Forests **2012**, *3*, 1104-1132; doi:10.3390/f3041104

OPEN ACCESS

forests

ISSN 1999-4907

www.mdpi.com/journal/forests

Article

Modeling Survival, Yield, Volume Partitioning and Their Response to Thinning for Longleaf Pine Plantations

Carlos A. Gonzalez-Benecke [1,*], Salvador A. Gezan [1], Daniel J. Leduc [2], Timothy A. Martin [1], Wendell P. Cropper, Jr. [1] and Lisa J. Samuelson [3]

[1] School of Forest Resources and Conservation, University of Florida, P.O. Box 110410, Gainesville, FL 32611-0410, USA; E-Mails: sgezan@ufl.edu (S.A.G.); tamartin@ufl.edu (T.A.M.); wcropper@ufl.edu (W.P.C.)

[2] USDA Forest Service, Southern Research Station, 2500 Shreveport Hwy, Alexandria Forestry Center, Pineville, LA 71360, USA; E-Mail: dleduc@fs.fed.us

[3] School of Forestry and Wildlife Sciences, 3301 SFWS Building, Auburn University, Auburn, AL 36849, USA; E-Mail: samuelj@auburn.edu

* Author to whom correspondence should be addressed; E-Mail: cgonzabe@ufl.edu; Tel.: +1-352-846-0851; Fax: +1-352-846-1277.

Received: 18 September 2012; in revised form: 25 November 2012 / Accepted: 11 December 2012 / Published: 18 December 2012

Abstract: Longleaf pine (*Pinus palustris* Mill.) is an important tree species of the southeast U.S. Currently there is no comprehensive stand-level growth and yield model for the species. The model system described here estimates site index (SI) if dominant height (H_{dom}) and stand age are known (inversely, the model can project H_{dom} at any given age if SI is known). The survival (N) equation was dependent on stand age and H_{dom}, predicting greater mortality on stands with larger H_{dom}. The function that predicts stand basal area (BA) for unthinned stands was dependent on N and H_{dom}. For thinned stands BA was predicted with a competition index that was dependent on stand age. The function that best predicted stand stem volume (outside or inside bark) was dependent on BA and H_{dom}. All functions performed well for a wide range of stand ages and productivity, with coefficients of determination ranging between 0.946 (BA) and 0.998 (N). We also developed equations to estimate merchantable volume yield consisting of different combinations of threshold diameter at breast height and top diameter for longleaf pine stands. The equations presented in this study performed similarly or slightly better than other reported models to estimate future N, H_{dom} and BA. The system presented here provides important new tools for supporting future longleaf pine management and research.

Keywords: longleaf pine; growth and yield modeling; merchantable volume yield; stand dynamics

1. Introduction

Longleaf pine (*Pinus palustris* Mill.) once dominated forests in the southeast U.S., occupying about 36 million ha prior to European settlement [1]. By 1935, the area was reduced to about 8 million ha. Currently, there are only about 1.2 million ha of longleaf pine stands left [2], extending along the Gulf and Atlantic Coastal Plains from Virginia, south into central Florida, and north into the Piedmont and mountains of northern Alabama and Georgia [2]. In recent years various organizations have begun promoting longleaf plantation establishment, directing most of their effort to private landowners with objectives that include production, but also aesthetics and wildlife habitat enhancement.

In order to improve stand management planning, researchers, managers and landowners need reliable information about stand dynamics and development. While a number of long-term experimental and permanent plot datasets exist for the species, these data, for the most part, have not been summarized in a comprehensive manner. As forest management decisions are based on information about current and future resource conditions, forest growth and yield modeling plays an important role by quantifying and summarizing relationships observed in field studies, and by providing stand projections under alternative management scenarios. Whole-stand-level growth and yield models predict future yields as a function of previous stand-level attributes such as age, stand density and site quality [3].

A number of models have been produced that predict elements of longleaf pine plantation stand dynamics [4–8]. To our knowledge, however, no comprehensive stand-level growth and yield system has been produced for longleaf plantations that includes growth for thinned stands and merchantable volume estimations, and that can be applied to planted stands across a wide range of ages.

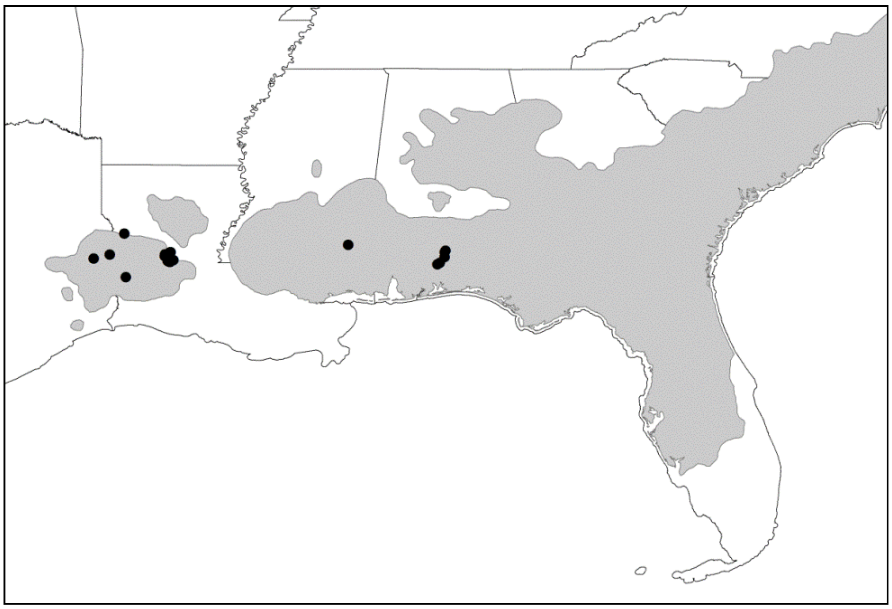
The objective of this study was to develop a stand-level growth and yield model system for thinned and unthinned longleaf pine plantations, using a long-term (>40 years) dataset measured and maintained by the U.S. Forest Service. A system of equations was developed to summarize the dynamics observed in the extensive, long-term dataset, and to provide a tool to predict and project stand growth and yield, including merchantable volume breakdown functions.

2. Materials and Methods

2.1. Data Description

The dataset used to estimate growth and yield parameters comes from 267 permanent plots measured and maintained by the U.S. Forest Service's Laboratory at Pineville, LA [9]. The data were collected from regularly remeasured plots in a combination of seven studies exploring the effects of spacing and thinning on longleaf plantations distributed through the Western Gulf Coastal Plain from Santa Rosa County in Florida to Jasper County in Texas (Figure 1) and representing its current range in the Western Gulf Coastal Plain [9,10]. Plantations were established on both old field and cutover sites. Soil texture for plots were primarily silt loams, very fine sandy loams, or fine sandy loams, characteristic of the U.S. Upper Coastal Plain. Most plots were burned regularly by prescribed burns or wild fires. Each plot was measured for ~40 years at ~five-year intervals, averaging eight measurements per plot. Plots were rectangular and ranged in size from 0.04 to 0.1 ha^{-1} [5].

Figure 1. Location of 267 permanent plots measured within the Western Gulf Coastal Plain longleaf pine natural distribution range.



For each tree, stem diameter outside bark at 1.37 m height (dbh, cm) was measured to the nearest 0.25 cm and total tree height (H, m) was measured to the nearest 0.3 m on a subsample of 4 to 15 trees per plot. Using the model proposed by Quicke and Meldahl [11] that relates H to the inverse of dbh, individual plot by measurement time regressions were determined ($P < 0.0001$) to estimate H in all trees without H measurement (MAE% = 4.3%; RMSE% = 5.6%; Bias% = −0.4%; $R^2 = 0.97$). Mean dominant height (H_{dom}, m) was determined for each plot at every measurement time as the mean of the top 25th percentile tree height. Site index (SI, m) was defined as H_{dom} at a reference age of 50 years after planting. As several plots were not measured at exactly age 50 yrs, SI was assessed using H_{dom} at index age plus/minus one year if necessary (*i.e.*, 49 and 51 years).

From the complete dataset, 30 plots were randomly selected and removed to use for model evaluation and the rest (*i.e.*, 237 plots) for model fitting. A total of 81 plots were thinned to constant basal area levels at five-year intervals; however, only pre-thinning measurements were considered on those plots. Summary statistics of individual trees and stand characteristics of both sub-datasets are shown in Table 1.

Table 1. Summary statistics and stand characteristics for 267 permanent longleaf pine plots measured (thinned and unthinned).

Variable	**Model fitting dataset (237 plots)**					**Model evaluation dataset (30 plots)**				
	Mean	**SD**	**Minimum**	**Maximum**	***n***	**Mean**	**SD**	**Minimum**	**Maximum**	***n***
Age	35.9	15.7	7.0	73.0	725	36.8	16.3	7.0	73.0	140
dbh	21.6	8.3	6.8	44.1	725	21.6	7.8	6.8	42.4	140
H	18.6	5.3	5.3	30.1	725	19.3	5.8	5.4	30.5	140
N	865	504	99	2849	725	982	548	198	2422	140
BA	27.0	11.3	6.6	62.9	725	31.5	13.1	6.8	65.9	140
Dq	22.6	8.4	7.0	44.3	725	22.6	8.0	7.1	42.8	140
SDI	566	222	129	1222	725	655	250	144	1287	140
H_{dom}	20.6	5.6	6.7	32.0	725	21.5	6.1	6.4	32.8	140
SI	25.8	1.9	19.6	30.8	173 *	26.4	1.6	22.1	29.3	21 *
VOL_{OB}	274.6	141.2	46.7	688.6	725	320.7	161.4	55.0	701.3	140

Age: stand age (year); dbh: arithmetic mean diameter outside bark at breast height (cm); H: total height (m); N: trees per hectare (trees ha^{-1}); BA: basal area ($m^2 \cdot ha^{-1}$); Dq: quadratic mean diameter (cm); SDI: Reineke's stand density index (trees ha^{-1}); H_{dom}: height of dominant and codominant trees (m); SI: site index (m); VOL_{OB}: total stem volume outside-bark ($m^3 \cdot ha^{-1}$); SD: standard deviation; *n*: number of plot-level observations; *: SI reported only for plots measured at age 50 yrs.

For all trees with H measurement (28,083 observations) a form factor F = H/dbh (m cm^{-1}) was calculated. In order to eliminate broken and malformed individuals, trees with F less than 0.54 m cm^{-1} and trees with F greater than 13.5 $m \cdot cm^{-1}$ were discarded for H_{dom} determination (5.4% of H observations). Plots with less than four trees with H measured were also not considered for H_{dom} fitting (7.9% of total plots).

The distribution of total observations (used for model fitting and model evaluation) by age, SI and surviving trees (N, ha^{-1}) is shown in Table 2.

Table 2. Distribution of observations by age, site index and surviving density for 267 permanent longleaf pine plots measured (thinned and unthinned).

Surviving Density Class (ha^{-1})	**Stand Age Class (yrs.)**				
	7–20	**20–40**	**40–60**	**60–73**	**Total**
99–500	8	66	105	61	240
500–1000	51	112	91	17	271
1000–1500	69	153	27	-	249
1500–2000	36	49	2	-	87
2000–2849	10	8	-	-	18
Site Index Class (m) *					
19–22	4	45	12	4	35
22–25	46	78	46	21	191
25–28	49	217	132	49	447
28–31	75	78	35	4	192
Total	**174**	**388**	**225**	**78**	**865**

*: SI reported for plots not measured at age 50 yrs. was estimated with model presented in this study.

Only 2% of plots had N > 2000 ha^{-1}, while 28% of data points had N < 500 ha^{-1}. About 29% of data had N between 1000 and 1500 ha^{-1}. Most stands (52%) had SI between 25 and 28 m, and only 4% of data had SI < 22 m. About 22% of stands had SI > 28 m. In term of age distribution, about 20% of data had age < 20 yrs. and 9% had age > 60 yrs.

2.2. Model Description

2.2.1. Survival and Yield Models for Unthinned Stands

Data from all unthinned plots and from thinned plots prior to thinning were used to estimate survival, H_{dom}, stand basal area and stand volume (inside and outside bark) parameters.

Following the guide curve method to produce an anamorphic model [12], a dominant height function was fitted based on the Chapman-Richards function using the following expression:

$$H_{dom} = a_0 \cdot SI \cdot (1 - e^{(a_1 \cdot Age)})^{a_2} + \varepsilon_1 \quad (1)$$

where Age is the stand age (yrs.), a_0, a_1 and a_2 are curve fit parameters and ε_1 is the error term, with $\varepsilon_1 \sim N(0, \sigma_1^2)$. For the selected site index age of 50 yrs., the model can be re-written as:

$$H_{dom} = SI \cdot \left(\frac{1 - e^{(a_1 \cdot Age)}}{1 - e^{(a_1 \cdot 50)}}\right)^{a_2} + \varepsilon_1 \quad (2)$$

This equation can be inverted to determine SI if stand age and H_{dom} are known. This anamorphic model has the assumption that the shape of the height-age curve is independent of SI, and differences between any two curves are proportional to the ratio of their SI's [13].

A negative-exponential survival model that includes H_{dom} was used to estimate survival using a modified version of the model proposed by Dieguez-Aranda *et al.* [14,15] and Zhao *et al.* [16]:

$$N_j = N_i \cdot e^{\left[\left(b_1 + b_2 \cdot H_{dom_i}{}^{b_3}\right) \cdot \left(Age_j^{b_4} - Age_i^{b_4}\right)\right]} + \varepsilon_2 \quad (3)$$

where N_j is the number of trees ha^{-1} at age *j* (yr.), N_i is the number of trees ha^{-1} at age *i* (yr.) ($i < j$), H_{dom_i} is the dominant height (m) at age *i* (yr.), b_1 to b_4 are curve fit parameters and ε_2 is the error term, with $\varepsilon_2 \sim N(0, \sigma_2^2)$. Several models proposed by Dieguez-Aranda *et al.* [14], Zhao *et al.* [16] and Burkhart and Tome [17] were also tested, but the model that we selected showed the best fit. After model testing, similar to Zhao *et al.* [16], the parameters b_1 and b_3 were set equals to 0 and 1, respectively, due to no improvement in predictive ability and convergence difficulties. The final model to estimate H_{dom} was:

$$N_j = N_i \cdot e^{\left[\left(b_1 \cdot H_{dom_i}\right) \cdot \left(Age_j^{b_2} - Age_i^{b_2}\right)\right]} + \varepsilon_2 \quad (4)$$

The following generic equation, proposed by Borders [18], was initially used to predict basal area:

$$\ln(BA) = c_1 + c_2 \cdot \ln(N) + c_3 \cdot \ln(H_{dom}) + c_4 \cdot \ln(SI) + c_5 \cdot \left(\frac{1}{Age}\right) + c_6 \cdot \ln(N/Age) + c_7 \cdot \ln(H_{dom}/Age) + \varepsilon_3 \quad (5)$$

where BA is the stand basal area ($m^2 \cdot ha^{-1}$), N is the survival (trees ha^{-1}), c_1 to c_7 are curve fit parameters and ε_3 is the error term, with $\varepsilon_3 \sim N(0, \sigma_3^2)$. After step-wise procedure and variance inflation factor (VIF) analysis, parameters non-significant and/or with high multicollinearity were discarded, resulting in the following final model to estimate BA:

$$\ln(\mathrm{BA}) = c_1 + c_2 \cdot \ln(\mathrm{N}) + c_3 \cdot \ln(\mathrm{H_{dom}})\, \varepsilon_3 \quad (6)$$

The equations reported by Gonzalez-Benecke *et al.* [19], which depend on the individual dbh and stand parameters N, H_{dom} and SI, were used to estimate individual tree volume outside and inside bark for each living tree in the dataset. After aggregating all individual tree volumes within each plot, stand volume outside and inside bark was determined for each plot. This information at the plot level was used to fit a model for stand volume prediction, which was initially based in the following generic model proposed by Borders [18] and Pienaar [20]:

$$\begin{aligned}\ln(\mathrm{VOL}) = d_1 + d_2 \cdot \ln(\mathrm{N}) + d_3 \cdot \ln(\mathrm{BA}) + d_4 \cdot \ln(\mathrm{SI}) + d_5 \cdot \ln(\mathrm{H_{dom}}) + d_6 \cdot (1/\mathrm{Age}) + \\ d_7 \cdot \ln(\mathrm{N/Age}) + d_8 \cdot \ln(\mathrm{H_{dom}/Age}) + d_9 \cdot \ln(\mathrm{BA/Age}) + \varepsilon_4\end{aligned} \quad (7)$$

where VOL is the stand stem volume outside or inside bark ($m^3 \cdot ha^{-1}$), d_1 to d_9 are curve fit parameters and ε_4 is the error term, with $\varepsilon_4 \sim N(0, \sigma_4^2)$. Similar to BA, after the step-wise procedure and VIF analysis, parameters non-significant and/or with high multicollinearity were discarded, resulting in the following final model to estimate VOL:

$$\ln(\mathrm{VOL}) = d_1 + d_2 \cdot \ln(\mathrm{N}) + d_3 \cdot \ln(\mathrm{BA}) + d_4 \cdot \ln(\mathrm{BA/Age}) + d_5 \cdot \ln(\mathrm{SI}) + \varepsilon_4 \quad (8)$$

2.2.2. Basal Area Growth Model for Thinned Stands

As the effects of thinning on survival and H_{dom} are small for southern pines (Westfall and Burkhart, 2001; Sharma *et al.* 2006) [21,22], we only modeled the response in BA growth after thinning. Several models, presented in Burkhart and Tome [17], were also tested in order to simulate BA growth after thinning, but the methodology reported by Pienaar [20,23] was selected. Following Pienaar [23], BA projection for thinned stands (BA_t, $m^2 \cdot ha^{-1}$) was determined by using a competition index (CI) and the basal area of an unthinned counterpart stand (BA_u, $m^2 \cdot ha^{-1}$), assuming that BA_t can be expressed as a proportion of the basal area of an unthinned stand of the same age, H_{dom} and number of surviving trees (*i.e.*, an unthinned counterpart) that changes over time. The CI is the rate of competition decline, a measure of the relative degree of competition affecting tree size in the thinned compared to the unthinned stands, and it was determined as follows:

$$\mathrm{CI} = \frac{(\mathrm{BA_u} - \mathrm{BA_t})}{\mathrm{BA_u}} \quad (9)$$

From Equation 7, when BA_t equals BA_u with the same number of trees, the CI is zero. Similarly, when BA_t is less than BA_u (that is the general case in operational thinnings), the CI is larger than zero, but approaching zero as stand ages, as BA_t will converge to BA_u [20]. As the permanent plots of thinned stands do not have an unthinned counterpart, projections of BA_u over time were estimated using Equations 2, 4 and 5. The BA growth response after thinning was determined indirectly by projecting the time trend of CI, assuming an asymptotic trajectory towards a value of zero. Thus, reflecting that the thinned stand, which has the same age, H_{dom} and number of trees as the unthinned counterpart, will approach, over time, the unthinned stand in terms of total BA [23]. The projected CI after thinning was estimated using a modified version of the model proposed by Pienaar [23], including the effect of stand age on the rate of competition decline:

$$\mathrm{CI_j} = \mathrm{CI_i} \cdot e^{\left[\left(\frac{f_1}{\mathrm{Age_j}}\right)\cdot(\mathrm{Age_j}-\mathrm{Age_i})\right]} + \varepsilon_5 \tag{10}$$

where CI_i and CI_j are the competition index at age i and j (yr.) ($i < j$), respectively, and f_1 is the curve fit parameters and ε_5 is the error term, with $\varepsilon_5 \sim \mathrm{N}(0, \sigma_5^2)$. The exponential of the coefficient term, $\frac{f_1}{\mathrm{Age}_j}$, corresponds to the annual decline rate of the CI as the stand ages after thinning.

After combining Equations 5 and 6, BA of a thinned stand is estimated using the projected CI as:

$$\mathrm{BA_{t_j}} = \mathrm{BA_{u_j}} \cdot (1 - \mathrm{CI_j}) \tag{11}$$

where $\mathrm{BA}_{\mathrm{t}_j}$ and $\mathrm{BA}_{\mathrm{u}_j}$ are the projected BA ($m^2 \cdot ha^{-1}$) in the thinned and unthinned counterpart stands at age j (yr.), respectively.

2.2.3. Merchantable Volume

For each tree in the fitting dataset, merchantable stem volume (both outside and inside bark), from the stump to any top diameter, was estimated using the equations reported by Gonzalez-Benecke *et al.* [19] for a range of combinations of threshold dbh values (d, from 5.08 to 40.64 cm) and top diameter limit values (t, from 5.08 to 45.72 cm) that incremented at steps of 5.08 cm. Finally, for each plot, merchantable stem volume per hectare for each combination of d and t was calculated based on all living trees within each plot.

The merchantable volume yield breakdown at the stand level function was determined following Amateis *et al.* [24], where total volume yield outside or inside bark (*i.e.*, $\mathrm{VOL_{OB}}$ and $\mathrm{VOL_{IB}}$, $m^3 \cdot ha^{-1}$) was proportionally assigned to product classes defined by two variables: top stem diameter outside bark merchantability limit (t, cm) and a dbh threshold limit (d, cm):

$$\mathrm{VOL_m} = \mathrm{VOL} \cdot e^{\left[m_1 \cdot \left(\frac{t}{\mathrm{Dq}}\right)^{m_2} + m_3 \cdot (\mathrm{N}^{m_4}) \cdot \left(\frac{d}{\mathrm{Dq}}\right)^{m_5}\right]} \tag{12}$$

where $\mathrm{VOL_m}$ is merchantable volume per hectare ($m^3 \cdot ha^{-1}$) for trees with dbh larger than d cm, to a top diameter of t cm outside bark, VOL is the total volume per hectare ($m^3 \cdot ha^{-1}$), Dq is the quadratic mean diameter (cm), N the survival (trees ha^{-1}), and m_1 to m_5 are curve fit parameters.

2.3. Model Evaluation

The predictive ability of the fitted models for N (Equation 4), $\mathrm{H_{dom}}$ (Equation 2), BA of unthinned stands (Equation 6), VOL of unthinned stands (Equation 8) and BA of thinned stands (Equation 11) was assessed with the 30 plot evaluation dataset. In the case of $\mathrm{VOL_m}$ (Equation 12), two combinations of d and t were selected to evaluate this model. The selected values of d and t correspond to the threshold values used to estimate breakdown volume yield for other southern pine species [25–27], corresponding to chip-and-saw (d = 21.6 cm; t = 10.2 cm) and sawtimber (d = 29.2 cm; t = 20.3 cm) products.

Four measures of accuracy were used to evaluate the goodness-of-fit between observed and predicted (simulated) values for each variable originated from the dataset obtained in the model evaluation: (i) mean absolute error (MAE); (ii) root mean square error (RMSE); (iii) mean bias error (Bias); and (iv) coefficient of determination (R^2) [28–31]. For BA and VOL, the statistics MAE, RMSE and Bias were back-transformed from logarithmic values.

The system of equations was also compared against other models reported in the literature for longleaf pine plantations using the same model evaluation dataset indicated above. The models compared were: (i) survival equations reported by Lohrey and Bailey [5], Brooks and Jack [7] and Lauer and Kush [32], (ii) dominant height equations reported by Farrar [4] and Brooks and Jack [7], and (iii) VOL_{OB} equations reported by Lohrey and Bailey [5] and Brooks and Jack [7]. The breakdown volume outside bark yield function was also compared against the functions reported for *Pinus taeda* [25] and *Pinus elliottii* [26] across different Dq and stand densities, and for three product classes (sawtimber: d = 29.2 cm and t = 20.3 cm; chip-and-saw: d = 21.6 cm and t = 11.2 cm; pulpwood: d = 11.4 cm and t = 5.1 cm), assuming stands with VOL_{OB} of 100 $m^3 \cdot ha^{-1}$. This value of VOL_{OB} was selected to facilitate percent comparisons. The results of the breakdown volume yield function are independent of the value assumed.

An overall evaluation of the model was carried out for unthinned plots of the validation dataset. On each plot, for known initial stand age, N and SI, stand BA and VOL_{OB} were estimated on the same ages where they were originally measured by using the final equations fitted to estimate N, H_{dom}, BA and VOL_{OB}. The same four measures of accuracy described previously were used to assess the agreement between observed and predicted values.

All of the summary, model fitting and model evaluation statistics were obtained using SAS 9.3 (SAS Inc., Cary, NC, USA) [33]. When multiple linear regressions were carried out, the variance inflation factor (VIF) was monitored to detect multicollinearity between predicting variables, discarding all variables included in the model with VIF larger than 5, as suggested by Neter *et al.* [34]. In the case of BA and VOL fitting, where multiple linear regressions were carried out, step-wise procedure was used with a threshold significance value of 0.15 as variable selection criteria to enter and to stay [34]. For these responses, a logarithm transformation was preferred as it allows controlling for heterogeneity of variances, approximate to normality and uses the linear model framework to select among the large set of, potentially collinear, predicting variables.

2.4. Model Application Example

The system of equations developed was used to predict stand growth of unthinned and thinned (3 thinnings, removing 33% of living trees at ages 30, 40 and 50 yrs.) longleaf pine stands growing at sites with two different SI's: 20 and 30 m. The initial planting density used was 1400 trees ha^{-1}, the survival after the first year was assumed to be 95%, and the simulation length was 70 yrs. Here it was assumed that the percentage of removed trees was the same as the percentage removal of BA during thinning.

3. Results

3.1. Model Fitting

The parameter estimates for the growth and yield predictive and projective equations (Equations 2, 4, 6, 8, 10 and 12) for longleaf pine plantations growing in Western Gulf Coastal Plain U.S. are reported in Table 3. All parameter estimates were significant at $P < 0.05$. Non-linear versions of the models presented in Equation 6 (BA) and 8 (VOL) were also evaluated, but these resulted in no improvement in model performance (data not shown), therefore, natural logarithm-transformed response variables were used. Parameter estimates for the intercept in Equations 6 (c_1) and 8 (d_1) include the correction proposed by Snowdon [35]. The correction factor proposed by Baskerville [36] was also evaluated, but it presented lower bias reduction (data not shown).

Parameter estimates for the model that projects dominant height (Equation 2) are shown in Table 3. For SI of 20 m, the model projects dominant height of 5.4 and 22.6 m at age 10 and 70 yrs., respectively. If SI increased to 29 m, the model projects dominant height of 7.9 and 32.8 m at age 10 and 70 yrs., respectively. For all 194 plots where SI was measured, the mean observed and predicted SI was 25.84 and 25.88 m, respectively.

The survival model (Equation 4) was dependent on stand age and H_{dom}. The performance of the N model for the range of SI present on the dataset used for model fitting (*i.e.*, between 20 and 29 m, see Tables 1 and 2) and using a planting density of 1500 trees ha^{-1} showed little mortality and only small differences in survival at age 10 yrs. (between 1450 and 1429 trees ha^{-1}, for SI 20 and 29 m, respectively). At age 70 yrs., however, the model estimated large differences in survival across SI's (between 493 and 300 trees ha^{-1}, for SI = 20 and 29 m, respectively).

After applying the step-wise procedure and checking variance inflation factors (VIF), the final selected model that predicts BA (Equation 6) was only dependent on N and H_{dom} (Table 3). Although the variables 1/Age, ln(N)/Age and ln(H_{dom})/Age were significant after the step-wise variable selection procedure ($P < 0.001$, data not shown), their VIF's were high with values of 296, 173 and 35, respectively (data not shown). Therefore, these variables were discarded from the model and the goodness-of-fit of the final model was lower than the full model, having a CV of 3.6% and a R^2 of 0.944. Partial R^2 of H_{dom} and N were 0.579 and 0.366, respectively (data not shown).

The final model that predicts stand volume (Equation 8), after the step-wise variable selection procedure and VIF checking, was dependent on N, BA, ln(BA)/Age and SI (Table 2). The variable H_{dom} was discarded from the final model, even though they were selected after step-wise variable selection procedure ($P < 0.001$, data not shown), due to its high multicollinearity (VIF = 42.3, data not shown). The final models that predict stand V_{OB} and V_{IB} had a CV of about 1% and R^2 greater than 0.99. Stand BA explained most of the variability in V_{OB} and V_{IB}, with partial R^2 of about 0.912 and 0.867, respectively. Stand density presented partial R^2 of about 0.079 and 0.121, for V_{OB} and V_{IB}, respectively. Even though SI and ln(BA)/Age were significant, both explained less than 0.1% of changes in stand volume (data not shown).

Table 3. Parameter estimates and fit statistics of Western Gulf Coastal Plain U.S. longleaf pine plantation growth and yield equations.

Model	*n*	Parameter	Parameter estimate	Approx. SE	Approx. Pr > F	VIF	R^2	RMSE	CV %
$H_{dom} = SI \cdot \left(\frac{1-e^{(a_1 \cdot Age)}}{1-e^{(a_1 \cdot 50)}}\right)^{a_2}$	569	a_1	−0.0369815	0.0015463	<0.0001	n.a.	0.998	0.87	4.1
		a_2	1.2928702	0.0454849	<0.0001	n.a.			
$N_j = N_i \cdot e^{\left[\left(b_1 \cdot H_{dom\ i}\right) \cdot \left(Age_j^{b_2} - Age_i^{b_2}\right)\right]}$	622	b_1	−0.0015002	0.0006992	0.0324	n.a.	0.997	52.89	6.9
		b_2	0.8635401	0.1000509	<0.0001	n.a.			
$\ln(BA) = c_1 + c_2 \cdot \ln(N) + c_3 \cdot \ln(H_{dom})$	725	c_1 *	−4.6484039	0.0736689	<0.0001	0	0.944	1.12	3.6
		c_2	0.4452486	0.0064583	<0.0001	1.16			
		c_3	1.6526307	0.0155728	<0.0001	1.16			
$\ln(VOL_{OB}) = d_1 + d_2 \cdot \ln(N) + d_3 \cdot \ln(BA) + d_4 \cdot [\ln(BA)]/Age + d_5 \cdot \ln(SI)$	569	d_1 *	3.1110579	0.0809271	<0.0001	0	0.997	0.04	0.72
		d_2	−0.1406022	0.0045948	<0.0001	4.41			
		d_3	1.1826310	0.0040024	<0.0001	2.48			
		d_4	−2.4435259	0.0989071	<0.0001	4.02			
		d_5	−0.0782880	0.0265719	0.0033	1.49			
$\ln(VOL_{IB}) = d_1 + d_2 \cdot \ln(N) + d_3 \cdot \ln(BA) + d_4 \cdot [\ln(BA)]/Age + d_5 \cdot \ln(SI)$	569	d_1 *	3.0888853	0.1026120	<0.0001	0	0.996	0.05	1.0
		d_2	−0.1943861	0.0058271	<0.0001	4.41			
		d_3	1.2580580	0.0050738	<0.0001	2.48			
		d_4	−3.1281571	0.1254092	<0.0001	4.02			
		d_5	−0.098259	0.0336921	0.0037	1.49			
$CI_j = CI_i \cdot e^{\left[\left(\frac{f_1}{Age_j}\right) \cdot \left(Age_j - Age_i\right)\right]}$	292	f_1	−1.5476196	0.1881092	<0.0001	n.a.	0.874	0.05	96.5

Table 3. *Cont.*

Model	*n*	Parameter	Parameter estimate	Approx. SE	Approx. Pr > F	VIF	R^2	RMSE	CV %
$\mathrm{VOL_{m-OB}} = \mathrm{VOL_{OB}} \cdot e^{\left[g_1 \cdot \left(\frac{t}{\mathrm{Dq}}\right)^{g_2} + g_3 \cdot (N^{g_4}) \cdot \left(\frac{d}{\mathrm{Dq}}\right)^{g_5}\right]}$	21,541	g_1	−1.0385828	0.0026438	<0.0001	n.a.	0.990	0.07	11.1
		g_2	4.2526170	0.0147436	<0.0001	n.a.			
		g_3	−0.6266850	0.0596972	<0.0001	n.a.			
		g_4	−0.1246646	0.0185442	<0.0001	n.a.			
		g_5	9.1649608	0.1878172	<0.0001	n.a.			
$\mathrm{VOL_{m-IB}} = \mathrm{VOL_{IB}} \cdot e^{\left[g_1 \cdot \left(\frac{t}{\mathrm{Dq}}\right)^{g_2} + g_3 \cdot (N^{g_4}) \cdot \left(\frac{d}{\mathrm{Dq}}\right)^{g_5}\right]}$	21,541	g_1	−1.0537628	0.0027184	<0.0001	n.a.	0.990	0.07	11.2
		g_2	4.2527499	0.0148697	<0.0001	n.a.			
		g_3	−0.6545719	0.0641831	<0.0001	n.a.			
		g_4	−0.1365633	0.0191092	<0.0001	n.a.			
		g_5	9.3108306	0.1971518	<0.0001	n.a.			

H_{dom}: average total height (m) of dominant and codominant trees; SI: site index (m); N_j: trees per hectare at stand age "*j*" yrs.; N_i: trees per hectare (ha^{-1}) at stand age "*i*" yrs. ($i < j$); H_{dom}: average total height (m) of dominant and codominant trees at stand age "*i*" yrs.; ln(BA): natural logarithm of basal area of unthinned stands [$\ln(m^2 \cdot ha^{-1})$]; ln(VOL): natural logarithm of total stem volume [$\ln(m^3 \cdot ha^{-1})$]; CI_j: competition index at stand age '*j*' yrs.; CI_i: competition index at stand age '*i*' yrs. ($i < j$); $_{OB}$: outside bark; $_{IB}$: inside bark; VOL_m: merchantable stem volume ($m^3 \cdot ha^{-1}$); VOL is total stem volume ($m^3 \cdot ha^{-1}$); *t*: top diameter (outside bark) merchantability limit (cm); Dq: quadratic mean diameter (cm); *d*: dbh threshold limit (cm); n: number of observations used for model fitting; SE: standard error; VIF: variance inflation factor; R^2: coefficient of determination; CV: coefficient of variation (100·RMSE/mean); *: Parameters estimates for c_1 and d_1 include the correction proposed by Snowdon [35].

The model that projects the time trend of CI after thinning (Equation 10) was dependent on stand age (Table 3). The exponential of the coefficient for a 36 year-old stand (mean values of stand age reported in Table 1), represents an average annual decline rate of the CI as the stand ages after thinning of 4.3%.

Parameter estimates for merchantable volume yield breakdown function (Equation 12) for both, outside ($VOL_{m\text{-}OB}$, $m^3 \cdot ha^{-1}$) and inside ($VOL_{m\text{-}IB}$, $m^3 \cdot ha^{-1}$) bark total volume yield, are shown in Table 3. The models had a CV of about 11% and an approximate R^2 of 0.99 for both outside and inside bark volume yield breakdown estimates.

There was a good agreement between predicted and observed values of N (Figure 2a), H_{dom} (Figure 2c) and BA (Figure 2e). The slope and the intercept of the relationship between predicted and observed values were not statistically different from one ($P = 0.32$) and zero ($P = 0.14$), respectively.

Figure 2. Validation of dominant height (Hdom) (**a**, **b**), surviving trees per hectare (N) (**c**, **d**) and basal area for unthinned stands (BA) (**e** to **h**) models based on 30 plots from the dataset used for model evaluation. Observed *versus* predicted (simulated) values (**a**, **c**, **e** and **g**) and residuals (predicted-observed) *versus* stand age (yrs.) relationship of Hdom (**b**) and N (**d**), and residuals *versus* observed values of predicting (**f**) and projecting (**h**) BA. Solid line represents linear fit between observed and predicted values and dotted lines for plots (**a**, **c**, **e** and **g**) correspond to the 1-to-1 relationship. Residuals are presented as a proportion of observed values.

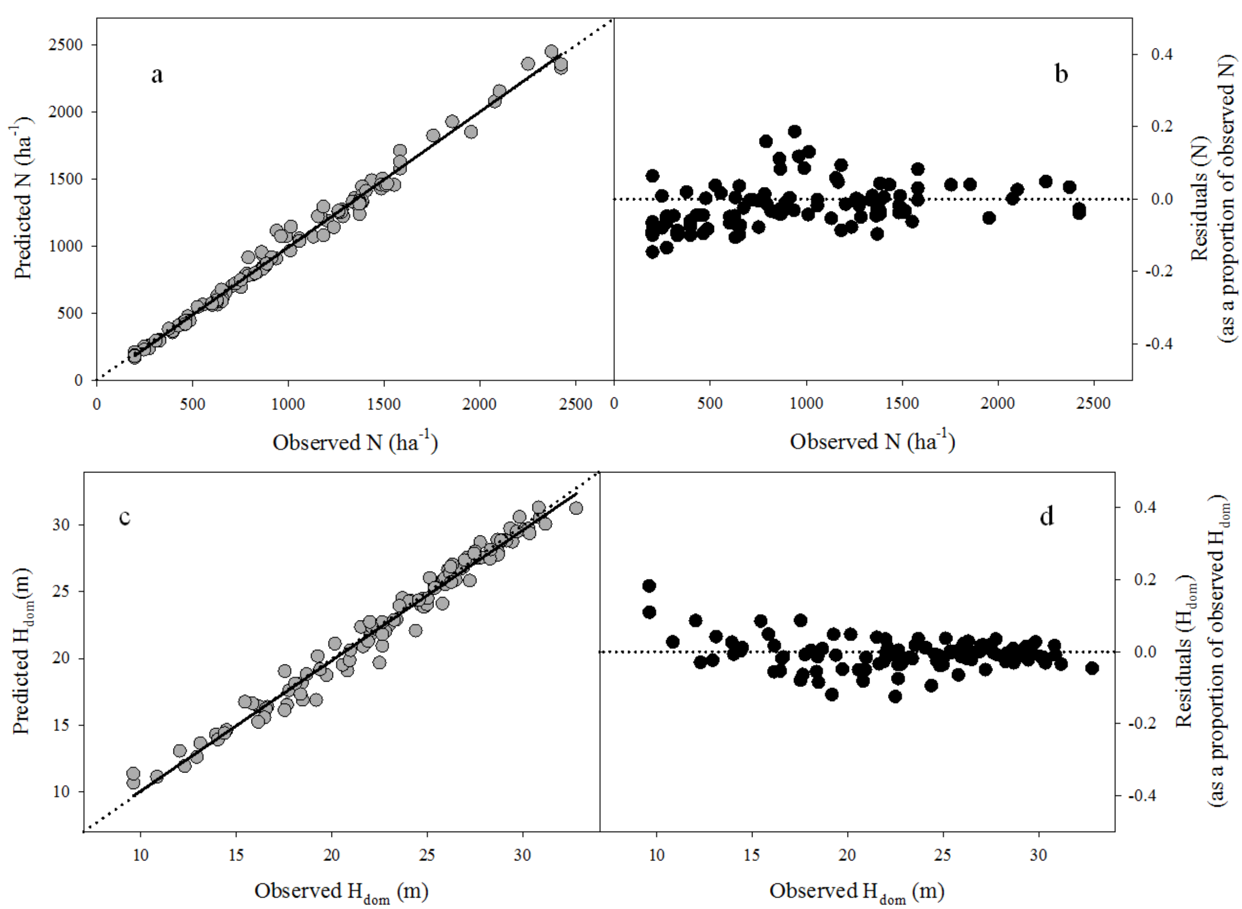
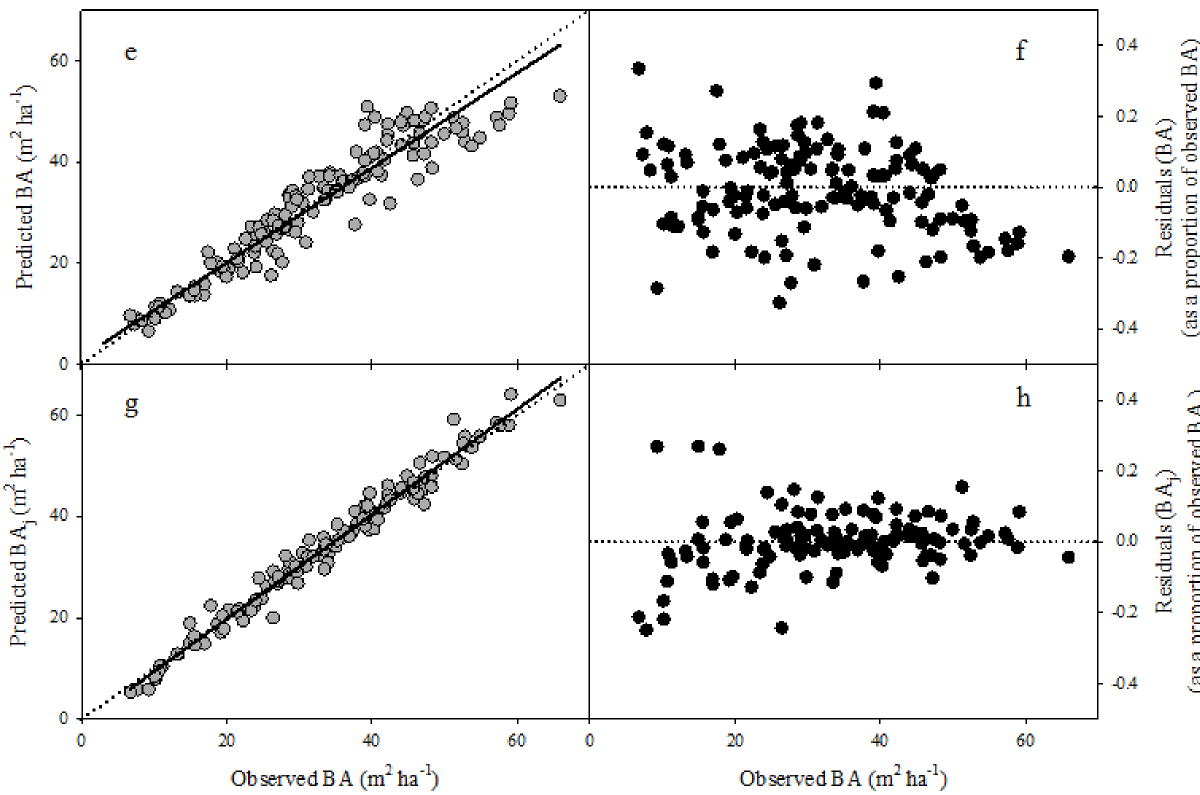


Figure 2. *Cont.*



If residuals are expressed as a percentage of the observed value, maximum absolute residuals observed represent about 17% and 16% of observed N and H_{dom}, respectively. Residuals for predicting the BA model were larger, with maximum residuals of about 30% of observed BA, but centered around zero. There was no noticeable trend in residuals with observed values (Figure 2b for N; Figure 2d for H_{dom} and Figure 2e for BA) or stand age (data not shown).

A growth model to project, or update, BA (BA_j) when some stand measurements are available, including current BA (BA_i), along with current (i) and future (j) Age, N and H_{dom}, was derived from the fitted BA model (Equation 5), and is expressed as:

$$BA_j = BA_i \cdot \left(\frac{N_j}{N_i}\right)^{0.4452486} \cdot \left(\frac{H_{dom_j}}{H_{dom_i}}\right)^{1.6516307} \quad (13)$$

As expected, this projecting growth model improved the estimations of BA, reducing the residuals as compared with BA predicting model (Figure 2g,h).

There was good agreement between predicted and observed values for VOL outside and inside bark (Figure 3a,c). In both cases, the intercept of those relationships was not statistically different from zero ($P > 0.16$). The slopes of the relationship between predicted and observed values (1.006 and 1.011, for VOL_{OB} and VOL_{IB}, respectively) were statistically different to one ($P < 0.02$). There was a good agreement between predicted and observed values of BA_t (Figure 3e). The intercept and slope were not different from zero ($P = 0.18$) and one ($P = 0.12$), respectively. If residuals are expressed as a percentage of observed value, maximum residuals observed in Figure 3 represent about 15% and 17% of observed VOL_{OB} and VOL_{IB}, respectively. There was no noticeable trend in residuals with observed values (Figure 3b for VOL_{OB}; Figure 3d for VOL_{IB} and Figure 3e for BA_t) or stand age (data not shown).

For the two combinations of *t* and *d* tested, there was good agreement between predicted and observed VOL_m (Figure 3g,i). For the two examples shown in Figure 3, the slope and intercept of those relationships were not different from one ($P > 0.41$) and zero ($P > 0.36$), respectively. For all variables listed above, there was no noticeable trend of residuals with observed values. Only for sawtimber VOL_m larger than about 500 $m^3 \cdot ha^{-1}$ (Figure 3i,j), there was a small tendency to increase residuals as VOL_m increased, but the magnitude of that overestimation was less than 5% of observed values.

Figure 3. Validation of total stem volume outside (VOL_{OB}) (**a**, **b**) and inside (VOL_{IB}) (**c**, **d**) bark, BA after thinning (BA_t) (**e**, **f**) and merchantable volume breakdown (VOL_m) (**g** to **j**) models based on 30 pots from the model evaluation dataset. Observed *versus* predicted (simulated) values (**a**, **c**, **e**, **g**, **i**) and residuals (predicted-observed) *versus* observed values of VOL_{OB} (b) VOL_{IB} (d), BA_t (f) and VOL_m (**h**, **j**). Two examples of VOL_m outside bark are shown: using d = 10.16 cm and t = 20.32 cm (**g**, **h**) and d = 20.32 cm and t = 30.48 cm (**i**, **j**). Solid line represents linear fit between observed and predicted values and dotted lines for plots **a**, **c**, **e**, **g** and **i** correspond to the 1-to-1 relationship. Residuals are presented as a proportion of observed values.

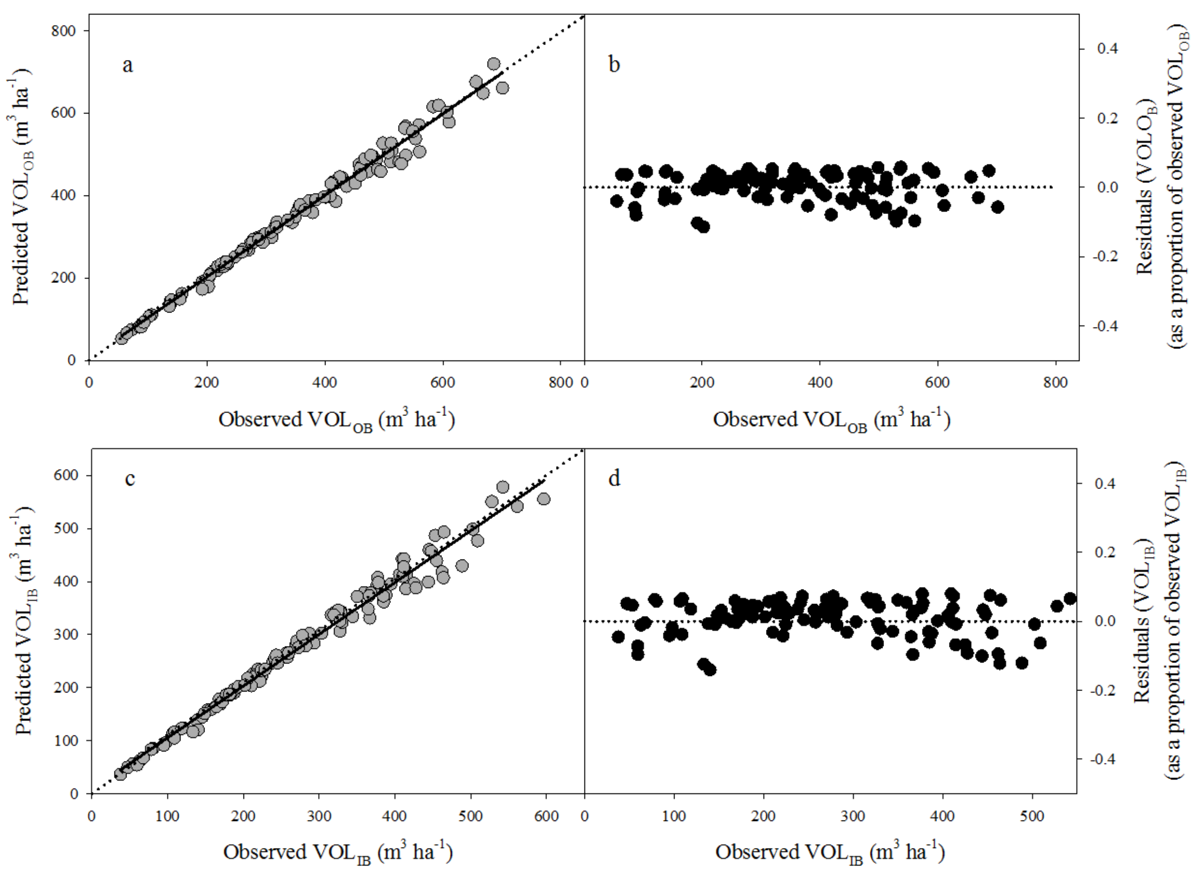
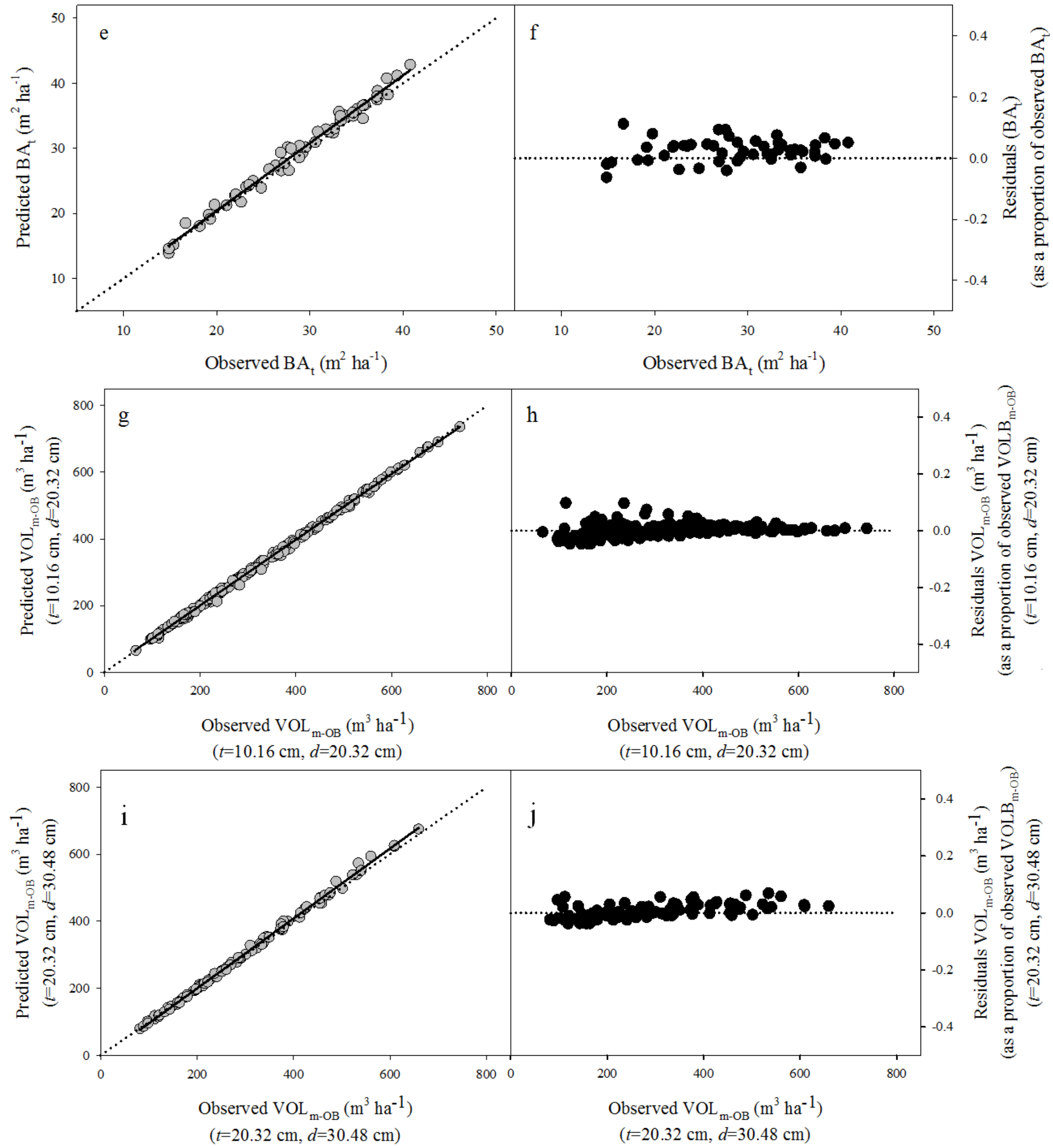


Figure 3. *Cont.*



All model performance tests showed that N, H_{dom}, BA, BA_t, VOL and VOL_m estimations agreed well with measured values (Table 4). For all estimations, MAE and RMSE ranged between 2.4% to 10.3%, and 3.4% to 13.4% of the observed values, respectively. In all cases, BA estimations presented the larger differences between the observed and predicted values. The Bias ranged between 1.9% under-estimations for projected BA and 1.4% over-estimations for BA_t, with no clear tendency to over- or under-estimate. Estimated and observed values were highly correlated, with R^2 values greater than 0.91. The performance of the BA model that included the variables with high collinearity was also tested, showing lower MAE and RMSE than the final model (8.8, 12.6%, respectively) and larger absolute Bias (−3.3%) (data not shown).

Table 4. Summary of model evaluation statistics for N, H_{dom}, BA, BA_t, VOL, and VOL_m estimations based on 30 plots.

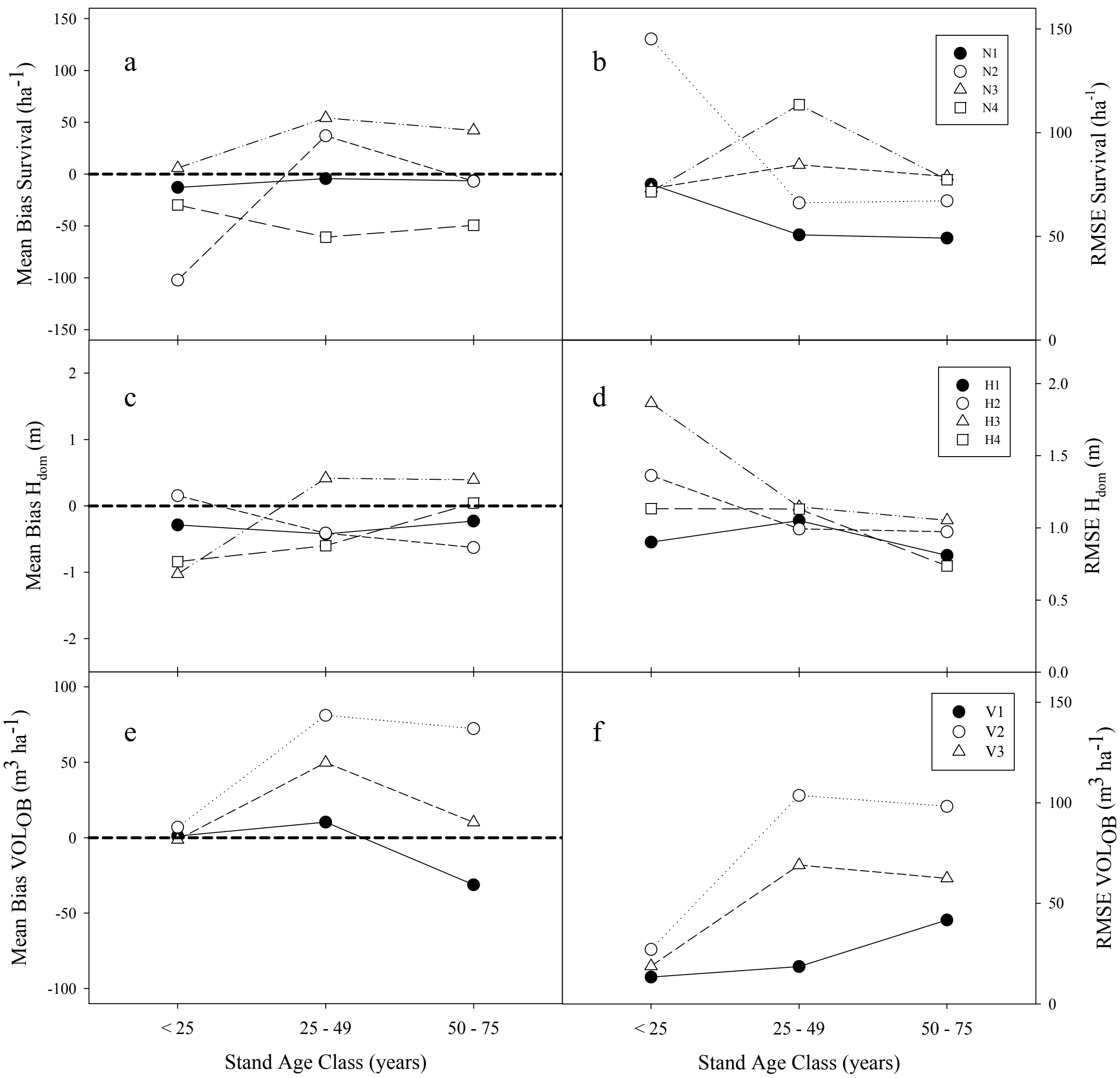
Variable	$\overline{O}$	$\overline{P}$	*n*	MAE	RMSE	Bias	R^2
N	938	929	120	40.3 (4.3)	53.1 (5.7)	−9.46 (−1.0)	0.991
H_{dom}	23.0	22.8	111	0.6 (2.7)	0.8 (3.6)	−0.20 (−0.9)	0.978
BA	31.5	30.8	140	3.1 (10.0)	4.2 (13.5)	−0.65 (−2.1)	0.898
BA_j	33.1	33.3	120	1.9 (5.8)	2.6 (7.8)	0.45 (1.4)	0.970
VOL_{OB}	340.4	341.1	115	11.9 (3.5)	16.4 (4.8)	0.61 (0.2)	0.990
VOL_{IB}	269.8	270.9	115	12.3 (4.6)	17.2 (6.4)	1.06 (0.4)	0.984
BA_t	28.5	27.9	52	0.9 (3.1)	1.1 (3.8)	−0.65 (−2.3)	0.984
$VOL_{m\text{-}OB\text{-}t = 10,\, d = 20}$	137.1	138.3	70	2.5 (1.9)	4.0 (1.9)	1.25 (0.9)	0.999
$VOL_{m\text{-}IB\text{-}t = 10,\, d = 20}$	109.9	110.8	70	1.9 (1.7)	3.0 (1.7)	0.94 (0.9)	0.999
$VOL_{m\text{-}OB\text{-}t = 20,\, d = 30}$	140.4	141.5	20	7.9 (5.6)	9.0 (5.6)	1.14 (0.8)	0.998
$VOL_{m\text{-}IB\text{-}t = 20,\, d = 30}$	115.0	114.4	20	6.3 (5.5)	7.2 (5.5)	−0.63 (−0.5)	0.998

N: trees per hectare (ha^{-1}); H_{dom}: average total height of dominant and codominant trees (m); BA: predicted basal area of unthinned stands ($m^2 \cdot ha^{-1}$); BA_j: projected basal area of unthinned stands ($m^2 \cdot ha^{-1}$); VOL: total stem volume ($m^3 \cdot ha^{-1}$); BA_t: basal area of thinned stands ($m^2 \cdot ha^{-1}$); VOL_m: merchantable stem volume for trees *d* cm and above to a *t* cm top diameter limit ($m^3 \cdot ha^{-1}$); $\overline{O}$: mean observed value; $\overline{P}$: mean predicted value; *n*: number of observations; MAE: mean absolute error; RMSE: root of mean square error; Bias: absolute bias; R^2: coefficient of determination. $_{OB}$: outside bark; $_{IB}$: inside bark; *t*: top diameter (outside bark) merchantability limit (cm); *d*: dbh threshold limit (cm). Values in parenthesis are percentage relative to observed mean.

When tested on the dataset used for model evaluation, predicted values of the models proposed in this study for N, H_{dom} and VOL_{OB} are within the range of variation of the estimations using other published growth and yield models. The effects of stand age on survival, H_{dom}, and VOL_{OB} were predicted using several models for longleaf pine (Figure 4). Across three stand age classes (<25, 25–49 and 50–75 yrs.), the models predict stand growth consistently, with no clear trend to over- or under-estimate. For example, N and H_{dom} estimations of all models performed adequately with Bias less than 10% (Figure 4a) and RMSE less than 15% with no apparent trend to change across stand age classes (Figure 4b). The estimates of VOL_{OB} were similar for all models for age less than 25 yrs., but for older stands the model reported by [7] Brooks and Jack (2006) over-estimated VOL_{OB} by around 70 $m^3 \cdot ha^{-1}$, while the model reported by [5] Lohrey and Bailey (1977) over-estimated VOL_{OB} by about 50 and 10 $m^3 \cdot ha^{-1}$ for stand age between 25–49 and 50–75 yrs., respectively.

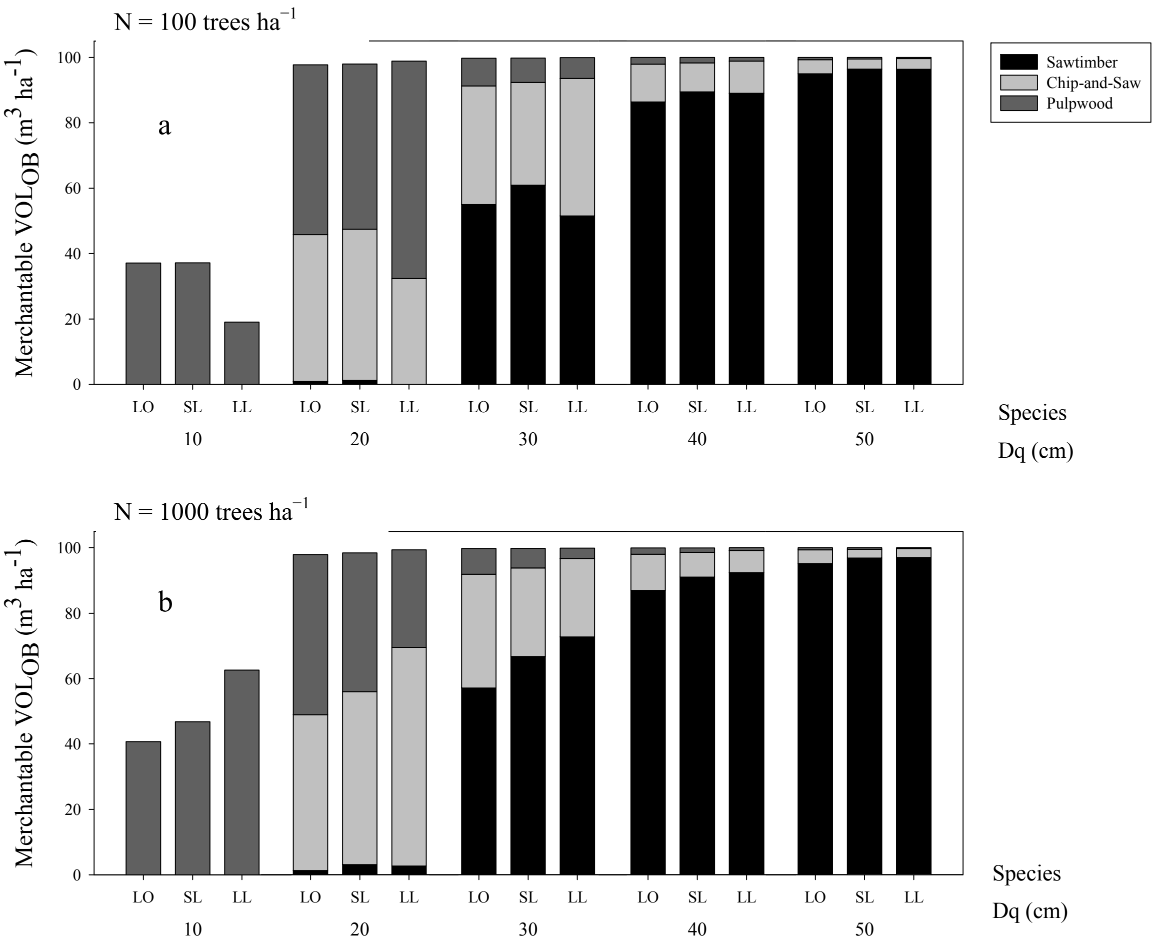
Similarly, the model presented in this study under-predicted VOL_{OB} by about 30 $m^3 \cdot ha^{-1}$ (or around 7%) for older stands (Figure 4e). The RMSE of VOL_{OB} estimations for the models reported in literature increased with stand age, averaging about 85 $m^3 \cdot ha^{-1}$ at age class 25–75 yrs., whereas the model presented in this study had an error of about 19 m^3 ha^{-1} at age class 25–49 yrs., and 42 $m^3 \cdot ha^{-1}$ at age class 50–75 yrs. (Figure 4f).

Figure 4. Mean bias and RMSE of the models presented in this study and reported in literature to predict survival (**a**, **b**), H_{dom} (**c**, **d**) and VOL_{OB} (**e**, **f**) of longleaf pine plantations across four stand age classes: <25, 25–49 and 50–75 yrs. The survival models are: current report (N1), Brooks and Jack [7] (N2), Lohrey and Bailey [5] (N3), and Lauer and Kush [34] (N4). The H_{dom} models are: current report (H1), Brooks and Jack [7] (H2), Farrar [4] using SI and base age 25 yrs. (H3) and using SI and base age 50 yrs. (H4). The VOL_{OB} models are: current report (V1), Brooks and Jack [7] (V2) and Lohrey and Bailey [5] (V3).



Examples of merchantable yield breakdown function of VOL_{OB} estimations for *P. taeda* [25], *P. elliottii* [26] and *P. palustris* (this study) are presented in Figure 5, showing, notably, similar results across species.

Figure 5. Comparison of merchantable volume yield breakdown functions published for *P. taeda* (LO, Harrison and Borders [25]), *P. elliottii* (SL, Pienaar *et al.* [26]) and *P. palustris* (LL, this study). Effect of Dq (from 10 to 50 cm) and stand density [N = 100 trees ha^{-1}, upper panel (**a**); N = 1000 trees ha^{-1}, lower panel (**b**)] on volume yield breakdown for three product classes (sawtimber: d = 29.2 cm and t = 20.3 cm; chip-and-saw: d = 21.6 cm and t = 11.4 cm; pulpwood: d = 11.4 cm and t = 5.1 cm), assuming a VOL_{OB} of 100 m^3·ha^{-1}.



For example, for sawtimber, defined as stem volume of trees with dbh larger than 29.2 cm outside bark (threshold dbh limit) to a top diameter of 20.3 cm outside bark (merchantability limit), when Dq was smaller than 20 cm there was no sawtimber volume production, but when Dq was 30 cm, sawtimber yield was about 55, 61 and 52% (N = 100 trees ha^{-1}) or 57, 67 and 73% (N = 1000 trees ha^{-1}) for *P. taeda*, *P. elliottii* and *P. palustris*, respectively (Figure 5a,b). In the case of chip-and-saw yield, when Dq was 10 cm, all models predicted no volume production for that product, which has a threshold dbh limit of 21.6 cm. Independent of N, when Dq was larger than 50 cm, sawtimber yield was larger than 95% of VOL_{OB} and the production of chip-and-saw (Figure 5c,d) and pulpwood (Figure 5e,f) declined when the stands reached Dq larger than the merchantability limit for sawtimber. Overall, the merchantable yield breakdown functions presented in this study showed the expected behavior of product partitioning as Dq and N changed.

The overall test of the model indicated that, if only initial (*i.e.*, current) stand age, N and SI (reported at first measurement) are known, estimations of H_{dom}, BA and VOL_{OB} were not affected, in relative terms, by simulation length (Figure 6d,f,h). On the other hand, projections of N were sensitive to the length of the simulation (Figure 6b), with errors getting larger as simulation length increased. In all cases residuals were centered on zero. For all stand parameters simulated, there was no noticeable trend of residuals with observed values, and the slope and intercept of the relationships between observed and predicted values were not different from one ($P > 0.24$) and zero ($P > 0.42$), respectively.

Figure 6. Overall simulation validation of survival (N) (**a**, **b**), dominant height (H_{dom}) (**c**, **d**), basal area (BA) (**e**, **f**) and stem volume outside bark (VOL_{OB}) (**g**, **h**) predictions. Observed *versus* predicted (simulated) values (**a**, **c**, **e**, **g**) and residuals (predicted-observed) *versus* simulation length (yrs.) (**b**, **d**, **f**, **h**) relationships for unthinned stands if initial age, N and SI are known, using the models to estimate N, H_{dom}, BA and VOL_{OB} for all unthinned plots in the dataset based only on knowing the initial stand age, N and SI.

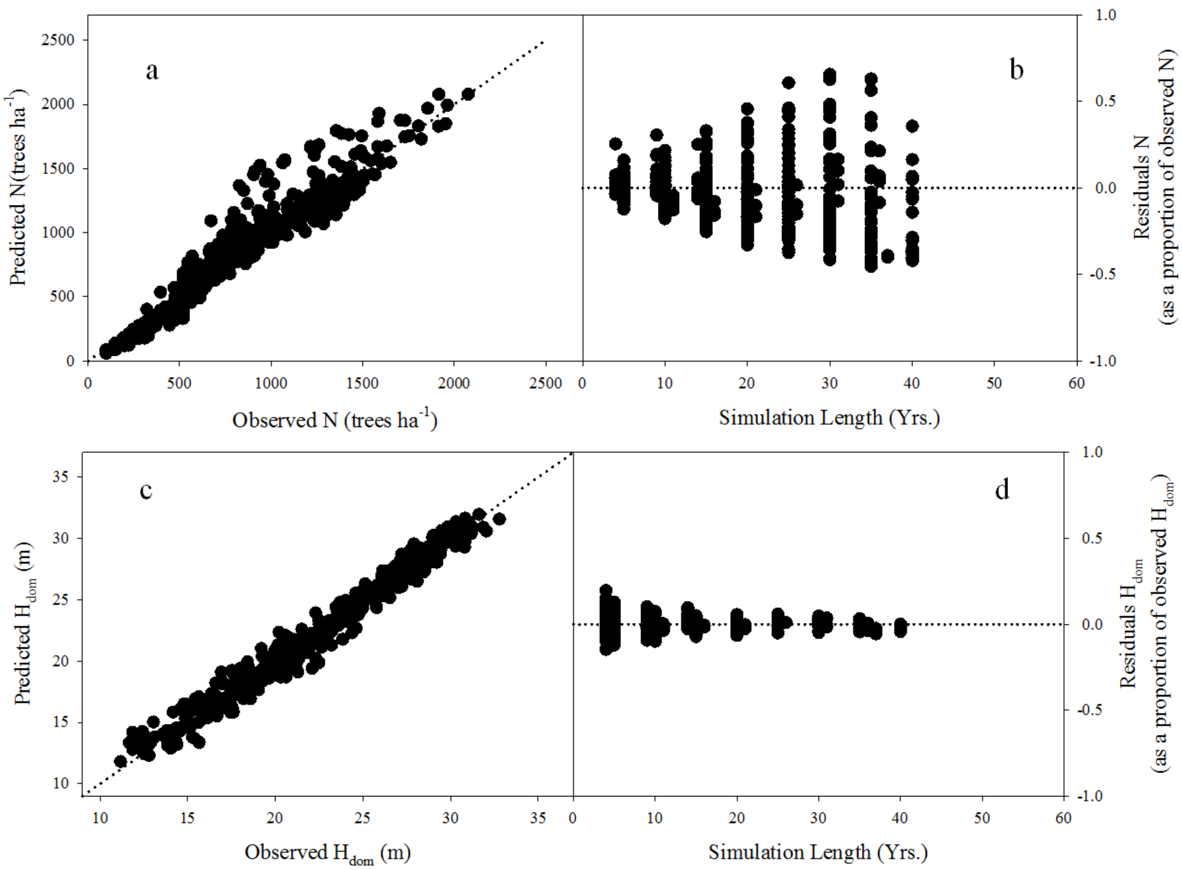
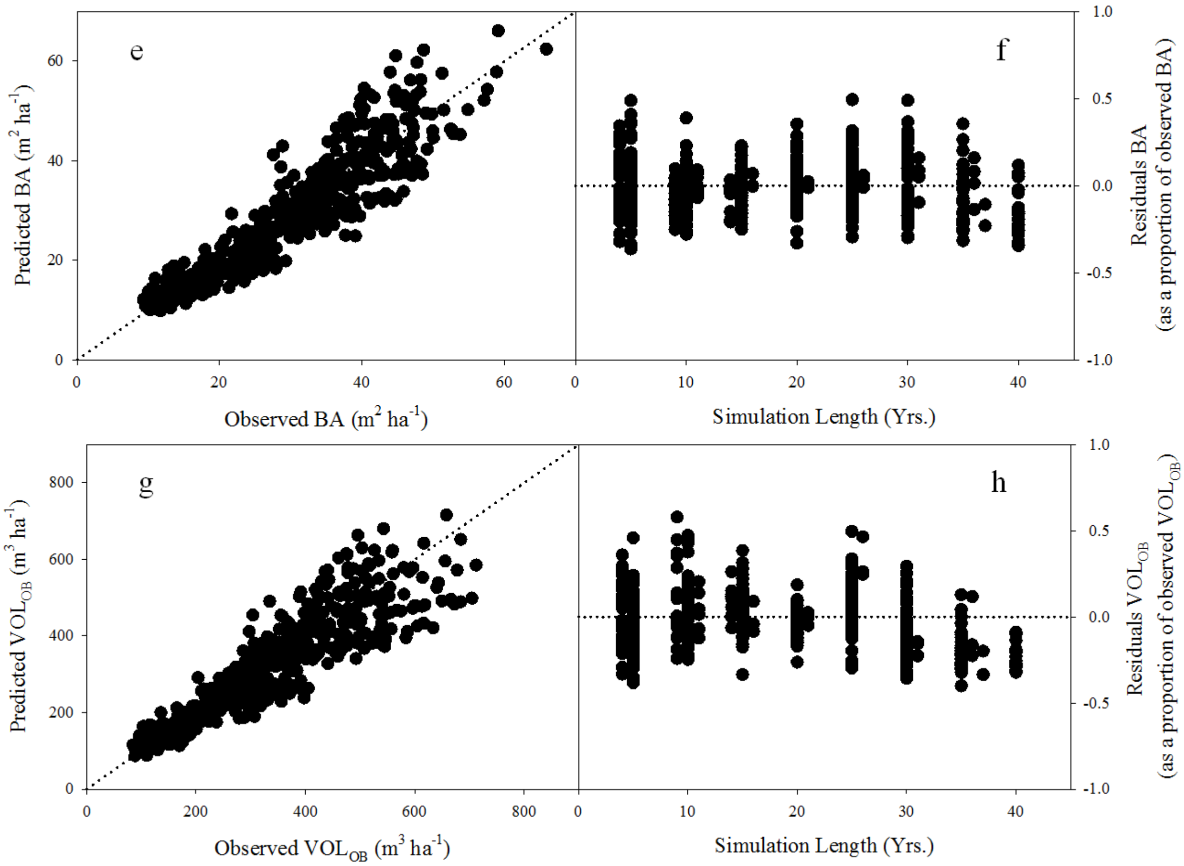


Figure 6. *Cont.*



If initial stand age, N and SI are known, the overall test of the model system indicated that projections of N, H_{dom} and predictions of BA and VOL_{OB} for less than ~40 yrs. simulation length presented a bias that ranged between −7% and 10% (Table 5). Across simulation lengths, the overall bias of the model system for N, H_{dom}, BA and VOL_{OB} were over-estimations of about 6 trees ha^{-1} and under-estimations of about 0.2 m, 0.9 $m^2 \cdot ha^{-1}$ and 13.4 $m^3 \cdot ha^{-1}$, respectively. The overall MAE and RMSE of the model system were about 12 and 18% for N, 3 and 3% for H_{dom}, 12 and 16% for BA and 13 and 18% for VOL_{OB}, respectively. The R^2 decreased as simulation length increased. The overall R^2 across simulation lengths were about 0.93, 0.97, 0.84 and 0.84, for N, H_{dom}, BA and VOL_{OB}, respectively. A trend of increasing error with simulation length was observed for Bias, MAE and RMSE (Table 5). Nevertheless, it is important to note that the number of observations decreases as the simulation length gets larger (Table 5), and therefore, the evaluation statistics on simulation lengths ~40 yrs. can be affected by the unbalanced sampling size and specific characteristics of the sampled plots for evaluations.

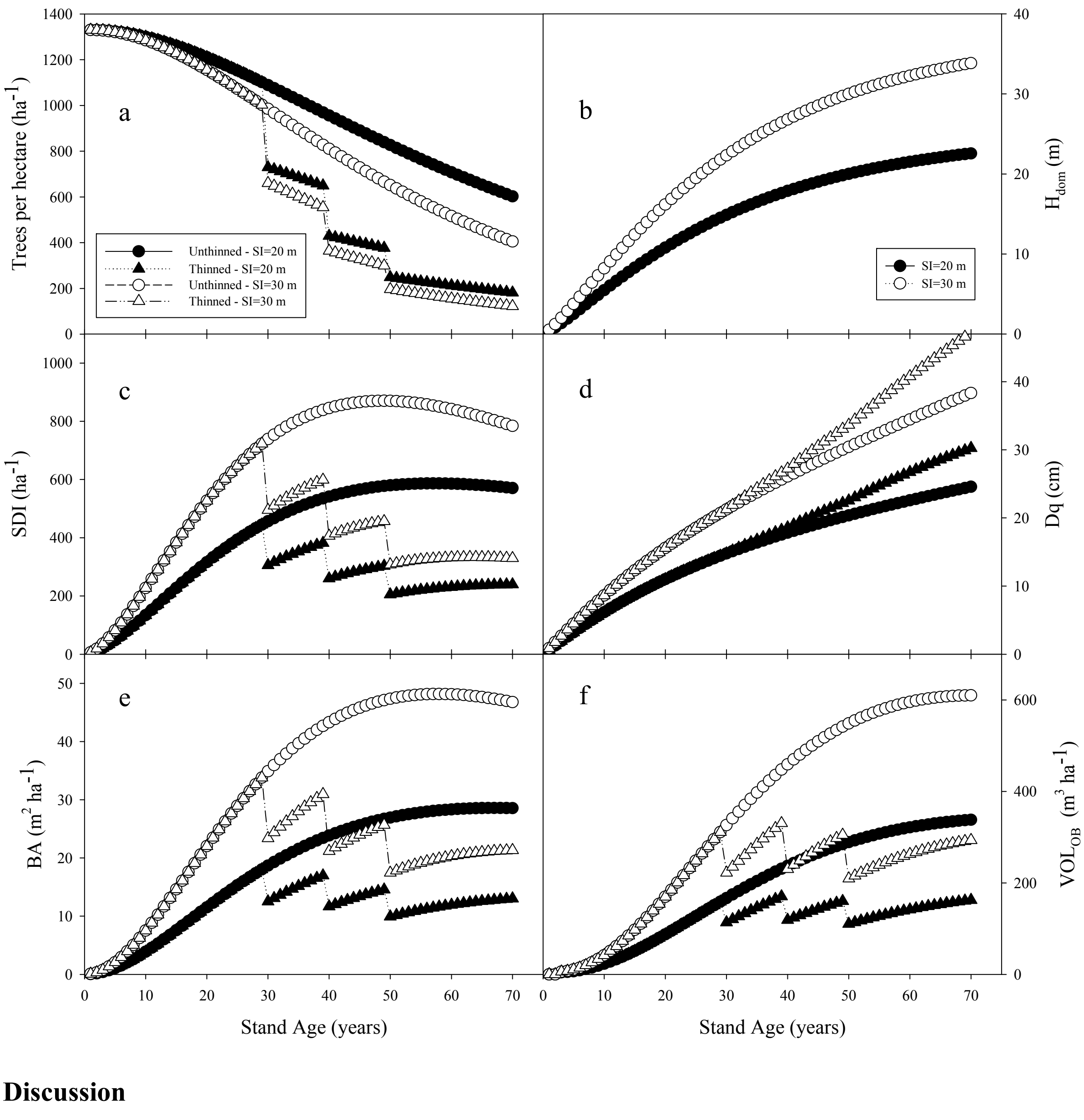
Table 5. Summary of overall model evaluation statistics for N, H_{dom}, BA and VOL_{OB} estimations using different reference age for SI for different simulation lengths.

Variable	Simulation length (yrs.)	$\overline{O}$	$\overline{P}$	*n*	MAE (%)	RMSE (%)	Bias (%)	R^2
N	0–20	818.5	818.3	339	8.3%	12.4%	0.0%	0.959
	21–40	541.1	560.9	172	21.3%	30.5%	3.5%	0.884
	All	20.9	20.9	339	11.6%	17.6%	0.9%	0.934
H_{dom}	0–20	27.2	27.2	172	3.3%	4.2%	−0.1%	0.960
	21–40	23.0	23.0	511	1.7%	2.1%	0.0%	0.948
	All	36.1	34.9	172	2.6%	3.4%	−0.1%	0.974
BA	0–20	30.6	29.7	511	9.8%	13.1%	−2.7%	0.887
	21–40	273.9	273.0	339	15.9%	19.1%	−3.5%	0.747
	All	333.6	320.1	511	12.2%	16.2%	−3.0%	0.837
VOL_{OB}	0–20	818.5	818.3	339	10.4%	13.6%	−0.3%	0.895
	21–40	541.1	560.9	172	19.6%	23.2%	−8.7%	0.557
	All	20.9	20.9	339	13.2%	18.3%	−4.2%	0.839

N: trees per hectare (ha^{-1}); H_{dom}: average total height of dominant and codominat trees (m); BA: stand basal area ($m^2 \cdot ha^{-1}$); VOL_{OB}: total stem volume outside bark ($m^3 \cdot ha^{-1}$); $\overline{O}$: mean observed value; $\overline{P}$: mean predicted value; *n*: number of observations; MAE: mean absolute error (m); RMSE: root of mean square error (m); Bias: absolute bias (m); R^2: coefficient of determination. Values of MAE, RSME and Bias are percentage relative to observed mean.

An example of model behavior for a hypothetical longleaf stands planted with 1400 trees ha^{-1} is shown in Figure 7. The unthinned stands growing on a site with SI = 20 m reached at age 70 yrs. a survival of about 46% of initial planting density, H_{dom} of 22.6 m, BA of 28.5 $m^2 \cdot ha^{-1}$, SDI of 571 tress ha^{-1} and VOL_{OB} of 338 $m^3 \cdot ha^{-1}$. When SI was 30 m instead, at the same age the survival was 31% and H_{dom} was 33.8 m. The unthinned stand reached a maximum BA of about 48.1 $m^2 \cdot ha^{-1}$ at age 58 yrs., and SDI peaked at about 870 trees ha^{-1} at age 49 yrs. and VOL_{OB} was still increasing, reaching about 610 $m^3 \cdot ha^{-1}$ at age 70 yrs. When a scenario of three thinnings was applied to both stands, at age 70 yrs. the number of surviving trees was about 181 and 122 trees ha^{-1} and Dq was increased from 24.6 and 38.3 cm (unthinned), to 30.2 and 47.2 cm, for SI of 20 and 30 m, respectively. The harvested volume from thinnings was about 171 and 331 $m^3 \cdot ha^{-1}$, and the final yield was 162 and 293 $m^3 \cdot ha^{-1}$ for SI of 20 and 30 m, respectively.

Figure 7. Example of model outputs. Simulation of survival (N, trees ha^{-1}): (**a**) dominant height (H_{dom}, m); (**b**) stand density index (SDI, trees ha^{-1}); (**c**) quadratic mean diameter (Dq, cm); (**d**) basal area (BA, $m^2 \cdot ha^{-1}$); (**e**) and stem volume outside bark (VOL_{OB}, $m^3 \cdot ha^{-1}$); (**f**) of unthinned (circle) and thinned (triangle) longleaf pine stands growing in sites with two different SI (20 m: black filled; 30 m: white filled).



4. Discussion

Bringing existing longleaf pine stands under management and restoring longleaf pine stands from degraded or otherwise converted forest stands is a priority for a number of land management entities in the southeastern U.S. [37,38]. Managers undertaking these tasks must have information about the response of growth and stand structure under alternative silvicultural scenarios. Growth and yield systems which incorporate long-term data from stands on a variety of sites and under a range of management regimes provide one of the best tools for exploring the possible outcomes of proposed management regimes. While a number of models predicting elements of longleaf pine plantation stand dynamics have been produced [4–8], this study represents, to our knowledge, the first comprehensive stand-level growth and yield model for longleaf pine plantations, including stand growth and merchantable volume estimations, that can be applied to plantations across a wide range of ages (from 7 to 73 years) and site quality (SI ranging from 20 to 29 m).

All choices of model structure involve compromise. Whole-stand level models, as the one presented here, provide reliable prediction of stand variables, such as BA and N; on the other hand, they do not provide the level of detail that individual-tree level models produce, which could allow for more flexibility in modeling silvicultural practices. However, individual-tree models typically are unreliable in prediction of cumulated stand information, and often have issues with propagation of errors. In this study, we opted to fit a stand level model to be used as a baseline, and in future work, we will consider incorporating individual-tree level information.

Site index is the most widely used measure of forest productivity, particularly in plantations. Base age selection for SI can have significant implications for the accuracy of estimations, as bias increases as the stand age is further from the base age [13]. For this study we decided to set SI at age 50 yrs., a widely used reference age in Southeast U.S. [4,5,32]. The H_{dom} model reported in this study, which behaved well for a wide range of stand age, performed similar or slightly better than the models reported by Farrar [4] and Brooks and Jack [7]. However, larger bias using the Brooks and Jack [7] model could be a result of applying their equation out of the age range and geographic zone of inference, as it was fitted from stands in southwest GA, with ages between 2 and 19 years. Dominant height is a major component of yield prediction systems for southern pine plantations. The anamorphic model obtained by this study seems suitable for H_{dom} estimations in the Western Gulf Coastal Plain, U.S.

In relation to the survival equations, the best model fitted was dependent on stand age and dominant height (a measure of site quality). Other models also incorporate the effect of site quality on survival, such as the models reported by Lauer and Kush [32] and Farrar and Matney [39] for naturally-regenerated longleaf pine stands, or the models reported for related southern pine species *P. elliottii* [40] and *P. taeda* [25,41]. A model that was only dependent on stand age, similar to that reported by Brooks and Jack [7] or Pienaar *et al.* [26], was also fitted, but even though the resulting equation did perform well across all stands included in this study, the final model selected had a slightly better fit (data not shown), and at the same time allows the inclusion of the effect of site quality (reflected in H_{dom}) on resource competition: the larger the SI (and hence H_{dom}), the larger the mortality rate after canopy closure. This process of accelerated self-thinning has been well documented for southern pines [16,42–45]. For example, 25 yrs. old *P. elliottii* and *P. taeda* stands in fertilized plots (with higher SI) had an accumulative mortality of about 59 and 43%, respectively, while non-fertilized plots showed lower mortality of about 43 and 22%, respectively [45]. Murphy and Farrar [46] reported that models that include H_{dom} performed better than models that rely only on stand age to project survival, especially on prepared sites.

Other models that included SI [14–17] were also tested, but H_{dom} was selected due to better predictive ability. An attempt was made to model survival as a two-step modeling approach [16], including an equation to predict the probability of survival of all trees in the stand over a measurement interval, but no improvement was observed. The model presented in this study performed similar to, or slightly better, than other reported models to estimate future survival, but performance can be influenced by the fact that, even though the validation plots are independent to the plots used for model fitting, they were located in the same geographic region and we are not using the model out of the geographic inference zone, as we did with the model of Brooks and Jack [7]. Nevertheless, the model of Lohrey and Bailey [5] was fitted with a subset of the same dataset used for this study, but perhaps the lower range of ages and N in their dataset influenced the results presented here. On the other hand, the model of Lauer and Kush [32] performed well across different combinations of stand density and productivity in this study. Residual analysis for each model did not indicate any unusual trends, even though the stands cover a wide range of productivity, planting density and age. The models obtained by this study appear suitable for survival estimations within the Western Gulf Coastal Plain U.S.

The model that presdict BA for unthinned stands was only dependent on N and H_{dom}. Other models reported for southern pine species include other simple or composite variables such as SI, Age, N/Age and H_{dom}/Age as well. In this study, all of these variables were significant and could be included in the model, but the high multicollinearity between those variables indicated the need to drop them from the final model. Therefore, it was decided to discard those variables, obtaining a simpler model to predict BA for unthinned longleaf pine stands with similar goodness-of-fit which avoided over-fitting problems. Widely used models for other southern pines [25,26] and for longleaf pine [32] include other stand variables to predict BA, but the existing publications contain no information regarding multicollinearity and/or their relative importance. The model that projects BA reported in this study had the same structure of the model reported by Brooks and Jack [7].

In the case of thinned stands, the use of the approach proposed by Pienaar [20,23], that uses CI and the basal area of the unthinned counterpart, fitted the available data well allowing the estimation of BA growth after thinning. Modified versions of the model used were also evaluated, which included H_{dom} or SI as dependent variables to modify the rate of decline of CI as stands ages after thinning, but none of those variables were significant into the model (data not shown) and the final model that estimates the decline of the CI as the stand ages after thinning was only dependent on stand age. For 25- and 50-year-old stands, the mean value of the annual rate of decline of the CI as the stand ages after thinning were 6.2% and 3.1%, respectively, reflecting the impact of stand age on the rate of decline of CI as stands ages after thinning. The value of the rate of decline of CI at age 50 yrs. is lower than the values reported for other southern pine species. For example, Pienaar [20] and Harrison and Borders [25] reported values of 9.3% and 7.6% for *P. elliottii* and *P. taeda*, respectively. Those authors reported CI's for stands thinned at younger ages of about 13 years and measured until age 30 in the most extended study [20]. The dataset used in this study included plots thinned at ages ranging from 17 to 63 years, and measured, in average, for about 20 yrs. The slope of the relationship between observed and predicted BA after thinning was not different from one, supporting the robustness of the model that projects BA growth for thinned stands.

The models that predict VOL (outside and inside bark) did not depend on stand age or N, and were similar or slightly better than other models reported for longleaf plantations [5,7] or naturally-regenerated stands [32]. In this study, as done previously with the BA model fits, variables that showed high levels of multicollinearity were dropped to obtain a parsimonious final model that was only dependent on BA and H_{dom} and provides good prediction ability. The residuals of this model showed a tendency toward under-estimation for observed VOL_{OB} greater than 600 $m^3 \cdot ha^{-1}$, a condition which is rare in longleaf plantations, which typically include multiple thinnings [5,47–49].

Nevertheless, the maximum residual found was less than 8% of the observed value, with residuals centered near zero at different age classes. For the dataset used for validation, the models reported by Brooks and Jack [5] and Lohrey and Bailey [7] showed very good prediction ability only for stands up to 25 yrs. old. This may be explained by the fact that the former was developed for stands younger than 20 yrs. in age and the latter includes a reduced range of ages and site quality as compared with the dataset used in the present study. This indicates that the new data used here, expanded the ability to accurately predict stand volume if compared with the model of Lohrey and Bailey [5].

One of the most important contributions of the system of equations presented in this study, in contrast to other longleaf models published, is the inclusion of the merchantable volume yield breakdown model. Similar to *P. elliottii* and *P. taeda*, it is now possible to estimate the merchantable volume for different combinations of threshold dbh and top diameter for longleaf pine stands by using equation 8. Although, the model presented in this study made similar predictions to some models currently used for *P. elliottii* and *P. taeda*, differences in diameter distribution between species could explain the disagreements observed in merchantable volume yield breakdown, especially in chip-and-saw and pulpwood products.

The overall evaluation, where N, H_{dom}, BA and VOL_{OB}, were calculated for all unthinned plots using the system of equations shown in Table 3 starting with a known initial age, N and SI (reported at first measurement), demonstrates the robustness of the model. As was expected, errors tended to get larger as the length of simulations increased, but overall, the residual centered on zero. Even though the number of observations was not balanced across simulation length classes, a fact that may explain the bias found for simulation lengths greater than 40 years, the results indicate that we can expect accurate estimations for simulation length of up to 40 years. Therefore, it is recommended that users update their stand inventories at least each 30–40 years, in order to improve the predictions from the use of the models presented here.

Despite the fact that the model system performed very well for the dataset used for validation, the functioning of the model outside the geographical range of the fitting data is uncertain. We strongly recommend using this system of equations only within the range of data used to fit (see Tables 1 and 2). In addition, the model does not include the effects of genetics, site preparation, weed control and fertilization. Nevertheless, the system presented here provides an important new tool for supporting present and future longleaf pine management decisions. Future research expanding the area of inference and including the effects of genetically improved material and intensive silvicultural management is needed to improve the predictive ability of the model and to address 21st century forest management approaches.

Acknowledgments

This research was supported by the U.S. Department of Defense, through the Strategic Environmental Research and Development Program (SERDP). The authors acknowledge the U.S. Forest Service Southern Research Station for their assistance and for providing the long term datasets.

Conflict of Interest

The authors declare no conflict of interest.

References

1. Frost, C.C. Four centuries of changing landscape patterns in the longleaf pine ecosystem. In *The Longleaf Pine Ecosystem: Ecology, Restoration and Management*, Proceedings of the 18th Tall Timbers Fire Ecology Conference, Tallahassee, FL, USA, 30 May–2 June 1991; Hermann, S.H., Ed.; Tall Timbers Research Station: Tallahassee, FL, USA, 1993; Volume 18, pp. 17–44.
2. Frost, C.C. History and future of the longleaf pine ecosystem. In *The Longleaf Pine Ecosystem—Ecology, Silviculture and Restoration*; Jose, S., Jokela, E.J., Miller, D.L., Eds.; Springer: New York, NY, USA, 2006; pp. 9–48.
3. Avery, T.R.; Burkhart, H.E. *Forest Measurements*, 5th ed.; McGraw-Hill Inc.: New York, NY, USA, 2002.
4. Farrar, R.M., Jr. Southern pine site index equations. *J. For*. **1973**, *71*, 696–697.
5. Lohrey, R.E.; Bailey, R.L. *Yield Tables and Stand Structure for Unthinned Longleaf Pine Plantations in Louisiana and Texas*; Research Paper SO-133 for USDA Forest Service Southern Forest Experiment Station: New Orleans, LA, USA, 1977.
6. Boyer, W.D. *Interim Site-Index Curves for Longleaf Pine Plantations*; Research Note SO-261 for USDA Forest Service Southern Forestry Experiment Station: New Orleans, LA, USA, 1980.
7. Brooks, J.R.; Jack, S.B. *A Whole Stand Growth and Yield System for Young Longleaf Pine Plantations in Southwest Georgia*; General Technical Report SRS-92 for USDA Forest Service Southern Research Station: Asheville, NC, USA, 2006; pp. 317–318.
8. VanderShaaf, C.L. *LONGLEAF: A Diameter-Distribution Growth and Yield Model and Decision Support System for Unthinned Longleaf Pine Plantations*; Texas Forest Service: College Station, TX, USA, 2010.
9. Goelz, J.C.G.; Leduc, D.J. Long-term studies on development of longleaf pine plantations. In *Forests for Our Future*, Proceedings of the Third Longleaf Alliance Regional Conference, Alexandria, LA, USA, 16–18 October 2000; Kush, J.S., Ed.; The Longleaf Alliance and Auburn University: Auburn, AL, USA, 2001; pp. 116–118.
10. Leduc, D.J.; Goelz, J.C.G. A height-diameter curve for longleaf pine plantations in the Gulf Coastal Plain. *South. J. Appl. For*. **2009**, *33*, 164–170.
11. Quicke, H.E.; Meldahl, R.S. Predicting pole classes for longleaf pine based on diameter breast height. *South. J. Appl. For*. **1992**, *16*, 79–82.
12. Clutter, J.L.; Forston, J.C.; Pienaar, L.V.; Brister, G.H.; Bailey, R.L. *Timber Management: A Quantitative Approach*; Krieger Publishing Company: Malabar, FL, USA, 1983.
13. Weiskittel, A.R.; Hann, D.W.; Kerhsaw, J.A., Jr.; Vanclay, J.K. *Forest Growth and Yield Modeling*; Wiley: Oxford, UK, 2011.
14. Diéguez-Aranda, U.; Castedo Dorado, F.; Álvarez González, J.G.; Rodriguez Soalleiro, R. Modelling mortality of Scots pine (*Pinus sylvestris* L.) plantations in the northwest of Spain. *Eur. J. For. Res*. **2005**, *124*, 143–153.
15. Diéguez-Aranda, U.; Castedo Dorado, F.; Álvarez González, J.G.; Rojo Alboreca, A. Dynamic growth model for Scots pine (*Pinus sylvestris* L.) plantations in Galicia (north-western Spain). *Ecol. Model*. **2006**, *191*, 225–242.

16. Zhao, D.; Borders, B.; Wang, M.; Kane, M. Modeling mortality of second-rotation loblolly pine plantations in the Piedmont/Upper Coastal Plain and Lower Coastal Plain of the southern United States. *For. Ecol. Manag*. **2007**, *252*, 132–143.
17. Burkhart, H.E.; Tomé, M. *Modeling Forest Trees and Stands*; Springer: New York, NY, USA, 2012.
18. Borders, B.E. Systems of equations in forest stand modeling. *For. Sci*. **1989**, *35*, 548–556.
19. Gonzalez-Benecke, C.A.; Gezan, S.A.; Martin, T.A.; Cropper, W.P., Jr.; Samuelson, L.; Leduc, D.J. Individual tree diameter, height and volume functions for longleaf pine. *For. Sci*. **2012**, submitted.
20. Pienaar, L.V. *Results and Analysis of a Slash Pine Spacing and Thinning Study in the Southeast Coastal Plain*; Technical Report 1995-3 for Plantation Management Research Cooperative (PMRC): University of Georgia, Athens, GA, USA, 1995.
21. Westfall, J.A.; Burkhart, H.E. Incorporating thinning response into a loblolly pine stand simulator. *South. J. Appl. For*. **2001**, *25*, 159–164.
22. Sharma, M.; Smith, M.; Burkhart, H.E.; Amateis, R.L. Modeling the impact of thinning on height development of dominant and codominant loblolly pine trees. *Ann. For. Sci*. **2006**, *63*, 349–354.
23. Pienaar, L.V. An approximation of basal area growth after thinning based on growth in unthinned plantations. *For. Sci*. **1979**, *25*, 223–232.
24. Amateis, R.L.; Burkhart, H.E.; Burk, T.E. A ratio approach to predicting merchantable yields of unthinned loblolly pine plantations. *For. Sci*. **1986**, *32*, 287–296.
25. Harrison, W.M.; Borders, B.E. *Yield Prediction and Growth Projection for Site-prepared Loblolly Pine Plantations in the Carolinas, Georgia, Alabama and Florida*; Technical Report 1996-1 for Plantation Management Research Cooperative (PMRC): University of Georgia, Athens, GA, USA, 1996.
26. Pienaar, L.V.; Shiver, B.D.; Rheney, J.W. *Yield Prediction for Mechanically Site-prepared Slash Pine Plantations in the Southeastern Coastal Plain*; Technical Report 1996-3 for Plantation Management Research Cooperative (PMRC): University of Georgia, Athens, GA, USA, 1996.
27. Yin, R.; Pienaar, L.V.; Aronow, M.E. The productivity and profitability of fiber farming. *J. For*. **1998**, *96*, 13–18.
28. Fox, D.G. Judging air quality model performance. *Bull. Am. Meteorol. Soc*. **1981**, *62*, 599–609.
29. Willmott, C.; Ackleson, S.; Davis, R.; Feddema, J.; Klink, K.; Legates, D.; O'Donnell, J.; Zhao, W.; Mason, E.G.; Brown, J. Modelling height-diameter relationships of *Pinus radiata* plantations in Canterbury, New Zealand. *N. Z. J. For*. **2006**, *51*, 23–27.
30. Loague, K.; Green, R.E. Statistical and graphical methods for evaluating solute transport models: Overview and application. *J. Contam. Hydrol*. **1991**, *7*, 51–73.
31. Kaboyashi, K.; Salam, M.U. Comparing simulated and measured values using mean squared deviation and its components. *Agron. J*. **2000**, *92*, 345–352.
32. Lauer, D.K.; Kush, J.S. *A Variable Density Stand Level Growth and Yield Model for Even-aged Natural Longleaf Pine*; Special Report No. 10 for Alabama Agricultural Experiment Station Auburn University: Auburn, AL, USA, 2011.
33. *SAS Software*, version 9.3; SAS Inc.: Cary, NC, USA, 2011.

34. Neter, J.; Kutner, M.H.; Nachtsheim, C.J.; Wasserman, W. *Applied Linear Statistical Models*, 4th ed.; Irwin: Chicago, IL, USA, 1996.
35. Snowdon, P. A ratio estimator for bias correction in logarithmic regressions. *Can. J. For. Res*. **1991**, *21*, 720–724.
36. Baskerville, G.L. Use of logarithmic regression in the estimation of plant biomass. *Can. J. For. Res*. **1972**, *2*, 49–53.
37. Johnson, E.E.; Gjerstad, D. Restoring the overstory of longleaf pine ecosystems. In *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration*; Jose, S., Jokela, E.J., Miller, D.L., Eds.; Springer: New York, NY, USA, 2006; pp. 271–295.
38. Outcalt, K.W.; Brockway, D.G. Structure and composition changes following restoration treatments of longleaf pine forests on the Gulf Coastal Plain of Alabama. *For. Ecol. Manag*. **2010**, *259*, 1615–1623.
39. Farrar, R.M., Jr.; Matney, T.G. A dual growth simulator for natural even-aged stands of longleaf pine in the South's East Gulf Region. *South. J. Appl. For*. **1994**, *18*, 147–155.
40. Pienaar, L.V.; Rheney, J.W. Yield prediction for mechanically site-prepared slash pine plantations in the southeastern Coastal Plain. *South. J. Appl. For*. **1993**, *17*, 163–173.
41. Clutter, J.L.; Harms, W.R.; Brister, G.H.; Rheney, J.W. *Stand Structure and Yields of Site-Prepared Loblolly Pine Plantations in the Lower Coastal Plain of the Carolinas, Georgia and North Florida*; General Technical Report SE-27 for USDA Forest Service Southeastern Forest Experiment Station: Asheville, NC, USA, 1984.
42. Bailey, R.L.; Borders, B.E.; Ware, K.D.; Jones, E.P. A compatible model relating slash pine plantation survival to density, age site index, and type and intensity of thinning. *For. Sci.* **1985**, *31*, 180–189.
43. Dean, T.J.; Jokela, E.J. A density management diagram for slash pine plantations in the lower Coastal Plain. *South. J. Appl. For*. **1992**, *16*, 178–185.
44. Samuelson, L.J.; Butnor, J.; Maier, C.; Stokes, T.A.; Johnsen, K.; Kane, M. Growth and physiology of loblolly pine in response to long-term resource management: Defining growth potential in the southern United States. *Can. J. For. Res*. **2008**, *38*, 721–732.
45. Jokela, E.J.; Martin, T.A.; Vogel, J.G. Twenty-five years of intensive forest management with southern pines: Important lessons learned. *J. For*. **2010**, *108*, 338–347.
46. Murphy, P.A.; Farrar, R.M., Jr. *A New Mortality (or Survival) Function for Longleaf Pine Plantations*; General Technical Report SO-74 for U.S. Department of Agriculture Forest Service Southern Research Station: New Orleans, LA, USA, 1988; pp. 427–432.
47. Beers, B.L.; Bailey, R.L. *Yield Stand Structure and Economic Conclusions from a 22-Year-Old Site Preparation Study with Planted Loblolly and Longleaf Pines*; General Technical Report SO-54 for U.S. Department of Agriculture Forest Service Southern Research Station: New Orleans, LA, USA, 1985.
48. Farrar, R.M., Jr.; Boyer, W.D. Managing longleaf pine under the selection system—Promises and problems. In *Proceedings of the Sixth Biennial Southern Silvicultural Research Conference*, Memphis, TN, USA, 30 October–1 November 1990; Coleman, S.S., Neary, D.G., Eds.; USDA Forest Service Southeastern Forest Experiment Station: New Orleans, LA, USA, 1991; pp. 357–368.

49. Jack, S.B.; Mitchell, R.J.; Pecot, S.D. *Silvicultural Alternatives in a Longleaf Pine/Wiregrass Woodland in Southwest Georgia: Understory Hardwood Response to Harvest-created Gaps*; General Technical Report SRS-92 for USDA Forest Service Southern Research Station: Asheville, NC, USA, 2006; pp. 85–89.