Modeling the Effects of Stand Development, Site Quality, and Silviculture on Leaf Area Index, Litterfall, and Forest Floor Accumulations in Loblolly and Slash Pine Plantations

Carlos A. Gonzalez-Benecke, Eric J. Jokela, and Timothy A. Martin

Abstract: Leaf area index (LAI), needlefall (NF), and forest floor (FF) dynamics are tightly linked with stand productivity, nutrient cycling, and carbon, water, and energy exchange. We analyzed a long-term data set to quantify the impacts of stand development, site quality, and silviculture on LAI and litterfall (LF) in loblolly and slash pine plantations. LAI was significantly correlated with stand density index (SDI) for each stand studied ($P < 0.001$), and the parameters of the fitted sigmoidal function were correlated with site index independently for each species. The maximum LAI that a loblolly or slash pine stand attained was linearly correlated with site index ($P < 0.001$), and the slope of that relationship was different for each species ($P = 0.003$). Soil resource availability affected the relationship between SDI and LAI. When weed control or fertilizer treatments were applied, the maximum attainable mean yearly LAI and the value of SDI that corresponded with the attainment of 50% of the maximum LAI (inflection point) were increased ($P < 0.05$). NF production was linearly related to the previous year's LAI ($P < 0.001$), and this relationship was independent of resources availability ($P > 0.086$); however, the relationship was different for both species ($P < 0.001$). Comparison of simulations of NF, LF, and FF with diverse data sets from the literature, encompassing the natural ranges of both species, indicated that these relationships captured the primary drivers of variation, and therefore the models provide a robust synthesis and prediction system for these important variables. FOR. SCI. 58(5):457–471.

Keywords: loblolly pine, slash pine, forest floor, needlefall, leaf area index

THE FOREST FLOOR (FF), consisting of shed vegetative parts in various stages of decomposition resting on the mineral soil surface, is a central component of forest nutrient and carbon (C) cycling (Miller 1984). In pine forests, the FF is one of the main ecosystem C pools, accounting for between 10 and 30% of total ecosystem C storage (Kinerson et al. 1977, Gholz and Fisher 1982, Harding and Jokela 1994, Shan et al. 2001, Noormets et al. 2010). Plant materials comprising the pine FF include pine needles, cones and twigs, and understory leaves and twigs, as well as bark and woody stems (Smith and Heath 2002). Other ecological functions of the FF include being a major source of humus in the mineral soil, supplying both inorganic and organic leachates to lower horizons, and serving as a source of organic soil C. The FF also provides habitat and food for meso and micro fauna, insulates the soil surface from extreme temperatures and moisture, improves water infiltration, and offers mechanical protection from raindrop impact and erosional forces (Van Lear and Goebel 1976, Lee et al. 1983, McColl and Gressel 1995, Chapin et al. 2002).

Accumulation of FF mass depends on rates of detrital inputs (in pine forests mainly through needlefall [NF]) and the rate of loss through decomposition, physical damage, or removal (Smith and Heath 2002). The total amount of needle mass in a stand has been shown to be correlated with stand productivity (Jarvis 1985, Hennessey et al. 1992) and NF production has been correlated with stand basal area (Gresham 1982, Hennessey et al. 1992, Gonzalez-Benecke et al. 2010). Changes in long-term forest productivity are closely related to changes in soil organic matter, including the mineral soil and FF (McColl and Gressel 1995). The potential long-term sustainable benefits of short-rotation forest management systems cannot be attained if soil elemental pools are depleted, leading to decreased productivity over subsequent rotations (Jorgensen et al. 1975, Miller 1984).

Understanding how stand development, stand structure, site, and management factors affect leaf area index (LAI), NF, and FF dynamics is important for several reasons. First, LAI has a direct correspondence with the ability of the canopy to absorb light and produce photosynthates; therefore, LAI is a key parameter for estimating plantation productivity (Vose and Allen 1988, Innes et al. 2005, Shoemaker and Cropper 2010), as well as for understanding the rates of material and energy exchanges between plant canopies and the atmosphere (Gholz et al. 1991, Cropper and Gholz 1993). Second, LAI is the primary biophysical parameter used in forest productivity

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modeling and carbon sequestration studies, and is commonly used by forest managers seeking to quantify canopy responses to silvicultural treatments (Landsberg and Gower 1997, Gower et al. 1999). Third, understanding NF dynamics is important because it reflects the amount of foliage biomass added to the FF, which ultimately represents a major source of plant recycled nutrients as decomposition and mineralization processes occur (Hennessey et al. 1992, Polglase et al. 1992; Perry 1983, Miller 1984); the FF is also one of the main C pools in southern pine forest ecosystems (Gholz and Fisher 1982).

The southeastern United States has more than 13 million ha of southern pine plantations (Fox et al. 2007). Approximately 58% of the total US timber harvest is from the southeastern United States, making this region one of the most important timber production zones in the world (McKeand et al. 2003, Allen et al. 2005). In terms of greenhouse emissions mitigation, the forests in the southeastern and south central United States could potentially capture CO_2 equivalent to approximately 23% of the regional emissions (Han et al. 2007). In this region, loblolly pine (*Pinus taeda* L.) grows on a variety of site types from East Texas to southern Tennessee to north Florida to southern New Jersey and is one of the fastest growing pine species, accounting for more than 84% of the planted seedlings in the United States (McKeand et al. 2003). Slash pine (*Pinus elliottii* var. elliottii) has been planted on more than 4.2 million ha, covering a wide range from eastern Texas to southern North Carolina to south central Florida, with 79% of the planted slash pine occurring in Florida and Georgia (Barnett and Sheffield 2005).

In this article, we perform an analysis using loblolly and slash pine LAI, LF, and FF data from a long-term experiment (Martin and Jokela 2004, Jokela et al. 2010) and present functions describing key relationships between these variables and stand developmental and site factors. We hypothesize that stand LAI, NF, and FF dynamics can be determined from stand structure variables obtained from forest inventories. We then compare predictions from these functions with independent data from the literature to determine whether the site and stand structural determinants of LAI and FF accumulations are consistent across the ranges of species and under diverse management and site conditions.

Materials and Methods

Site and Stand Description

The Intensive Management Practices Assessment Center (IMPAC) experiment, established in 1982 as a collaborative effort between the University of Florida, USDA Forest Service, and forest industry, represents a unique opportunity to analyze the factors that control the productivity of loblolly and slash pine stands in the southern United States (Swindel et al. 1988, Jokela and Martin 2000). The combinations of different levels of competition control and nutrient amendments created a large gradient in productivity for both species over a 25-year period (Jokela et al. 2010). The IMPAC site, located approximately 10 km north of Gainesville, Florida (29°30′ N, 82°30′ W), was site-prepared by roller drum chopping and conventional bedding and planted in January 1983 at a 1.8 × 3.6 m spacing using genetically improved seedlings. 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 design (species as main plot and fertilization and weed control as subplots) (Jokela and Martin 2000). Four treatments were randomized within each species block: control (C); complete and sustained understory competition control (W); annual fertilization with macro- and micronutrients from establishment through age 10 years (F); and combined competition control and fertilization (FW) treatments. From age 15 to 17 years, a nitrogen and phosphorus fertilization regime was reinitiated in the F and FW treatments. In total, the F and FW treatments cumulatively received (kg ha^{-1}) 1,088 nitrogen, 230 phosphorus, 430 potassium, 108 calcium, 72 magnesium, 72 sulfur, 4.1 manganese, 5.4 iron, 0.9 copper, 4.0 zinc, and 0.90 boron. More details about the experimental design and treatment applications can be found elsewhere

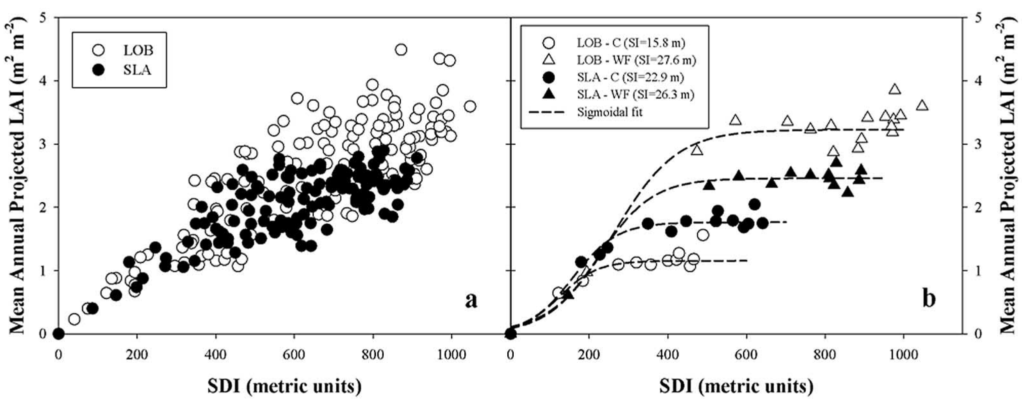


Figure 1. Relationship between SDI and mean annual projected LAI for all plots pooled by species (a) and example of sigmoidal curve fitting for selected plots (b) that received the following silvicultural treatments: control (C) and fertilizer + weed control (FW). LOB, loblolly pine; SLA, slash pine.

(Swindel et al. 1988, Dalla-Tea and Jokela 1991, Jokela and Martin 2000). Treatment plots were approximately 820 m^2 in size, with 40 measured trees in an interior plot of 260 m^2 dbh and height of each tree were measured periodically for each plot.

NF and LAI

Data from 15 years of monthly sampling of LF at the IMPAC study were used to estimate the long-term dynamics of foliage production in loblolly and slash pine stands. Beginning at age 5 years, pine LF (Mg ha^{-1} $year^{-1}$) was collected monthly in six circular litter traps (0.7 m^2) installed in each plot (Dalla-Tea 1990). The litter collected was separated into needles and other pine materials (branch, bark, twigs, and cones) and then was oven-dried at 70°C and weighed to the nearest 0.1 g (Dalla-Tea 1990, Jokela and Martin 2000). LAI was calculated from NF and the logistic models of foliage accretion as described by Kinerson et al. (1974) and Dougherty et al. (1995). As Jokela and Martin (2000) reported, NF was corrected for senescence-related biomass reductions and transformed to all-sided leaf area using specific leaf area of 0.0100 and 0.0115 m^2 g^{-1} for loblolly and slash pine, respectively (Dalla-Tea 1990). Monthly values of NF and projected LAI (the ratio of leaf surface area supported by a plant to its corresponding horizontal projection on the ground, m^2 m^{-2}) were determined for each plot. Total yearly NF (Mg ha^{-1} $year^{-1}$) was calculated as the sum of all NF collected within the calendar year. Mean annual projected LAI was determined as the average of monthly projected LAI determined within each calendar year.

Model Fitting

We parameterized key relationships by combining experimental data between ages 5 and 20 years at the IMPAC site on stand basal area (BA) (m^2 ha^{-1}), number of living trees per ha (N), stand density index (SDI) (number of trees of 25.4-cm diameter that the stand can support in 1 ha for a given BA; Reineke 1933), LAI, and NF production under contrasting resource availability conditions. SDI was computed using the equation proposed by Reineke (1933):

$$\mathrm{SDI} = \mathrm{N} \cdot ([200 \cdot \sqrt{BA/N \cdot \pi})]/25.4)^{1.6} \qquad (1)$$

For each plot, SDI was correlated with LAI using several nonlinear models, and the three-parameter sigmoidal model gave the best fit and was selected for further analysis. Analysis of variance (ANOVA) was used to test the effect of species and treatments on the model parameter estimates:

$$\mathrm{LAI} = \beta_0/(1 + e^{-\left(\frac{(\mathrm{SDI}-\beta_2)}{\beta_1}\right)}) \qquad (2)$$

where β_0 represents the maximum LAI that can be attained, β_1 is the scale parameter that represents the distance on the x-axis between the inflection point and the point where the response is $\beta_0/(1 + e^{-(1)}) \approx 0.73\beta_0$, and β_2 is the inflection point, the SDI at which 50% of maximum LAI is attained (Pinheiro and Bates 2000).

Current year NF was correlated with previous year mean annual projected LAI. A linear regression was fitted, and species and treatment effects on that relationship were analyzed using covariance analysis.

LF was determined from NF using literature estimates that reported NF/LF ratios for loblolly and slash pine. A total of 15 reports were used for loblolly pine ranging in ages from 3 to 37 years. The slash pine data set was composed of five reports, ranging in ages from 2 to 35 years. A nonlinear model that related stand age and the NF/LF ratio was fitted for stands with and without weed control treatments at planting. Biomass was transformed to carbon mass using an average C content of 50% for NF and LF (Clark et al. 1999, Smith et al. 2006).

FF (Mg ha^{-1}) accumulation was determined as the

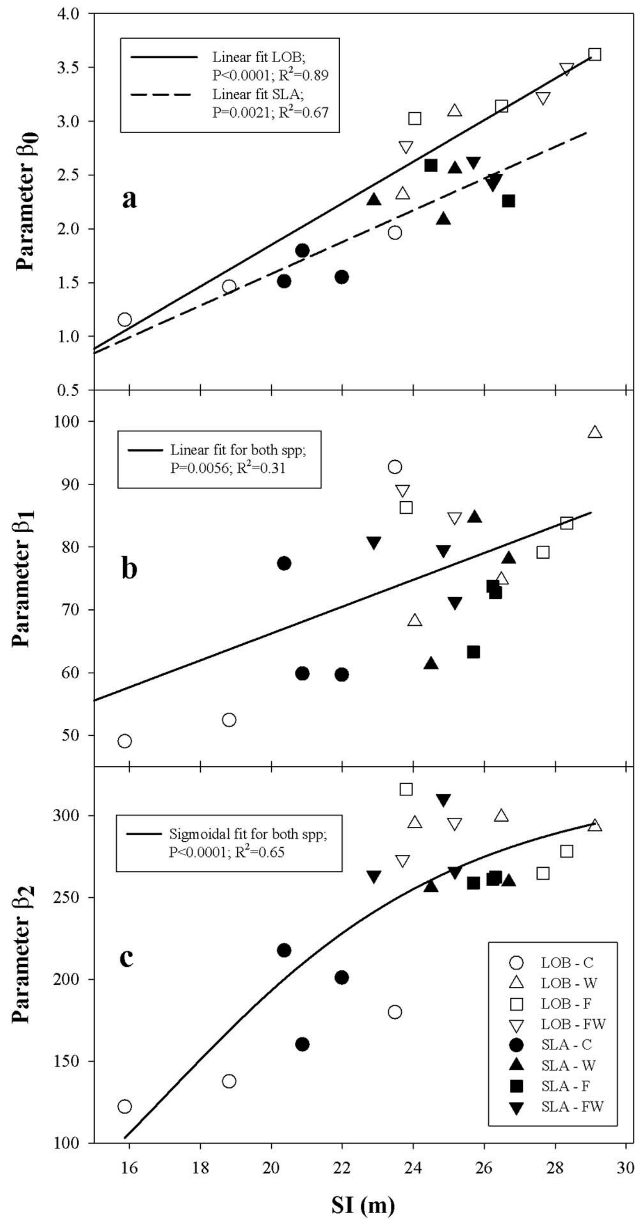


Figure 2. Relationship between SI and curve parameters of the relationship between SDI and mean annual projected LAI for loblolly (LOB) and slash (SLA) pine plantations grown under the following silvicultural treatments: control (C), weed control (W), fertilization (F), and fertilizer + weed control (FW).

Table 1. Summary of parameter estimates.

Variable	Model	Species	Parameter	Value	SE	Observation
LAI	$= \beta_0/(1 + e^{-((SDI - \beta_2)/\beta_1)})$	LOB/SLA				SDI in metric units
β_0	$= a_0 + b_0 \cdot SI$	LOB	a_0	−2.0287	0.531	SI in m
			b_0	0.19665	0.021	
		SLA	a_0	−1.3707	0.838	
			b_0	0.14758	0.034	
β_1	$= a_1 + b_1 \cdot SI$	LOB/SLA	a_1	12.0950	17.003	
			b_1	2.5869	0.696	
β_2	$= a_2/[1 + (SI/b_2)]^{c_2}$	LOB/SLA	a_2	327.234	42.616	
			b_2	18.5717	2.096	
			c_2	−4.929	1.148	
ln NF	$= a_3 + b_3 \cdot \ln(LAI)$	LOB	a_3	0.62455	0.0159	Mean annual projected LAI
		LOB	b_3	0.97146	0.0163	
		SLA	a_3	0.80235	0.0163	
		SLA	b_3	0.96529	0.0211	
NF/LF	$= (a_4 \cdot b_4 + c_4 \cdot Age^{d_4})/b_4 + Age^{d_4})$	LOB/SLA	a_4	0.7399	0.047	For stands without weed control at planting and age ≥10 yr; for stands with weed control at planting at any age
			b_4	0.00837	0.021	
			c_4	1.007	0.040	
			d_4	−2.007	0.870	
	$= a_4 + b_4 \cdot Age + c_4 \cdot Age^2 + d_4 \cdot Age^3$	LOB/SLA	a_4	−1.2312	0.216	For stands without weed control at planting and age <10 yr
			b_4	0.8740	0.132	
			c_4	−0.1204	0.024	
			d_4	0.00547	0.001	

LAI, previous year mean annual projected LAI ($m^2\ m^{-2}$); SDI, Reineke's stand density index in metric units; β_0, β_1, and β_2, sigmoidal fit parameters (see text for details); SI, site index (m); NF, current year needlefall biomass (Mg ha^{-1} $year^{-1}$); LF, current year litterfall biomass (Mg ha^{-1} $year^{-1}$); Age, stand age (years); SE, standard error of the parameter value; SLA, slash pine; LOB, loblolly pine.

sum of yearly LF inputs corrected for mass loss using an equation to estimate the decay rate of the FF by Radtke et al. (2009). This equation used site coordinates as inputs to estimate decay rate, and results were in good agreement with values of decay rate reported by Gholz et al. (1986) and Binkley (2002):

$$M_t = M_i \times \left(\frac{Lon}{Lat}\right)^{-0.1247 \times t} \quad (3)$$

where M_t is the mass of the FF at the time t (years), M_i is the initial mass of the FF, Lon is the longitude (in positive decimal degrees west), and Lat is the latitude (in positive decimal degrees north).

Model Validation

The model was validated against values of NF, LF, and FF reported in the peer-reviewed literature. Summary tables of all data used for validation for NF and LF (Table A1) and for FF (Table A2) are found in the Appendix. For each reported value used to validate the model, stand productivity characteristics such as dominant height, BA, N, site index (SI) (the height reached by the stand's dominant and codominant trees at a reference age of 25 years), and management inputs (site preparation, weed control, fertilization, and thinning) were used to determine a time series of SDI, from time of planting up to the reported age. We used growth and yield models developed by the University of Georgia Plantation Management Research Cooperative for loblolly and slash pine, as reported by Peter et al. (2007) and Gonzalez-Benecke et al. (2010), respectively.

The model was also validated against 10 years of monthly LF and LAI data from a long-term C flux study in a commercial slash pine plantation in north central Florida (15 km northeast of Gainesville, Alachua County, Florida, USA; 29°44′ N, 82°9′30″ W) (Clark et al. 1999, 2004, Gholz and Clark 2002, Bracho et al. 2011). The site was harvested in 1998, double-bedded, treated with herbicide, replanted with approximately 1,864 trees ha^{-1} in December 1998–January 1999, and fertilized during fall 2002 (Clark et al. 1999, 2004). Stem dbh, total tree height, and number of trees surviving were measured yearly in four permanent inventory plots (625 m^2 per plot). The model inputs were the average yearly time series of stand age, BA and N from the inventory plots, and SI estimated with the last height measurement carried out at age 11 and the equation reported by Pienaar et al. (1996). The site had a mean SI of 24.3 m.

Sensitivity Analysis

A sensitivity analysis was performed to determine the effects of changes in input values (SI, BA, and N) on NF and FF estimations for both species. The effect of SI was assessed by evaluating the model with SI ±2 m from the default value of 22 m. The effect of BA and N was assessed by evaluating the model with continuous 25% under- or overestimations in each variable separately. The variability margins used were arbitrary but corresponded to acceptable values observed in loblolly and slash pine plantations in the southeastern United States. A plot with average SI was selected for each species from the IMPAC study, and its time series of BA and N were used for all simulations as

Table 2. Treatment effects on parameter estimates of the logistic relationship between SDI and projected mean annual LAI for loblolly and slash pine under silvicultural treatments.

Species and treatment	Average parameter estimates*		
	β_0	β_1	β_2
LOB			
C	1.52 a	64.7 a	146.6 a
F	3.26 c	80.3 a	295.8 b
W	2.54 b	84.9 a	284.5 b
FW	3.17 b	83.1 a	286.4 b
SLA			
C	1.62 a	65.6 a	193.0 a
F	2.38 bc	74.6 a	258.2 b
W	2.29 b	77.2 a	279.9 b
FW	2.50 c	69.9 a	260.9 b
Source of variation†			
Whole plot			
Block (df = 2)			
Species (df = 1)	0.083	0.496	0.629
Error (df = 2)			
Split plot			
F (df = 1)	<0.001	0.353	<0.001
W (df = 1)	<0.001	0.105	<0.001
F × W (df = 1)	<0.001	0.069	<0.001
S × F (df = 1)	<0.001	0.461	0.018
S × W (df = 1)	0.519	0.371	0.326
S × F × W (df = 1)	0.014	0.978	0.121
Error (df = 1)			

LOB, loblolly pine; SLA, slash pine; C, control; W, weed control; F, fertilization; FW, fertilizer + weed control; S, species.
* For each parameter estimate within each species, significant differences ($P < 0.05$) among treatments are indicated by different letters.
† Significant P values ($P < 0.05$, ANOVA) were determined using a mixed-model procedure.

base conditions. The SI, N, and BA at age 25 were 22.5 m, 965 trees ha^{-1}, and 39.4 m^2 ha^{-1} for the loblolly pine stand and 22.0 m, 1003 trees ha^{-1}, and 18.4 m^2 ha^{-1} for the slash pine stand. At age 25 years, the loblolly and slash pine stands selected had NF estimates of 4.1 and 4.2 Mg ha^{-1} year^{-1} and FF accumulations of 39.1 and 36.9 Mg ha^{-1}, respectively. The sensitivity analysis was also tested on extreme low and high productivity plots for each species, and the magnitude of the results was similar to that of the average productivity plot.

Statistical Analysis

Four measures of accuracy were used to evaluate the goodness of fit between observed and predicted (simulated) values for each variable from the data set obtained in the model validation: (1) mean absolute error; (2) root mean square error; (3) mean bias error (Bias); and (4) Pearson product-moment correlation coefficient (r) (Fox 1981, Willmott 1982, Willmott et al. 1985, Loague and Green 1991, Kobayashi and Salam 2000).

All of the model fitting and summary statistics computations were made using SAS 9.2 (SAS, Inc., Cary, NC). Effects of species and treatments on model fitting were assessed using an extra sum of squares F-test. Treatment and species effects on parameter estimates were determined using a split-plot ANOVA (PROC MIXED; SAS, Inc.) for a factorial experiment (Jokela and Martin 2000). The whole plot was species, and block and block by species were treated as random effects.

Results

The general relationships between mean annual projected LAI and SDI for each species are illustrated in Figure 1a (all silvicultural treatments were pooled within each species). The relationship between SDI and LAI was strong ($P < 0.001$) but was unique for each plot. Examples of curve fitting for loblolly and slash pine plots with contrasting levels of productivity are shown in Figure 1b. When the plots were analyzed individually, that relationship followed a sigmoidal shape (Figure 1b).

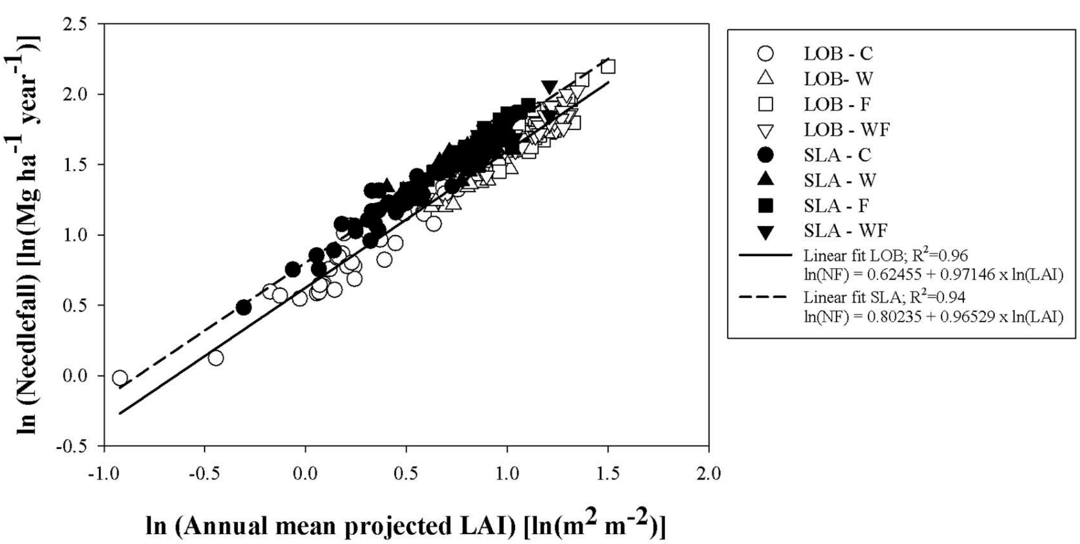


Figure 3. Relationship between previous year mean annual projected leaf area index (LAI) and current year needlefall (NF) for loblolly (LOB) and slash (SLA) pine plantations grown under the following silvicultural treatments: control (C), weed control (W), fertilization (F), and fertilizer + weed control (FW).

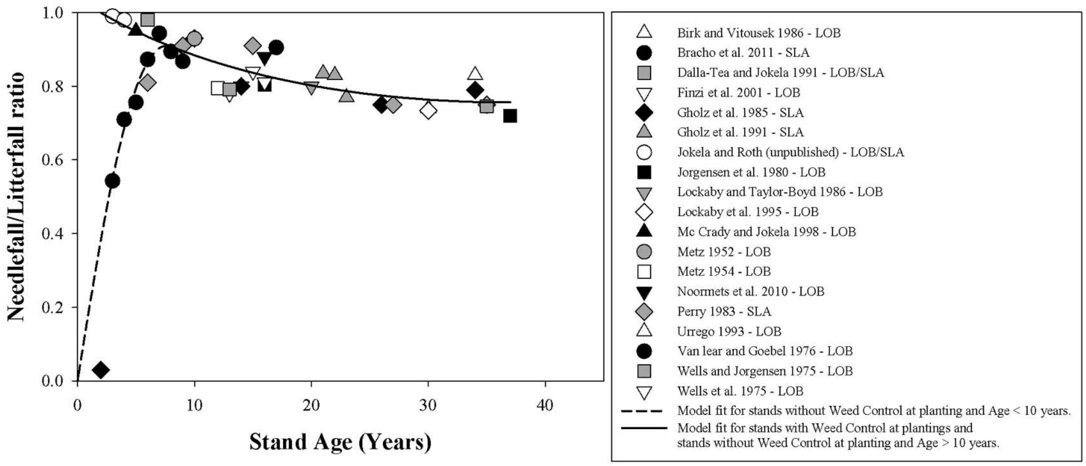


Figure 4. Relationship between stand age and the NF/LF ratio for slash (SLA) and loblolly (LOB) pine plantations.

To generalize the relationships in Figure 1b, we correlated the three sigmoidal equation parameter estimates with site index calculated from individual plot data (Figure 2; Table 1). The parameter β_0 (the asymptote) was linearly related to SI ($P < 0.0001$), and that relationship was different for each species ($P = 0.017$; Table 1). Changes in SI explained 67 and 89% of the variability in parameter β_0 for slash and loblolly pine, respectively.

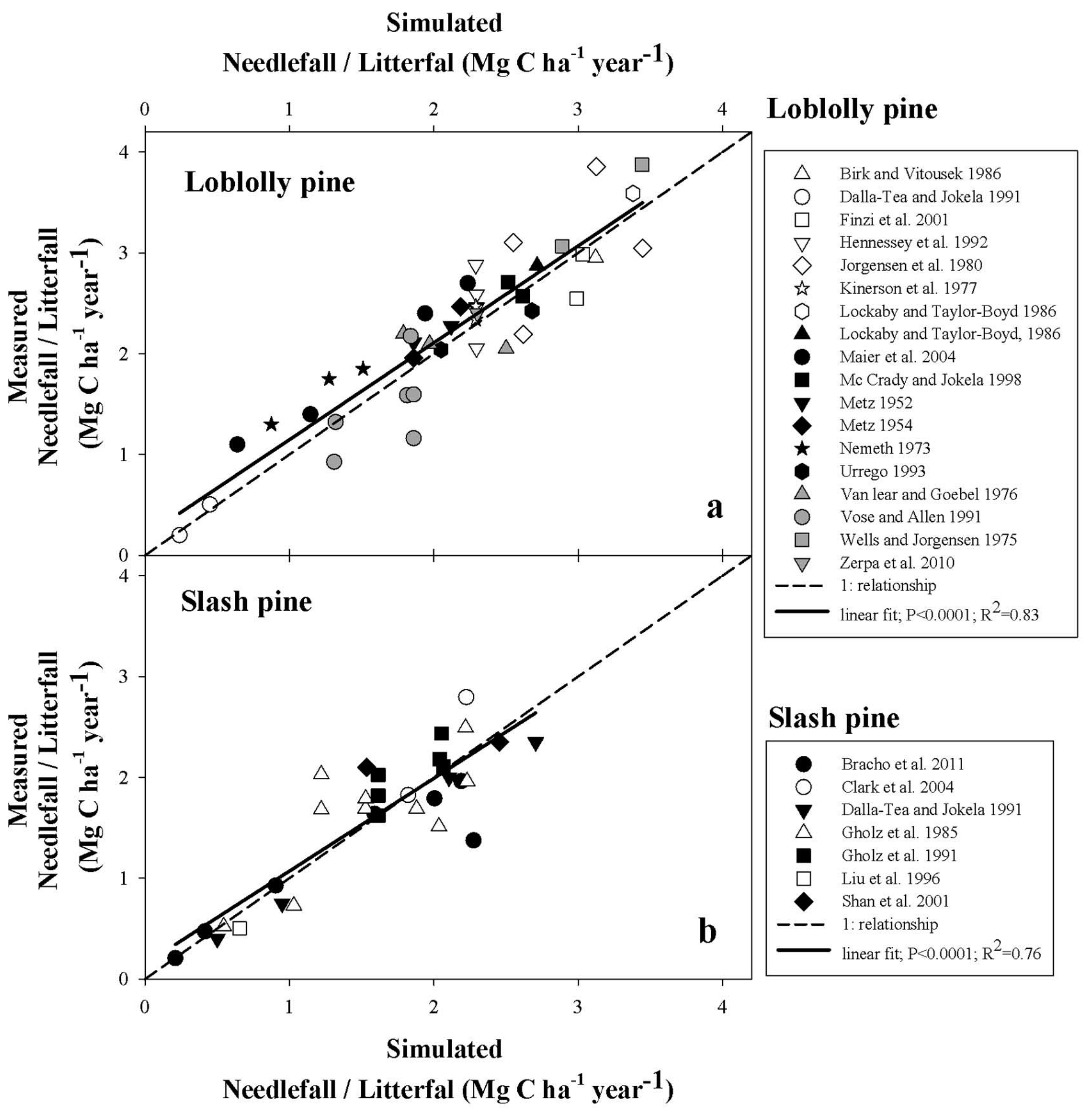


Figure 5. Simulated versus measured NF or LF for slash (a) and loblolly (b) pine plantations.

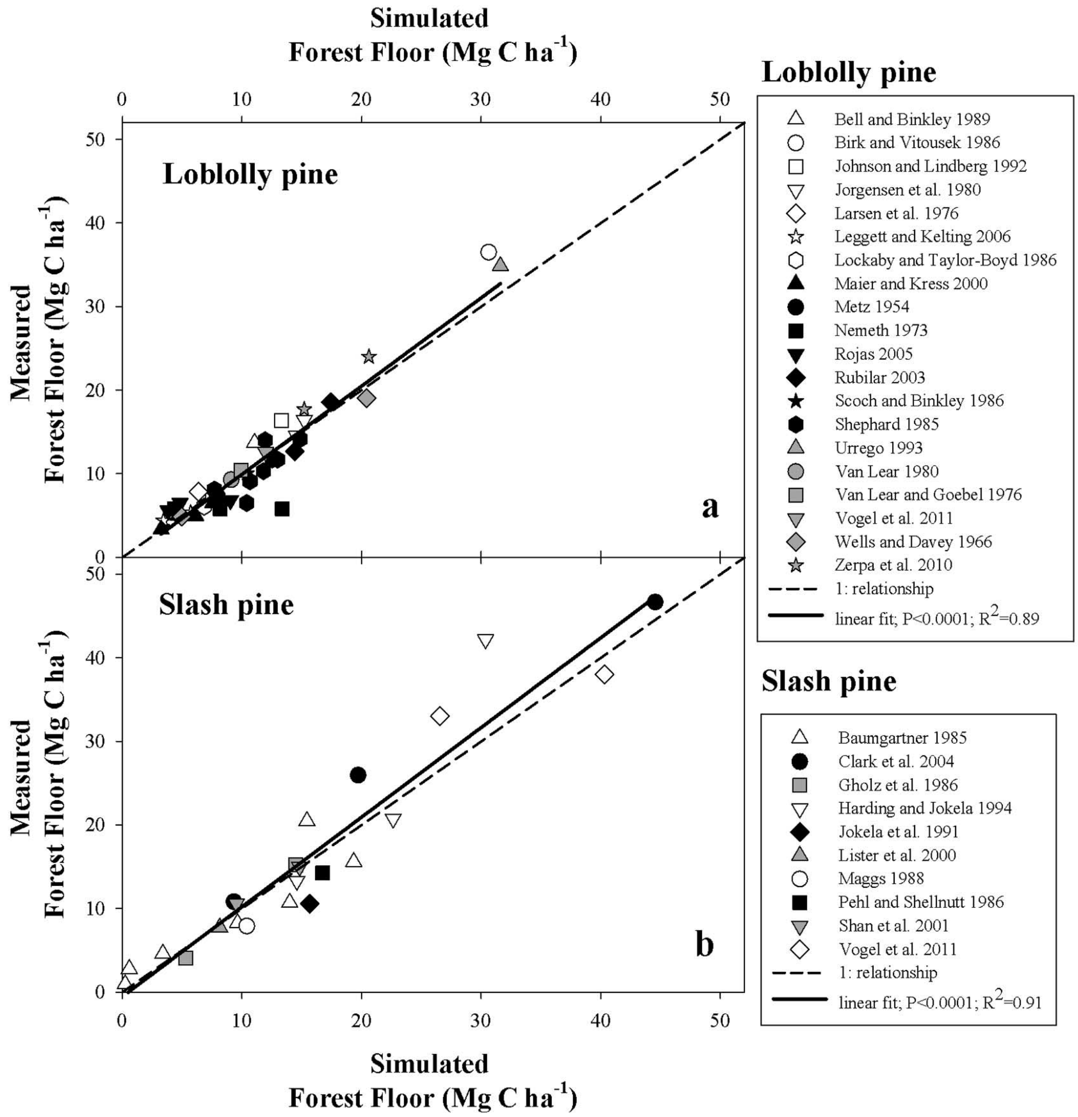


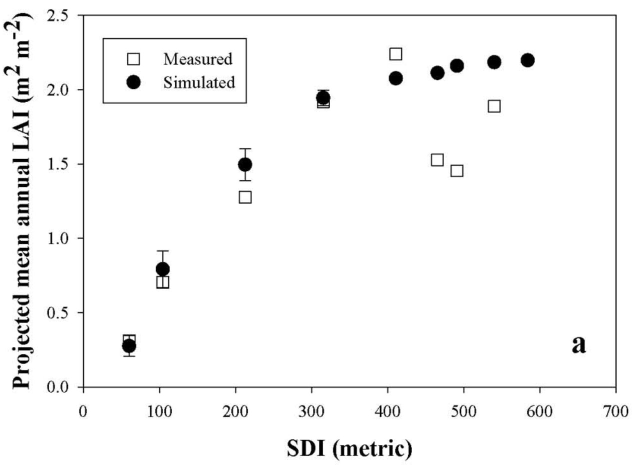
Figure 6. Simulated versus measured forest floor for slash (a) and loblolly (b) pine stands.

The parameter β_1 (the scale parameter) was linearly related to SI ($P = 0.005$; $R^2 = 0.31$), and that relationship was not different between species ($P = 0.19$; Table 1). The parameter β_2 (the inflection point) was also correlated with SI and was not different between species ($P = 0.81$; Table 1). For this parameter, the best fit was a sigmoidal curve; this model better represented the loss of linearity as SI exceeded ~24 m and where β_2 reached asymptotic values of SDI between 250 and 300. Details of the parameter estimates are presented in Table 1.

Species and treatment effects were also tested for each model parameter. The maximum attainable mean yearly LAI (i.e., parameter β_0) was increased by the F and W treatments (Table 2). The response to fertilization differed between species because the F and FW treatments for slash pine supported lower maximum LAI than the fertilized loblolly stands, and the W plots of slash pine supported LAI levels similar to the weed control loblolly stands. The scale parameter of the sigmoidal model (β_1) was not different between species and treatments (Table 2). The SDI corresponding with 50% of the maximum attainable mean yearly LAI (i.e., parameter β_2, the inflection point) was increased by the F and W treatments, and no significant species × treatment interactions were found (Table 2). The inflection point of the SDI-LAI curve was shifted from SDI = 147 and 193 to SDI = 289 and 266 for loblolly and slash pine, respectively, when the F or W treatments were applied.

The total NF of the current year was proportional to LAI in that stand from the previous year. There was a strong relationship between mean annual projected LAI during the previous year and NF ($P < 0.0001$); the data were log transformed to satisfy statistical assumptions for the constant variance test (Figure 3). The intercept and slope of this relationship were independent of treatments ($P > 0.086$) but were different for both species ($P < 0.0001$; Table 1).

To determine LF from NF estimates, we used 35 observations from the peer-reviewed literature that reported the proportion between NF and LF (NF/LF) at a given stand age for slash and loblolly pine. Two curves were fitted to explain the changes in the NF/LF ratio; one



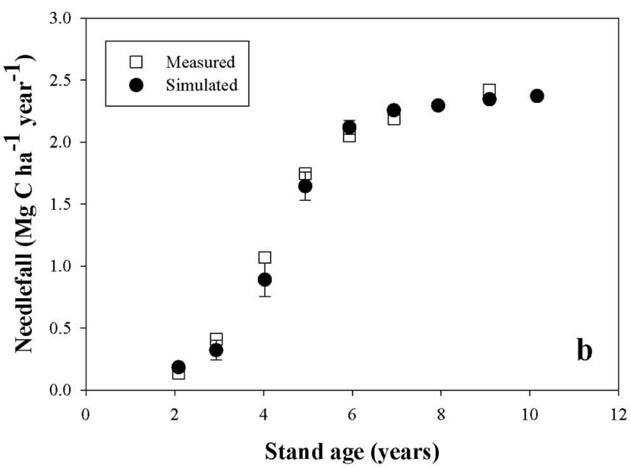


Figure 7. Simulated versus measured relationship between SDI and mean yearly projected LAI (a) and NF time series (b) in a slash pine stand. Error bars represent SE.

curve was generated for stands younger than 10 years old that did not receive a weed control treatment (dashed line in Figure 4), and a second curve was developed for any stand that included a history of weed control from establishment to year 40 (solid line in Figure 4). This latter model could be applied to stands without a weed control treatment after age 10 years. In general, the NF/LF ratio stabilized after year 20, with NF representing between 75 and 80% of total LF (Table 1).

We compared our model results with reported values for LF or NF in the peer-reviewed literature. Overall, there was good agreement between the simulated and measured NF and LF values (Figure 5). The slope of that relationship was not different from 1 (P = 0.267 and 0.528 for slash and loblolly pine, respectively), and the intercept was not different from 0 (P = 0.09 and 0.247 for slash and loblolly pine, respectively).

There was also good agreement between simulated and measured FF estimates reported in the peer-reviewed literature (Figure 6). The slope of the relationship was not different from 1 (P = 0.254 and 0.112 for slash and loblolly pine, respectively), and the intercept was not different from 0 (P = 0.569 and 0.252 for slash and loblolly pine, respectively).

In addition, we compared simulated LAI and LF to measured time series data from Bracho et al. (2011) (Figure 7). There was no statistical difference between the average measured and simulated mean annual LAI from year 2 to 9 (P = 0.713), averaging 1.41 and 1.45 m^2 m^{-2}, respectively (Table 3). Between ages 2 and 9, there was also no statistical difference in measured and simulated LF (P = 0.14), averaging 1.43 and 1.32 Mg C ha^{-1} $year^{-1}$, respectively (Table 3).

All model performance tests showed that LAI, LF, and FF estimations agreed well with measured values (Table 3). Mean absolute error and root mean square error ranged between 12.5 and 18.8 and 6.9 and 25.2% of the observed values, for loblolly and slash pine, respectively. The Bias ranged between 4.7% underestimations for LF/NF in loblolly pine publications and 15.2% overestimations for LAI in the slash pine time series, with no clear tendency toward under- or overestimating the results. Estimated and observed values were highly correlated, ranging between r = 0.87 and 0.99.

An error in estimating SI by 2 m could lead, after the age of 15 years, to constant over- and underestimation of NF by approximately 0.67 and 0.61 Mg ha^{-1} $year^{-1}$ for loblolly and slash pine stands, respectively (Figure 8a). This constant Bias in NF estimation was reflected in the FF accumulation error of 3.9 and 6.0 Mg ha^{-1} for loblolly pine and 2.6 and 5.3 Mg ha^{-1} for slash pine, at ages 15 and 25 years, respectively (Figure 8b). At ages younger than the age of peak maximum LAI, differences in NF or FF estimations were generally small when SI was changed. Bias in BA determinations produced a transient error in NF that peaked 1 year before the onset of maximum LAI, afterward gradually trending to reach similar values of NF (Figure 8c). Maximum under- and overestimation errors in NF, due to systematic bias in BA, reached values of approximately −0.8 and 0.6 Mg

Table 3. Summary of model evaluation statistics.

Species	Variable	$\bar{O}$	$\bar{P}$	n	MAE	RMSE	Bias	r
LOB	LF-NF^{l}	2.21	2.11	43	0.29	0.34	−0.104	0.91
	FF^{l}	10.63	10.66	39	1.51	2.05	0.035	0.95
SLA	LF-NF^{l}	1.61	1.59	32	0.25	0.34	−0.023	0.87
	FF^{l}	16.49	15.90	23	2.06	3.49	−0.561	0.95
	NF^{ts}	1.43	1.32	7	0.22	0.20	−0.036	0.99
	LAI^{ts}	1.41	1.62	8	0.26	0.36	0.215	0.91

LOB, loblolly pine; SLA, slash pine; LF, litterfall biomass (Mg C ha^{-1} $year^{-1}$); NF, needlefall biomass (Mg C ha^{-1} $year^{-1}$); FF, forest floor biomass (Mg C ha^{-1}); LAI, mean annual projected leaf area index (m^2 m^{-2}); $\bar{O}$ is the mean observed value; $\bar{P}$, mean predicted value; n, number of observations; MAE, mean absolute error; RMSE, root mean square error; Bias, bias estimator; r, Pearson's correlation coefficient. l, model evaluation data obtained from literature estimates; ts, model evaluation data from times series measurements.

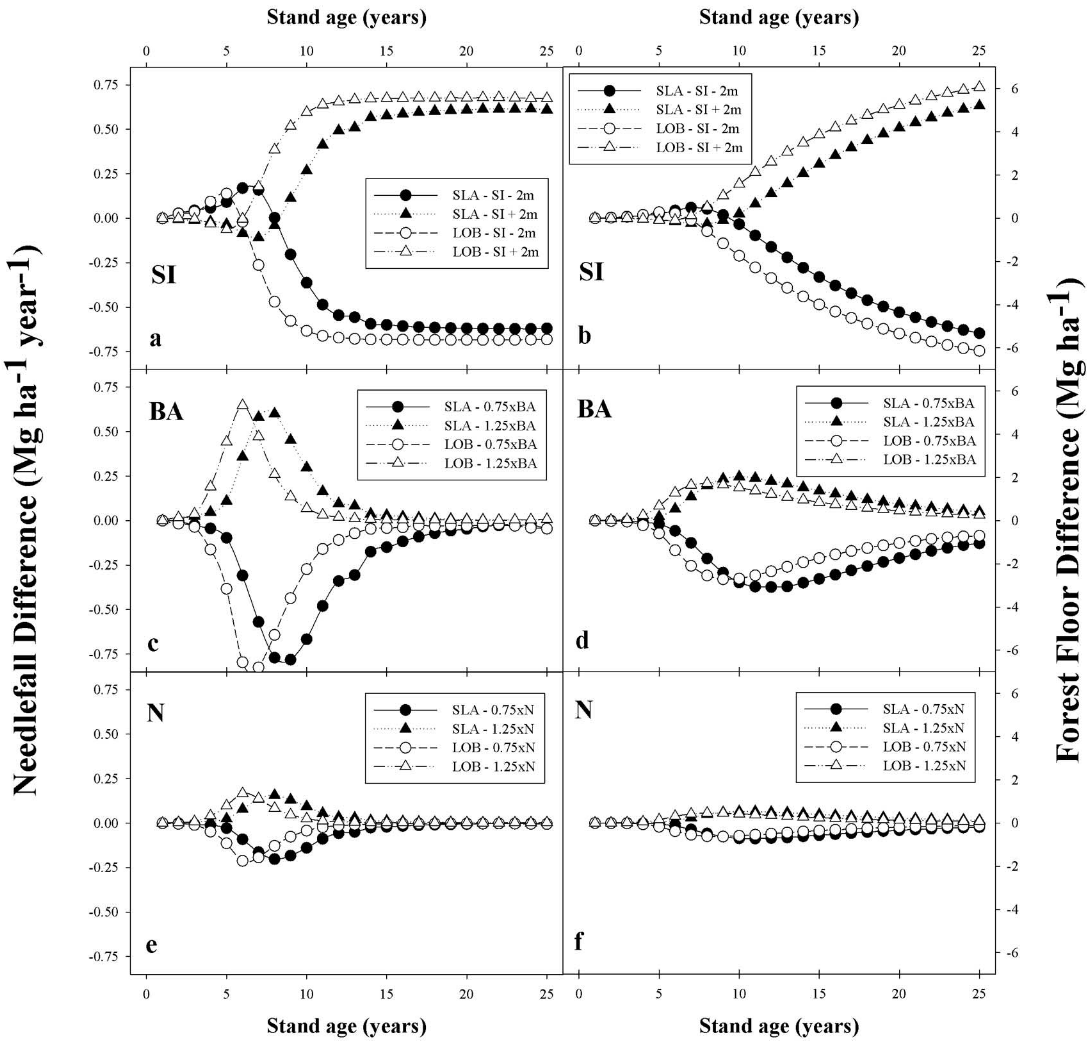


Figure 8. Effect of SI (a and b), BA (c and d), and N (e and f) on estimations of NF (a, c, and e) and FF accumulation (b, d, and f) in loblolly (LOB) and slash (SLA) pine plantations. The values are expressed as the difference from the default inventory data.

ha^{-1} $year^{-1}$ for both species. The transitory bias in NF affected FF estimations, with similar maximum errors for both species of approximately 2.0 and -3.0 Mg ha^{-1}; these errors peaked approximately 3–4 years after the maximum error in NF. At age 25 years, the mean under- and overestimations in FF were -0.85 and 0.35 Mg ha^{-1}, respectively (Figure 8d). Underestimations in BA led to higher absolute errors than overestimations because the square root of BA was included in the numerator for the SDI calculation. Constant errors of 25% in the number of trees estimated per ha resulted in only a small and transitory error in NF estimation (Figure 8e). For both species the maximum under- and overestimation errors in NF were similar, averaging -0.2 and 0.16 Mg ha^{-1} $year^{-1}$, respectively. At age 25 years, the cumulative error in FF estimation was <0.2 Mg ha^{-1} (Figure 8f).

Discussion

The model presented here summarizes the three major determinants of LAI, LF, and FF in southern pine plantations: stand development, site quality, and silviculture. Along with radiation and water availability, nutrition regulates and limits net primary production in these forest ecosystems. Common nutritional limitations observed in the southeastern United States result in suboptimal levels of LAI (Vose and Allen 1988, Jokela 2004, Jokela et al. 2004); however, previous research has demonstrated that competition control and/or fertilization can increase LAI and productivity in southern pines (Vose and Allen 1988, Colbert et al. 1990, Dalla-Tea and Jokela 1991, Jokela and Martin 2000, Albaugh et al. 2004, Samuelson et al. 2004). Because current silvicultural practices in the southeastern United States focus on improving resource availability through fertilization and weed control treatments (Fox et al. 2007), it follows that they have important effects on LAI and NF dynamics as well as on FF accumulation.

Several authors have correlated BA with foliage biomass production and LAI or NF with southern pines (Gresham 1982, Dalla-Tea and Jokela 1991, Vose and Allen 1991, Hennessey et al. 1992, Dougherty et al. 1995, Gonzalez-Benecke et al. 2010), but few studies have included SDI in that relationship in loblolly pine (Dean and Baldwin 1996) or other conifers (Jack and Long 1991, 1996, Innes et al. 2005). In our analysis, we decided to use SDI instead of BA because SDI implicitly includes both BA and stocking. Our rationale was based on the fact that it is possible to reach the same BA with different numbers of living trees and that effect can be captured by SDI. Vose and Allen (1991) reported no correlation between BA and NF in nonfertilized stands (and a weak relationship in nitrogen-fertilized stands), arguing that when stand resource demand exceeds the supply capacity of the site, the relationship may not hold. However, Dean and Baldwin (1996) reported a positive relationship between LAI and SDI for loblolly pine stands, but the lack of information on early stages of stand development (data from trees between 22 and 37 years old) restricted their analyses to stands that had already reached maximum LAI and had SDI values >400. In *Pinus strobus* L. stands, Innes et al. (2005) reported that LAI was not correlated with SDI or SI separately, but when both parameters were incorporated into a multiple linear model, a significant relationship emerged. Jack and Long (1991) reported a nonlinear relationship between SDI and LAI for *Pinus contorta* Douglas ex Louden and *Abies lasiocarpa* (Hook.) Nutt. In all of these studies the relationships reported resembled that shown in Figure 1a, in which stand development and site quality were mixed after data from a set of plots with different structure and productivity were pooled. In that sense, the current study offers an important advantage: long-term, repeated measurements in stands of both species with large differences in site productivity (produced by applied treatments) allowed us to develop the relationships and models that predicted LAI, NF, and FF over time. From simple inventory data such as stand BA, N, and SI, the mean annual projected LAI and NF could be successfully estimated for both loblolly and slash pine stands.

At an early developmental stage, before intraspecific competition begins, all stands followed the same relationship between SDI and LAI, independent of site productivity (Figure 1). However, when SDI was ~200 the curves separated, creating the scattering of data points observed in Figure 1a. Resource availability made each stand reach a different maximum level of LAI. In our study, SI was used as a surrogate of stand-carrying capacity, and a strong positive correlation was observed between SI and the maximum LAI that the stand could attain (parameter β_0 in Figure 2). As was reported by Dalla-Tea and Jokela (1991) and Jokela and Martin (2000), loblolly pine had greater sensitivity than slash pine in LAI response to resource availability. In our study, the correlations between maximum LAI and SI were larger for loblolly than for slash pine. The linear relationship between SI and maximum LAI allowed us to estimate accurately LAI and NF in stands with varying levels of productivity.

In general, after canopy closure there was stabilization in loblolly and slash pine foliage production. Several authors have reported similar patterns, but the time of stabilization differed, depending on site quality and planting density (Switzer and Nelson 1972, Gholz and Fisher 1982, Perry 1983, Gholz et al. 1985, Vose and Allen 1988, Dalla-Tea and Jokela 1991). After this stage, seasonal dynamics in LAI and NF are often affected by crown disturbance factors such as windstorms, ice, or hail, as well as variations in weather, such as water stress due to drought conditions.

Variation in weather can have large effects on LAI and NF in southern pine stands, affecting not only the magnitude but also the phenology of foliage production. Hennessey et al. (1992) reported variation in yearly needle biomass production of 29% due to weather fluctuations in 10- to 13-year-old loblolly pine stands. Water stress due to drought conditions and the downward adjustment in canopy leaf area needed to balance reduced availability of water has been attributed to LAI and NF fluctuations in southern pines (Gholz et al. 1985, Hennessey et al. 1992, Dougherty et al. 1995, Powell et al. 2008, Bracho et al. 2011). The effects of site water balance in needle biomass and NF of loblolly pine were studied by Hennessey et al. (1992) and Dougherty et al. (1995). Even though weather fluctuations were not addressed by our model, there was still very good agreement between observed values from the literature and predicted values from our model (Figures 5 and 6; Table 3), probably because weather variation causes fluctuations around the "inherent" stand and site LAI predicted by our model. Further research is planned to incorporate weather variability into the model, which would allow better prediction of LAI and NF for specific years and weather conditions and might enable projections for climate change scenarios.

Conclusions

Our analyses showed that LAI, NF, and FF dynamics in loblolly and slash pine plantations could be summarized by functions incorporating the effects of stand development (age), stand structure (planting density, BA, and SDI), and site quality (SI). Comparison of simulations to diverse data sets from across the natural ranges of both species indicated that these relationships captured the primary drivers of variation and, thus, provided a robust synthesis and prediction system for these important variables. Because the functions were based on growth-and-yield and allometric relationships, they were well suited to describing mean responses, but further development may be necessary to incorporate additional functions to capture year-to-year or stand-to-stand variation caused by climatic fluctuations.

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Appendix

Table A1. Reported values of NF and LF for loblolly and slash pine stands.

Species	Age (yr)	NF	LF	Citation
		. . .(Mg C ha^{-1} year^{-1}). . .		
Loblolly	4	2.71		Mc Crady and Jokela 1998
	5	0.20		Dalla-Tea and Jokela 1991
	5	2.57		McCrady and Jokela 1998
	6	0.51		Dalla-Tea and Jokela 1991
	9	1.30		Nemeth 1973
	10		2.40	Zerpa et al. 2010
	10	2.11	2.27	Metz 1952
	10	2.88		Hennessey et al. 1992
	10	1.75		Nemeth 1973
	11	1.59		Vose and Allen 1991
	11	2.05		Hennessey et al. 1992
	11	1.85		Nemeth 1973
	12	1.96	2.46	Metz 1954
	12		2.55	Finzi et al. 2001
	12	2.17		Vose and Allen 1991
	12	2.59		Hennessey et al. 1992
	12		1.10	Maier et al. 2004
	12		1.40	Maier et al. 2004
	12		2.40	Maier et al. 2004
	12		2.70	Maier et al. 2004
	12	2.34		Kinerson et al. 1977
	13		2.99	Finzi et al. 2001
	13	3.07	3.87	Wells and Jorgensen 1975
	13	2.46		Hennessey et al. 1992
	13	2.47		Kinerson et al. 1977
	14	1.16		Vose and Allen 1991
	15		2.20	Van Lear and Goebel 1976
	15	1.60		Vose and Allen 1991
	16	3.10	3.86	Jorgensen et al. 1980
	16	0.93		Vose and Allen 1991
	17	1.32		Vose and Allen 1991
	20	2.87	3.59	Lockaby and Taylor-Boyd 1986
	21		2.10	Van Lear and Goebel 1976
	32		2.05	Van Lear and Goebel 1976
	34		2.04	Urrego 1993
	34	2.43		Urrego 1993
	37	2.19	3.05	Jorgensen et al. 1980
Slash	3		0.21	Bracho et al. 2011
	4		0.47	Bracho et al. 2011
	5		0.93	Bracho et al. 2011
	6	0.52		Gholz et al. 1985
	6		1.64	Bracho et al. 2011
	6	0.40		Dalla-Tea and Jokela 1991
	6	2.00		Dalla-Tea and Jokela 1991
	7	0.73		Gholz et al. 1985
	7		1.79	Bracho et al. 2011
	7	0.75		Dalla-Tea and Jokela 1991
	7	2.35		Dalla-Tea and Jokela 1991
	8		1.96	Bracho et al. 2011
	9	1.69		Gholz et al. 1985
	9		1.37	Bracho et al. 2011
	10	1.51		Gholz et al. 1985
	11		1.83	Clark et al. 2004
	15	2.49		Gholz et al. 1985
	16	1.96		Gholz et al. 1985
	17	2.10		Shan et al. 2001
	17	2.35		Shan et al. 2001
	22	1.82	2.18	Gholz et al. 1991
	23	2.02	2.44	Gholz et al. 1991
	24	1.62	2.11	Gholz et al. 1991
	25		2.80	Clark et al. 2004
	27	1.69		Gholz et al. 1985
	28	1.79		Gholz et al. 1985
	30	0.50		Liu et al. 1997
	35	2.03		Gholz et al. 1985
	36	1.68		Gholz et al. 1985

Table A2. Reported values of FF for loblolly and slash pine stands.

Species	Age (yr)	FF (Mg C ha^{-1})	Citation
Loblolly	7	5.59	Rojas 2005
	8	6.48	Rojas 2005
	9	5.80	Nemeth 1973
	10	5.80	Nemeth 1973
	10	6.81	Rojas 2005
	10	4.87	Zerpa et al. 2010
	10	19.05	Zerpa et al. 2010
	11	5.35	Leggett and Kelting 2006
	11	4.40	Leggett and Kelting 2006
	11	5.02	Maier and Kress 2000
	11	4.95	Maier and Kress 2000
	11	3.35	Maier and Kress 2000
	11	6.50	Maier and Kress 2000
	11	5.80	Nemeth 1973
	12	7.24	Metz 1954
	13	7.85	Larsen et al. 1976
	16	14.52	Jorgensen et al. 1980
	17	16.36	Johnson and Lindberg 1992
	18	12.65	Rubilar 2003
	18	11.70	Shepard 1985
	18	9.29	Van Lear 1980
	18	17.70	Vogel et al. 2010
	19	14.15	Shepard 1985
	20	6.06	Lockaby and Taylor-Boyd 1986
	20	10.30	Shepard 1985
	20	12.60	Wells and Davey 1966
	21	8.10	Shepard 1985
	22	18.55	Rubilar 2003
	22	11.70	Shepard 1985
	23	7.07	Johnson and Lindberg 1992
	24	14.00	Shepard 1985
	25	6.50	Shepard 1985
	25	9.10	Shepard 1985
	25	24.00	Vogel et al. 2010
	31	10.41	Van Lear and Goebel 1976
	34	34.85	Urrego 1993
	37	16.43	Jorgensen et al. 1980
	55	10.05	Schoch and Binkley 1986
	56	13.70	Bell and Binkley 1989
Slash	1	46.66	Clark et al. 2004
	2	0.95	Baumgartner 1985
	5	2.78	Baumgartner 1985
	8	4.61	Baumgartner 1985
	9	4.06	Gholz et al. 1986
	11	10.80	Clark et al. 2004
	14	6.85	Baumgartner 1985
	16	10.56	Jokela et al. 1991
	16	7.90	Maggs 1988
	17	10.60	Shan et al. 2001
	17	15.00	Shan et al. 2001
	18	11.3	Baumgartner 1985
	22	14.25	Pehl and Shelnutt 1986
	25	25.96	Clark et al. 2004
	25	13.30	Harding and Jokela 1994
	25	20.75	Harding and Jokela 1994
	25	42.20	Harding and Jokela 1994
	25	38.00	Vogel et al. 2011
	25	33.00	Vogel et al. 2011
	26	16.90	Baumgartner 1985
	27	15.25	Gholz et al. 1986
	34	21.45	Baumgartner 1985
	40	7.73	Lister et al. 2000