area per unit of time) as the product of two terms: radiation use efficiency ( $\varepsilon$ , in units of dry mass biomass per megajoule of photosynthetically active radiation [PAR] intercepted or absorbed by the plant canopy) and the sum of PAR intercepted or absorbed by the canopy ( $\Phi_{\text{par}}$ , in units of megajoules per unit of radiation area per unit of time). Predicting productivity in a biologically realistic manner requires an understanding of how model components are affected by natural and anthropogenic environmental factors, as well as other influences such as aging or stand development. We measured or calculated all components of the  $\varepsilon$  model (aboveground woody biomass increment,  $I_{\text{WB}}$ ; foliage biomass increment,  $I_{\text{FB}}$ ; aboveground net primary production, ANPP; leaf area index, LAI;  $\Phi_{\text{par}}$ ; and aboveground radiation use efficiency,  $\varepsilon_A$ ) from ages 4 to 18 yr in loblolly and slash pine stands in north-central Florida grown under replicated fertilizer and understory vegetation control treatments that induced a large gradient in soil nutrient availability. Treatments impacted all measured components, which in turn led to strong responses in aboveground radiation use efficiency. Age 6–9 yr  $\varepsilon_A$ , averaged across species, ranged from 0.78 g/MJ to 0.83 g/MJ in treatments receiving fertilizer or vegetation control vs. 0.53 g/MJ in untreated plots. Stand developmental processes modified these responses, however, with  $\varepsilon_A$  declining by over 40% in treated plots from age 6–9 yr to age 15–16 yr. Variation in  $\varepsilon_A$  in both species was linked to development of stand basal area (BA), with a positive, linear relationship between  $\varepsilon_A$  and BA for values of BA < 18 m<sup>2</sup>/ha and a declining, linear relationship for values of BA > 18 m<sup>2</sup>/ha. Loblolly pine  $\varepsilon_A$  was positively correlated with foliar nitrogen concentration, [N]. These data highlight the dynamic nature of  $\varepsilon_A$  and suggest that both stand developmental and nutritional processes drive changes in ANPP and  $\varepsilon_A$  in southern pines.

**Key words:** *aboveground net primary production; basal area; Florida, USA; Pinus elliottii; Pinus taeda; stand development.*

### INTRODUCTION

The biological complexity of forest growth models ranges from empirical, statistical descriptions of forest growth and yield (e.g., Curtis et al. 1981, Wyckoff et al. 1982, Burkhardt et al. 1987) to bottom-up models incorporating some or all of the known biological processes responsible for tree growth (e.g., Friend et al. 1993, Kimmins et al. 1999, Kirschbaum 1999, Cropper 2000). Trade-offs associated with this range of models include their ease of use for management applications (high for empirical models, low for biologically complex ones) and their ability to predict forest growth under new or unique management or climate scenarios (high for biology-based models, low for empirical growth and yield models).

Somewhere between these extremes lie a number of contemporary models that predict forest productivity using some variation of a growth efficiency ( $\varepsilon$ ), APAR

(absorbed photosynthetically active radiation) or IPAR (intercepted photosynthetically active radiation) approach (e.g., Monteith 1977, Sievänen 1993, Landsberg and Hingston 1996, Battaglia and Sands 1997, Landsberg and Waring 1997). In its simplest form, the  $\varepsilon$  model can be expressed as

$$\text{ANPP} = \varepsilon \Phi_{\text{par}} \quad (1)$$

This model has some conceptual appeal because of its simplicity, since production (aboveground net primary production, ANPP, in units of dry mass biomass per unit of area per unit of time) is described as the product of only two terms: radiation use efficiency ( $\varepsilon$ , in units of dry mass biomass per megajoule of photosynthetically active radiation intercepted or absorbed by the plant canopy) and the sum of photosynthetically active radiation (PAR) intercepted or absorbed by the canopy ( $\Phi_{\text{par}}$ , in megajoules per unit of radiation area per unit of time). At the same time, the approach retains a degree of process-level sophistication, as both the  $\varepsilon$  and  $\Phi_{\text{par}}$  terms subsume considerable biological complexity. The applications of this approach are diverse. For example,  $\varepsilon$  models frequently include modifying

Manuscript received 18 August 2003; revised 13 February 2004; accepted 18 March 2004. Corresponding Editor: B. J. Bond.

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PLATE 1. Understory views in loblolly pine plots in (A) the control and (B) fertilizer plus understory vegetation control treatments. Photo credits: E. Jokela.

terms that reduce  $\varepsilon$  below a theoretical optimum due to the effects of environmental constraints such as soil fertility, drought, or temperature (Monteith 1977, McMurtrie et al. 1994, Runyon et al. 1994, Prince and Goward 1995). The growth efficiency approach has been used to simulate forest net primary production, aboveground net primary production (ANPP), and even hourly net carbon exchange (Runyon et al. 1994, Landsberg et al. 1996, Anderson et al. 2000). The  $\varepsilon$  approach is especially powerful when used in conjunction with remotely sensed estimates of leaf area index (LAI) and  $\Phi_{\text{par}}$  to predict productivity of ecosystems at the landscape to global scales (Prince and Goward 1995, Gower et al. 1999, Anderson et al. 2000).

In order to parameterize and utilize  $\varepsilon$  models to accurately predict forest growth in a biologically realistic manner, it will be necessary to understand how the components of this model are affected by environment, including both natural and anthropogenic factors, and how they may change with other factors, such as aging or stand development. In this study, we examined changes in  $\varepsilon_A$  (the A subscript denoting an efficiency incorporating only aboveground production); the two components of  $\varepsilon_A$  (ANPP and  $\Phi_{\text{par}}$ ); and the subcomponent parameters that comprise ANPP and  $\Phi_{\text{par}}$  (aboveground woody biomass increment [ $I_{\text{WB}}$ ], foliage biomass increment [ $I_{\text{FB}}$ ], and leaf area index [LAI]) under treatments inducing a gradient in soil nutrient availability during 18 yr of stand development in single-cohort, monospecific stands of loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* var. *elliottii*). Previous research at this site has characterized nutrient cycling (Polglase et al. 1992, Grierson et al. 1999), early growth dynamics (Colbert et al. 1990), biomass distribution, long-term production dynamics, and leaf area efficiency (Jokela and Martin 2000, Martin and Jokela 2004), and  $\varepsilon_A$  over short time periods (Dalla-Tea and Jokela 1991). However, the current study is the first at this site or in these species to integrate

variation in ANPP, LAI,  $\Phi_{\text{par}}$ , and  $\varepsilon_A$  along a strong gradient in soil nutrient availability, over a long period of stand development.

The objectives of this study were: (1) to quantify changes in  $I_{\text{WB}}$ ,  $I_{\text{FB}}$ , ANPP, LAI,  $\Phi_{\text{par}}$ , and  $\varepsilon_A$  under replicated experimental treatments inducing a large gradient in soil nutrient availability, in a model system utilizing both loblolly and slash pine, two commercially important tree species; (2) to quantify how the responses in (1) were altered with stand age or stand development; and (3) to determine whether ecosystem variables such as foliar nitrogen concentration ([N]) or stand basal area or environmental variables such as site water balance could explain patterns of variation in  $\varepsilon_A$ . Many of the relationships and patterns described here changed with stand age. We assume from the outset that these changes were caused less by stand age, per se, than by alterations in stand structure (e.g., mean tree height, stand basal area, stem density, leaf area index) that occur as populations of trees grow and develop. We follow the silvicultural convention of referring to these age-related alterations in structure as stand development.

## MATERIALS AND METHODS

### *Study site and experimental treatments*

The study utilized data from the Intensive Management Practices Assessment Center experiment near Gainesville, Florida, USA (29°30' N, 82°20' W; see Plate 1). The study was established in January 1983 as a  $2 \times 2 \times 2$  factorial of species (loblolly pine and slash pine), complete and sustained control of competing understory vegetation and annual fertilization with both macro- and micronutrients. This resulted in four treatments within each species: control (C), fertilizer only (F), understory vegetation control only (V), and fertilizer + vegetation control (FV). Each treatment–species combination was replicated three times, for a total

TABLE 1. Summary of fertilizer treatments from the Intensive Management Practices Assessment Center experiment near Gainesville, Florida, USA.

Time period	Stand age (yr)	Mean annual application rate (kg·ha <sup>-1</sup> ·yr <sup>-1</sup> )										
		N	P	K	Ca	Mg	Mn	Fe	Cu	Zn	B	S
1983–1993	0–10	36.0	14.3	31.7	10.8	7.2	0.3	0.3	0.05	0.3	0.05	7.2
1998–2000	15–17	242.6	29.0	37.7	0.0	0.0	0.4	0.8	0.13	0.3	0.13	0.0
Cumulative total (kg/ha)		1088.0	230.0	430.0	108.0	72.0	4.1	5.4	0.9	4.0	0.90	72.0

of 24 plots. Full establishment details are reported in Swindel et al. (1988). Fertilizer was applied annually for the first 10 yr of the study, then fertilization was suspended for 5 yr. In 1998 at age 15 yr, an aggressive N and P refertilization regime was initiated in the F and FV treatments to determine whether previously observed growth decreases in those treatments could be attributed to induced nutrient deficiency (Jokela and Martin 2000). Table 1 shows details of the fertilizer regimes.

#### Biomass parameters

Biomass harvests at ages 4 and 13 yr were used to develop equations relating dbh to total aboveground woody biomass (i.e., all aboveground biomass except foliage; Jokela and Martin 2000). These equations were corrected for logarithmic bias (Baskerville 1972) and were used in combination with periodic inventories to estimate aboveground woody biomass accumulation through time. The age 4 yr equations were applied for stand ages 4–6 yr, and the age 13 yr equations were applied to subsequent years. Aboveground woody biomass increment ( $I_{WB}$ ) was calculated as a gross increment:

$$I_{WB} = \sum WB_{t_2} - \sum WB_{t_1} + \sum_{t_1}^{t_2} M \quad (2)$$

where  $WB_{it}$  is stand woody biomass at time  $i$ , and  $\sum_{t_1}^{t_2} M$  is the summed woody biomass of trees that died during the interval between  $t_1$  and  $t_2$  ("Approach 2" of Clark et al. [2001]). This approach minimizes underestimates of  $I_{WB}$  that can result when large trees die in small plots (Clark et al. 2001). Application of the 13 yr equations to age 7–13 yr inventory data should not be problematic, as the range of tree sizes sampled for equation development overlapped completely with the inventory data. There may be some error associated with extrapolation of the 13 yr equations to inventory data for older stand ages, but the alternative of utilizing equations for older trees developed on other sites would likely introduce much greater uncertainty. Wood density sampling at this site indicated that ring specific gravity increased from about 0.4 at age 5 yr to a plateau of  $\sim 0.5$  at age 8 yr (Martin and Jokela 2004), suggesting that the timing and application of the biomass equations captured variation in wood density.

#### Leaf area and light interception

Foliage biomass production ( $I_{FB}$ ) and leaf area index (LAI) were calculated from litterfall data. Pine litterfall was collected monthly from age 5 yr to age 18 yr from six 0.7-m<sup>2</sup> litter traps randomly located within each plot. The collected litter was sorted into needles and other pine materials (branch, bark, twigs, cones), dried at 70°C, and weighed to the nearest 0.1 g. In this report, data analyses and interpretations will consider only the needlefall component, as needles constituted >90% of the annual pine litterfall mass. Monthly canopy biomass was calculated from needlefall and logistic models of foliage accretion as described by Kinerson et al. (1974), Dougherty et al. (1995), and Liu et al. (1997). This approach assumes that: (1) foliage accretion begins on 1 March and that the accretion curve is not affected by treatment; and (2) needles formed in a year are dead and fallen from the tree by 28 February in the second year after their formation (i.e., maximum leaf lifespan is just under 2 yr). If these assumptions are met, it follows that total needlefall in a given phenological year (1 March–28 February) represents total needle production in the previous year. Dalla-Tea (1990), Gholz et al. (1991), and Liu et al. (1997) present data for both loblolly and slash pine that support the validity of these assumptions. Needlefall data were corrected for senescence-related biomass reductions of 13 and 14% for slash and loblolly pine, respectively, and were converted to hemi-surface leaf area (all-sided leaf area/2) using mean values of specific leaf area for slash (0.0050 m<sup>2</sup>/g) and loblolly pine (0.0058 m<sup>2</sup>/g) (Dalla-Tea 1990, Dalla-Tea and Jokela 1991). This approach folds variation in specific leaf area due to foliage age and season into a single average. Liu et al. (1997) made the same simplifying assumption for their litterfall-based estimates of LAI in slash pine stands and found that they compared well with independent, gap fraction-based estimates. Foliage biomass production was added to  $I_{WB}$  to obtain aboveground net primary production (ANPP).

The Beer-Lambert law was used to estimate  $\Phi_{par}$  for each year in each plot by combining the monthly canopy LAI data with the 30-yr mean monthly incoming radiation for north Florida (National Renewable Energy Laboratory 1992). We utilized empirically derived, season-specific, sun-angle corrected values of the Beer-

Lambert extinction coefficient  $k$  as reported for these same stands by Dalla-Tea and Jokela (1991). We assumed that PAR comprises 50% of total incoming radiation (Landsberg and Waring 1997, Waring and Running 1998). In addition, we assumed that the Beer-Lambert law is sufficient for estimating radiation interception in pine canopies. This assumption can be troublesome in non-closed canopies or in canopies with clumped foliage (Stenberg et al. 1994). Landsberg and Gower (1997) argue, however, that these problems with Beer-Lambert estimations of  $\Phi_{\text{par}}$  become less severe when estimates are averaged over longer time steps (i.e., days, weeks, and seasons). As one test of these assumptions, we compared our monthly plot-level  $\Phi_{\text{par}}$  estimates with equivalent estimates derived from monthly ceptometer measurements made in all plots over an 11-mo period at age 6 yr ( $\Phi_{\text{par-c}}$ ; Dalla-Tea 1990, Dalla-Tea and Jokela 1991). The two estimates were highly correlated with each other ( $\Phi_{\text{par}}$  [in megajoules per square meter] =  $26.8 + 0.99 \times \Phi_{\text{par-c}}$ ,  $P < 0.0001$ ,  $R^2 = 0.72$ ,  $n = 264$ ), suggesting that the method described here produces reasonable  $\Phi_{\text{par}}$  and LAI estimates.

Aboveground radiation use efficiency ( $\epsilon_A$ ) was calculated by dividing ANPP by  $\Phi_{\text{par}}$  during the time period. All parameters were calculated over the following time intervals: ages 4–6, 6–9, 9–11, 11–13, 13–15, and 15–16 yr. In addition,  $I_{\text{WB}}$  was calculated for ages 16–18 yr.

#### Transpiration and water balance

To examine the influence of site water balance on radiation use efficiency, a transpiration model was constructed to simulate changes in annual site water balance (precipitation – transpiration) with treatment over the course of the experiment. The model simulated hourly stomatal conductance by adjusting the maximum midday measured stomatal conductance in these species ( $110 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  all-sided leaf area basis,  $220 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  hemi-surface area basis; T. A. Martin, unpublished data) downward based on the radiation level for that day and then varied stomatal conductance linearly upward from zero at the hour before sunrise toward the maximum at noon and then linearly downward to zero at the hour after sunset in the afternoon. Hourly leaf-level transpiration was calculated from vapor pressure deficit (VPD) and stomatal conductance using the Penman-Monteith equation (Monteith 1965), assuming that boundary layer conductance was much larger than stomatal conductance (Ewers and Oren 2000). Leaf-level transpiration was then scaled to the plot level using monthly values of leaf area index, assuming that at hemi-surface LAI above 2.5, additional leaf area becomes increasingly shaded and therefore has a lower stomatal conductance and transpiration rate (Iritz and Lindroth 1996, Phillips and Oren 2001). Because information on understory vegetation was very limited (Neary et al. 1990a), we assumed that under-

story LAI in the C and F treatments were at a steady state level of 0.75 and 1.0, respectively. Hourly transpiration was then summed by year and subtracted from annual precipitation to produce a simple water balance estimate for each plot. We did not attempt to model soil water balance explicitly, as the hydrology of flatwoods spodosols in this region is quite complex (Abrahamson and Hartnett 1990).

Hourly meteorological data to drive the model were not available for the entire length of the experiment, so we used daily maximum and minimum air temperature and precipitation measurements from the Gainesville airport, located ~8 km from our site, and simulated hourly VPD (Landsberg 1986) and daily radiation (Weiss and Hays 2004) from the measured data. Comparisons of one year of simulated hourly VPD with measurements from a nearby meteorological station (Gholz and Clark 2002) showed that the simulated data matched the timing, patterns, and peaks of the measured data quite well. To assess the model, we compared simulations with four months of sap flow transpiration measurements made on one FV plot in each species at the site (Martin 2000). Model predictions of cumulative stand transpiration were within 10% of measured values for both species.

#### Foliar N concentration

At ages 6, 7, and 14 yr, foliage was collected from the upper crown of four trees per plot, composited, dried, and ground. The foliage was then analyzed for [N] using either a semi-micro-Kjeldahl method (Wilde et al. 1979) or an elemental analyzer (NCS 2500, CE Elantech, Lakewood, New Jersey, USA). Foliar [N] was expressed as percentage of N on a dry mass basis. Foliage was sampled in August or September, corresponding to the period of peak LAI and minimum foliar [N] (T. A. Martin and E. J. Jokela, unpublished data).

#### Statistical analysis

The statistical significance of main effects (species [S], fertilizer [F], and understory vegetation control [V]) and interactions was analyzed separately for each time period using mixed model analysis of variance (ANOVA) for a split-plot factorial experiment. Block and the interaction of block with species were treated as random effects, and all others were treated as fixed. For all tests, an effect was judged statistically significant when  $P < 0.05$ . When the three-way interaction term ( $S \times F \times V$ ) was significant, the differences between means of individual treatment–species combinations were compared using pairwise  $t$  tests, with  $P$  values adjusted using the Tukey-Kramer method to control the family confidence coefficient (Neter et al. 1990). To test for changes in treatment effects over time, each species was analyzed separately using a repeated measures ANOVA (Littell et al. 1998). Although the full experiment could have been analyzed and presented as a repeated measures analysis, the num-

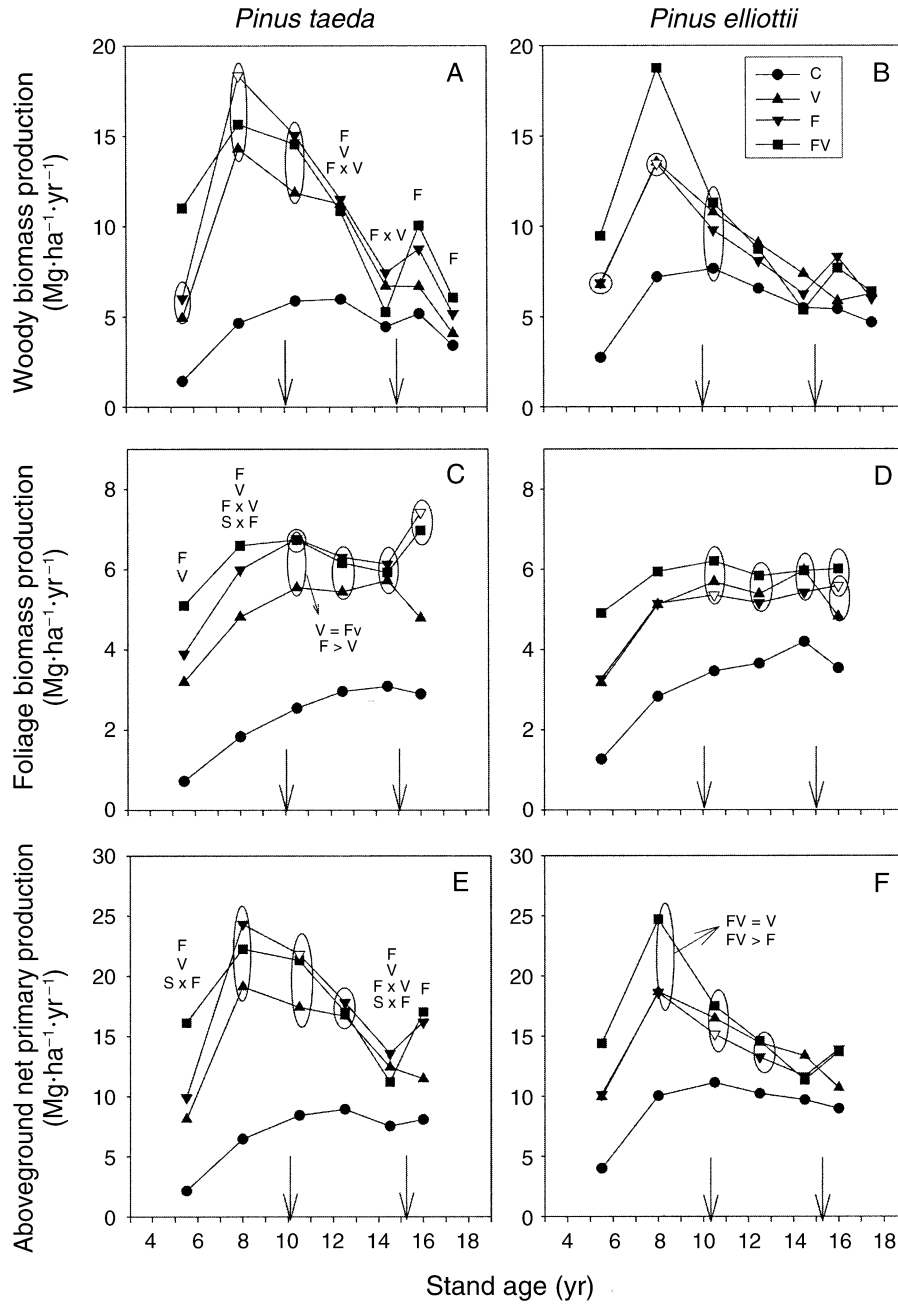


FIG. 1. Changes in (A, B) aboveground woody biomass production, (C, D) foliage biomass production, and (E, F) aboveground net primary production with stand age for loblolly and slash pine stands receiving control (C), fertilizer (F), understory vegetation control (V), and combination (FV) treatments. Each symbol is the mean of three replicate plots. Significance of ANOVA main effects and interactions for the full experiment (species [S] × fertilizer [F] × vegetation control [V]) for each time period are indicated by letters on the loblolly pine graph. For time periods when the three-way interaction (S × F × V) was significant, ellipses enclose treatments within a species that are not significantly different from each other ( $P > 0.05$ ). Open symbols indicate a significant difference between species for that particular treatment and time period. The first arrow along each x-axis indicates the time at which fertilization was stopped; the second arrow indicates the time at which fertilization was resumed. The study utilized data from the Intensive Management Practices Assessment Center experiment near Gainesville, Florida, USA.

ber of terms was intractable (15 main effect and interaction terms, hundreds of potential pairwise comparisons), so the single time point analyses were utilized for treatment- and species-related inferences, and the repeated measures analyses were used only for inferences involving time. In subsequent discussions, references to changes in magnitudes of variables over time indicate a significant ( $P < 0.05$ ) time main effect or time  $\times$  treatment interaction. All analyses of variance were performed with the SAS mixed procedure (SAS Institute 1992). Linear regression analysis was performed with the SAS GLM procedure (SAS Institute 1992).

### RESULTS

Aboveground radiation use efficiency and ANPP subsume a number of ecological parameters, all of which are likely to vary independently in response to environmental and plant physiological conditions. Because we were interested in better understanding the mechanisms driving changes in  $\epsilon_A$  and ANPP, we examined variation in the three terms of Eq. 1 (ANPP,  $\epsilon_A$ , and  $\Phi_{\text{par}}$ ), as well as the components that are used to calculate these three terms ( $I_{\text{WB}}$ ,  $I_{\text{FB}}$ , and LAI).

#### *Aboveground woody biomass increment*

Aboveground woody biomass increment was significantly impacted by silvicultural treatment, with strong additional variation associated with stand development (Fig. 1A, B). Within any particular treatment, loblolly pine and slash pine tended to have similar  $I_{\text{WB}}$ . At age 4–6 yr,  $I_{\text{WB}}$  in the FV treatment was higher than in all other treatments, at 10.2 Mg·ha<sup>-1</sup>·yr<sup>-1</sup>, vs. 6.4, 5.8, and 2.1 Mg·ha<sup>-1</sup>·yr<sup>-1</sup> in the F, V, and C treatments, respectively, averaged across species.

Aboveground woody biomass production in the treated plots (F, V, and FV treatments) peaked at age 6–9 yr for both species, with  $I_{\text{WB}}$  in treated plots as much as three times greater than in the controls. In the following two time periods (ages 9–11 and 11–13 yr),  $I_{\text{WB}}$  declined sharply for both species. By age 11–13 yr,  $I_{\text{WB}}$  for F, V, and FV was the same across species and exceeded the controls by ~55%, compared to >200% difference at age 6–9 yr. In the year after refertilization at age 15, a significant F main effect was manifested. Plots receiving refertilization showed a mean increase in  $I_{\text{WB}}$  of 51% over plots not receiving fertilizer. The significant F effect continued through age 18, although production in all plots declined during that time period, and  $I_{\text{WB}}$  in plots receiving refertilization exceeded nonfertilized plots by only ~30%.

#### *Foliage biomass production*

Foliage biomass production ( $I_{\text{FB}}$ ) was also affected by silvicultural treatments and to some extent by stand development. As was the case for  $I_{\text{WB}}$ ,  $I_{\text{FB}}$  within a treatment tended not to differ between species (Fig. 1C, D). At age 4–6 yr, F and V treatments caused mean

increases in  $I_{\text{FB}}$  of 1.96 Mg·ha<sup>-1</sup>·yr<sup>-1</sup> (45%) and 1.51 Mg·ha<sup>-1</sup>·yr<sup>-1</sup> (33%), respectively. Foliage biomass production peaked at age 9–11 yr for treated plots in both species and declined (loblolly pine) or remained relatively constant at around 5.5 Mg·ha<sup>-1</sup>·yr<sup>-1</sup> (slash pine) through age 13–15 yr. By age 13–15 yr, the differential effects of F and V treatments had declined, and there was no difference in  $I_{\text{FB}}$  among treated plots or between species for those treatments (mean 5.9 Mg·ha<sup>-1</sup>·yr<sup>-1</sup>). After refertilization at age 15 yr, loblolly pine  $I_{\text{FB}}$  in the F and FV treatments increased by 19.3% over the previous time period, in contrast to slash pine, which showed no response of  $I_{\text{FB}}$  to the refertilization.

#### *Aboveground net primary production*

Trends in ANPP with silvicultural treatment and stand development (Fig. 1E, F) reflected the combined effects of its component variables,  $I_{\text{WB}}$  and  $I_{\text{FB}}$ . With few exceptions, species ANPP within any particular treatment did not differ. At age 4–6 yr, the greater fertilizer response of loblolly pine (7.88 Mg·ha<sup>-1</sup>·yr<sup>-1</sup>) vs. slash pine (5.29 Mg·ha<sup>-1</sup>·yr<sup>-1</sup>) led to a significant S  $\times$  F interaction. As with  $I_{\text{WB}}$  and  $I_{\text{FB}}$ , ANPP peaked in all treated plots at age 6–9 yr (mean of treated plots across species = 21.3 Mg·ha<sup>-1</sup>·yr<sup>-1</sup>) and declined to age 13–15 yr. At age 13–15 yr there was again a significant S  $\times$  F interaction; fertilized loblolly pine plots maintained a higher ANPP than nonfertilized plots (12.4 vs. 10.0 Mg·ha<sup>-1</sup>·yr<sup>-1</sup>, respectively), while ANPP of slash pine fertilized and nonfertilized treatments were not different (11.5 Mg·ha<sup>-1</sup>·yr<sup>-1</sup>). The refertilization treatment at age 15 yr resulted in a significant across-species F response at age 16 yr, with ANPP in fertilized plots averaging 15.2 Mg·ha<sup>-1</sup>·yr<sup>-1</sup> vs. 9.8 Mg·ha<sup>-1</sup>·yr<sup>-1</sup> in nonfertilized plots.

#### *Leaf area index*

The responses of hemi-surface leaf area index to fertility manipulations were large and differed consistently by species, with loblolly pine producing higher LAI in situations in which fertilizer was applied (Fig. 2A, B). This result is in contrast to the patterns of  $I_{\text{FB}}$ , which did not differ greatly by species (Fig. 1C, D). This contrast is attributable to specific leaf area: loblolly pine has higher specific leaf area than slash pine, which results in greater leaf area production per unit leaf biomass produced. The S  $\times$  F interaction was significant for LAI at ages 4–6 and 6–9 yr, showing that the increase in LAI with fertilizer was greater for loblolly pine than for slash pine in these two time periods. For example, at age 4–6 yr, fertilizer increased LAI in loblolly pine by 1.9 m<sup>2</sup>/m<sup>2</sup> (129%) over plots not receiving fertilizer, compared to 1.3 m<sup>2</sup>/m<sup>2</sup> (97%) for slash pine. LAI in loblolly pine F and FV plots peaked at ~5 m<sup>2</sup>/m<sup>2</sup> at age 9–11 yr and declined over the next two time periods. Slash pine, in contrast, reached an apparent “steady state” in LAI of ~3.8 m<sup>2</sup>/m<sup>2</sup> in F, V, and FV treatments at age 6–9 yr, which persisted

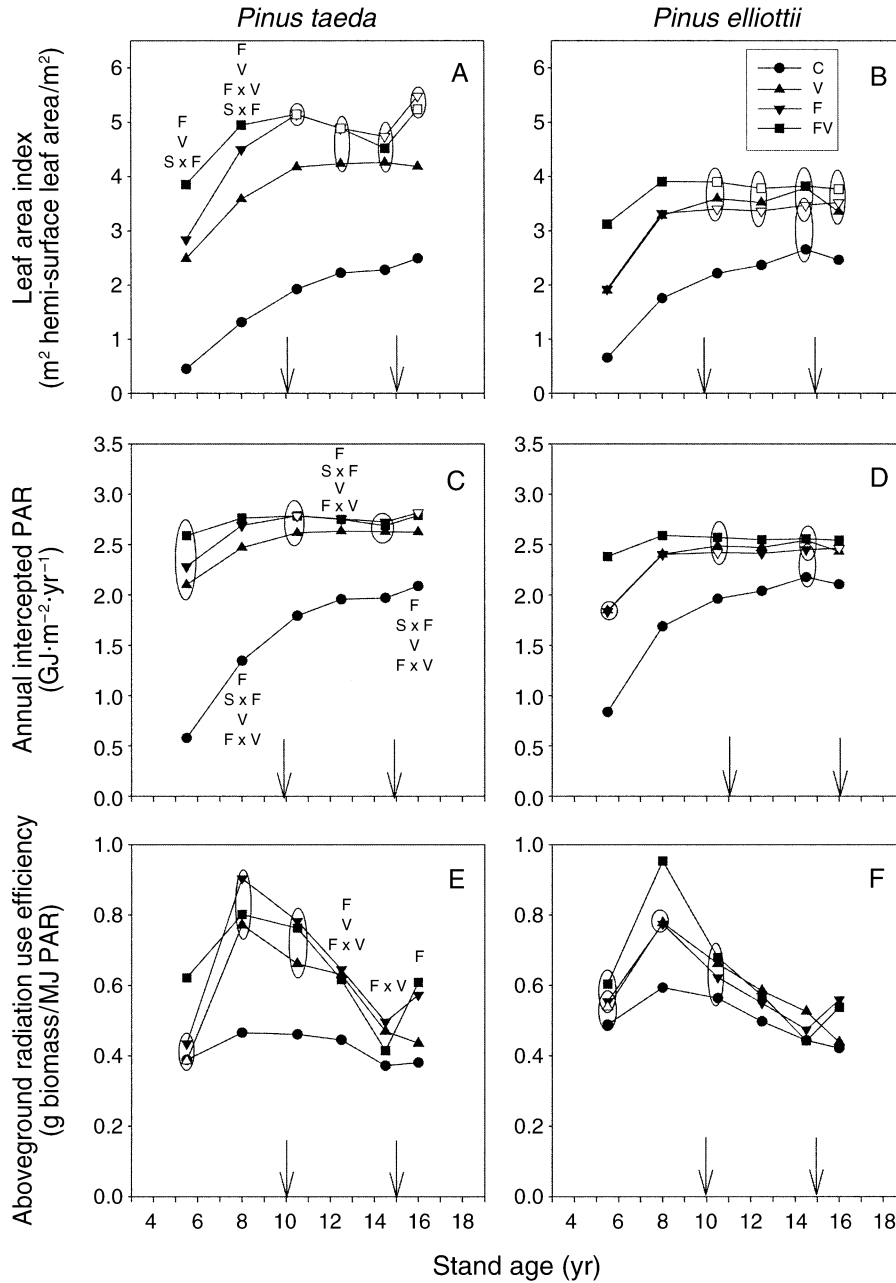


FIG. 2. Changes in (A, B) leaf area index, (C, D) annual intercepted photosynthetically active radiation (PAR), and (E, F) aboveground radiation use efficiency with stand age for loblolly and slash pine stands receiving control (C), fertilizer (F), understory vegetation control (V), and combination (FV) treatments. Each symbol is the mean of three replicate plots. Significance of ANOVA main effects and interactions for the full experiment (species [S] × fertilizer [F] × vegetation control [V]) for each time period are indicated by letters on the loblolly pine graph. For time periods when the three-way interaction (S × F × V) was significant, ellipses enclose treatments within a species that are not significantly different from each other ( $P > 0.05$ ). Open symbols indicate a significant difference between species for that particular treatment and time period. The first arrow along each x-axis indicates the time at which fertilization was stopped; the second arrow indicates the time at which fertilization was resumed.

through age 16 yr. LAI for both loblolly and slash pine C treatments remained significantly lower than all other plots through the duration of the experiment. Loblolly pine LAI in plots receiving fertilizer (F and FV treatments) was significantly higher than in any slash pine

plots for ages 9–11 and 11–13 yr. By age 13–15 yr, LAI of fertilized loblolly pine plots had declined to the point that LAI of loblolly pine FV, F, and V and slash pine FV and V were not significantly different from each other (mean = 4.3 m<sup>2</sup>/m<sup>2</sup>). There were marked

differences in species responses to refertilization at age 15 yr. Loblolly pine LAI responded rapidly, with refertilized plots showing significant positive responses to fertilizer, in contrast to slash pine LAI, which did not respond to refertilization.

#### Intercepted photosynthetically active radiation

Both fertilizer and vegetation control treatments increased annual  $\Phi_{\text{par}}$  above C treatments for the duration of the experiment (Fig. 2C, D). Intercepted PAR in all treatments increased for the first two measurement periods, but reached a plateau at age 6–9 yr; this plateau was between 2.4 and 2.7  $\text{GJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  in treated plots, while  $\Phi_{\text{par}}$  in the control treatments leveled off at a significantly lower level between 1.8 and 2.0  $\text{GJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ . There were consistent differences in species responses to fertilizer, with significant species by fertilizer interactions at ages 6–9, 11–13, and 15–16 yr. For all three time periods, this interaction was the result of slash pine having the same  $\Phi_{\text{par}}$  as loblolly pine in plots not receiving fertilizer, but loblolly pine having significantly greater radiation interception in treatments with added fertilizer. In other words, loblolly pine tended to have about twice the increase in  $\Phi_{\text{par}}$  in response to fertilizer than did slash pine.

#### Aboveground radiation use efficiency

As was the case with its component parameters,  $\epsilon_A$  responded both to experimental treatments and stand development. At age 4–6 yr,  $\epsilon_A$  was highest in the FV treatment for both species, at approximately 0.61 g biomass/MJ intercepted PAR (Fig. 2E, F). For loblolly pine, this value was significantly higher than the other three treatments, which averaged 0.40 g/MJ. Similarly, slash pine C, F, and V treatments were not significantly different from one another at 0.53 g/MJ. By age 6–9 yr,  $\epsilon_A$  had peaked in treated plots of both loblolly and slash pine. Aboveground radiation use efficiency of loblolly pine F, V, and FV treatments averaged 0.83 g/MJ, a 77% increase over  $\epsilon_A$  in the C treatment (0.47 g/MJ). In slash pine,  $\epsilon_A$  of the FV treatment (0.95 g/MJ) exceeded that of the F and V treatments by 22% (0.78 g/MJ) and the C treatment by 61% (0.59 g/MJ). Over the next three time periods (9–11, 11–13, and 13–15 yr),  $\epsilon_A$  continued to decline in the F, V, and FV treatments. At ages 11–13 and 13–15, the F  $\times$  V interaction was highly significant ( $P = 0.0093$  and  $0.0012$ , respectively), as plots receiving both fertilizer and vegetation control (FV) tended to have lower  $\epsilon_A$  than did plots receiving only F or only V. Immediately after the resumption of refertilization treatments at age 15 yr,  $\epsilon_A$  showed a highly significant F response ( $P = 0.0002$ ), which was consistent across species; plots receiving fertilizer had an  $\epsilon_A$  of 0.57 g/MJ (averaged across species), compared to 0.42 g/MJ in the V and C treatments (Fig. 2E, F). For both species, there was no significant change in  $\epsilon_A$  over time in the C treatment.

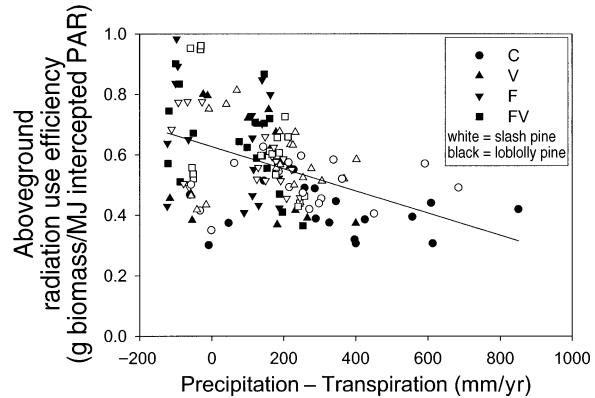


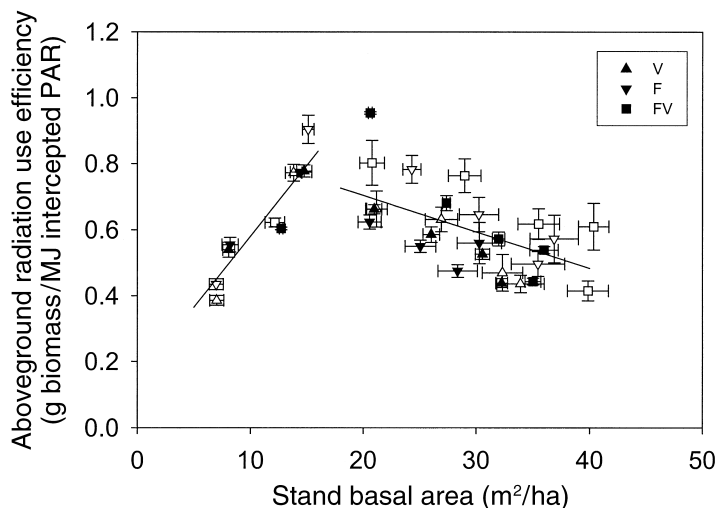
FIG. 3. Relationship between aboveground radiation use efficiency and simulated annual site water balance in loblolly and slash pine stands receiving control (C), fertilizer (F), understory vegetation control (V), and combination (FV) treatments. PAR is photosynthetically active radiation. The line shows a linear regression through the data ( $\epsilon_A = 0.63 - 0.000367 \times (\text{precipitation} - \text{transpiration})$ ,  $R^2 = 0.18$ ,  $P < 0.0001$ ).

Aboveground radiation use efficiency was negatively correlated with an index of site water balance, precipitation – transpiration ( $\epsilon_A = 0.63 - 0.000367 \times [\text{precipitation} - \text{transpiration}]$ ,  $R^2 = 0.18$ ,  $P < 0.0001$ , Fig. 3). The relationship between  $\epsilon_A$  and stand basal area for plots receiving the F, V, or FV treatment was two phased, with a positive, linear relationship for values of BA  $< 18 \text{ m}^2/\text{ha}$  ( $\epsilon_A = 0.15 + 0.0429 \times \text{BA}$ ,  $R^2 = 0.80$ ,  $P < 0.0001$ ) and a declining, linear relationship for values of BA  $> 18 \text{ m}^2/\text{ha}$  ( $\epsilon_A = 0.92 - 0.015 \times \text{BA}$ ,  $R^2 = 0.25$ ,  $P < 0.0001$ ; Fig. 4). Loblolly pine  $\epsilon_A$  for ages 4–6, 6–9, and 13–15 yr was significantly correlated with foliar [N] ( $\epsilon_A = -1.37 + 1.98 \times [\text{N}]$ ,  $R^2 = 0.51$ ,  $P < 0.0001$ ; Fig. 5). There was not a significant relationship between  $\epsilon_A$  and foliar [N] for slash pine.

#### DISCUSSION

This study examined long-term patterns of radiation use efficiency and its components in two even-aged forest model systems: loblolly pine, one of the best studied and most commercially important tree species in North America, and slash pine, a much less thoroughly studied southern pine with a range contained entirely within that of loblolly pine. The availability of long-term inventory and litterfall measurements in this replicated, multi-treatment experiment provided a unique and powerful opportunity to explore the mechanisms underlying changes in productivity and radiation use efficiency associated with nutrient availability and stand development. We found that gradients in soil nutrient availability, as induced by fertilizer additions and control of understory vegetation, impacted all the components of Eq. 1. However, stand developmental processes modified these responses, resulting in large variation in productivity and  $\epsilon_A$  that was dependent on both soil nutrient availability and stand basal area.

FIG. 4. Changes in aboveground radiation use efficiency,  $\epsilon_A$ , with stand basal area development in loblolly (filled symbols) and slash pine (open symbols) stands receiving fertilizer (F), understory vegetation control (V), and combination (FV) treatments. PAR is photosynthetically active radiation. Each symbol represents the  $\epsilon_A$  and basal area (BA; means with standard error bars) for a single treatment and time period. Regression lines are shown for BA < 18 m<sup>2</sup>/ha ( $\epsilon_A = 0.15 + 0.0429 \times BA$ ,  $R^2 = 0.80$ ,  $P < 0.0001$ ) and for BA > 18 m<sup>2</sup>/ha ( $\epsilon_A = 0.92 - 0.015 \times BA$ ,  $R^2 = 0.25$ ,  $P < 0.0001$ ).



#### Biomass, leaf area, and radiation interception dynamics

As in previous work at this site and in other studies, nutrient availability in the form of added fertilizer or nutrients released from competing understory vegetation had a strong impact on biomass increment and aboveground biomass accumulation (Colbert et al. 1990, Dalla-Tea and Jokela 1991, Gholz et al. 1991, Gower et al. 1992, Raison and Myers 1992, Albaugh et al. 1998, Samuelson et al. 2001). For example, at age 6–9 yr, any combination of fertilizer or vegetation control treatments increased ANPP by 200–300% over the untreated controls (Fig. 1E, F). While the magnitude of these productivity increases declined with stand development, the treated plots maintained significantly greater productivity than the C treatment throughout most of the experiment (Fig. 1). Leaf area index in both loblolly and slash pine was also highly responsive to treatments that increased soil nutrient availability, with

LAI in treated plots elevated from 97% (slash pine age 4–6 yr) to 129% (loblolly pine age 4–6 yr) above that in control treatments (Fig. 2A, B). A number of studies in southern pines (Vose and Allen 1988, Gholz et al. 1991, Dalla-Tea and Jokela 1994, Albaugh et al. 1998, Will et al. 2002) and in other conifers (Gower et al. 1992, Balster and Marshall 2000) have also shown positive responses of leaf biomass or LAI to either fertilizer or removal of competing vegetation.

Large treatment- or species-related differences in LAI did not necessarily translate into large differences in  $\Phi_{\text{par}}$ . For example, the 12.6% decline in loblolly pine LAI in the FV treatment from age 9–11 yr (5.2) to age 13–15 yr (4.5) resulted in only a 3.6% decrease in  $\Phi_{\text{par}}$  (2.8 vs. 2.7 GJ·m<sup>-2</sup>·yr<sup>-1</sup>). The relative insensitivity of  $\Phi_{\text{par}}$  to changes in LAI is due to the nonlinearity of the  $\Phi_{\text{par}}$  vs. LAI function, which begins leveling out at higher LAI values. As an example, at an all-sided LAI of 1.0 and extinction coefficient  $k = -0.23$ , 20.5% of incoming radiation would be intercepted, and a unit increase in LAI would result in a 19% increase in  $\Phi_{\text{par}}$ . At an LAI of 10.0, 90% of incoming radiation would be intercepted, and a unit increase in LAI would cause only a 2.4% increase in  $\Phi_{\text{par}}$ . In other words, as additional units of LAI are added to a canopy, that canopy becomes increasingly inefficient at intercepting radiation.

Most species-level differences in response to treatments involved the foliage parameters  $I_{\text{FB}}$  and LAI. Loblolly pine leaf biomass and leaf area was especially sensitive to nutrient availability. Loblolly pine LAI response to added fertilizer was proportionally greater than in slash pine, and LAI in fertilized loblolly pine plots began declining within a year of the cessation of fertilizer applications (Fig. 2A). In contrast, fertilized slash pine LAI did not decline after fertilizer applications ended (Fig. 2B).  $I_{\text{FB}}$  showed similar patterns. These data highlight the lower nutrient demand of slash pine and the substantial plasticity of loblolly pine leaf

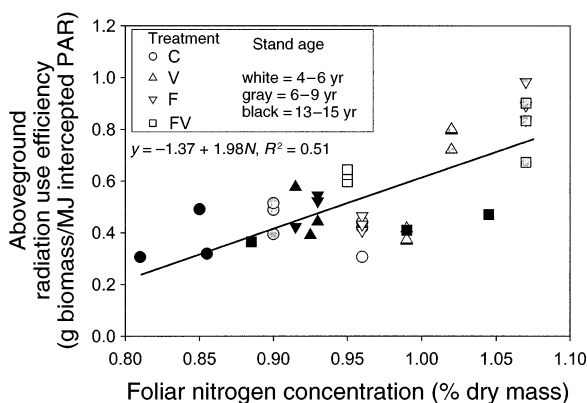


FIG. 5. Relationship between aboveground radiation use efficiency and foliar nitrogen concentration in loblolly pine stands receiving control (C), fertilizer (F), understory vegetation control (V), and combination (FV) treatments. PAR is photosynthetically active radiation.

area in response to changes in nutrient availability. The few other studies that have compared the production ecology of these two species have shown similar patterns. Colbert et al. (1990) observed that loblolly pine accumulated greater biomass when soil nutrient availability was high, while slash pine accumulated greater biomass when soil nutrient availability was low, as under control treatment conditions. On a site in southeastern Georgia, USA, Barron-Gafford et al. (2003) showed that when soil nutrient availability was increased with fertilizer and understory competition control treatments, loblolly pine accumulated both higher N and P concentrations and higher N and P contents in most biomass components compared to slash pine.

#### *Treatment effects on radiation use efficiency*

Aboveground radiation use efficiency in this study varied from 0.40 to almost 1.00 g/MJ across a range of cultural treatments and stages of stand development (Fig. 2E, F). This degree of variation in  $\epsilon_A$  for two species at one location is almost as large as the reported variation in  $\epsilon_A$  across temperate evergreen forests in North America, Australia, and New Zealand (0.18–1.48 g/MJ; Runyon et al. 1994, McCrady and Jokela 1998, Gower et al. 1999). However, the peak  $\epsilon_A$  values observed in this study were considerably lower than those measured by McCrady and Jokela (1998) for 4-yr-old loblolly pine stands in South Carolina, USA (1.33–1.44 g/MJ). It is likely that the high stem density (11 800 stems/ha), early stage in stand development, high quality genetic stock, and fertile soils contributed to the very high levels of  $\epsilon_A$  and ANPP observed in the McCrady and Jokela (1998) study.

Radiation use efficiency increased in response to treatments that elevated soil nutrient availability. Treatment-induced changes in  $\epsilon_A$  were largest at age 6–9 yr, with plots receiving fertilizer or understory competition control showing a 77% (loblolly pine) and 61% (slash pine) increase over the untreated controls (Fig. 2E, F). An earlier study in 21-yr-old slash pine showed increases in  $\epsilon_A$  from 0.46 g/MJ in a control treatment to 0.80 g/MJ in plots receiving fertilizer (Gholz et al. 1991). A limited number of studies have shown increases in  $\epsilon_A$  in response to fertilizer in other conifer species (Wang et al. 1991, Raison and Myers 1992, Balster and Marshall 2000), and Sinclair and Horie (1989) showed increases in  $\epsilon$  in several crop species in response to fertilizer application. Few other studies have documented responses of  $\epsilon$  to changes in soil nutrient availability, although several have documented changes in southern pine leaf area efficiency (the ratio of production to LAI). For example, Albaugh et al. (1998) found that loblolly pine NPP:LAI increased by 91% over control with addition of fertilizer and by 120% when treated with fertilizer and irrigation. In contrast, Samuelson et al. (2001) saw no change in  $I_{wB}$ :LAI in fertilized and irrigated loblolly pine. Will et al. (2002) showed that fertilizer addition increased

the ratio of stem biomass growth:LAI in 7-yr-old loblolly pine stands, but decreased the ratio in 13-yr-old stands. DeLucia et al. (2002) documented increased loblolly pine  $\epsilon$  in response to elevated atmospheric  $\text{CO}_2$  concentration.

Throughout stand development,  $\epsilon_A$  of both species responded similarly to treatments, i.e., there were no significant species  $\times$  treatment interactions detected (Fig. 2E, F). Burkes et al. (2003) similarly found that stemwood growth efficiency (expressed as stem biomass growth/leaf biomass) of loblolly and slash pine did not differ. McCrady and Jokela (1998) found significant variation in  $\epsilon_A$  among individual loblolly pine families, suggesting that in some situations, within-species genetic variation in  $\epsilon_A$  may be important.

#### *Site water balance effects*

Studies in other conifer forests have shown that  $\epsilon$  may be reduced by drought, cold temperatures, or other environmental stresses (McMurtrie et al. 1994, Runyon et al. 1994). Over the course of the current study, precipitation regimes ranged from very dry to very wet (e.g., 871 mm in 2000, 1480 mm in 1997, study period mean = 1203 mm). When we plotted  $\epsilon_A$  against a stand water balance index obtained by subtracting annual modeled plot-level transpiration from annual precipitation, there was a weak negative relationship between the two variables (Fig. 3;  $R^2 = 0.18$ ). While this analysis does not definitively test the dependence of  $\epsilon_A$  on soil water availability, it does suggest that any negative effects of drought were probably overwhelmed by the impact of stand developmental and nutritional factors (see subsequent discussions).

Previous field and modeling studies have suggested that soil drought is not a strong determinant of productivity for pine forests on flatwoods soils (Neary et al. 1990b, McMurtrie et al. 1994, Teskey et al. 1994). To a large extent, this is probably because these flat, somewhat poorly to poorly drained sites maintain a water table within reach of tree roots for much of the year, even as the surface soil dries (Abrahamson and Hartnett 1990). Several modeling and irrigation studies on loblolly pine across a range of sites have also suggested that nutrient availability is a stronger determinant of productivity than soil water availability (Neary et al. 1990b, Albaugh et al. 1998, Sampson and Allen 1999, Samuelson et al. 2001).

The analysis in Fig. 3 implies that  $\epsilon_A$  declines as site water balance increases, which is somewhat counter-intuitive. One explanation could be that on the poorly drained soils of this site, higher water balance values might be associated with prolonged root zone inundation, leading to plant stress and reduced  $\epsilon_A$ . This hypothesis has some grounding in the experience of practitioners: avoidance of root system inundation is one of the primary motivations for the widespread silvicultural practice in this region of planting tree seed-

lings on raised beds (Kaufman et al. 1977, Wheeler et al. 2002).

#### Effects of stand development

As the stands in the current study aged,  $\epsilon_A$  declined rapidly in the treated plots, with the most intensive treatment (FV) showing the largest decline (Fig. 2E, F). Aboveground radiation use efficiency remained responsive to fertilizer, however, increasing significantly after the refertilization treatment at age 15 yr (Fig. 2E, F). While changes in  $\epsilon$  with stand development have been anticipated in the literature (Russell et al. 1989, Landsberg et al. 1996, McCrady and Jokela 1998), few studies have documented such variation in a forest tree species. Saldarriaga and Luxmoore (1991) showed that Amazonian rainforest  $\epsilon_A$  declined from  $\sim 0.32$  g/MJ in young stands in a chronosequence to nearly 0.00 g/MJ in 70-yr-old stands. Will et al. (2002) examined stemwood growth efficiency (expressed as stemwood biomass growth:leaf biomass) in 5-, 10- and 12-yr-old loblolly pine stands. They found that plot-level stemwood growth efficiency was linearly and negatively related to mean tree height and suggested that age- or tree-size-related increases in maintenance respiration costs or partitioning of biomass to belowground components may have contributed to declining efficiency. In the current study, stand basal area appeared to be a good index of the effect of stand development on  $\epsilon_A$  in treated plots (Fig. 4). This relationship showed a linear rise in  $\epsilon_A$  at lower BA levels to a peak at  $\sim 15$  m<sup>2</sup>/ha and a linear decline in  $\epsilon_A$  with BA above that point. This relationship did not hold for the control stands, where  $\epsilon_A$  was relatively insensitive to BA throughout the study (data not shown). The decline in  $\epsilon_A$  was largely caused by decreasing  $I_{WB}$  (Fig. 1A, B). Variations in  $I_{FB}$  (Fig. 1C, D) and  $\Phi_{par}$  (Fig. 2C, D) during this time period were not large enough to greatly influence  $\epsilon_A$ .

It has long been observed that  $I_{WB}$  and ANPP decline at higher BA levels in even-aged forests (see reviews by Gower et al. [1996] and Ryan et al. [1997]), and this information has been incorporated into guidelines for density management. For example, published stocking guides specify minimum basal area levels that should be maintained in order to obtain "full site occupancy" by trees. Stocking guides also stipulate maximum basal area levels above which competition-induced reductions in stand productivity and self-thinning will occur. Stocking guides for loblolly pine (Dean and Baldwin 1993) and slash pine (Dean and Jokela 1992) indicate minimum basal area levels of  $\sim 10.0$  m<sup>2</sup>/ha and maximum basal area levels of 23.0 m<sup>2</sup>/ha for the stand conditions examined in the current study. These values correspond to the range of BA around the inflection point of the relationship shown in Fig. 4. The implication of this relationship is that the declines in growth associated with aging of even-aged southern pine stands (Fig. 1E, F) are driven by large reductions

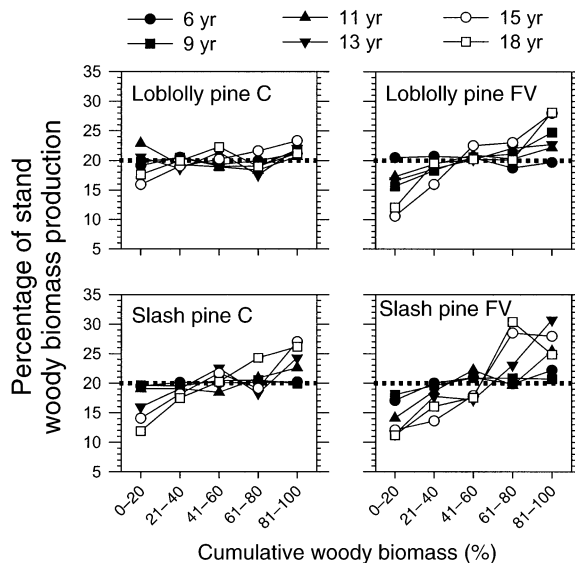


FIG. 6. Distribution of age 6–18 yr stand-level woody biomass production across different size classes of trees in loblolly and slash pine stands under control (C) and fertilizer + understory vegetation control (FV) treatments. The x-axis was generated by ranking all trees from smallest to largest woody biomass for each time period, then grouping the list into five categories, each holding 20% of the stand's woody biomass. Points falling on the dotted line represent woody biomass production that is proportional to woody biomass.

in stand-level radiation use efficiency with increasing stand basal area.

Binkley et al. (2002) and Binkley (2004) similarly hypothesize that the decline in growth following canopy closure in even-aged forests is associated with decreasing stand-level resource use efficiency. More specifically, they suggest that after canopy closure tree size differentiation results in dominance of site resources by larger trees and declining resource use efficiency of smaller trees, leading to an overall decline in stand-level resource use efficiency. Binkley (2004) tested this hypothesis in mixed species stands in Oregon, USA, by determining the proportional distribution of stand-level growth across different size classes of trees. At 74 yr, the age coinciding with declining stand-level growth, the largest 20% of trees contributed 39% of stand-level growth, compared to the smallest fifth of trees, which accounted for only 9% of stand-level growth. In the present experiment, growth differentiation or dominance (as defined by Binkley [2004]) around the time of stand-level growth declines was less extreme (Fig. 6). At the time of the largest  $I_{WB}$  declines in the treated plots (ages 9–11 yr and 11–13 yr, Fig. 1A, B), there was only a slight shift in growth towards larger trees, with the largest 20% of the FV stands producing about 22% (loblolly pine) or 28% (slash pine) of the stands'  $I_{WB}$  and the smallest fifth producing 17% and 13% of stand  $I_{WB}$  in loblolly and slash pine, respectively. Differentiation increased as the stands

aged (Fig. 6), but the patterns of shifting differentiation were not large enough or early enough to suggest that declining efficiency in only small trees was driving the changes in stand-level efficiency (D. Binkley, *personal communication*).

Smith and Long (2001) also invoked decreasing resource use efficiency as a primary mechanism for post-canopy closure growth declines. Their hypothesis differs slightly from Binkley (2004), because they suggest that the redistribution of a relatively constant amount of foliage onto larger trees that are differentiating into increasingly contrasting crown classes results in declining production efficiency of both larger and smaller trees, causing decreased stand level growth efficiency. Our analysis (Fig. 6) appears to be consistent with this hypothesis. Smith and Long (2001) further hypothesized that stand-level growth declines are an emergent property, not attributable to decreasing individual tree growth. Previous analyses have shown this is not the case for our study: all size classes of trees follow similar patterns of growth throughout the study period (Martin and Jokela 2004).

#### Nutrition effects

Our data suggest that nitrogen nutrition may play an important role in mediating changes in  $\epsilon_A$ , at least in loblolly pine. Loblolly pine radiation use efficiency at ages 4–6, 6–9, and 13–15 yr was significantly correlated with late summer (August–September) foliar [N] (Fig. 5). The relationship was linear and explained about half of the variation in  $\epsilon_A$ . The same relationship did not hold for slash pine. There are a number of physiological mechanisms that might be invoked to explain this pattern. One is leaf net photosynthesis rate ( $A_{\text{net}}$ ). All other factors being equal, increases in  $A_{\text{net}}$  should result in increased  $\epsilon$  (Monteith 1977, Sinclair and Horie 1989, Landsberg et al. 1996). If  $A_{\text{net}}$  was positively correlated with foliar [N], it would be predicted that  $\epsilon_A$  would also rise with foliar [N]. A number of species have demonstrated a positive response of  $A_{\text{net}}$  to leaf [N] (Brix 1971, Evans 1989, Sinclair and Horie 1989, Mitchell and Hinckley 1993, Bond et al. 1999). In fact, leaf [N] is used to scale  $A_{\text{net}}$  within trees and among sites in many physiological process models (e.g., Kull and Jarvis 1995, Leuning et al. 1995, Williams et al. 1996, Lai et al. 2002). It is not entirely clear that a strong  $A_{\text{net}}$ –leaf [N] relationship exists for loblolly pine, though. While several studies have reported a positive response of loblolly pine  $A_{\text{net}}$  to foliar [N] (Tjoelker and Luxmoore 1991, Green and Mitchell 1992, Tissue et al. 1993, Murthy et al. 1996, Samuelson 2000, Lai et al. 2002), a number have found little or no relationship between the two variables (Samuelson 1998, Tang et al. 1999, Samuelson et al. 2001, Munger et al. 2003). Other conifers have also failed to show a strong  $A_{\text{net}}$ –leaf [N] relationship (Kloppel et al. 2000, Nippert and Marshall 2003). A one-time sampling of net photosynthesis for 36 loblolly pine trees from the

F and FV treatments in the present study was consistent with the “no response” pattern. Current-year, upper crown foliage in the FV treatment had a foliar [N] of 1.66%, significantly greater ( $P < 0.0001$ ) than in the V treatment (1.14%), while light-saturated net photosynthesis rate of the same foliage was not affected by fertilizer ( $P = 0.9545$ ,  $3.83 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  FV treatment vs.  $3.85 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  V treatment; T. A. Martin and R. C. McGarvey, *unpublished data*). Area-based foliar [N] and mass-based photosynthesis followed the same patterns.

A second possible mechanism that could contribute to the response in Fig. 5 is a shift in allocation of C from belowground to aboveground biomass in response to increased foliar [N]. A number of studies in southern pines (Johnson 1990, Li et al. 1991, Albaugh et al. 1998, Samuelson 2000) and other conifers (Keyes and Grier 1981, Axelsson and Axelsson 1986, Ingestad and Agren 1991, Haynes and Gower 1995, Beets and Whitehead 1996) have shown decreased allocation of C to belowground biomass, especially fine roots, in response to increased soil nutrient availability. A shift in C allocation in response to increased fertility would be expected to increase the “efficiency” of aboveground biomass production and could reasonably produce a response such as the one in Fig. 5.

Unfortunately, the relative importance of changes in  $A_{\text{net}}$  or C allocation for productivity responses to soil fertility has not been determined and remains a pressing research topic (Cropper and Gholz 1994, Beets and Whitehead 1996, Waring and Running 1998, Samuelson et al. 2001). A modeling analysis of a slash pine fertilizer study showed that either a small increase in net photosynthesis rate or a small decrease in C allocation to fine roots could initiate a positive feedback loop leading to sufficient increased C gain to explain fertilizer growth responses (Cropper and Gholz 1994), suggesting that in southern pines, either or both processes could be involved.

It should be noted that evidence from other tree species has suggested that declines in productivity with stand development can be attributable to hydraulic limitations associated with increasing tree height and hydraulic resistance (e.g., Mencuccini and Grace 1996, Bond 2000). We were not able to rigorously test this hypothesis with our data, as possible indices of hydraulic resistance such as tree height or size were highly correlated with stand basal area. In other long-term studies in southern pines in which fertility treatments were maintained throughout the course of the rotation, growth declines were not as severe as those seen in the present study, in which nutrient additions were curtailed in the middle of the study (Jokela et al. 2004). These studies, in addition to the data presented here, make a strong case for competition for soil nutrients as an important driver of productivity patterns in pine species adapted to low nutrient soils.

### Future research needs

This study has highlighted the dynamic nature of  $\epsilon_A$  in southern pine forests. The results show that both stand developmental and nutritional processes are associated with changes in ANPP and  $\epsilon_A$  (Figs. 1E, F, 2E, F, 4, and 5). Our data suggest that in southern pine, increasing intraspecific competition occurring with rising stand BA results in lowered stand-level resource use efficiency. The biological mechanisms responsible for these changes in efficiency remain obscure. Previous researchers have identified shortcomings in our understanding of post-canopy-closure growth declines in even-aged forests (Gower et al. 1996, Ryan et al. 1997, Jokela and Martin 2000), and a number of avenues for further research are being pursued, including age- or size-related changes in plant hydraulics and carbon dynamics (Mencuccini and Grace 1996, Ryan and Yoder 1997, Hunt et al. 1999, Bond 2000). It is apparent, however, that nutrient uptake and utilization research should take high priority in southern pines (Jokela and Martin 2000, Ducey and Allen 2001, Landsberg et al. 2001). Landsberg (2003) pointed out that our lack of understanding of nutrient uptake and utilization mechanisms remains one of the primary barriers to development of robust process-based models for forests in general. Clearly, if we are to use some form of efficiency model (Eq. 1) to predict forest growth over long periods of time and in diverse management and soil environments, we must better understand the factors controlling variation in  $\epsilon_A$ , especially in relation to stand development and soil nutrient supply.

### ACKNOWLEDGMENTS

The Forest Biology Research Cooperative at the University of Florida funded this research. Rayonier provided access to the study site. Wendell Cropper helped with the modeling analyses, and Dan Binkley provided valuable discussions. The comments of John Marshall, Barbara Bond, and an anonymous reviewer are appreciated. We thank S. Brooker, R. J. English, A. J. Kegley, D. R. Nolletti, J. E. Smith, D. S. Wilson, and W. Wood for technical field assistance. This is Florida Agricultural Experiment Station Journal Series Paper Number R-10024.

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