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# Regional validation and improved parameterization of the 3-PG model for *Pinus taeda* stands

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ABSTRACT

The forest simulation model, 3-PG, has the capability to estimate the effects of climate, site and management practices on many stand attributes using easily available data. The model, once calibrated, has been widely applied as a useful tool for estimating growth of forest species in many countries. Currently, there is an increasing interest in estimating biomass and assessing the potential impact of climate change on loblolly pine (*Pinus taeda* L.), the most important commercial tree species in the southeastern U.S. This paper reports a new set of 3-PG parameter estimates for loblolly pine, and describe new methodologies to determine important estimates. Using data from the literature and long-term productivity studies, we parameterized 3-PG for loblolly pine stands, and developed new functions for estimating NPP allocation dynamics, biomass pools at variable starting ages, canopy cover dynamics, effects of frost on production, density-independent and density-dependent tree mortality and the fertility rating. The model was tested against data from replicated experimental measurement plots covering a wide range of stand characteristics, distributed across the southeastern U.S. and also beyond the natural range of the species, using stands in Uruguay, South America. We used the largest validation dataset for 3-PG, and the most geographically extensive within and beyond a species' native range. Comparison of modeled to measured data showed robust agreement across the natural range in the U.S., as well as in South America, where the species is grown as an exotic. Across all tested sites, estimations of survival, basal area, height, quadratic mean diameter, bole volume and above-ground biomass agreed well with measured values, with $R^2$ values ranging between 0.71 for bole volume, and 0.95 for survival. The levels of bias were small and generally less than 13%. LAI estimations performed well, predicting monthly values within the range of observed LAI. The results provided strong evidence that 3-PG could be applied over a wide geographical range using one set of parameters for loblolly pine. The model can also be applied to estimate the impact of climate change on stands growing across a wide range of ages and stand characteristics.



## 1. Introduction

Loblolly pine (*Pinus taeda* L.) is one of the fastest growing pine species and has been planted on more than 10 million ha in the southeastern U.S. (Huggett et al., 2013). Its native range covers a wide area from the Atlantic coast to eastern Texas and from northern Florida to southern New Jersey (Fig. 1). Loblolly pine has also been introduced into many countries, and large-scale plantations for timber production are found in Argentina, Brazil, China, New Zealand, South Africa and Uruguay (Borders and Bailey, 2001; Fassola et al., 2012).

Forest simulation models can be used to estimate forest productivity or biomass under diverse management and/or climate scenarios, and those estimates are of interest to landowners, managers and researchers. The semi-process-based simulation model, 3-PG (Physiological Processes Predicting Growth; Landsberg and Waring, 1997), has been extensively used to estimate stand attributes such as volume growth or biomass dynamics (Landsberg et al., 2001; Stape et al., 2004; Fontes et al., 2006; Sampson et al., 2006; Coops et al., 2010; Bryars et al., 2013; Gonzalez-Benecke et al., 2014a). The model uses species-specific

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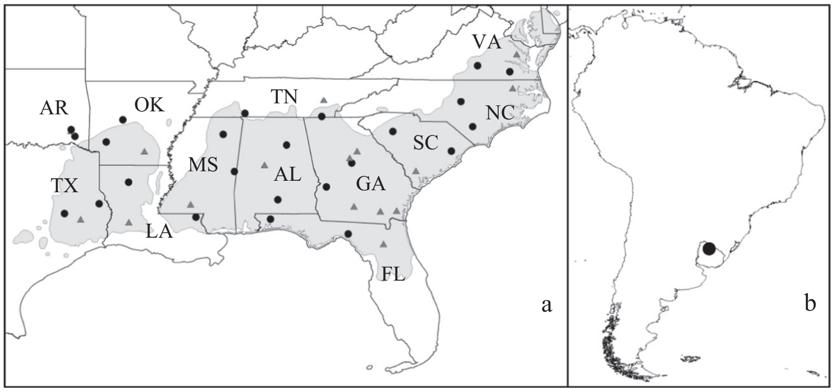


**Fig. 1.** (a) Location of sites used for validation (black circle, $n = 91$ plots in 24 sites) or FR/SI analysis (grey triangle, $n = 63$ plots in 16 sites) in the U.S.: the species natural distribution range is the shaded area. (b) Location of sites used for validation in Uruguay ($n = 10$ plots). AL: Alabama; AR: Arkansas; FL: Florida; GA: Georgia; LA: Louisiana; MS: Mississippi; NA: North Carolina; OK: Oklahoma; SC: South Carolina; TN: Tennessee; TX: Texas; and VA: Virginia.

empirical tree- and stand-level traits in combination with physiological attributes to quantify Net Primary Production (NPP, Mg ha$^{-1}$), allocation to the various biomass pools, population dynamics and soil water balance (Landsberg and Sands, 2011).

The 3-PG model can be used to estimate the effects on stand productivity of management, site characteristics and climate and has been parameterized for different tree species (Booth et al., 2000; Law et al., 2000; Waring, 2000; Dye, 2001; Rodríguez et al., 2002; Sands and Landsberg, 2002; Almeida et al., 2004; Flores and Allen, 2004; Coops et al., 2005, 2010; Waring et al., 2008; Rodríguez et al., 2009; Pérez-Cruzado et al., 2011; Gonzalez-Benecke et al., 2014a). Even though the model has been parameterized for loblolly pine (Landsberg et al., 2001, 2003; Sampson et al., 2006; Bryars et al., 2013), questions have arisen about the generality of these parameterizations and the accuracy of model predictions across the southeastern U.S. and in other countries (Bryars et al., 2013). The modular implementation of the 3-PG model allows improvement of specific sub-routines. Several have been reported as requiring further refinement, including NPP partitioning, stand mortality, light interception, canopy closure and the fertility rating (FR) (Pinjuv et al., 2006; Almeida et al., 2010; Landsberg and Sands, 2011; Bryars et al., 2013). To improve model performance we used long-term datasets to obtain new species-specific parameters, and changed the structure of the model by introducing some new species-specific functions.

The objectives of this study were to parameterize the 3-PG model for loblolly pine, and validate it using data from measurement plots covering a wide range of age, productivity, management and geographical distribution in the southeastern U.S. and Uruguay, South America. We used published data and long-term productivity studies from five university-forest industry research cooperatives in the southeastern U.S.: the Forest Biology Research Cooperative (FBRC) at the University of Florida, the Forest Productivity Cooperative (FPC) at North Carolina State University and Virginia Tech University, the Forest Modelling Research Cooperative (FMRC) at Virginia Tech University, the Western Gulf Forest Tree Improvement Program (WGFTIP) at Texas A&M University, and the Plantation Management Research Cooperative (PMRC) at the University of Georgia. This collaborative effort was part of the integrative research of the Pine Integrated Network: Education, Mitigation and Adaptation Project (PINEMAP, http://www.pinemap.org/). These shared datasets represented the outcome of frequently remeasured permanent plots established for a range of purposes, from monitoring plots of operational plantations to studies that included a variety of replicated treatments such as genetics, planting density, fertilization, weed control and thinning.

As we had access to the large datasets of PINEMAP, we were able to revise some important parameters of 3-PG using the alternative methods suggested by Gonzalez-Benecke et al. (2014a) to estimate species-specific parameters for FR, monthly needlefall rate, canopy cover, density-independent and density-dependent tree mortality, bole volume bark fraction, mean tree height, stemwood specific gravity, and initial biomass pools at any starting age. In addition, we incorporated new functions for estimating NPP partitioning, quadratic mean diameter and effect of frost temperature. We suggest that this new set of parameters could be applied across the native range of loblolly pine in the southeastern U.S.; however, certain parameters, when necessary, could be modified to improve predictions in other parts of the world where loblolly pine is grown.

## 2. Materials and methods

### 2.1. An overview of the 3-PG model

The 3-PG model (Landsberg and Waring, 1997) is a stand-level model that uses monthly weather data (e.g., global radiation, rainfall, number of rainy days, number of frost days and mean minimum and maximum temperatures) to predict growth of even-aged, mono-specific stands. The model also requires initial values of site characteristics such as soil texture class and upper and lower limits of available soil water (mm), as well as stand data about initial age, latitude of stand location, stocking (trees ha$^{-1}$) and biomass (Mg ha$^{-1}$) in roots (WR), foliage (WF) and stem (stemwood + bark + branches, WS). The 3-PG model has different submodules to estimate NPP, biomass allocation, population dynamics and soil water balance at monthly intervals. A detailed description of the model can be found in Landsberg and Waring (1997) and Landsberg and Sands (2011). In this study we used the 3-PG version 3-PGpjs2.7 (Sands, 2010), implemented as a Microsoft Excel spreadsheet. The user-interface was modified allowing the user to change FR using SI, and initial biomass using tree density, age, mean dbh and mean tree height.

### 2.2. Parameter estimation

Table 1 shows a summary of stand characteristics of the studies used for model fitting and parameter estimation. SI was estimated as the mean height of dominant and co-dominant trees at a base age of 25 years. For all sites in the U.S., SI was estimated with the height measurement at the age closest to 25 years using the equation reported by Diéguez-Aranda et al. (2006). For sites in Uruguay, SI

**Table 1**
Summary of data used for parameter estimation.

| Project | Site | Institution | $n$ | Lat. | Long. | AGE (yrs) | Dq (cm) | Nha (trees $ha^{-1}$) | BA ($m^2$ $ha^{-1}$) | SI (m) | Parameters estimated |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Ameriflux | US-NC2 | NCSU | 4 | 35.80 | −76.67 | 15–16 | 25.0–26.4 | 630–650 | 31.0–34.2 | 20.3–22.7 | I |
| IMPAC | Gainesville | FBRC | 12 | 29.76 | −82.29 | 3–25 | 1.0–24.9 | 692–1538 | 0.1–50.1 | 13.9–27.2 | II, IV, V, VI, VII, VIII |
| PPINES | Sanderson | FBRC | 96 | 30.24 | −82.33 | 2–14 | 2.0–20.7 | 988–2964 | 0.4–45.5 | 17.1–30.7 | III, IV |
| PPINES | Waverly | FBRC | 86 | 31.13 | −81.75 | 2–14 | 2.2–21.5 | 988–2964 | 0.5–52.9 | 24.4–31.7 | III, IV, VIII |
| SAGCD | Various (18)[a] | PMRC | 250 | | | 2–12 | 1.1–32.1 | 205–1810 | 0.1–54.8 | 14.0–29.2 | III, VII |
| CPCD | Various (14)[a] | PMRC | 192 | | | 4–12 | 0.1–24.3 | 401–4485 | 0.1–46.3 | 16.8–33.2 | II, III, VI |
| GSSS | Various (25)[a] | WGFTIP | 437 | | | 5–20 | 0.1–27.0 | 232–4483 | 0.1–55.0 | 18.3–30.4 | III, VII |
| RS2 | Various (11)[a] | FPC | 141 | | | 4–23 | 0.2–30.9 | 156–2050 | 0.1–48.2 | 15.5–26.8 | III |
| RS5 | Various (8)[a] | FPC | 196 | | | 11–31 | 14.1–30.3 | 225–2032 | 9.0–47.6 | 15.6–25.6 | III |
| RS8 | Various (26)[a] | FPC | 96 | | | 9–33 | 7.5–30.7 | 252–2590 | 4.7–52.1 | 15.1–24.3 | III |
| N.A. | Tacuarembó | CAMBIUM | 24 | | | 3–34 | 6.9–40.1 | 256–1381 | 5.1–55.3 | 20.9–29.8 | V, VII |
| Total | | | 1506 | | | 2–34 | 0.1–40.1 | 156–4485 | 0.1–55.3 | 13.9–33.2 | |

$n$: number of plots; AGE: range of age (yrs); Dq: range of quadratic mean diameter (cm); BA: range of basal area ($m^2$ $ha^{-1}$); SI: range of site index (m).
I: canopy conductance; II: NPP partitioning; III: density-dependent tree mortality; IV: canopy cover; V: needlefall; VI: dbh–Ht relationship; VII: Dq–STEM relationship; VIII: FR–SI relationship.
[a] Multiple sites were used.

was estimated with an operational function used by Cambium Forestal Uruguay S.A. and a reference age of 15 years (Daniel Ramirez, personal communication).

All model fitting and data analyses were performed using SAS 9.3 (SAS Inc., Cary, NC, USA). When boundary line fitting was performed, we used the quantile regression procedure with a quantile threshold of 0.99. When multiple variables were included in the fitted model, we used a logarithm transformation and a stepwise procedure with a threshold significance value of 0.15 as variable selection criteria. All variables included in the model with a variance inflation factor (VIF) larger than 5 were discarded, as suggested by Neter et al. (1996). As non-linear model fitting was carried out, an empirical $R^2$ (Myers, 2000) was determined as:

$$R^2 = 1 - \frac{\mathrm{SSE}/df_e}{\mathrm{SST}/df_t} \quad (1)$$

where SSE and SST are the sum of squares of residuals and total, respectively, and $df_e$ and $df_t$ are the degrees of freedom of error and total, respectively.

*2.2.1. Canopy conductance*

Estimates of maximum (MaxCond, m $s^{-1}$) canopy conductance and stomatal response to VPD (CoeffCond, $mb^{-1}$) were obtained using two years of data from the US-NC2 long-term eddy covariance site, located in the lower Coastal Plain of North Carolina, USA (39°48′N, 76°40′W) (Noormets et al., 2010). The stand was 15–16 years old, with peak projected LAI of 4.0–4.3 $m^2$ $m^{-2}$ and mean tree height of 12–15 m. Further details of the study sites and measurement techniques can be found in Domec et al. (2009) and Noormets et al. (2010). Similar to Gonzalez-Benecke et al. (2014a), MaxCond and CoeffCond were estimated using meteorological measurements recorded with an automated weather station, latent heat fluxes from eddy-covariance measurements, and canopy conductance for water vapor was computed using an inverted form of the Penman–Monteith equation.

*2.2.2. NPP partitioning*

Previous versions of 3-PG allocated NPP to the three main tree components (foliage, stem and roots) using the ratio of foliage to stem mass (pFS) as a function of tree diameter. To better understand allocation pattern dynamics we used data from two long-term, replicated studies: CPCD (Coastal Plain Intensive Culture/Density Studies, from PMRC) and IMPAC (Intensive Management Practices Assessment Center, from FBRC). The CPCD dataset consisted of 192 plots that ranged in age from 4 to 12 years and the IMPAC dataset consisted of 12 plots that ranged in age from between 3 and 25 years (Table 1). For each study, we had access to the repeated measures raw inventory data. For all plots, above-ground biomass (foliage, branch, bark, stemwood) was calculated using the general functions reported in Gonzalez-Benecke et al. (2014b). Aboveground Net Primary Production (ANPP, Mg $ha^{-1}$ $year^{-1}$) was calculated for each measurement interval as the net increment in woody biomass + foliage production during that period. Woody Biomass included increments in woody biomass (Iw, Mg $ha^{-1}$ $year^{-1}$) and the biomass of dead trees as suggested by Martin and Jokela (2004). For each plot and measurement, needlefall (NF, Mg $ha^{-1}$ $year^{-1}$), branchfall (BF, Mg $ha^{-1}$ $year^{-1}$) and litterfall (LF, Mg $ha^{-1}$ $year^{-1}$) were calculated using the functions reported by Gonzalez-Benecke et al. (2012). Foliage production (If, Mg $ha^{-1}$ $year^{-1}$) was assumed to be equal to the average of needlefall for the measurement interval. Woody biomass production (Iw) was assumed to be equal to net increment in woody biomass and included BF for the measurement interval.

We fitted a non-linear model to estimate the ratio between NPP allocation to foliage and NPP allocation to stem (pFS). The original equation used in 3-PG was an exponential decay to a non-zero asymptote function that correlated Age and pFS (Landsberg and Waring, 1997). That model was later modified by Gonzalez-Benecke et al. (2014a) using BA instead of Age. Upon further analysis we examined Age, BA and other stand attributes such as Nha, Dq and SDI. The model finally selected included stand Age and Dq to estimate pFS:

$$\mathrm{pFS} = a1 \cdot \mathrm{Age}^{a2} \cdot \mathrm{Dq}^{a3} \quad (2)$$

where $a1$ to $a3$ are curve fit parameters (denoted in 3-PG as pFSC, pFSAge and pFSQMD, respectively).

*2.2.3. Tree mortality and self-thinning*

Parameter estimates for density-independent tree mortality (i.e. stochastic mortality that occurs prior to the onset of mortality due to intra-specific competition) were obtained after adapting the survival model reported by Harrison and Borders (1996). Similar to Gonzalez-Benecke et al. (2014a), we ran the model of Harrison and Borders (1996) under different conditions of planting density and SI, and then fitted the model of Sands (2004) to that dataset to maintain parsimony in the 3-PG model structure:

$$\gamma Nt = \gamma N1 + (\gamma N0 - \gamma N1) \cdot e^{\left(-\ln(2) \cdot \frac{\mathrm{Age}}{\mathrm{Age}_\gamma}\right)} \quad (3)$$

where $e$ is the base of natural logarithm, $\gamma N1$ is the mortality rate of mature stands, $\gamma N0$ is the mortality rate at age = 0 (seedling mortality rate), and $\mathrm{Age}_\gamma$ is the age at which $\gamma Nt = \frac{1}{2} \cdot (\gamma N0 + \gamma N1)$.

Parameter estimates for density-dependent tree mortality (WSx1000, the single tree stem biomass at a stand density of 1000 trees $ha^{-1}$, and thinPower, the self-thinning rule parameter) were computed from permanent plot data (Table 1), after using a species-specific general biomass equation for WS reported by Gonzalez-Benecke et al. (2014b). The dataset used for model fitting consisted of 8842 observations (repeated plot x age measurements), including trees from 2 to 33 years old, with WS ranging between 0.1 and 367 kg $tree^{-1}$, growing in stands with Nha and SI ranging between 156 and 4485 trees $ha^{-1}$ and 14–33 m, respectively. Similar to Gonzalez-Benecke et al. (2014a), value of thinPower was determined using linear fitting to the boundary line of the transformed data of mean plot WS and Nha for each year and each site; the value of WSx1000 was calculated after solving the fitted equation using Nha = 1000.

*2.2.4. Allometric relationships*

Initial biomass pools (WF, WS and WR) are needed for model initialization. If the model user has no initial biomass estimations for the stand to be simulated, general biomass functions for foliage and stem that use dbh, Ht and age can be used as predictors. Using the dataset reported in Gonzalez-Benecke et al. (2014b), allometric relationships for WS, WF and branch and bark fraction (pBB) were obtained. The model for pBB was needed to estimate stemwood biomass by subtracting branch and stembark biomass from WS. The dataset consisted of a collection of several sources used previously for site-specific allometric functions (further details can be found in Gonzalez-Benecke et al., 2014b), including 744 trees measured at 25 sites, with age, dbh and height ranging between 2 and 30 years old, 1.3–32.6 cm and 1.5–22.9 m, respectively. For stands where dbh and Ht were known, WF and WS were estimated by the model:

$$W_{F,S} = w1 \cdot \mathrm{dbh}^{w2} \cdot \mathrm{Ht}^{w3} \cdot \mathrm{Age}^{w4} \tag{4}$$

where $W_{F,S}$ is the dry mass of foliage ($F$) or stem ($S$), and $w1$–$w4$ are curve fit parameters.

In order to estimate WR, a model was fitted to estimate the ratio between WR and WS (RFrac) using data from Kinerson et al. (1977), Gibson et al. (1985), Tuttle (1978), Adegbidi et al. (2002), and Roth et al. (2007). When RFrac was known, WR was determined as: WR = RFrac · WS. The dataset consisted of 168 trees from 2 to 27 years old, with dbh and height ranging between 0.3–26.7 cm and 2.0–18.6 m, respectively. The data were collected across the natural range of the species distribution, under different management and stand development conditions. The root systems were excavated to a depth of 40 cm in a 1 $m^2$ pit around the stump of each selected tree, and all live pine roots larger than a 2 mm diameter were weighed. We determined RFrac as a function of age as follows:

$$\mathrm{RFrac} = r0 + r1 \cdot e^{(r2 \cdot \mathrm{Age})} \tag{5}$$

where $e$ is the base of natural logarithm, and $r0$–$r2$ are curve fit parameters. Other predictors were tested, such as dbh, height and Nha, but this model showed the better goodness of fit.

Similar to Gonzalez-Benecke et al. (2014a), alternative allometric models were developed to estimate initial WS, WF and WR for young stands when dbh was not available, using total tree height (Ht, m) and age as the main predictors. For WS and WF, the data consisted of 338 trees measured at 10 sites, including trees from 1 to 4 years old, with Ht ranging between 0.9 and 6.0 m (Colbert et al., 1990; Roth et al., 2007; Samuelson et al., 2004; Maier et al., 2012). For WR we used the same relationship described previously. For young stands, when dbh data were not available, the model selected was:

$$W_{F,S} = w1 \cdot \mathrm{Ht}^{w2} \cdot \mathrm{Age}^{w3} \tag{6}$$

where $W_{F,S}$ is the dry mass of foliage ($F$) or stem ($S$), and $w1$–$w3$ are curve fit parameters.

The relationship between age and pBB was fitted using an exponential decay to a non-zero asymptote function (Sands and Landsberg, 2002):

$$\mathrm{pBB} = \mathrm{pBB1} + (\mathrm{pBB0} - \mathrm{pBB1}) \cdot e^{\left(-\ln(2) \cdot \frac{\mathrm{Age}}{\mathrm{Age_{BB}}}\right)} \tag{7}$$

where $e$ is the base of natural logarithm, pBB1 is the branch and bark fraction of mature stands, pBB0 is the branch and bark fraction at age = 0 (planting), and $\mathrm{Age_{BB}}$ is the age at which $\mathrm{pBB} = \frac{1}{2} \cdot (\mathrm{fracBB0} + \mathrm{fracBB1})$. Similar to allometric relationships described previously, we used the dataset reported by Gonzalez-Benecke et al. (2014b). This dataset included 427 trees measured at 11 sites, with age, dbh and height ranging between 2 and 25 years old, 1.3–30.1 cm and 1.5–21.3 m, respectively.

The relationship between Dq and mean tree height ($H$, $m$) was obtained from permanent plot data. We fitted separate models for stands growing in the southeastern U.S. (7334 paired Dq–$H$ data were used, including trees from 2 to 25 years old, with Dq and $H$ ranging between 0.3–37.8 cm and 1.4–26.3 m, respectively) and stands growing in Uruguay (175 paired Dq–$H$ data were used, including trees from 3 to 34 years old, with Dq and $H$ ranging between 6.9–40.1 cm and 4.5–26.6 m, respectively) (Table 1). The relationship between Dq and $H$ was fitted using several stand-level variables as covariates. The variables considered were Age, Nha and BA, which represented different characteristics of the stands, such as stocking, productivity and competition, which could affect the height-diameter relationships. The model finally selected to estimate mean height was:

$$H = h1 \cdot \mathrm{Dq}^{h2} \cdot \mathrm{Age}^{h3} \cdot \mathrm{Nha}^{h4} \tag{8}$$

where $h1$–$h4$ are curve fit parameters (denoted in 3-PG as aH, nHD, nHAge and nHN, respectively).

The original equation in 3-PG used the relationships between WS and dbh to estimate dbh from a known WS (Landsberg and Waring, 1997). As the model used stem diameter to estimate BA, and considering that the model estimated WS (in Mg $ha^{-1}$) directly from NPP, we decided to estimate Dq (the dbh of the tree of mean BA) from stand-level WS, including age and stand density (Nha) as covariates. The model finally selected was:

$$\mathrm{Dq} = b1 + b2 \cdot \mathrm{WS}^{b3} \cdot \mathrm{Age}^{b4} \cdot \mathrm{Nha}^{b5} \tag{9}$$

where $b1$–$b5$ are curve fit parameters (denoted in 3-PG as a11Ws, a1Ws, n1Ws, n2Ws and n3Ws, respectively). For stands growing in the southeastern U.S. we computed WS using the general biomass equation reported by Gonzalez-Benecke et al. (2014b); for stands growing in Uruguay, South America, we computed WS using the biomass equations reported by Fassola et al. (2012). Table 1 describes the data used for the Dq–WS analysis.

After bole volume inside bark (VIB, $m^3$ $ha^{-1}$) was computed, we estimated bole volume outside bark (VOB, $m^3$ $ha^{-1}$) from VIB using the term Vratio, which is the ratio between VOB and VIB using the same approach described by Gonzalez-Benecke et al. (2014a). We created the dataset needed for model fitting by running the growth and yield model reported by Harrison and Borders (1996) for a rotation length of 30 years under different conditions of planting density (500, 1500 and 2500 trees $ha^{-1}$) and SI (15, 23 and 30 m). The relationship between Vratio and VIB was also fitted using several stand-level variables as covariates. The model finally selected to estimate Vratio was:

$$\mathrm{Vratio} = r1 \cdot \mathrm{VIB}^{r2} \cdot \mathrm{Nha}^{r3} \cdot \mathrm{Age}^{r4} \tag{10}$$

where $r1$–$r4$ are curve fit parameters (denoted in 3-PG as aVR, nVRVi, nVRN and nVRAge, respectively).

### 2.2.5. Wood specific gravity

Wood specific gravity (SG) was needed to convert stemwood mass (Mg $ha^{-1}$) to VIB. As it has been documented that SG differs between trees growing in the United States and South America (Higa et al., 1973; Barrichelo et al., 1977), we developed separate models for each geographic location. For trees growing in the southeastern U.S. we used the data reported by Gonzalez-Benecke et al. (2011) and fitted a new model that maintained parsimony with the 3-PG model structure. For trees growing in South America (Argentina, Brazil and Uruguay), we used data reported by Higa et al. (1973), Barrichelo et al. (1977), Pereyra and Gelid (2002), Weber (2005), Von Wallis et al. (2007), Pezzutti (2011), and Barth et al. (2013). The relationships between age and wood specific gravity (SG) were determined by fitting the model proposed by Sands (2010):

$$SG = \rho_1 + (\rho_0 - \rho_1) \cdot e^{\left(-\ln(2) \cdot \frac{Age}{Age_\rho}\right)} \quad (11)$$

where $e$ is the base of natural logarithm, $\rho_1$ is the SG of mature stands, $\rho_0$ is the SG at age = 0, and $Age_\rho$ is the age at which $SG = \frac{1}{2} \cdot (\rho_0 + \rho_1)$.

### 2.2.6. Specific needle area

Data used to determine the relationships between age and specific needle area (SNA, $m^2$ $kg^{-1}$) were obtained from the literature review (see Fig. 8 for list of references used). We fitted the model proposed by Sands (2010):

$$SNA = \sigma_1 + (\sigma_0 - \sigma_1) \cdot e^{\left(-\ln(2) \cdot \left(\frac{Age}{Age_\sigma}\right)^2\right)} \quad (12)$$

where $e$ is the base of natural logarithm, $\sigma_1$ is the SNA of mature stands $\sigma_0$ is the SNA at age = 0; and $Age_\sigma$ is the age at which $SNA = \frac{1}{2} \cdot (\sigma_0 + \sigma_1)$.

### 2.2.7. Canopy cover

We used data from 182 plots installed in two PPINES (Pine Productivity Interactions on Experimental Sites, from FBRC) studies in FL and GA (Table 1) to analyze canopy cover dynamics of young loblolly pine stands. These studies were selected because they provided long-term repeated measurements of canopy cover development under contrasting conditions. The studies included the combinations of two contrasting silvicultural treatments (operational and high intensity), two contrasting planting densities (1334 and 2990 trees $ha^{-1}$), and seven different loblolly pine full-sib genetic families. Further details can be found in Roth et al. (2007). The dataset included yearly measurements of dbh and Ht, from age 2 to 14 years, and live crown widths at ages 3, 4 and 5 years. For each measured tree, live crown area (CA, $m^2$) was determined assuming an elliptical crown shape. Following the approach of Gonzalez-Benecke et al (2014a), for each site and plot (that included the combination of planting density, culture and genetic family), a model was fitted to estimate CA as a function of dbh:

$$CA = a \cdot dbh^b \quad (13)$$

Only the effect of genetic family was significant in the allometry of CA and no effect of site, planting density and culture was detected ($P > 0.18$, data not shown). Using family-specific models, CA was calculated for all measured trees. Following Gonzalez-Benecke et al. (2014a), the sum of CA for each plot was expressed as a proportion of the area of the plot and the variable CanCover was determined for each age. After canopy closure the relationship used in this study would not be adequate as the allometry of crown width changes (Pretzsch et al., 2012). As 3-PG uses a maximum value of CanCover of 1 (not accounting for overlapping branches), values of CanCover greater than 1 were assumed to be 1. A function to describe the dynamics of CanCover prior to reaching full canopy closure was fitted using age and other stand attributes such as Dq, SDI, BA and Nha. The model finally selected to estimate mean CanCover was:

$$CanCover = c1 \cdot BA^{c2} \cdot Age^{c3} \quad (14)$$

where $c1$–$c3$ are curve fit parameters (denoted in 3-PG as aCan, nCanBA, nCanAge, respectively).

### 2.2.8. Needlefall, litterfall and forest floor accumulation

We followed the approach of Gonzalez-Benecke et al. (2014a) to analyze the dynamics of monthly fractional rate of needlefall ($\gamma N$, $month^{-1}$), using needlefall (NF, Mg $ha^{-1}$ $month^{-1}$) data from the IMPAC study (Dalla-Tea and Jokela, 1991; Jokela and Martin, 2000). Phenological month for needlefall (NMonth) was defined as starting in May (NMonth = 1) and ending in April (Nmonth = 12). After expressing $\gamma N$ as a proportion of annual maximum $\gamma N$ ($\gamma Nx$, $month^{-1}$), a non-linear model was fitted to the relationship between NMonth and the monthly average $\gamma N$. The final model was:

$$\frac{\gamma N}{\gamma Nx} = \frac{\gamma N1 + \gamma N2 * NMonth}{1 + \gamma N3 * NMonth + \gamma N4 * NMonth^2 + \gamma N5 * NMonth^3} \quad (15)$$

where $\gamma N1$ to $\gamma N5$ are curve fit parameters.

To estimate litterfall (LF, Mg $ha^{-1}$ $month^{-1}$), we used the model ratio between NF and LF reported by Gonzalez-Benecke et al. (2014a). Using LF and a litter decay rate = 0.15 (Binkley, 2002), we incorporated into 3-PG the calculation of forest floor accumulation (Mg $ha^{-1}$).

### 2.2.9. Effect of frost on production

Previous versions of 3-PG have incorporated the effects of frost on canopy conductance by using a factor called kF, the number of days of production lost per frost day. The frost-dependent growth modifier fFrost depended on kF and the number of frost days (FrostDay) and was calculated as fFrost = 1 − kF·FrostDay/30. The effect of frost on stand production was assumed to be independent of frost intensity. For example, Sands and Landsberg (2002) used kF = 0 for *Eucalyptus globulus*, assuming that there is no effect of frost on production, or Bryars et al. (2013) used kF = 1 for loblolly pine, assuming that there is one day of production lost per each frost day. Based on observations of Teskey et al. (1987) and Polster and Fuchs (1963), as redrawn in Larcher (1995), the reduction in photosynthesis or leaf conductance depended on the intensity of frost. Thus, we modified the fFrost function to account for the effect of frost intensity. The impact of frost on growth reduction was conducted using data reported in Teskey et al. (1987), where maximum leaf conductance during the day following a frost night was correlated with minimum night temperature on 8 year-old trees. After expressing conductance relative to conductance at 0 °C (fractional conductance, kF), the model used was:

$$kF = e^{(tF \cdot Tmin)} \quad (16)$$

where $e$ is the base of natural logarithm, tF is the rate of production loss per degree celsius below zero and Tmin is the minimum temperature of each frost day. For days when Tmin > 0, fFrost was set equal to 1. Using this parameter, fFrost was calculated as:

$$fFrost = 1 - (1 - e^{(tF \cdot Tmin)}) \cdot FrostDay/30 \quad (17)$$

where $e$ is the base of natural logarithm and FrostDay is the number of frost days of each month.

### 2.2.10. Fertility rating

Following Gonzalez-Benecke et al. (2014a), we used the approach of correlating FR with changes in site index (SI, m). Using this approach, FR was the only parameter obtained from calibration and not from observed/reported data. The relationship between FR and SI was analyzed using data from 47 permanent plots from the PINEMAP dataset, installed at 12 sites, one site per state: two studies from FBRC, one from FMRC, six from FPC, one from PMRC and two from WGFTIP. The first selection criteria was that all sites would have at least 10 years of measurement interval. Then, all sites were randomly selected to account for variability in geographic location within each state (avoid two sites in same county). On each site, 3–4 plots were randomly selected. We also included data from 16 permanent plots from the CAPPS study (Consortium for Accelerated Pine Production Studies, from PMRC) installed in GA. The treatments applied in each of the 63 plots created a wide range in productivity, similar to the range in productivity found in operational and experimental plots in the southeastern United States (Fox et al., 2007). The dataset consisted of 510 plot-level data points, including stands from 2 to 27 years old, with Nha and SI ranging between 302–4434 trees $ha^{-1}$ and 13.9–33.1 m, respectively (Table 2). On each plot, total above-ground biomass (AGB, Mg $ha^{-1}$) was determined using the general biomass function reported by Gonzalez-Benecke et al. (2014b).

Similar to Gonzalez-Benecke et al. (2014a), after obtaining all parameter estimates required by 3-PG, we determined the value of FR that minimized the error of AGB, by recording for each plot the value that had the minimum mean square error of the fitting between the observed and predicted AGB (including all measurements). Finally, after pooling all paired data from all 63 plots, SI was correlated with the optimum FR. The following sigmoidal curve was finally selected to estimate FR:

$$\mathrm{FR} = \frac{f1}{1 + f2 \cdot e^{(-f3 \cdot \mathrm{SI})}} \tag{18}$$

where $e$ is the base of natural logarithm $f1$–$f3$ are curve fit parameters. Once the FR function had been developed by calibration, it was applied unchanged to the validation data set. This is in contrast to most applications of the model, in which the FR parameter is used as a "tuning" parameter.

### 2.2.11. Parameters obtained from literature review

All other parameter estimates shown in Table 4 were obtained from previous reports of 3-PG parameterizations for loblolly pine (Table 4). From Sampson et al. (2006), canopy quantum yield $\alpha_c$ = 0.053 mol C $mol^{-1}$ photon, and the age modifiers MaxAge, nAge and rAge = 200, 1.5 and 0.75. From Bryars et al. (2013), maximum (pRx) and minimum (pRn) fraction of NPP to roots = 0.4 and 0.2; temperature modifiers Tmin, Topt and Tmax = 4, 25 and 38 °C; fertility effects factors m0, fNo and fNn = 0, 0.3 and 1; maximum proportion rainfall canopy interception Maxintcptn = 0.2; LAI for maximum rainfall interception LAImaxIntcp = 5; light extinction coefficient $k$ = 0.57; monthly root turnover = 0.0168.

## 2.3. Model evaluation

The independent validation dataset included data from 91 permanent plots distributed in 24 sites in 12 states in the southeastern U.S. (two sites per state). The model was also validated against data from 10 permanent plots growing in operational stands in Tacuarembó, Uruguay (properties of Cambium Forestal Uruguay S.A.). Fig. 1 shows the location of all validation sites. An additional validation was conducted on projected LAI (LAI, $m^2\,m^{-2}$) estimates using data from IMPAC study (Jokela and Martin, 2000), where monthly LAI was estimated from needlefall collected monthly from age 6 to 19 years, using six circular litter traps (1 $m^2$) installed in each of the 12 study plots (see Section 2.2.8). Further details of LAI calculations can be found in Jokela and Martin (2000). On each plot, we modified FR using the observed SI and the FR–SI relationship reported in this study.

The performance of 3-PG for loblolly pine was compared against independent data not used in model development. The goodness-of-fit between the observed and predicted values was evaluated using three measures of accuracy: (i) root mean square error (RMSE); (ii) mean bias error (Bias, the difference between observed and predicted values); and (iii) coefficient of determination ($R^2$). Variables evaluated included BA, Nha, H, AGB and VOB. For each plot, observed VOB was computed with the function reported by Van Deusen et al. (1981); observed AGB was computed using the general biomass function reported by Gonzalez-Benecke et al. (2014a). For sites in Uruguay, functions to estimate VOB were not available and VIB was used instead, and was computed with the function reported by Rachid et al. (2014). Observed AGB for the Uruguay sites was computed using the function reported by Fassola et al. (2012). For each variable, we used $F$-tests to determine if the relationship between predicted and observed values had a slope and intercept different than one and zero, respectively. All statistical analyses were performed using SAS 9.3 (SAS Inc., Cary, NC, USA).

Model validation was conducted by running the model from age of first measurement to the age of last measurement. Initial biomass pools to initialize the model were determined for each plot using the equations for WF, WS and WR reported in this study. Table 2 shows a summary of stand characteristics for each site used for model validation and FR/SI calibration.

## 2.4. Climate and soil data

The weather data consisted of monthly average daily maximum (Tmax, °C) and minimum (Tmin, °C) temperature, monthly total rainfall (Rain, mm $month^{-1}$), monthly average daily total solar radiation (MJ $m^{-2}\,day^{-1}$), number of rainy days (the number days with rainfall > 1 mm, $month^{-1}$) and number of frost days (the number of days with Tmin < 0 °C, $month^{-1}$). For the AMERIFLUX study, weather data were collected from an automatic weather station installed at the site (Noormets et al., 2010). For all other sites in the U.S., daily weather data were obtained online from the University of Idaho Gridded Surface Meteorological Dataset (http://climate.nkn.uidaho.edu/METDATA/), and selecting the weather station nearest to each study site. For sites from Uruguay, daily weather data were obtained online from the Instituto Nacional de Investigación Agropecuaria (http://www.inia.org.uy/online/site/gras.php), and selecting the weather station at INIA-Tacuarembó. The soils data collected were texture class (s: sandy; sl: sandy-loam; cl: clay), and maximum and minimum available soil water (mm). For all sites in the U.S., soils data were obtained online from the USDA's National Resources Conservation Service (http://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx), using site coordinates. For sites in Uruguay, soils data were available from soil classification maps for each site using the soil classification of CONEAT (Comisión Nacional de Estudio Agro económico de la Tierra; www.prenader.gub.uy/coneat/). A summary of soil and weather data of all sites used for model validation and FR/SI analysis is presented in Table 3.

**Table 2**
Summary of data used for model validation and FR/SI calibration.

| State | County | Institution | *n* | Lat. | Long. | AGE (yrs) | Dq (cm) | Nha (trees $ha^{-1}$) | BA ($m^2$ $ha^{-1}$) | SI (m) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|
| AL | Bibb | FPC | 4[a] | 33.03 | −87.21 | 18–26 | 18.8–28.8 | 302–336 | 8.4–21.9 | 17.8–19.8 | 1 |
| | Butler | FPC | 4 | 31.57 | −86.67 | 4–18 | 2.7–20.8 | 923–1369 | 0.5–36.2 | 20.8–23.7 | 2 |
| | St. Clair | PMRC | 4 | 33.84 | −86.30 | 2–12 | 0.1–24.1 | 355–1494 | 0.1–38.3 | 21.6–25.4 | 3 |
| AR | Bradley | FPC | 4[a] | 33.59 | −92.17 | 19–27 | 21.9–29.4 | 358–494 | 15.6–30 | 18.3–20.1 | 1 |
| | Hempstead | WGFTIP | 4 | 33.96 | −93.75 | 5–20 | 6.6–27.8 | 333–969 | 2.6–34.4 | 20.5–21.6 | 4 |
| | Perry | FMRC | 3 | 34.88 | −93.07 | 15–30 | 15.8–29.2 | 652–1265 | 17.8–47 | 17.2–18.5 | 5 |
| FL | Alachua | FBRC | 4[a] | 29.76 | −82.29 | 4–25 | 2.4–21.8 | 1010–1497 | 0.6–44.3 | 15.0–23.0 | 6 |
| | Santa Rosa | FPC | 4 | 30.77 | −86.97 | 5–13 | 4–13.7 | 1262–1441 | 1.6–20.9 | 15.5–19.9 | 7 |
| | Taylor | FBRC | 4 | 30.16 | −83.75 | 2–14 | 2.7–25.4 | 1070–2902 | 0.7–54.8 | 27.2–32.9 | 8 |
| GA | Camden | FBRC | 4[a] | 31.13 | −81.75 | 2–14 | 3.3–22.3 | 1098–2779 | 1.1–48.6 | 27.1–28.8 | 8 |
| | Jones | FPC | 4 | 33.10 | −83.60 | 25–33 | 19.8–30.3 | 333–428 | 12.9–24.7 | 15.5–18.5 | 1 |
| | Stewart | FMRC | 3 | 32.12 | −84.66 | 6–17 | 7.1–17.1 | 1532–1775 | 7.0–37.7 | 17.7–18.8 | 5 |
| | Clarke | PMRC | 4[a] | 33.60 | −83.38 | 2–15 | 0.5–21.0 | 1230–1580 | 0.1–45.2 | 24.5–29.5 | 9 |
| | Jasper | PMRC | 4[a] | 33.32 | −83.39 | 2–15 | 0.7–20.5 | 1200–1588 | 0.2–42.2 | 23.7–29.3 | 9 |
| | Tift | PMRC | 4[a] | 31.30 | −83.51 | 3–15 | 1.6–22.1 | 1070–1440 | 0.5–40.9 | 27.6–29.0 | 9 |
| | Pierce | PMRC | 4[a] | 31.10 | −82.42 | 2–15 | 0.8–20.9 | 1356–1660 | 0.2–46.6 | 26.1–32.8 | 9 |
| LA | Allen | WGFTIP | 4[a] | 30.65 | −92.82 | 5–20 | 2.1–22.6 | 890–1268 | 0.4–40.5 | 18.2–20.1 | 4 |
| | Bienville | FPC | 4 | 32.32 | −92.83 | 16–24 | 14.6–20.2 | 1161–1482 | 23.9–40.6 | 16.8–17.7 | 10 |
| | Washington | FPC | 4 | 30.85 | −90.04 | 14–24 | 12.5–17.2 | 1418–1912 | 21.6–36.5 | 14.1–17.7 | 10 |
| MS | Kemper | FPC | 4 | 32.75 | −88.45 | 11–19 | 15.1–22.5 | 787–896 | 14.2–35.8 | 20.3–22.4 | 10 |
| | Marion | FPC | 4[a] | 31.38 | −90.27 | 4–14 | 4–18.8 | 914–1778 | 1.8–30.7 | 22.0–24.6 | 2 |
| | Pontotoc | WGFTIP | 4 | 34.28 | −88.92 | 5–20 | 7.3–24.1 | 458–1339 | 4.2–37.4 | 21.3–22.6 | 4 |
| NC | Bertie | FPC | 4[a] | 36.21 | −76.95 | 10–20 | 12.3–20.5 | 1428–1517 | 17.2–50.2 | 19.7–20.5 | 10 |
| | Bladen | FPC | 4 | 34.60 | −78.60 | 4–23 | 3–26.9 | 726–1508 | 1.0–42.8 | 23.1–26.8 | 2 |
| | Chatham | FMRC | 3 | 35.63 | −79.08 | 24–39 | 19.1–25.6 | 396–1260 | 17.4–39.9 | 15.4–17.1 | 5 |
| OK | McCurtain | FMRC | 4 | 34.20 | −95.05 | 17–26 | 18.4–36.6 | 226–1252 | 13.3–45.5 | 16.2–18.1 | 5 |
| | Pushmataha | WGFTIP | 4[a] | 34.43 | −95.22 | 5–15 | 3.7–20.5 | 1041–1627 | 1.4–47.6 | 18.7–20.2 | 4 |
| | Pushmataha | WGFTIP | 4 | 34.47 | −95.20 | 5–20 | 4.5–21.6 | 1145–1517 | 2.2–52 | 19.8–21.4 | 4 |
| –SC | Hampton | PMRC | 4 | 32.79 | −80.95 | 2–12 | 2.8–24.2 | 672–1476 | 0.4–39.2 | 28.5–30.3 | 11 |
| | Laurens | PMRC | 4[a] | 34.40 | −81.90 | 4–12 | 2.7–23.2 | 486–4434 | 0.3–46.9 | 21.3–23.4 | 11 |
| | Williams | FPC | 4 | 33.59 | −79.48 | 4–22 | 0.4–23.2 | 736–1340 | 0.1–39.0 | 18.6–20.9 | 2 |
| TN | Bradley | FPC | 4 | 35.02 | −84.84 | 12–22 | 12–18.5 | 1468–2040 | 19.1–48.3 | 17.0–19.3 | 10 |
| | Hardin | FPC | 4 | 35.15 | −88.01 | 5–17 | 4.8–18.2 | 1366–1655 | 2.6–36.2 | 19.3–21.7 | 2 |
| | Rhea | FPC | 4[a] | 35.72 | −84.77 | 12–22 | 14–20.9 | 1330–1411 | 21–45.7 | 16.9–18.4 | 10 |
| TX | Polk | FMRC | 4[a] | 30.77 | −94.82 | 4–14 | 7.6–20.6 | 907–1072 | 4.4–30.4 | 22.3–23.5 | 5 |
| | San Augustine | PMRC | 4 | 31.40 | −94.05 | 2–8 | 0.9–20.7 | 469–2938 | 0.1–35.0 | 23.8–24.6 | 1 |
| | Walker | FMRC | 4 | 31.00 | −95.48 | 19–31 | 16.8–25.3 | 693–1502 | 24–37.3 | 15.2–17.0 | 5 |
| VA | King & Queen | FPC | 4[a] | 37.62 | −76.78 | 4–18 | 2.2–22.3 | 999–1655 | 0.6–41 | 18.2–23.5 | 2 |
| | Prince Edward | FMRC | 3 | 37.13 | −78.40 | 19–34 | 15.2–29.8 | 516–1729 | 19.7–46.1 | 18.8–19.3 | 5 |
| | Sussex | FPC | 4 | 36.88 | −77.07 | 4–18 | 1.5–18.6 | 1314–1550 | 0.2–38.4 | 19.4–21.2 | 2 |
| Uruguay | Tacuarembó | CAMBIUM | 10 | −31.48 | −55.99 | 7–17 | 15.8–40.1 | 255–1000 | 8.8–55.3 | 20.9–29.8 | 1 |
| Total | | | 148 | | | 2–39 | 0.1–30.3 | 226–4434 | 0.1–55.3 | 14.0–32.9 | |

n: number of plots; AGE: range of age (yrs); Dq: range of quadratic mean diameter (cm) across AGE and plots; BA: range of basal area ($m^2$ $ha^{-1}$) across AGE and plots, SI: range of site index at base age = 25 years (m) across plots.
FBRC: Forest Biology Research Cooperative; FMRC: Forest Modeling Research Cooperative; FPC: Forest Productivity Cooperative; PMRC: Plantation Management Research Cooperative; WGFTIP: Western Gulf Forest Tree Improvement Program; CAMBIUM: Cambium S.A.
References: 1: Carlson et al. (2014); 2: Nilsson and Allen (2003); 3: Zhao et al. (2012); 4: Koralewski et al. (2015); 5: Russell et al. (2010); 6: Jokela and Martin (2000); 7: Leggett and Kelting (2006); 8: Roth et al. (2007); 9: Borders et al. (2004); 10: Zhao et al. (2011); and 11: Hynynen et al. (1998).
AL: Alabama; AR: Arkansas; FL: Florida; GA: Georgia; LA: Louisiana; MS: Mississippi; NA: North Carolina; OK: Oklahoma; SC: South Carolina; TN: Tennessee; TX: Texas; and VA: Virginia.
[a] Site used for FR/SI analysis.

## 3. Results

### 3.1. Model fitting

The parameter estimates used by 3-PG for loblolly pine are reported in Table 4. All parameter estimates from model fitting were significant at $P < 0.05$.

There was a negative relationship between canopy conductance (Gc, m $s^{-1}$) and mean daily VPD ($n = 132$; $P < 0.001$; $R^2 = 0.96$). The model fitted to estimate Gc parameters is shown in Fig. 2. Maximum (MaxCond) and minimum (MinCond) canopy conductance, and the response of canopy conductance to VPD (CoeffCond) were 0.0188 m $s^{-1}$, 0 m $s^{-1}$ and 0.0408 $mb^{-1}$, respectively (Table 4).

NPP partitioning was set as a function of Dq and age ($n = 924$; $P < 0.001$; $R^2 = 0.95$). NPP allocation to stem (pS) increased rapidly until reaching values ranging between 0.6 and 0.8 at Dq larger than about 2 cm. Conversely, NPP allocation to foliage (pF) decreased sharply until reaching values ranging between 0.2 and 0.4 at Dq larger than about 3 cm (Fig. 3a). The ratio between pF and pS (pFS) ranged between 0.25 and 0.6 for Dq larger than 5 cm and there was a good agreement between observed and predicted values (Fig. 3b). The parameter estimates of the new pFS function were 0.406, 0.311 and −0.288, for pFSC, pFSAge and pFSD, respectively (Table 4).

Allometric relationships for Dq as a function of stem biomass (WS), mean height (H) as a function of Dq, pBB as a function of

**Table 3**
Summary of soil and weather data of sites used for model validation and FR/SI calibration ([a]).

| State | County | Institution | Soil Class | ASW | Tmin-w | Tmax-s | Rad-w | Rad-s | Rain | Nrain | Nfrost |
|---|---|---|---|---|---|---|---|---|---|---|---|
| AL | Bibb | FPC[a] | SL | 187 | 3.0 | 33.0 | 11.0 | 19.4 | 1,460 | 150 | 31 |
| | Butler | FPC | SL | 227 | 1.0 | 32.6 | 10.4 | 20.0 | 1,421 | 148 | 47 |
| | St. Clair | PMRC | SL | 155 | 0.4 | 32.3 | 10.1 | 20.2 | 1,390 | 148 | 50 |
| AR | Bradley | FPC[a] | SL | 165 | 0.9 | 32.9 | 10.1 | 20.6 | 1,380 | 129 | 44 |
| | Hempstead | WGFTIP | SL | 164 | 0.0 | 32.8 | 10.1 | 20.7 | 1,330 | 131 | 52 |
| | Perry | FMRC | SL | 140 | −1.7 | 32.5 | 10.0 | 20.8 | 1,332 | 129 | 68 |
| FL | Alachua | FBRC[a] | S | 116 | 6.8 | 32.8 | 11.8 | 18.0 | 1,310 | 138 | 11 |
| | Santa Rosa | FPC | SL | 150 | 4.8 | 32.9 | 11.0 | 18.7 | 1,662 | 156 | 20 |
| | Taylor | FBRC | S | 125 | 5.7 | 33.2 | 11.5 | 18.3 | 1,442 | 152 | 17 |
| GA | Camden | FBRC[a] | SL | 213 | 5.3 | 32.7 | 11.2 | 18.5 | 1,284 | 144 | 14 |
| | Jones | FPC | CL | 218 | 0.5 | 32.6 | 10.5 | 19.8 | 1,207 | 150 | 42 |
| | Stewart | FMRC | SL | 190 | 2.0 | 32.8 | 10.9 | 19.6 | 1,271 | 145 | 33 |
| | Clarke | PMRC[a] | CL | 205 | 4.1 | 36.7 | 12.2 | 22.2 | 1,236 | 131 | 27 |
| | Jasper | PMRC[a] | C | 205 | 4.1 | 35.9 | 11.6 | 22.5 | 1,198 | 130 | 25 |
| | Tift | PMRC[a] | CL | 198 | 1.1 | 36.4 | 10.9 | 22.8 | 1,175 | 119 | 44 |
| | Pierce | PMRC[a] | SL | 178 | 1.3 | 36.7 | 10.7 | 22.8 | 1,181 | 123 | 42 |
| LA | Allen | WGFTIP[a] | SL | 214 | 4.2 | 33.1 | 11.0 | 19.2 | 1,617 | 153 | 23 |
| | Bienville | FPC | CL | 211 | 5.3 | 33.3 | 10.8 | 19.4 | 1,600 | 140 | 15 |
| | Washington | FPC | CL | 241 | 2.4 | 33.6 | 10.5 | 20.3 | 1,379 | 131 | 33 |
| MS | Kemper | FPC | CL | 173 | 3.1 | 32.8 | 11.0 | 19.7 | 1,543 | 149 | 30 |
| | Marion | FPC[a] | CL | 256 | 1.9 | 33.0 | 10.4 | 19.8 | 1,362 | 147 | 40 |
| | Pontotoc | WGFTIP | SL | 175 | 0.6 | 32.5 | 9.8 | 20.4 | 1,470 | 144 | 48 |
| NC | Bertie | FPC[a] | S | 169 | 1.2 | 31.6 | 9.9 | 19.4 | 1,259 | 133 | 44 |
| | Bladen | FPC | SL | 203 | −0.3 | 31.2 | 9.2 | 19.8 | 1,217 | 148 | 56 |
| | Chatham | FMRC | SL | 228 | −1.5 | 31.6 | 9.7 | 20.2 | 1,129 | 140 | 72 |
| OK | McCurtain | PMRC | S | 128 | −0.1 | 33.1 | 10.3 | 21.1 | 1,290 | 131 | 53 |
| | Pushmataha | WGFTIP[a] | SL | 146 | −0.8 | 32.9 | 10.3 | 21.2 | 1,271 | 127 | 61 |
| | Pushmataha | WGFTIP | SL | 184 | −0.8 | 33.1 | 10.2 | 21.1 | 1,278 | 127 | 62 |
| SC | Hampton | PMRC | SL | 148 | 2.4 | 32.2 | 10.2 | 18.9 | 1,263 | 151 | 31 |
| | Laurens | PMRC[a] | S | 166 | 2.9 | 32.9 | 10.6 | 19.1 | 1,258 | 149 | 31 |
| | Williams | FPC | SL | 176 | −0.6 | 32.3 | 10.1 | 20.2 | 1,158 | 140 | 60 |
| TN | Bradley | FPC | CL | 247 | −1.7 | 31.6 | 9.5 | 20.7 | 1,430 | 160 | 72 |
| | Hardin | FPC | SL | 184 | −0.8 | 31.2 | 9.6 | 20.3 | 1,415 | 155 | 62 |
| | Rhea | FPC[a] | S | 123 | −1.8 | 30.7 | 9.2 | 20.3 | 1,391 | 163 | 71 |
| TX | Polk | FMRC[a] | SL | 254 | 2.2 | 33.8 | 10.9 | 20.7 | 1,329 | 127 | 36 |
| | San Augustine | PMRC | SL | 166 | 3.8 | 34.5 | 11.1 | 20.9 | 1,118 | 120 | 22 |
| | Walker | FMRC | SL | 161 | 3.5 | 33.8 | 11.1 | 20.7 | 1,276 | 128 | 31 |
| VA | King & Queen | FPC[a] | CL | 241 | −1.2 | 31.1 | 9.0 | 19.9 | 1,204 | 144 | 67 |
| | Prince Edward | FMRC | SL | 221 | −1.4 | 31.0 | 8.7 | 20.0 | 1,149 | 134 | 69 |
| | Sussex | FPC | SL | 202 | −2.6 | 30.6 | 9.2 | 20.4 | 1,117 | 141 | 81 |
| URUGUAY | Tacuarembó | CAMBIUM | SL | 195 | 4.2 | 33.1 | 11.0 | 19.2 | 1,617 | 153 | 23 |

Soil Class: Soil texture class (s: sandy; sl: sandy-loam; cl: clay); ASW: Available soil water, the difference between maximum and minimum ASW (mm); Tmin-w: average daily minimum temperature of winter months (°C); Tmax-s: average daily maximum temperature of summer months (°C); Rad-w: average daily total solar radiation of winter months (MJ $m^{-2}$ $day^{-1}$); Rad-s: average daily total solar radiation of summer months (MJ $m^{-2}$ $day^{-1}$); Rain: average yearly total rainfall (mm $year^{-1}$), Nrain: average yearly total number of rainy days, Nfrost: average yearly total number of frost days.
Winter months: December 1 to February 28 in U.S., June 1 to August 31 in Uruguay; summer months: June 1 to August 31 in U.S., December 1 to February 28 in Uruguay.
AL: Alabama; AR: Arkansas; FL: Florida; GA: Georgia; LA: Louisiana; MS: Mississippi; NA: North Carolina; OK: Oklahoma; SC: South Carolina; TN: Tennessee; TX: Texas; and VA: Virginia.
Weather data from years used for validation or FR/SI analysis.
[a] Site used for FR/SI calibration.

age, and volume ratio (Vratio) as a function of bole volume inside bark (VIB) are shown in Fig. 4. The model to estimate Dq (Fig. 4a) was dependent on WS (Mg $ha^{-1}$), age and Nha. We fitted separate models for stands growing in the southeastern U.S. ($Dq_{US}$) and Uruguay ($Dq_{UR}$):

$$Dq_{US} = -3.707 + 54.449 \cdot WS^{0.253} \cdot Age^{0.0374} \cdot Nha^{-0.3065}$$
$$(n = 4380;\ P < 0.001;\ R^2 = 0.97)$$
$$Dq_{UR} = -0.142 + 43.721 \cdot WS^{0.353} \cdot Age^{0.0099} \cdot Nha^{-0.3424}$$
$$(n = 181;\ P < 0.001;\ R^2 = 0.98)$$

In this model, the parameter estimate associated with Nha was negative, indicating that for the same WS and age, stands with higher density would have smaller diameters. Differences in model estimations reflect differences in allocation and/or wood specific gravity between geographic areas. For example, a 15-year-old stand with 1000 trees per ha and a WS of 200 Mg $ha^{-1}$, would have, on average, Dq = 24.0 or 29.9 cm, if growing in the southeastern U.S. or Uruguay, respectively.

The model to estimate mean height (Fig. 4b) was dependent on Dq, age and Nha. We fitted separate models for stands growing in the southeastern U.S. ($H_{US}$) and Uruguay ($H_{UR}$):

$$H_{US} = 0.2304 \cdot Dq^{0.9171} \cdot Age^{0.2616} \cdot Nha^{0.1098}$$
$$(n = 7334;\ P < 0.001;\ R^2 = 0.99)$$
$$H_{UR} = 0.0799 \cdot Dq^{0.9226} \cdot Age^{0.3080} \cdot Nha^{0.2439}$$
$$(n = 175;\ P < 0.001;\ R^2 = 0.98).$$

**Table 4**
Description of 3-PG parameters and values for loblolly pine.

| Meaning/Comment | 3-PG symbol | Unit | Value | Sources |
|---|---|---|---|---|
| Biomass partitioning and turnover | | | | |
| *Allometric relationships and partitioning* | | | | |
| Constant in the foliage: stem partitioning ratio relationship | pFSC | – | 0.406 | This study |
| Power of Age in the foliage: stem partitioning ratio relationship | pFSAge | – | 0.311 | This study |
| Power of Dq in the foliage: stem partitioning ratio relationship | pFSD | – | −0.288 | This study |
| Intercept in the Dq v. stem mass relationship | a11Ws | – | −3.707[a] | This study |
| Constant in the Dq v. stem mass relationship | a1Ws | – | 54.44[a] | This study |
| Power in the Dq v. stem mass relationship | n1Ws | – | 0.253[a] | This study |
| Power of Age in the Dq v. stem mass relationship | n2Ws | – | 0.037[a] | This study |
| Power of Nha in the Dq v. stem mass relationship | n3Ws | – | −0.306[a] | This study |
| Maximum fraction of NPP to roots | pRx | – | 0.40 | 1 |
| Minimum fraction of NPP to roots | pRn | – | 0.20 | 1 |
| *Needlefall, litterfall, litter decay and root turnover* | | | | |
| Maximum needlefall rate | $\gamma$Fx | month$^{-1}$ | 0.157 | This study |
| Month at which needlefall rate has maximum value | t$\gamma$Fx | | 11 | This study |
| Average yearly decay rate of litter | | year$^{-1}$ | 0.15 | This study |
| Needlefall to litterfall ratio at age 0 | $NF_0$ | – | 0.733 | This study |
| Needlefall to litterfall ratio for mature stands | $NF_1$ | – | 1.0 | This study |
| Age at which Needlefall to litterfall ratio = ($\sigma$0 + $\sigma$1)/2 | $Age_{NLR}$ | year | 21.5 | This study |
| Average monthly root turnover rate | $\gamma$R | month$^{-1}$ | 0.0168 | 1 |
| NPP and conductance modifiers | | | | |
| *Temperature modifier (fT)* | | | | |
| Minimum temperature for growth | Tmin | °C | 4 | 1 |
| Optimum temperature for growth | Topt | °C | 25 | 1 |
| Maximum temperature for growth | Tmax | °C | 38 | 1 |
| *Frost modifier (fFrost)* | | | | |
| Reduction rate of production per degree Celsius below zero | tF | Day °C$^{-1}$ | 0.178 | This study |
| *Soil water modifier (fSW)* | | | | |
| Moisture ratio deficit for *fq* = 0.5 | SWconst | – | 0.7 | 1 |
| Power of moisture ratio deficit | SWpower | – | 9 | 1 |
| *Fertility effects* | | | | |
| Value of '*m*' when FR = 0 | m0 | – | 0 | 1 |
| Value of 'fNutr' when FR = 0 | fN0 | – | 0.3 | 1 |
| Power of (1-FR) in 'fNutr' | fNn | – | 1 | 1 |
| *Age modifier (fAge)* | | | | |
| Maximum stand age used in age modifier | MaxAge | year | 200 | 2 |
| Power of relative age in function for fAge | nAge | – | 1.5 | 2 |
| Relative age to give fAge = 0.5 | rAge | – | 0.5 | 2 |
| *Stem mortality and self-thinning* | | | | |
| Mortality rate for large t | $\gamma$Nx | % year$^{-1}$ | 0.392 | This study |
| Seedling mortality rate (*t* = 0) | $\gamma$N0 | % year$^{-1}$ | 2.320 | This study |
| Age at which mortality rate has median value | t$\gamma$N | year | 10.853 | This study |
| Shape of mortality response | n$\gamma$N | – | 1 | This study |
| Max. stem mass per tree @ 1000 trees/hectare | wSx1000 | kg tree$^{-1}$ | 230 | This study |
| Power in self-thinning rule | thinPower | – | 1.174 | This study |
| Fraction mean single-tree foliage biomass lost per dead tree | mF | – | 0 | 1 |
| Fraction mean single-tree root biomass lost per dead tree | mR | – | 0.2 | 1 |
| Fraction mean single-tree stem biomass lost per dead tree | mS | – | 0.4 | 1 |
| Canopy structure and processes | | | | |
| *Specific needle area ($\sigma$)* | | | | |
| Specific needle area at age 0 | $\sigma$0 | m$^2$ kg$^{-1}$ | 5.529 | This study |
| Specific leaf area for mature leaves | $\sigma$1 | m$^2$ kg$^{-1}$ | 3.875 | This study |
| Age at which specific needle area = ($\sigma$0 + $\sigma$1)/2 | $t\sigma$ | year | 5.971 | This study |
| *Light interception* | | | | |
| Extinction coefficient for absorption of PAR by canopy | k | – | 0.57 | 1 |
| Constant in the CanCover relationship | aCan | – | 0.258 | This study |
| Power of BA in the CanCover relationship | nCanBA | – | 0.688 | This study |
| Power of Age in the CanCover relationship | nCanAge | – | −0.198 | This study |
| Maximum proportion of rainfall evaporated from canopy | MaxIntcptn | – | 0.2 | 1 |
| LAI for maximum rainfall interception | LAImaxIntcptn | – | 5 | 1 |
| *Production and respiration* | | | | |
| Canopy quantum efficiency | $\alpha_c$ | mol C mol PAR$^{-1}$ | 0.053 | 2 |
| Ratio NPP/GPP | Y | – | 0.47 | 1 |
| *Canopy Conductance (gc)* | | | | |
| Minimum canopy conductance | MinCond | m s$^{-1}$ | 0 | This study |
| Maximum canopy conductance | MaxCond | m s$^{-1}$ | 0.0118 | This study |
| LAI for maximum canopy conductance | LAIgcx | – | 3 | 1 |
| Defines stomatal response to VPD | CoeffCond | mb$^{-1}$ | 0.0408 | This study |

(*continued on next page*)

**Table 4** (*continued*)

| Meaning/Comment | 3-PG symbol | Unit | Value | Sources |
|---|---|---|---|---|
| Canopy boundary layer conductance | BLcond | m s$^{-1}$ | 0.1 | 1 |
| Wood and stand properties | | | | |
| *Branch and bark fraction (pBB)* | | | | |
| Branch and bark fraction at age 0 | pBB0 | – | 1.198 | This study |
| Branch and bark fraction for mature stands | pBB1 | – | 0.235 | This study |
| Age at which pBB = (pBB0 + pBB1)/2 | tBB | year | 1.737 | This study |
| *Wood basic specific gravity* | | | | |
| Minimum basic density – for young trees | $\rho$0 | – | 0.358[b] | This study |
| Maximum basic density – for older trees | $\rho$1 | – | 0.482[b] | This study |
| Age at which rho = (rhoMin + rhoMax)/2 | tRho | year | 7.054[b] | This study |
| *Stem height* | | | | |
| Constant in the Dq v. height relationship | aH | – | 0.230[c] | This study |
| Power of Dq in the Dq v. height relationship | nHD | – | 0.91[c] | This study |
| Power of Age in the Dq v. height relationship | nHAge | – | 0.261[c] | This study |
| Power of Nha in the Dq v. height relationship | nHN | – | 0.110[c] | This study |
| *Volume ratio* | | | | |
| Constant in the bole volume ratio relationship | aVR | – | 1.232 | This study |
| Power of VIB in the bole volume ratio relationship | nVRVi | – | −0.017 | This study |
| Power of Nha in the bole volume ratio relationship | nVRN | – | 0.025 | This study |
| Power of Age in the bole volume ratio relationship | nVRAge | – | −0.030 | This study |

References: 1: Bryars et al. (2013) and 2: Sampson et al. (2006).

[a] For Uruguay a11Ws = −0.143; a1Ws = 43.721; n1Ws = 0.353; n2Ws = −0.0099; and n3Ws = −0.342.

[b] For Uruguay $\rho$0 = 0.328; $\rho$1 = 0.478; and tRho = 6.913.

[c] For Uruguay aH = 0.080; nHD = 0.923; nHAge = 0.308; and nHN = 0.244.

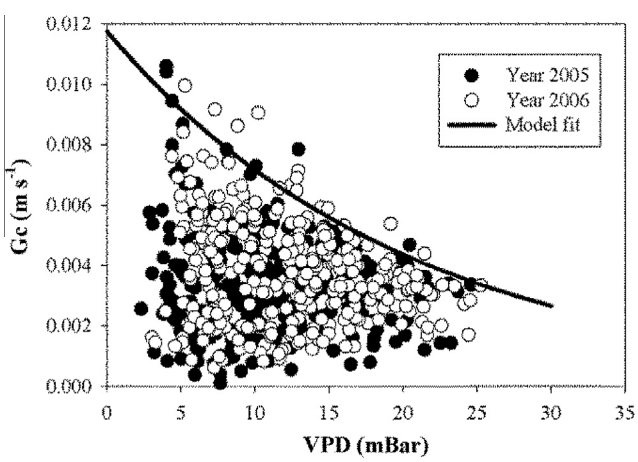


**Fig. 2.** Model fitting for canopy conductance sensitivity to VPD. Data from a 15–16 year-old eddy-covariance site located in the Lower Coastal Plain of North Carolina, U.S.

The model to estimate fraction of branch and bark to stem biomass (Fig. 4c) was dependent on age. In this model the average pBB for seedlings was about 1, decreasing to about 0.235 as the trees aged:

$$\mathrm{pBB} = 0.235 + (1.198 - 0.235) \cdot e^{\left(-\ln(2)\cdot\frac{\mathrm{Age}}{1.737}\right)} \quad (n = 114;\ P < 0.001;\ R^2 = 0.51)$$

Bole volume ratio (Fig. 4d) was dependent on age and Nha. In this model, too, the parameter estimate associated with age was negative, indicating that older trees were likely to have a larger bark fraction:

$$\mathrm{Vratio} = 1.232 \cdot \mathrm{VIB}^{-0.0166} \cdot \mathrm{Nha}^{0.0248} \cdot \mathrm{Age}^{-0.0299} \quad (n = 324;\ P < 0.001;\ R^2 = 0.99).$$

Parameter estimates of models needed to estimate initial biomass pools for stands growing in the southeastern U.S. are shown in Table 5. For WF when dbh data were available (Ht > 3 m), the parameter estimate associated with Ht was negative, indicating that for the same dbh and Age, taller trees had less living needle biomass than shorter trees. In all cases, the parameter estimate associated with Age was negative, indicating that for the same size (dbh and/or H), older trees had less WS or WF. For young trees (Ht < 3 m), WF was dependent on Ht and age, and WS was dependent only on Ht. For RFrac, the parameter estimate associated with Age was negative, indicating that as trees aged, the ratio between WR and WS decreased, reaching a value of about 0.233 for trees older than about 15 years.

Fig. 5 shows the tree mortality relationships. The model of Harrison and Borders (1996) was used to calculate mortality rate (Fig. 5a). The parameter estimates for the model fitted for density-independent mortality are shown in Table 4. When using boundary line analysis for density-dependent mortality (Fig. 5b), the slope of the self-thinning line (thinPower) was −1.174 and the maximum stem mass per tree at 1000 trees ha$^{-1}$ (WSx1000) was 230 kg (Table 4).

Family-specific allometric relationships were used to estimate crown area for each plot (models not shown). Using these relationships, the fractional canopy cover for each plot was calculated for both PPINES studies. Fig. 6a shows the relationship between age and canopy cover development, which affected the timing to reach full canopy closure (fractional canopy cover = 1). In the PPINES studies, plots with a narrow planting density and high culture (*N–H*) reached full canopy cover at about 3 years, while plots with a wide planting density and low culture (WL) reached full canopy cover at ages older than 10 years. After canopy closure the allometry of branches changes (Valentine et al., 2012) and the relationship used in this study may not be adequate, but for 3-PG any value of CanCover > 1 is assumed to be 1.When the fractional canopy cover was plotted against BA, a suite of curves was observed, and those curves were expressed as:

$$\mathrm{CanCover} = 0.258 \cdot \mathrm{BA}^{0.6883} \cdot \mathrm{Age}^{-0.1986} \quad (n = 559;\ P < 0.001;\ R^2 = 0.98).$$

Fig. 7 shows average monthly WF (Fig. 7a), NF (Fig. 7b) and $\gamma N$ (Fig. 7c) for the IMPAC study, where fertilization (*F*) and weed control (*W*) treatments created a wide range in foliage biomass and

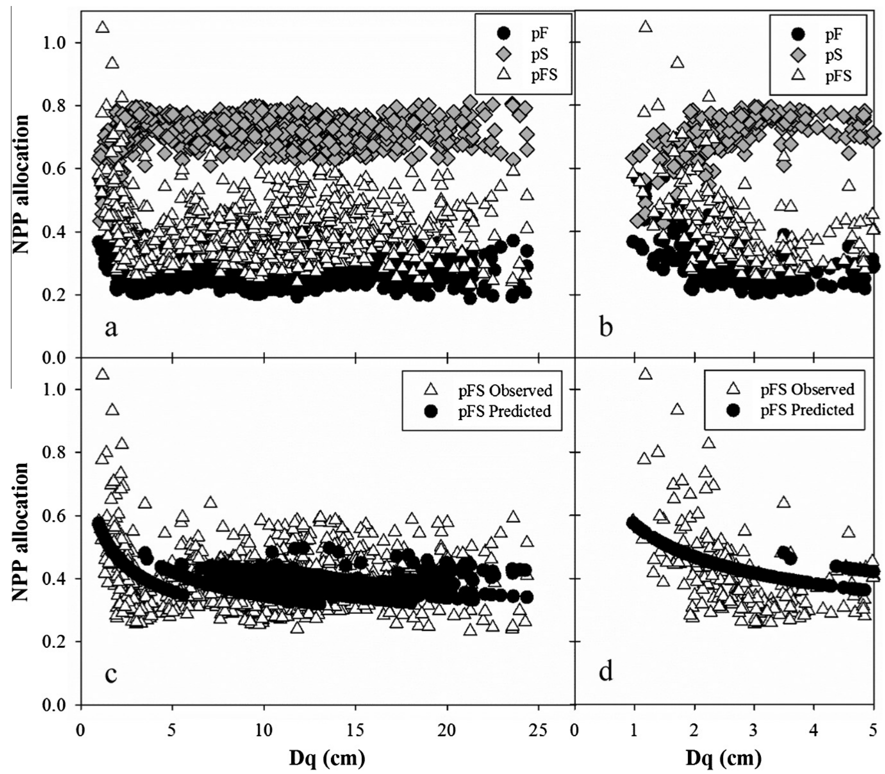


**Fig. 3.** (a) Relationship between observed values of Dq and NPP allocation to foliage (pF), stem (pS) and stem to foliage ratio (pFS) for loblolly pine stands ranging in age from 2 to 25 years old (all data points are observed values). (b) Observed and predicted values of pFS. Panels (c) and (d) shows inserts for Dq smaller than 5 cm.

needlefall (Jokela and Martin, 2000). In general, across all 14 years of measurements, control plots (*C*) that did not receive fertilization and weed control, showed lower monthly WF and NF. Maximum and minimum WF was reached in July (NMonth = 3) and February (NMonth = 10), respectively, and maximum and minimum NF was attained in November (NMonth = 7) and March (NMonth = 11). All treatments showed similar $\gamma N$ within each month, reaching maximums and minimums in November (NMonth = 7) and April (NMonth = 12), respectively. The final model fitted was:

$$\frac{\gamma N}{\gamma \mathrm{Nx}} = \frac{0.1183 + 11.9827 * \mathrm{NMonth}}{1 + 1.1522 \cdot \mathrm{NMonth} - 0.8833 \cdot \mathrm{NMonth}^2 + 0.0713 \cdot \mathrm{NMonth}^3} \quad (n = 144;\ P < 0.001;\ R^2 = 0.96)$$

We left the model flexible to account for site-specific needlefall dynamics, allowing the user to change $\gamma$Nx and the month when $\gamma N$ reached the maximum (t$\gamma$Nx). As default values, we determined a mean $\gamma$Nx of 0.157 month$^{-1}$ ($n$ = 12; SE = 0.031) and November (t$\gamma$Nx = 11) as the month when $\gamma$Nx peaked (Table 3). Mean monthly $\gamma N$ was 0.062 month$^{-1}$.

Fig. 8 shows the age-dependent relationships for SNA (Fig. 8a) and whole-tree SG for trees growing in the southeastern U.S. ($SG_{US}$) and Uruguay ($SG_{UR}$) (Fig. 8b). For both variables, an exponential decay to a non-zero asymptote was fitted from the data:

$$\mathrm{SNA} = 3.875 + (5.529 - 3.875) \cdot e^{\left(-\ln(2)\cdot\frac{\mathrm{Age}}{5.971}\right)} \quad (n = 94;\ P < 0.001;\ R^2 = 0.37)$$

$$\mathrm{SG_{US}} = 0.482 + (0.358 - 0.482) \cdot e^{\left(-\ln(2)\cdot\frac{\mathrm{Age}}{7.054}\right)} \quad (n = 30;\ P < 0.001;\ R^2 = 0.98)$$

$$\mathrm{SG_{UR}} = 0.478 + (0.328 - 0.478) \cdot e^{\left(-\ln(2)\cdot\frac{\mathrm{Age}}{6.913}\right)} \quad (n = 20;\ P < 0.001;\ R^2 = 0.86)$$

Average SNA for 1-year-old trees was about 5.5 m$^2$ kg$^{-1}$, decreasing as trees aged to values of about 3.9 m$^2$ kg$^{-1}$ (Fig. 8a).The models for whole-tree SG indicated that for trees growing in the southeastern U.S. ($SG_{US}$) and South America ($SG_{SA}$), SG of seedlings at planting was about 0.36 and 0.32, respectively, increasing as the trees aged to values of about 0.48 and 0.47, respectively (Table 3). The models predict that at an age of 20 years, $SG_{US}$ = 0.48 and $SG_{SA}$ = 0.45 (Fig. 8b).

The curve that showed the best fit between minimum daily temperature (Tmin) and fractional leaf conductance (kF) is was:

$$\mathrm{kF} = e^{(0.178\cdot\mathrm{Tmin})} \quad (n = 8,\ P < 0.001;\ R^2 = 0.96).$$

On frost days, for each degree Celsius below zero during the night before, leaf conductance during the daytime was reduced at an exponential rate of 17.8%. For example, if a month had Frostday = 5 and Tmin = -3 °C, productivity would be reduced by Ffrost = 0.902 ($\mathrm{Ffrost} = 1 - (1 - e^{(\mathrm{tF}\cdot\mathrm{Tmin})}) \cdot \mathrm{Frostday}/30$).

### 3.2. Iterative calibration of FR

We analyzed the relationship between FR and SI using iterative calibration on 63 plots randomly selected across the distribution range of loblolly pine. The silvicultural treatments applied in each of the selected plots created a wide span in productivity, resulting in SI ranging between 13.9 and 33.1 m (Table 2). Fig. 9 shows the relationship between SI and FR. The model predicts a FR = 0.35 for stands with SI = 15 m and a FR = 0.96 for stands with SI = 35 m. The curve that showed the best fit and biological meaning was:

$$\mathrm{FR} = \frac{1.1272}{1 + 14.9144 \cdot e^{(-0.1277\cdot\mathrm{SI})}} \quad (n = 63;\ P < 0.001;\ R^2 = 0.68).$$

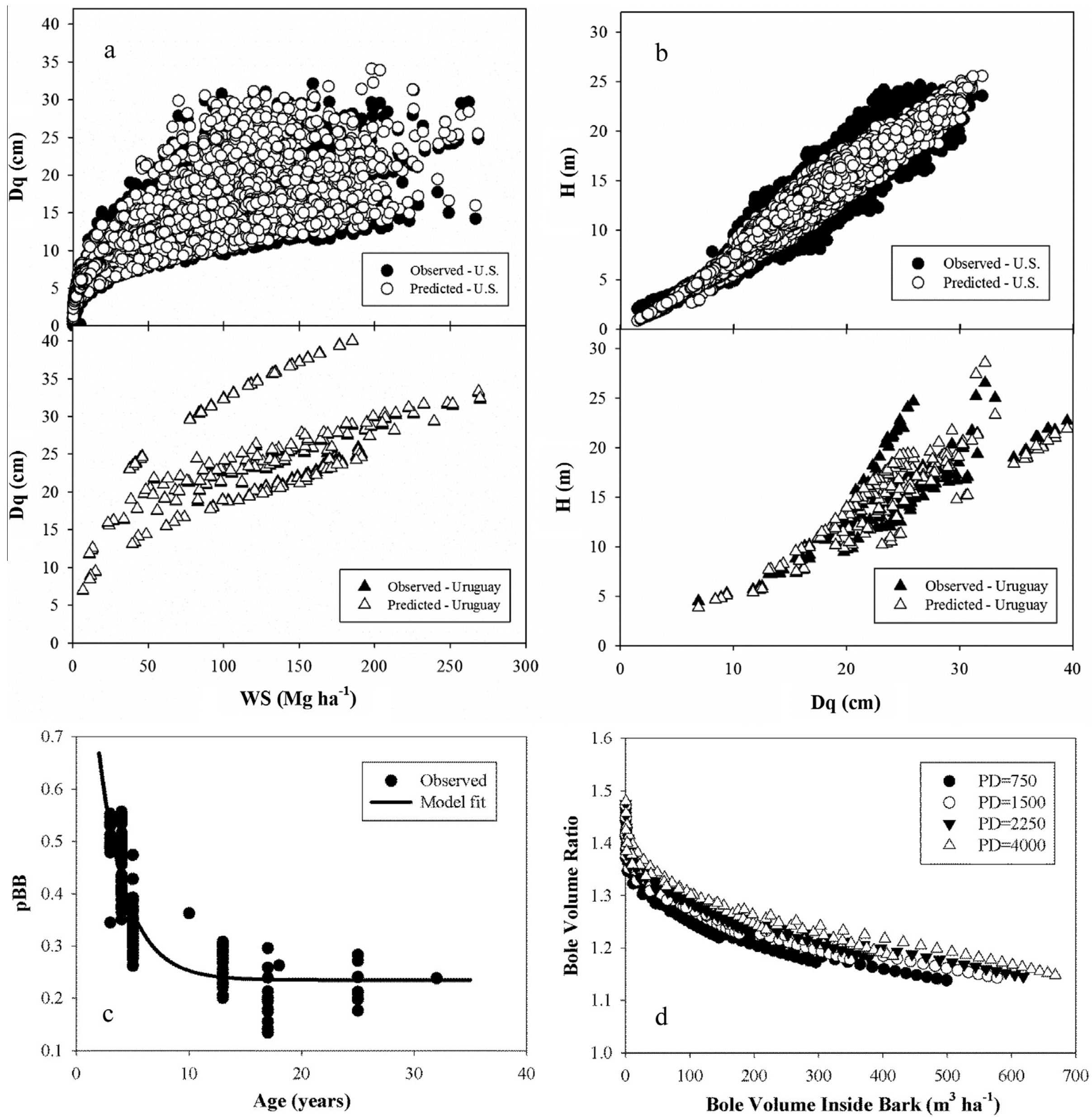


**Fig. 4.** Allometric relationships for (a) stem biomass (WS) and Dq, (b) Dq and mean height (H), (c) age and branch and bark fraction (pBB), and (d) bole volume inside bark (VIB) and bole volume ratio (Vratio) for different planting density (PD) and site index (not labeled). Panels (a) and (b) show observed (filled symbol) and predicted (open symbol)) values for stands goring in U.S. (circles) and Uruguay (triangles).

### 3.3. Model evaluation

There was agreement between observed and predicted values, with no clear tendencies to over or under-estimate for any of the variables tested. Across all sites, including stands growing in Uruguay, the slope and the intercept of the relationship between predicted and observed values were not statistically different from one ($P > 0.13$) and zero ($P > 0.09$), respectively (Fig. 10).

The LAI estimations performed well, predicting monthly values within the range of observed LAI reported for the IMPAC study. For the control plots that did not receive fertilization or herbicide treatments (Fig. 11a), predicted and observed LAI followed similar trends, continuing to increase after age 14 years. The model also accurately estimated the amplitude and timing of seasonal LAI variation. For plots that received sustained fertilization (Fig. 11b), herbicide (Fig. 11c) and the combination (Fig. 11d) of both treatments, the model showed adequate predictions also following similar seasonal trends, showing a mean bias of about 2.3%. On the other hand, maximum monthly LAI (LAI-peak) had a mean underestimation of about 11% (Table 6).

Using monthly values of LAI shown previously, mean annual LAI (LAI-mean) was calculated for each plot and year of observation (Fig. 12). There was a strong correlation between observed and predicted values ($P < 0.001$; $R^2 = 0.85$), showing a mean bias of 5.6% (data not shown).

All model performance tests showed that AGB, VOB, BA, Nha, Dq, H, LAI-mean, LAI-min and LAI-peak estimations agreed with measured values (Table 6). Across all sites and for all estimations, the RMSE ranged between 3% for Dq and 31% for VOB, both for stands growing in Uruguay. The Bias ranged between 14% underestimations for LAI-peak at the IMPAC study and 14% overestimations for VOB in Uruguay, both on stands with SI > 25 m.

**Table 5**
Parameter estimates and fitted statistics of equations for predicting initial WF, WS and RFrac for stands growing in the southeastern U.S.

| | Model | Equation | Parameter | Parameter estimate | SE | $R^2$ | RMSE |
|---|---|---|---|---|---|---|---|
| Ht > 3 m | WF = $w_1 \cdot \text{dbht}^{w2} \cdot \text{Ht}^{w3} \cdot \text{Age}^{w4}$ | 5 | *w*1 | 0.0997 | 0.0125 | 0.876 | 1.66 |
| | | | *w*2 | 2.2416 | 0.0886 | | |
| | | | *w*3 | −0.591 | 0.0866 | | |
| | | | *w*4 | −0.3184 | 0.0422 | | |
| | WS = $w_1 \cdot \text{dbht}^{w2} \cdot \text{Ht}^{w3} \cdot \text{Age}^{w4}$ | 5 | *w*1 | 0.015 | 0.000965 | 0.986 | 8.74 |
| | | | *w*2 | 2.0449 | 0.0303 | | |
| | | | *w*3 | 1.2165 | 0.039 | | |
| | | | *w*4 | −0.2078 | 0.0159 | | |
| Ht < 3 m | WF = $w_1 \cdot \text{Ht}^{w2} \cdot \text{Age}^{w3}$ | 6 | *w*1 | 0.3253 | 0.034 | 0.926 | 1.80 |
| | | | *w*2 | 2.5944 | 0.1336 | | |
| | | | *w*3 | −0.6389 | 0.1699 | | |
| | WS = $w_1 \cdot \text{Ht}^{w2}$ | 6 | *w*1 | 0.0904 | 0.00797 | 0.954 | 0.57 |
| | | | *w*2 | 2.4223 | 0.0559 | | |
| All | RFrac = $r0 + r1 \cdot e^{(r2 \cdot \text{Age})}$ | 7 | *r*0 | 0.2333 | 0.018 | 0.913 | 0.12 |
| | | | *r*1 | 10.6424 | 1.1156 | | |
| | | | *r*2 | −1.851 | 0.0994 | | |

WF: foliage dry mass (kg $\text{tree}^{-1}$); WS: stem dry mass (kg $\text{tree}^{-1}$); dbh: diameter outside-bark at 1.37 m height (cm); Ht: total tree height (m); RFrac: ratio between WR and WS; SE: standard error; $R^2$: coefficient of determination; and RMSE: root mean square error. For all parameter estimates: *P*-value < 0.001.

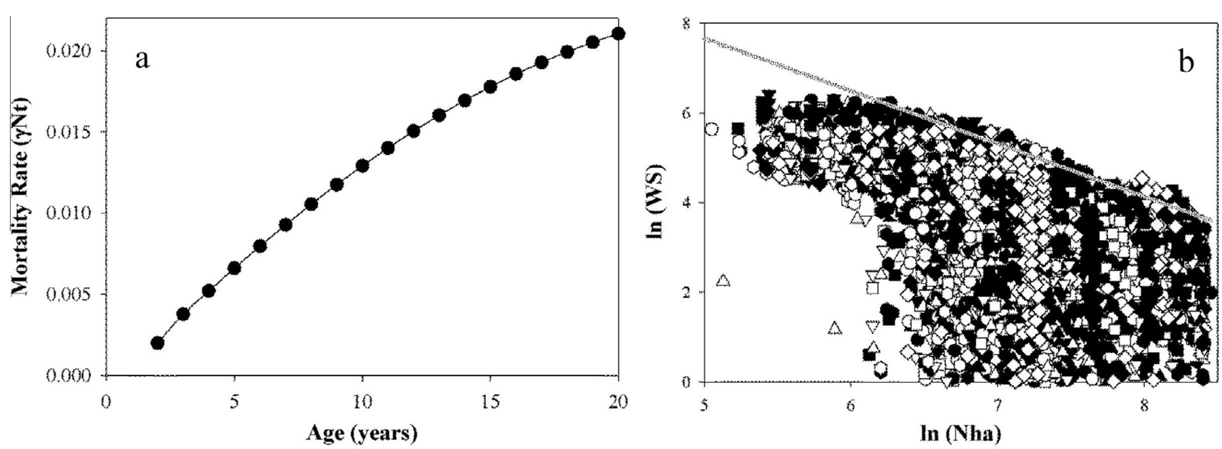


**Fig. 5.** Tree mortality relationships. (a) Relationship between age density-independent tree mortality (γNt) using the model of Harrison and Borders (1996). (b) Density-dependent tree mortality, based on the relationship between stem biomass (WS, kg $\text{tree}^{-1}$) and stand density (both in natural logarithm scale). The self-thinning line is the theoretical upper limit.

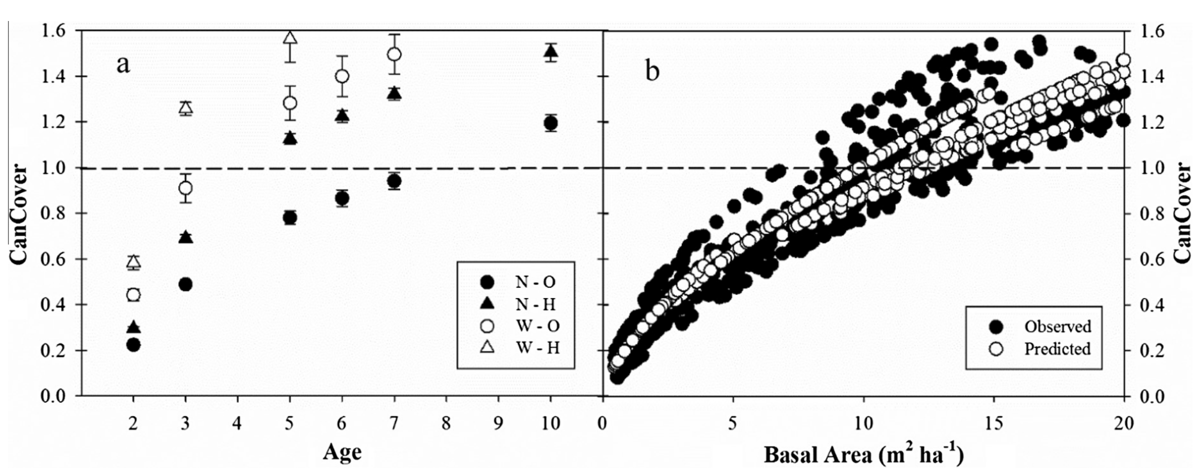


**Fig. 6.** Relationship between canopy development (expressed as fractional canopy cover, CanCover) and (a) age and (b) basal area for loblolly pine stands of PPINES study. Plots that received combinations of two contrasting silvicultural treatments (operational, O, and high intensity, H) and two contrasting planting densities (1334 trees $\text{ha}^{-1}$, W, and 2990 trees $\text{ha}^{-1}$, N). Panel (a) show mean values for stands growing in GA. Panel (b) show observed and predicted values for all plots growing on sites in FL and GA. Dashed line represents the point when the stand reach canopy closure (CanCover = 1).

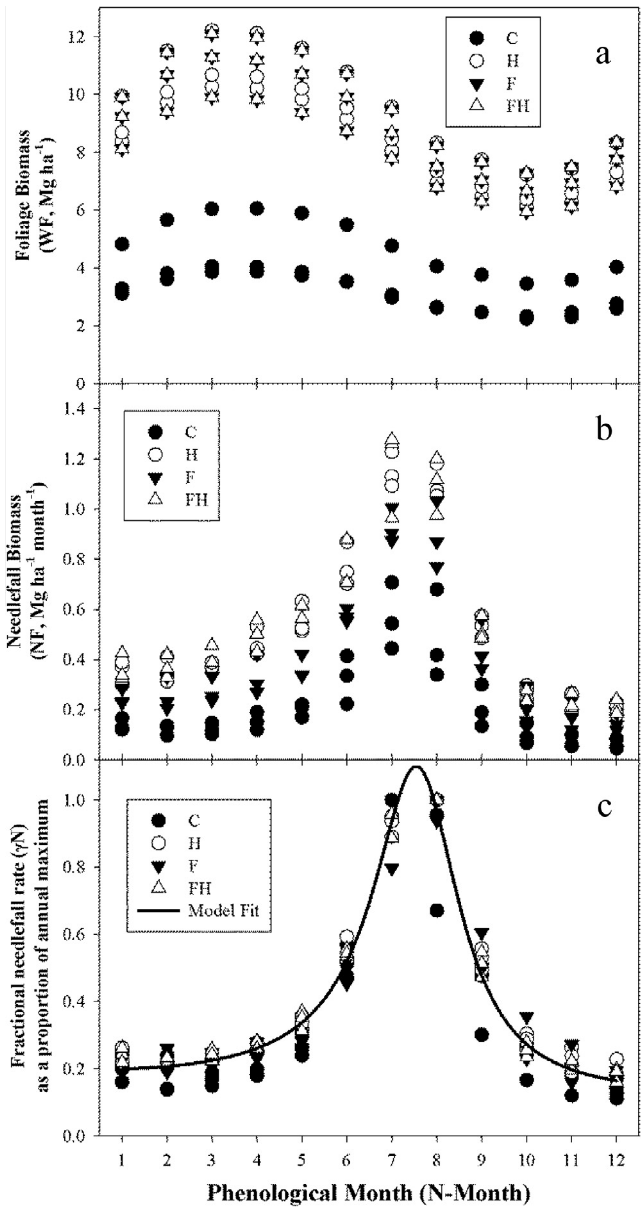


**Fig. 7.** Seasonal dynamics of foliage biomass and needlefall for the IMPAC study, showing average monthly (a) foliage dry mass (WF, Mg ha$^{-1}$), (b) needlefall (NF, Mg ha$^{-1}$ month$^{-1}$) and (c) fractional needlefall ($\gamma N$ as a proportion of annual maximum).

Estimated and observed values were highly correlated, with $R^2$ values ranging between 0.47 and 0.96. There was no clear trend indicating that there was different model behavior for stands with different SI. Even though the Bias percentage of AGB estimations increased from −2.6% for stands with SI < 20 m, to −16.3% for stands with SI > 25 m, the Bias percentage of VOB did not change. Furthermore, for LAI-min and LAI-mean, the Bias percentage was reduced as SI increased.

## 4. Discussion

The 3-PG model has broad potential for application, e.g., for regional analysis of loblolly pine stand dynamics or assessing the impact of future climate scenarios on stand productivity across a wide range of ages and stand characteristics. Because we had access to a large, previously-unavailable set of data, we were able to revise some important parameter estimates using the alternative methods suggested by Gonzalez-Benecke et al. (2014a,b) across a far broader range of climate, soils, and silvicultural intensity than previous researchers. The new approaches presented in this study provided new algorithms for canopy cover dynamics, fertility rating, needlefall dynamics, NPP allocation dynamics, mortality, frost intensity effects on production, quadratic mean diameter (and therefore, basal area), mean height and initial biomass estimations.

A critical variable used in 3-PG is FR, the empirical index that ranks soil fertility on a scale from 0 (extremely infertile) to 1 (optimum), and modifies canopy quantum efficiency and root allocation (Dye et al., 2004; Swenson et al., 2005; Fontes et al., 2006; Almeida et al., 2010; Gonzalez-Benecke et al., 2014a). Most previous applications of the 3-PG model relied on using arbitrary FR values determined by calibration which gave adequate results, but lacked a mechanistic basis and independence. Working with Douglas-fir (*Pseduotsuga menziesii*) stands, Swenson et al. (2005) indirectly correlated FR with SI by using 3-PG model to estimate SI, after computing FR from soil nitrogen content. The authors provided the logarithmic function but did not show any index of correlation or goodness of fit of the model fitted. Coops et al. (2011), working with five conifer species in Pacific Northwest of the U.S., also used 3-PG model to estimate SI, but used a constant value of FR = 0.7 in all their calculations.

Dye et al. (2004), also correlated FR with SI, but estimated FR from known SI. The authors showed an alternative approach to estimate FR. This method was successfully tested by Gonzalez-Benecke et al. (2014a) for slash pine (*Pinus elliottii var. elliottii* Engelm.), supporting that FR was positively correlated with changes in SI; SI integrated a variety of factors including nutrient dynamics and site water balance. The model reported in this study predicted a maximum FR of 1 for stands with a SI of 37 m, a value that was above the range of observed plots (in our dataset consisting of 148 plots, only 8 plots had SI larger than 32 m, and those plots corresponded to studies with sustained weed control and fertilization). It is expected that improved genetics and silviculture can lead to higher values than those observed in our current database (Fox et al., 2007). The use of SI as a determinant of FR allows the model to be applied across a range of sites without resorting to model "tuning" to estimate FR. Nevertheless, further research is needed to improve the goodness of fit of that relationship. In a recent publication, Subedi et al. (2015) used SI to estimate FR for loblolly pine stands. The authors determined the relationship between stem volume at age 11 years and SI for each plot and then assigned a value of FR = 0 for SI = 10.7 m and FR = 1 for SI of 30.5 m (plots with minimum and maximum volume at age 11 years observed in their dataset). Finally the authors arbitrarily assigned evenly the steps of FR associated to stem volume. We consider that our method is stronger as does not assume a linear relationship between FR and stem volume at age 11 years. Furthermore, instead of using one target age (11 years), we used all years of observations on each plot finding the value of FR that minimized the overall prediction error.

Assessments of mortality occurring prior to the onset of intraspecific competition (density-independent tree mortality) were not included in the original version of the model (Landsberg and Waring, 1997), that assumed no mortality until self-thinning was triggered (density-dependent tree mortality). Several authors reported inadequate results in model performance, especially in stand density estimations (Sands and Landsberg, 2002; Pinjuv et al., 2006; Bryars et al., 2013). Following Sands (2004), who first proposed the inclusion of the density-independent model shown in Eq. (4), Pérez-Cruzado et al. (2011) and Gonzalez-Benecke et al. (2014a) included, successfully, new species-specific parameter estimates for *Eucalyptus nitens* H. Deane

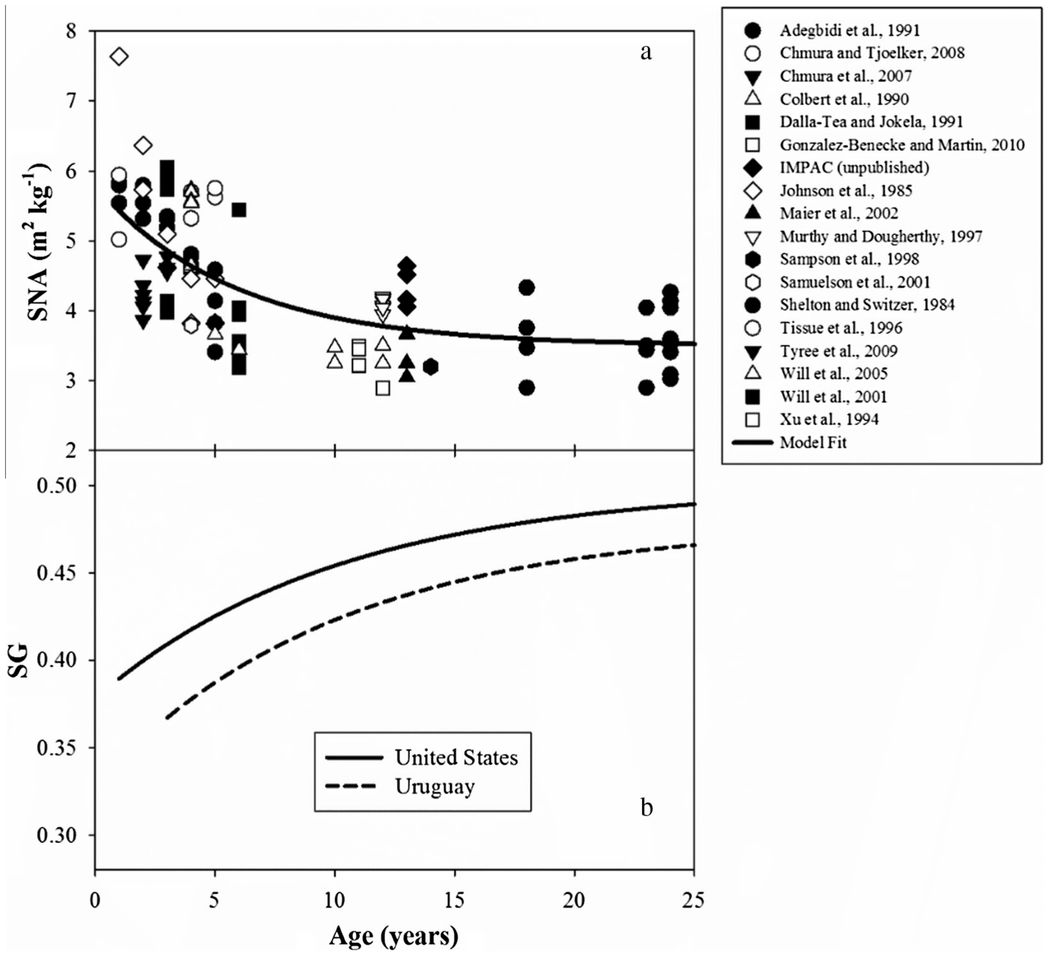


**Fig. 8.** Model fitted for age-dependent relationship between for (a) specific needle area (SNA) and (b) whole-tree wood specific gravity (SG) for trees growing in southeast U.S. ($SG_{US}$, solid line; adapted from Harrison and Borders, 1996) and Uruguay ($SG_{UR}$, dashed line).

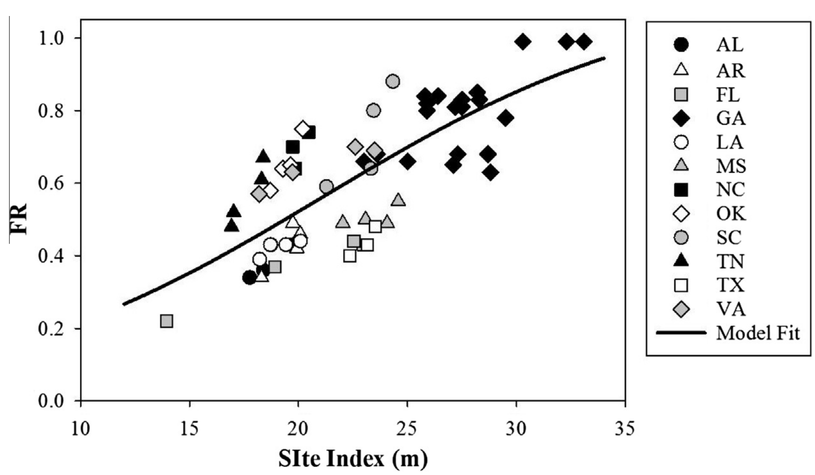


**Fig. 9.** Relationship between site index (SI, m) and FR after iterative calibration for 63 plots in 12 states in southeastern U.S. AL: Alabama; AR: Arkansas; FL: Florida; GA: Georgia; LA: Louisiana; MS: Mississippi; NA: North Carolina; OK: Oklahoma; SC: South Carolina; TN: Tennessee; TX: Texas; and VA: Virginia.

and Maiden and slash pine, respectively, allowing for the estimation of random or stress-induced mortality observed under field conditions. Gonzalez-Benecke et al. (2014a) reported an overall bias of about 1% on stand density estimations. The inclusion of the mortality function reported by Harrison and Borders (1996) in the form of the model proposed by Sands (2004), greatly improved the estimations of stand density. In our study the overall bias was less than 3%.

In general, the model assumes that the fractional ground covered by the canopy (CanCover) is proportional to stand age until the age of full canopy cover (fullCanAge, years). This parameter is uncertain, as the age for full canopy cover depends on genetics,

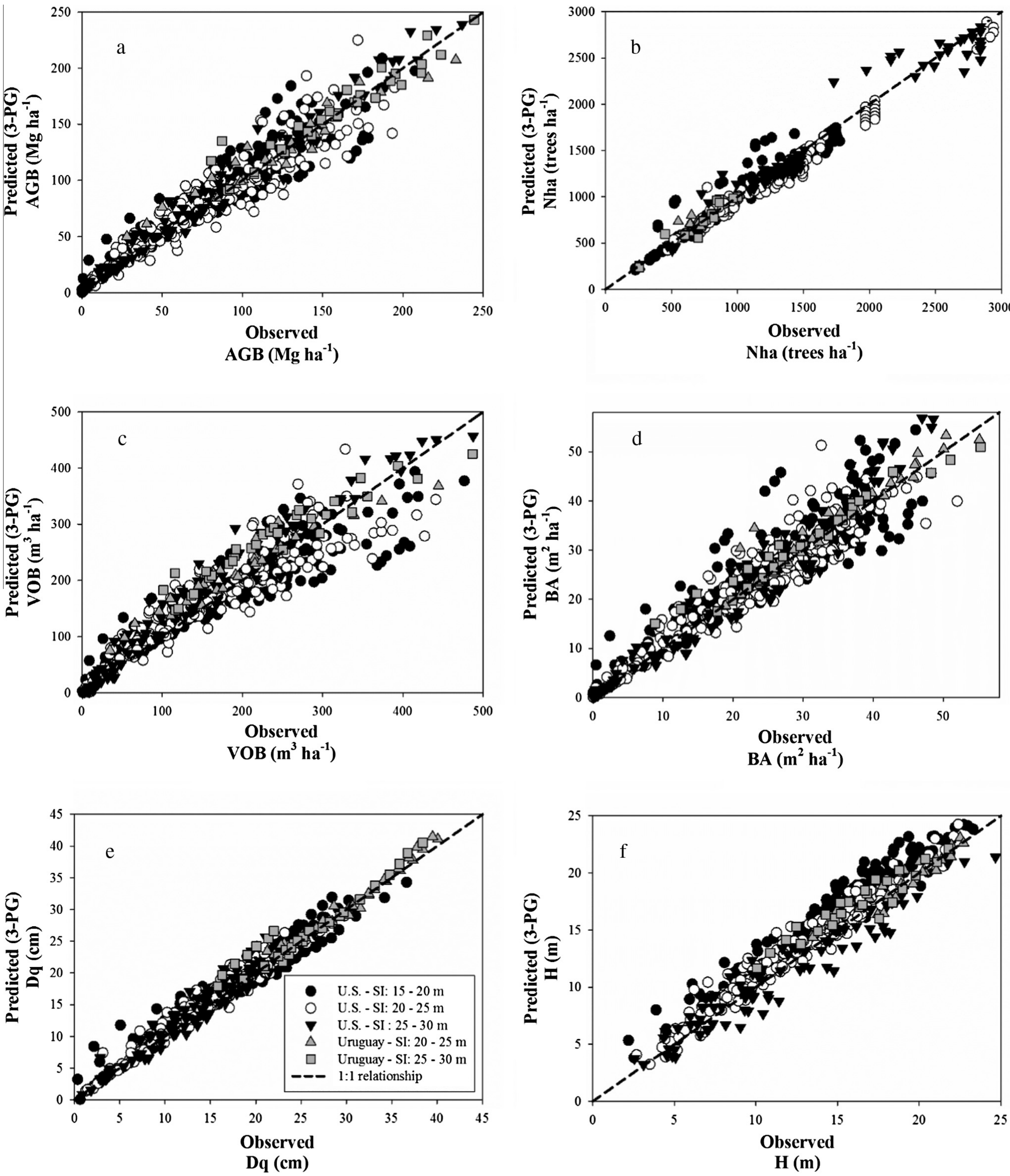


**Fig. 10.** Model validation for 34 tested sites (101 plots total; 91 in the southeastern U.S.; 10 in Uruguay, South America) for different site index. Observed versus predicted (simulated with 3-PG) values of (a) total above ground biomass (AGB, Mg ha$^{-1}$), (b) stand density (Nha, trees ha$^{-1}$); (c) bole volume over-bark (VOL, m$^3$ ha$^{-1}$); (d) stand basal area (BA, m$^2$ ha$^{-1}$); (e) quadratic mean diameter (Dq, cm), and (f) mean tree height (H, m). The dotted line corresponds to the 1-to-1 relationship. * For sites in Uruguay: VIB.

stand density and levels of productivity (Radtke and Burkhart, 1999). Bryars et al. (2013) reported a fullCanAge of 2 years, based on data reported by Burkes et al. (2003) for stands with high silviculture intensity and high planting density (between 3700 and 4400 trees ha$^{-1}$). Similar to our earlier findings (Gonzalez-Benecke et al., 2014a), we concluded that the use of a single age to determine the year to reach full canopy cover was not satisfactory. A relationship between fractional canopy cover, age and BA improved canopy cover estimations under different conditions of stand age, genetics, density and productivity in loblolly pine stands. This relationship was in agreement with our rationale that the moment when the stand reaches full canopy closure was

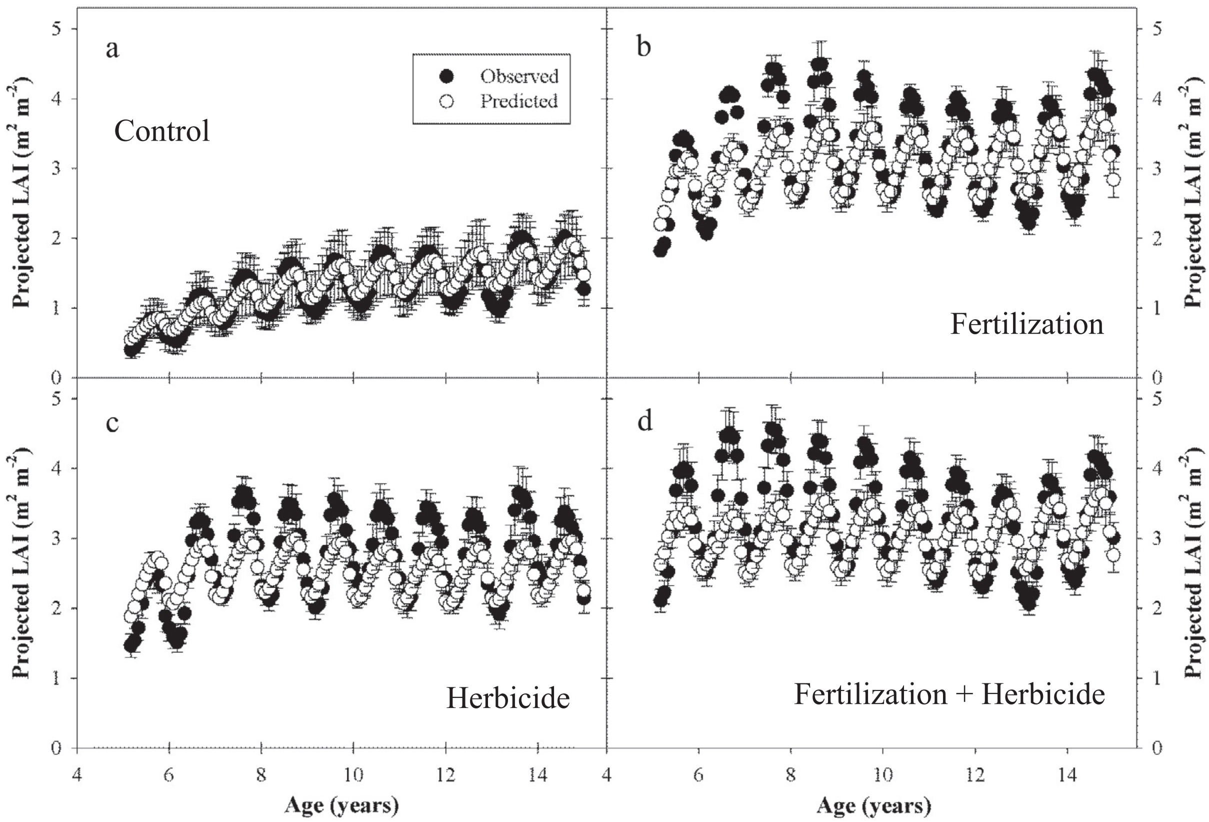


**Fig. 11.** Validation of monthly projected leaf area index (LAI, $m^2\,m^{-2}$). Observed (filled circle) and predicted (open circle) values for loblolly pine stands grown at the IMPAC study under the following silvicultural treatments (a) control, (b) fertilization, (c) herbicide, and (d) fertilization + herbicide (Jokela and Martin, 2000).

correlated with stand density and productivity. With our new approach, the estimations of absorbed PAR are less dependent on arbitrary tuning of the CanCover parameter.

The model needs as inputs initial biomass allocations to roots (WR), foliage (WF) and stem (stemwood + bark + branches, WS). Sands and Landsberg (2002) emphasized the importance of the initial biomass conditions, especially to initial canopy development. If the model user has no initial biomass estimations for the stand to be simulated, we provide general individual-tree biomass functions for loblolly pine that use dbh, Ht and age as predictors. We also provide new biomass functions that can be used for young stands, where individual-tree biomass can be estimated using Ht and age. Using the raw data from 764 measured trees, we adapted the models reported by Gonzalez-Benecke et al. (2014b) and produced alternative functions to estimate initial biomass pools. The parameter estimates and relationships presented in this study have a wide range of applicability, and not only for 3-PG initialization, but also life-cycle analysis (Puettmann et al., 2010), and estimation of stand biomass and carbon sequestration dynamics (Gonzalez-Benecke et al., 2011).

Landsberg and Sands (2011) remarked that relationships used for biomass allocation deserved further research. Previous versions of the model estimated NPP allocation to stem and foliage (pFS) based on individual-tree stem mass ($kg\,tree^{-1}$) and dbh. Gonzalez-Benecke et al. (2014a) introduced a new function to estimate pFS using BA rather than using dbh. For stands with a Dq of 20 cm, the modified model predicted pFS values between 0.35 and 0.45 (covering most of the distribution of observed values), and were larger than the comparable value of 0.25 reported by Bryars et al. (2013). Our new model used to estimate pFS included Dq and age, supporting our rationale that stand productivity and competition were correlated with changes in NPP allocation. These modifications contributed to our accurate predictions of stand biomass.

The model performed well when describing LAI dynamics, and mean annual LAI (LAI-mean) was well estimated (mean bias of 2.3% across all SI classes) in most cases. However, the model could not accurately reproduce the peak (mean bias of +11% across all SI classes) and minimum (mean bias of −10%, across all SI classes) LAI. This could be an effect of inadequacy of the model to capture the impacts of nutrition on foliage allocation and retention (Albaugh et al., 1998). Nevertheless, it is highly unlikely that stands receiving extremely high management inputs, such as those in some experimental plots, would be found under regular field conditions. An important area for future research is to better understand how intensive management and genetic selection affects LAI phenology.

Needlefall rate was a key factor that affected LAI estimations. Previous versions of the model used a function that described the dynamics of needlefall as trees developed, assuming a constant needlefall rate after canopy closure (Sands and Landsberg, 2002). Gonzalez-Benecke et al. (2014a) introduced equations to better describe the seasonal dynamics of needlefall for slash pine. We applied these equations to loblolly pine and found that the model was appropriate for the species, with needlefall also peaking in November; however, the maximum needlefall rate was 36% larger than for slash pine. Similar differences between species in total yearly needlefall were reported by Dalla-Tea and Jokela (1991). Our approach, that estimated a variable monthly needlefall rate, produced more realistic LAI dynamics than previous versions of the model, both in terms of average annual LAI, as well as within-year amplitude.

The dataset used for model validation includes plots with different treatments of fertilization and vegetation management. We

**Table 6**
Summary of model evaluation statistics for AGB, VOB, BA, Nha, Dq, H and LAI estimations for loblolly pine stands growing in sites with different SI in U.S. and Uruguay.

| Variable | Location | SI class | $\bar{O}$ | $\bar{P}$ | $n$ | RMSE | Bias | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| AGB | U.S. | 15–20 | 89.7 | 92.0 | 184 | 16.9 (18.9) | −2.3 (−2.6) | 0.854 |
| | | 20–25 | 68.3 | 66.9 | 222 | 17.1 (25.1) | 1.4 (2.1) | 0.874 |
| | | 25–30 | 71.2 | 82.9 | 104 | 16.9 (23.8) | −11.6 (−16.3) | 0.939 |
| | Uruguay | 20–25 | 130.3 | 132.4 | 30 | 15.5 (11.9) | −2.1 (−1.6) | 0.866 |
| | | 25–30 | 164.3 | 166.0 | 32 | 14.4 (8.8) | −1.7 (−1.0) | 0.891 |
| VOB[a] | U.S. | 15–20 | 184.6 | 176.9 | 184 | 44.2 (23.9) | 15.9 (8.6) | 0.729 |
| | | 20–25 | 133.4 | 131.3 | 222 | 41.1 (30.8) | 13.6 (10.2) | 0.814 |
| | | 25–30 | 132.7 | 162.8 | 104 | 25.3 (19.1) | −11.4 (−8.6) | 0.967 |
| | Uruguay | 20–25 | 191.6 | 214.8 | 30 | 37.5 (19.6) | −23.2 (−12.1) | 0.722 |
| | | 25–30 | 239.4 | 272.1 | 32 | 46.1 (19.2) | −32.7 (−13.7) | 0.602 |
| BA | U.S. | 15–20 | 25.6 | 27.2 | 184 | 5.4 (21.1) | −1.5 (−6.0) | 0.767 |
| | | 20–25 | 20.8 | 20.7 | 222 | 4.1 (19.5) | 0.1 (0.4) | 0.889 |
| | | 25–30 | 20.9 | 23.2 | 104 | 4.5 (21.7) | −2.2 (−10.7) | 0.917 |
| | Uruguay | 20–25 | 30.1 | 31.5 | 30 | 2.8 (9.4) | −1.5 (−4.8) | 0.911 |
| | | 25–30 | 33.8 | 35.1 | 32 | 3.0 (9.0) | −1.3 (−3.8) | 0.915 |
| Nha | U.S. | 15–20 | 1045 | 1042 | 184 | 117 (11.2) | 3 (0.3) | 0.923 |
| | | 20–25 | 1218 | 1156 | 222 | 95 (7.8) | 62 (5.1) | 0.945 |
| | | 25–30 | 1471 | 1437 | 104 | 147 (10.0) | 34 (2.3) | 0.956 |
| | Uruguay | 20–25 | 646 | 639 | 30 | 67 (10.3) | 8 (1.2) | 0.931 |
| | | 25–30 | 508 | 518 | 32 | 48 (9.5) | −10 (−1.9) | 0.961 |
| Dq | U.S. | 15–20 | 18.5 | 19.1 | 184 | 1.8 (9.7) | −0.6 (−3.2) | 0.912 |
| | | 20–25 | 14.4 | 14.8 | 222 | 1.4 (9.7) | −0.5 (−3.3) | 0.948 |
| | | 25–30 | 13.3 | 14.2 | 104 | 1.8 (13.8) | −1.0 (−7.2) | 0.925 |
| | Uruguay | 20–25 | 25.3 | 26.4 | 30 | 2.0 (7.7) | −1.1 (−4.3) | 0.889 |
| | | 25–30 | 30.6 | 31.2 | 32 | 1.0 (3.3) | −0.5 (−1.7) | 0.966 |
| H | U.S. | 15–20 | 13.9 | 16.6 | 184 | 2.3 (16.5) | −2.0 (−14.3) | 0.763 |
| | | 20–25 | 10.6 | 12.7 | 222 | 1.2 (11.2) | −0.7 (−6.4) | 0.921 |
| | | 25–30 | 10.0 | 11.2 | 104 | 1.2 (12.5) | 0.1 (0.7) | 0.920 |
| | URUGUAY | 20–25 | 15.7 | 17.2 | 30 | 1.5 (9.6) | −1.1 (−6.9) | 0.682 |
| | | 25–30 | 18.2 | 18.9 | 32 | 0.8 (4.3) | −0.1 (−0.8) | 0.889 |
| LAI-mean | IMPAC | 13–20 | 1.59 | 1.59 | 33 | 0.35 (22.1) | −0.001 (−0.13) | 0.862 |
| | | 20–25 | 2.90 | 2.90 | 55 | 0.48 (16.7) | −0.001 (−0.04) | 0.511 |
| | | 25–30 | 3.13 | 2.94 | 44 | 0.43 (13.9) | 0.184 (5.9) | 0.587 |
| LAI-min | IMPAC | 13–20 | 1.16 | 1.30 | 33 | 0.30 (26.2) | −0.143 (−12.3) | 0.814 |
| | | 20–25 | 2.11 | 2.39 | 55 | 0.47 (22.0) | −0.279 (−13.2) | 0.528 |
| | | 25–30 | 2.30 | 2.44 | 44 | 0.35 (15.3) | −0.135 (−5.9) | 0.540 |
| LAI-peak | IMPAC | 13–20 | 2.01 | 1.83 | 33 | 0.51 (25.0) | 0.18 (8.8) | 0.809 |
| | | 20–25 | 3.65 | 3.32 | 55 | 0.72 (19.6) | 0.34 (9.2) | 0.473 |
| | | 25–30 | 3.92 | 3.36 | 44 | 0.75 (19.3) | 0.56 (14.2) | 0.563 |

AGB: above-ground biomass (Mg $ha^{-1}$); VOB: stand bole volume outside bark ($m^3$ $ha^{-1}$); BA: stand basal area ($m^2$ $ha^{-1}$); Nha: trees per hectare ($ha^{-1}$); Dq: quadratic mean diameter (cm); H: mean tree height (m); LAI-mean: mean annual projected leaf area index ($m^2$ $m^{-2}$); LAI-min: minimum annual projected leaf area index ($m^2$ $m^{-2}$); LAI-peak: maximum annual projected leaf area index ($m^2$ $m^{-2}$); SI: site index class range (m); $\bar{O}$: mean observed value; $\bar{P}$: mean predicted value; $n$: number of observations; RMSE: root of mean square error (same unit as observed value); Bias: absolute bias (observed-predicted; same unit as observed value); $R^2$: coefficient of determination. Values in parenthesis are percentage relative to observed mean.
[a] For sites in Uruguay: VIB.

used a simple approach to address the effects of those treatments by changing the FR reflected on observed SI on each plot. Wei et al. (2014) included the effects of competing vegetation on water and light availability in a recent publication on *Pinus ponderosa* trees. We recognize the great contribution of their study in including explicitly understory biomass into light interception and water balance modules of the model, but we also have to mention that the authors used a value of FR calibrated for each plot assuming no effect of FR on canopy quantum yield and only effects on biomass allocation. We are aware that competing vegetation has not only effects on nutrient availability, but our approach showed adequate results for loblolly pine stands on a variety of sites.

No other study using 3-PG with any species has shown the range of validation sites as reported here. Previous versions used with loblolly pine were validated using datasets restricted to single U.S. state, i.e., Georgia for Bryars et al. (2013) and North Carolina for Landsberg et al. (2001) and Sampson et al. (2006). In this study, the model was regionally validated under different stand and site conditions, covering zones beyond the native range for loblolly pine, including stands growing in Uruguay, South America. Even

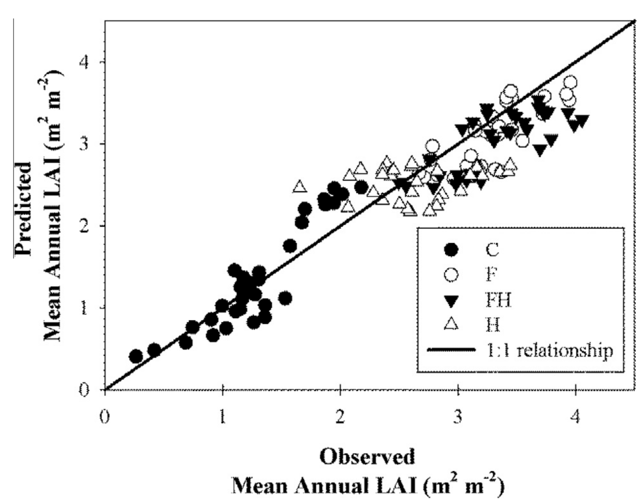


**Fig. 12.** Relationship between observed and predicted mean annual projected leaf area index (LAI, $m^2$ $m^{-2}$) for loblolly pine stands grown at the IMPAC study under the following silvicultural treatments: control (C), herbicide (H), fertilization (F), and fertilization + herbicide (FH) (Jokela and Martin, 2000).

though other factors such as storms, disease and pests could be significant (VanderSchaaf and Prisley, 2006; Aubrey et al., 2007; Coyle et al., 2015), the model showed adequate estimates over a range of climate and soil conditions. Interestingly, the validation results for stands in Uruguay were satisfactory, showing good agreement for all variables tested, and supported the robustness of the model. Even though the use of specific parameters for the Dq-WS, H-Dq and SG-Age functions greatly improved model performance, we consider that estimates of stem volume and LAI-peak could be improved as new data becomes available, e.g., whole-tree SG for older trees, seasonal phenology of SNA and NPP allocation or soil/site variables that can improve the FR–SI relationship. These results have important implications, as the model can be used to capture the variation in loblolly pine productivity across the southeastern U.S., including sites in South America.

## 5. Conclusions

This study reports a regional validation of and alternative parameterization for the 3-PG model for loblolly pine. The new model was successfully tested against data from stands of varying characteristics that were distributed across the species' native range in the southeastern U.S., as well as in Uruguay, South America. We used the largest and most geographically extensive validation dataset across a species' range with 3-PG. In addition, data from the literature and long-term studies were used to develop new functions for estimating important parameters for the model. Similar to previous work on slash pine, we estimated fertility rating based on a positive correlation with site index. The new parameterization and validation represents an improvement to previous published versions, allowing for improved assessments of stand productivity across a wide range of ages and stand characteristics for this species. The results in this study provide strong evidence that 3-PG can be applied over a wide geographical range using the same set of physiological parameters.

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