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Parameterization of the 3-PG model for *Pinus elliottii* stands using alternative methods to estimate fertility rating, biomass partitioning and canopy closure

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ABSTRACT

The forest simulation model, 3-PG, has been widely applied as a useful tool for predicting growth of forest species in many countries. The model has the capability to estimate the effects of management, climate and site characteristics on many stand attributes using easily available data. Currently, there is an increasing interest in estimating biomass and assessing the potential impact of climate change for slash pine (*Pinus elliottii* Engelm. var. *elliottii*), a commercially important tree species of the southeastern U.S. The 3-PG model had not been previously parameterized for this species. Using data from the literature and long-term productivity studies, we parameterized 3-PG for slash pine stands, developing new functions for estimating biomass pools at variable starting ages, canopy cover dynamics, allocation dynamics, density-independent tree mortality and the fertility rating. The model was tested against data from measurement plots covering a wide range of stand characteristics (age, productivity and management), distributed within and beyond the natural range of the species, including stands in Uruguay, South America. Across all tested sites, estimations of survival, basal area, height, volume and above-ground biomass agreed well with measured values. The bias was small and generally less than 7%. This paper reports the first set of 3-PG parameter estimates for slash pine, showing new methodologies to determine important estimates. The model can be applied to stands growing over a large geographical area and across a wide range of ages and stand characteristics.

1. Introduction

In the southeastern United States, slash pine (*Pinus elliottii* Engelm. var. *elliottii*) has been planted on more than 4.2 million ha, covering a wide range from eastern Texas to southern North Carolina to south-central Florida. Approximately 79% of the planted slash pine stands occur within Florida and Georgia (Barnett and Sheffield, 2004). Slash pine has also been introduced into many countries and large-scale plantations for timber production are found in Argentina, Australia, Venezuela, Brazil, China, South Africa, New Zealand, and Uruguay (Barnett and Sheffield, 2004).

Estimates of stand productivity are of interest to landowners, researchers, managers and policymakers, and are central to our ability to understand and predict forest carbon (C) stocks and dynamics. Measures of stand level biomass accumulation are required for multiple purposes such as estimating site productivity, planning prescribed fire, accounting for biomass harvested for bioenergy production, or accounting for the effects of biomass harvest removals on site nutrient supply and productivity (Shan et al., 2001; Powers et al., 2005; Sanchez et al., 2006).

The forest simulation model, 3-PG (Physiological Processes Predicting Growth; Landsberg and Waring, 1997; Landsberg and Sands, 2011), has been widely applied to estimate the effects of management, climate and site characteristics on different stand level attributes such as stem volume growth, biomass dynamics or water use efficiency (Coops and Waring, 2001; Landsberg et al., 2001; Sands and Landsberg, 2002; Stape et al., 2004; Sampson et al., 2006; Aylott et al., 2008; Zhao et al., 2009; Coops et al., 2010; Bryars et al., 2013). This model uses species-specific physiological traits in conjunction with empirical tree- and stand-level attributes to quantify Net Primary Production (NPP, Mg ha^{-1}), allocation of assimilates to the various biomass pools, population dynamics and soil water balance (Landsberg and Sands, 2011).

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The 3-PG model has been parameterized for many tree species, including *Acacia mangium* Willd. (Booth et al., 2000), *Dacrydium cupressinum* Sol. ex Lamb (Whitehead et al., 2002), *Eucalyptus globulus* Labill. (Sands and Landsberg, 2002), *Eucalyptus grandis* W.Hill ex Maiden (Almeida et al., 2004), *Eucalyptus nitens* H.Deane and Maiden (Rodríguez et al., 2009; Pérez-Cruzado et al., 2011), *Picea sitchensis* (Bong.) Carr. (Waring, 2000), *Pinus patula* Schiede ex Schltdl. and Cham. (Dye, 2001), *Pinus radiata* D.Don (Rodríguez et al., 2002; Flores and Allen, 2004), *Pinus taeda* L. (Landsberg et al., 2001, 2003; Sampson et al., 2006; Bryars et al., 2013), *Pinus ponderosa* Douglas ex C.Lawson (Law et al., 2000; Coops et al., 2005) and *Pseudotsuga menziesii* (Mirb.) Franco (Waring et al., 2008; Coops et al., 2010). There are no specifics 3-PG parameter estimates published for slash pine. Only one publication included the use of 3-PG for slash pine (Landsberg et al., 2003), but no species-specific parameter estimates were provided, and the authors indicated that estimates for "pine" were used instead.

Developing a general forest simulation model with applications across many species and regions is inherently difficult. There are trade-offs between level of aggregation and mechanistic representation of site-level processes. The 3-PG model is modular, thus allowing for refinement of specific sub-routines for better representation of new species or critical processes. Some sub-routines of 3-PG that could be addressed include stand mortality (Pinjuv et al., 2006; Bryars et al., 2013), light interception and canopy closure (Landsberg and Sands, 2011) and the fertility rating (FR), the empirical factor that modifies canopy quantum efficiency and root partitioning (Dye et al., 2004; Fontes et al., 2006; Xenakis et al., 2008; Almeida et al., 2010; Pérez-Cruzado et al., 2011). Using long-term datasets, we addressed these issues by incorporating new species-specific functions and changing the structure of the model.

Estimates of stand mortality occurring prior to the onset of intra-specific competition were not incorporated into earlier versions of the model (Landsberg and Waring, 1997; Landsberg et al., 2003; Coops et al., 2005); rather, tree mortality was computed as a function of density-dependent competition using Reinecke's -3/2 self-thinning principles (Reineke, 1933). Sands and Landsberg (2002), Pinjuv et al. (2006) and Bryars et al. (2013) concluded that the model was unable to predict tree mortality satisfactorily. In an attempt to improve tree mortality estimates, Sands (2004) introduced a density-independent tree mortality calculation. This model improvement allowed for the estimation of random or stress-induced mortality observed under field conditions. Pérez-Cruzado et al. (2011) included new species-specific parameter estimates for density-independent tree mortality for *E. nitens*, using the generic relationships described by Sands (2004). Following the same guidelines, we will introduce a density-independent tree mortality function for slash pine using results from well-established growth and yield models.

In some versions of 3-PG (Landsberg and Waring, 1997; Sands and Landsberg, 2002; Almeida et al., 2004; Sampson et al., 2006), the model assumed that all incoming PAR radiation was intercepted by the amount of LAI present in the stands at each time step, and it did not consider cases before canopy closure. The model assumption was that the fractional ground covered by the canopy (CanCover) was always maximum (100% canopy cover). Newer versions of the model have assumed that CanCover is proportional to stand age until the age of full canopy cover (fullCanAge, years.). This represents an improvement in the model, but this parameter is uncertain, as it depends on genetics, stand density and levels of productivity (Radtke and Burkhart, 1999). Landsberg and Sands (2011) indicated that light interception in open canopies was an area where research is needed for future model improvement. Following the results of Radtke and Burkhart (1999), there is no single age for full canopy cover for each species (see Fig. 3 in Radtke and Burkhart, 1999), as that value depends on planting density, site productivity and genetics. Because errors in the age of canopy closure can reduce model accuracy and performance, we decided to investigate a different way to correlate canopy cover as a function of parameters that are available within the model. We assumed that, for average genetic variability within the species, the year to reach full canopy cover would be correlated with stand density and site productivity.

A sensitive and controversial variable used in 3-PG is the FR term (Landsberg et al., 2003; Landsberg and Sands, 2011). FR is an empirical index that ranks soil fertility on a scale from 0 (extremely infertile) to 1 (optimum). Landsberg et al. (2003) remarked that the use of FR was problematic and unsatisfactory and could be used as a tunable parameter, as demonstrated by Fontes et al. (2006). An alternative approach to estimate FR was reported by Dye et al. (2004), who correlated FR with the stand's site index (SI, m). The SI corresponds to the mean height of the dominant and co-dominant trees at a reference age, and is widely used by foresters as an index of site quality (Burkhart and Tomé, 2012). The site index is the base for many empirical growth and yield

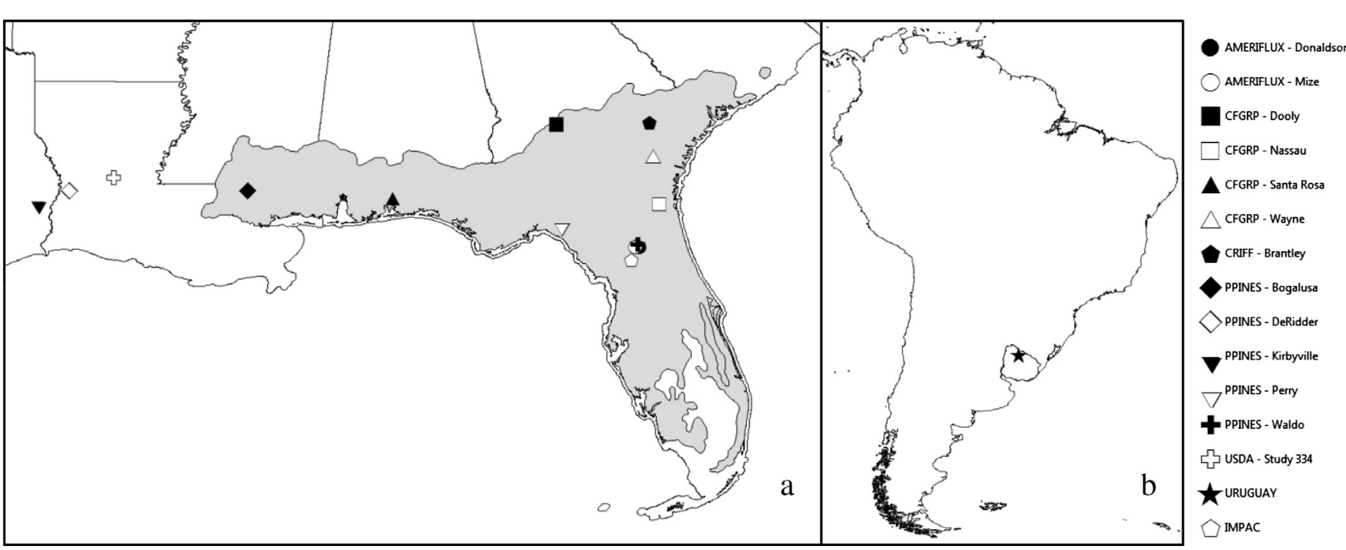

Fig. 1. Location of validation sites (a) in U.S., within the species natural distribution range (shaded area), and (b) in Uruguay.

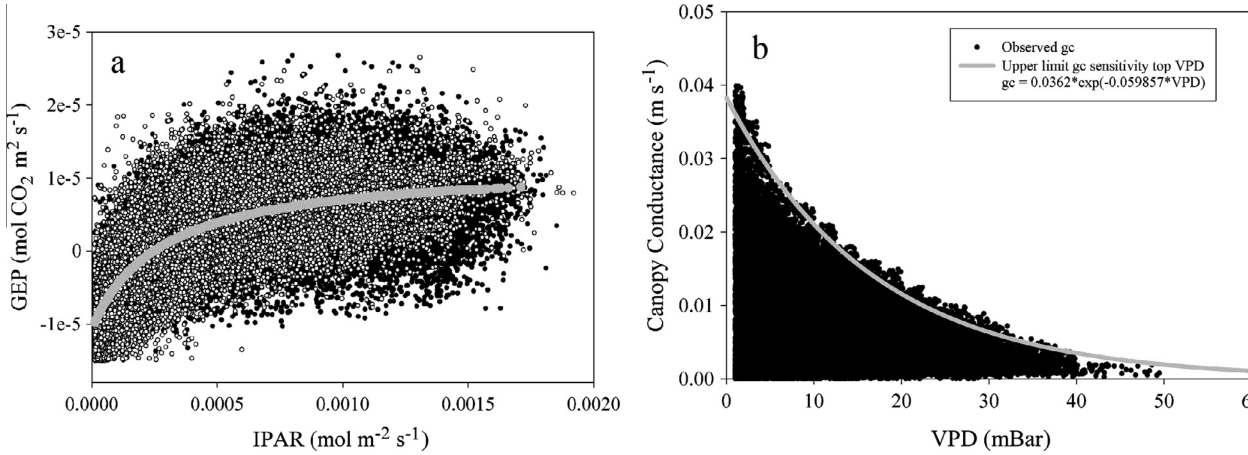

Fig. 2. Model fitting for (a) canopy quantum yield (the initial slope of the relationship showed as grey line) and (b) canopy conductance sensitivity to VPD.

models (Weiskittel et al., 2011). The site index presumably integrates a variety of factors including nutrient dynamics and site water balance, and it is reasonable to assume that FR was positively correlated with changes in SI.

The objective of this study was to parameterize the 3-PG model for slash pine using published data and long-term productivity studies for this species from the Forest Biology Research Cooperative (FBRC) at the University of Florida. We incorporated new functions for estimating canopy cover, density-independent tree mortality, fertility rating (FR) and initial biomass pools at any starting age. The model was tested against data from measurement plots covering a wide range in stand characteristics (age, productivity and management) for this species in the southeastern United States, and also plots from Uruguay, South America.

2. Materials and methods

2.1. The 3-PG model

The 3-PG model (Landsberg and Waring, 1997; Landsberg and Sands, 2011) is a stand-level model that predicts growth of even-aged, mono-specific stands. The model requires initial values of stand characteristics such as age, stocking (trees per hectare) and biomass (Mg ha^{-1}) in roots (WR), foliage (WF) and stem (stemwood + bark + branches, WS), as well as soil texture class and upper and lower limits of available soil water. The model also requires monthly weather data (e.g., global radiation, rainfall, number of rainy days, number of frost days and mean minimum and maximum temperatures). 3-PG has different sub-modules to

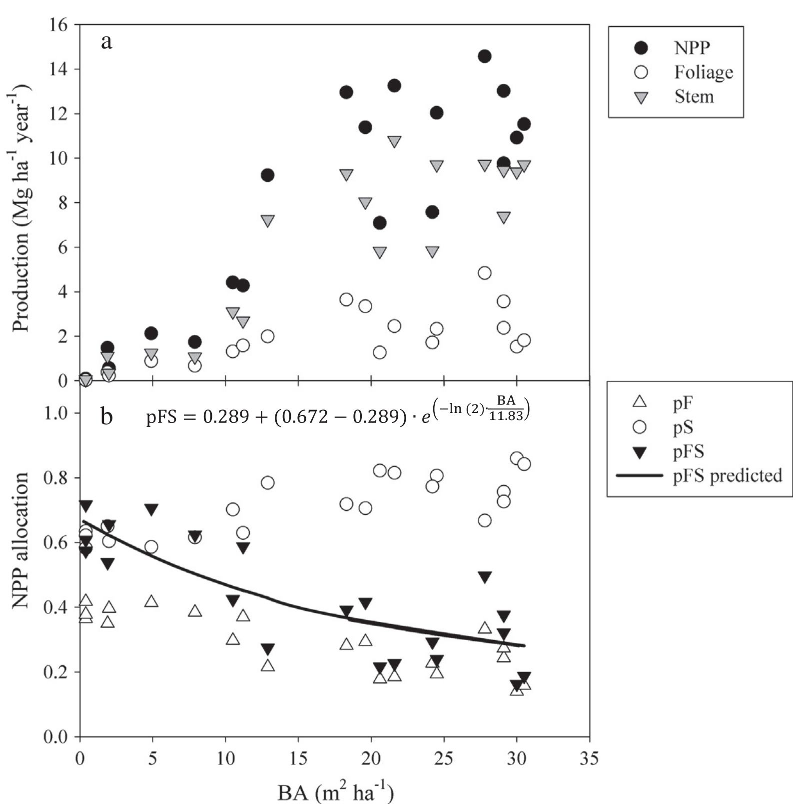

Fig. 3. Relationship between BA and (a) NPP, Foliage and Stem production (Mg ha^{-1} $year^{-1}$), and (b) NPP allocation to foliage (pF), stem (pS) and stem to foliage ratio (pFS) for slash pine stands of age ranging 2–34 years old growing in North Florida (data from Gholz and Fisher, 1982).

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). Briefly, the first step of the model calculates absorbed photosynthetically active radiation (APAR), using photosynthetically active radiation (PAR) computed from monthly mean solar radiation, and light interception. Canopy light interception is computed from projected leaf area index (LAI, $m^2\,m^{-2}$) using Beers Law. LAI was previously computed from WF and projected specific needle area (SNA, $m^2\,kg^{-1}$), corrected by foliage loss due to needlefall. For stands that have not reached canopy closure, a canopy closure index (CanCover, the proportion of ground area covered by the stand canopy) is computed to better calculate APAR. The utilized absorbed photosynthetically active radiation (APARu) is then calculated using APAR and the physiological modifier that incorporates the effects of vapor pressure deficit (VPD, mb), soil moisture and age. The canopy quantum efficiency (α_c, mol C mol^{-1} photon) is adjusted using a series of environmental modifiers that account for temperature, nutrition and frost damage. All the modifiers have values varying between 0 and 1. Gross primary production (GPP, Mg ha^{-1}) is computed using the adjusted α_c and APARu and NPP is calculated assuming a constant respiration proportion of 0.47. NPP is then allocated to the different biomass pools (WS, WF and WR) using partitioning coefficients. Root and foliage abscission are computed and discounted from the corresponding WR and WF pools.

In the water balance module, the model computes canopy conductance to water vapor, using the species-specific maximum canopy conductance ($m\,s^{-1}$), LAI, and adjusting the value depending on VPD and soil moisture. After that, stand transpiration ($mm\,month^{-1}$) is calculated using the Penman-Monteith model, and canopy evaporation is calculated using LAI, canopy interception and the amount of rainfall. Stand evapotranspiration is computed as canopy transpiration + canopy evaporation. Changes in available soil water are then computed as the difference between rainfall and evapotranspiration losses.

In the tree mortality module, the model first calculates average single tree stem biomass (kg $tree^{-1}$). If that value is lower than the target single tree stem biomass at a stand density of 1000 trees ha^{-1}, then mortality is computed using a density-independent mortality function. If the average single tree stem biomass exceeds the biomass of the target stem biomass, then the number of trees is reduced using the -3/2 self-thinning rule. If that average single tree stem biomass is smaller than the target stem biomass, then the number of trees is reduced using a mortality function from a published growth and yield model. After computing the number of dead trees, stocking and biomass pools are re-calculated. Then, stand basal area (BA, $m^2\,ha^{-1}$) is computed from mean diameter at breast height (dbh, cm) and the updated tree density; bole volume inside bark (VIB, $m^3\,ha^{-1}$) is computed from the updated WS (discounting the fraction of bark and branches, fracBB) and wood basic specific gravity (SG); bole volume outside bark (VOB, $m^3\,ha^{-1}$) is computed from VIB and the bark volume fraction. Finally, mean tree height is computed using a height-diameter function. For the next time step (month), using the updated values of trees per ha, WS, WF and WR, the cycle is repeated, adjusting the age-dependent functions of needlefall, SNA, fracBB and SG.

The 3-PG version used in this study was 3-PGpjs2.7 (Sands, 2010), which was implemented as a Microsoft Excel spreadsheet using Visual Basic for Applications. Modifications were made in the user-interface, allowing for FR and initial biomass calculations.

2.2. Experimental data for calibrating the 3-PG model

A summary of stand characteristics of the studies used for model fitting and validation is shown in Table 1. SI was estimated as the mean height of dominant and co-dominant trees at a base age of 25 years. For the IMPAC study, SI was determined directly from height measurements at age 25 years. For all other sites, SI was estimated with last height measurements and the equation reported by Pienaar et al. (1996).

2.2.1. Canopy quantum efficiency and canopy conductance

Estimates of α_c, minimum (MinCond, $m\,s^{-1}$) and maximum (MaxCond, $m\,s^{-1}$) canopy conductance, LAI for maximum canopy conductance (LAIgcx, $m^2\,m^{-2}$) and stomatal response to VPD (CoefCond, mb^{-1}) were obtained from data of the AMERIFLUX Project at the University of Florida, a long-term net ecosystem production study that uses eddy-covariance to quantify fluxes of CO_2 and H_2O (Bracho et al., 2012). This study was carried out for more than 14 years at two sites in North Central Florida. The sites represented two commercial slash pine plantations that were being managed for pulpwood production and were approximately 15 km northeast

Table 1
Summary of data used for parameter estimation and model validation.

Project	Site	*n*	Lat	Long	AGE (years)	Dq (cm)	Nha (trees ha^{-1})	BA ($m^2\,ha^{-1}$)	SI (m)	Parameters Estimated	Ref.
AMERIFLUX	Donaldson*	4	29.75	−82.16	9–23	9.0–17.8	592–2432	10.4–28.8	17.5–18.6	I, II, V	1
AMERIFLUX	Mize	4	29.76	−82.24	2–14	2.6–17.9	1152–2064	0.8–29.9	23.7–25.8		1
CFGRP	Wayne	5	31.55	−81.91	8–15	11.5–20.5	716–1083	9.6–28.6	17.9–24.1	II, V	2
CFGRP	Nassau	5	30.61	−81.77	9–15	13.6–22.2	631–1910	18.2–39.7	22.5–28.2		2
CFGRP	Santa Rosa	5	30.70	−87.02	8–15	10.5–18.2	1048–1654	10.5–33.4	21.8–26.6		2
CFGRP	Dooly	5	32.16	−83.80	9–15	10.2–18.0	1040–1637	10.8–27.5	17.9–24.1		2
CRIFF	Brantley	9	32.20	−81.98	8–18	10.0–17.2	1161–1606	10.6–33.2	20.4–26.6		3
E-PPINES	Perry	16	30.16	−83.74	3–10	5.4–19.7	737–2753	3.6–37.4	27.2–31.1	II, III, V	4
E-PPINES	Waldo	16	29.80	−82.21	3–12	4.5–20.7	709–2800	2.0–39.1	25.9–29.7		4
W-PPINES	Bogalusa	5	30.60	−93.99	3–10	4.9–18.2	641–1195	2.1–21.9	20.2–23.4	III, V	5
W-PPINES	DeRidder	5	30.87	−89.86	3–10	4.9–18.8	845–1195	2.1–26.9	23.2–27.4		5
W-PPINES	Kirbyville	5	30.86	−93.36	3–10	4.4–19.6	904–1224	1.8–35.0	26.3–27.7		5
USFS-334	Woodworth	25	31.12	−92.49	6–17	5.0–24.3	308–5573	0.9–48.8	22.3 5 23.5	II, V	6
URUGUAY	Tacuarembo	10	−31.48	−55.99	4–9	4.9–24.3	400–1167	0.8–42.3	19.8–28.5		7
IMPAC**	Gainesville	12	29.50	−82.33	3–25	3.5–26.4	538–1538	1.3–45.7	20.4–28.8	II, III, IV, V, VI	8
TOTAL***	14	118			2–23	2.6–24.3	308–5573	0.8–48.8	17.5–31.1		

n: number of plots; AGE: range of age (years); Dq: range of quadratic mean diameter (cm); BA: range of basal area ($m^2\,ha^{-1}$), SI: range of site index at base age = 25 years (m). I: Canopy quantum efficiency and canopy conductance; II: density-dependent tree mortality; III: canopy cover; IV: needlefall; V: dbh-Ht relationship; VI: fertility rating.
Ref.: Reference; 1: Bracho et al., 2012; 2: CFGRP, 2012; 3: Jokela et al., 2000; 4: Roth et al., 2007; 5: Chmura et al., 2007; 6: Baldwin et al., 1995; 7: Cambium S.A., unpublished; 8: Jokela and Martin, 2000.
* Stand thinned at age 19.
** Site used for FR-SI calibration.
*** Totals do not include IMPAC study.

of Gainesville, Alachua County, Florida, USA (29°44′N, 82°9′30″W). Further details of the study sites and measurement techniques can be found in Clark et al. (1999, 2004) and Bracho et al. (2012). Briefly, the first research site (Mize) was established in a 24-year-old slash pine plantation in 1996. The site was harvested in 1998, double-bedded, treated with herbicide and replanted with approximately 1864 trees ha^{-1} in December 1998–January 1999; the second research site (Donaldson) was established in an 8-year-old slash pine plantation in 1998. The site was replanted early in 1990 with approximately 2196 trees ha^{-1}, following clear cutting in 1988–1989 (Clark et al., 1999, 2004).

2.2.2. NPP partitioning

Traditional versions of 3-PG allocate 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. This approach has the risk that errors in tree-level allometry can lead to large errors in simulated NPP and stand level partitioning. We used data from a chronosequence study (from age 2 to 34) reported by Gholz and Fisher (1982) to better understand allocation pattern dynamics. That study included biomass sampling for each stand, allowing for accurate determinations of stand productivity. We had access to the raw data used in that study.

2.2.3. Allometric relationships

Allometric relationships for WS, WF and branch and bark fraction (pBB) were obtained from the dataset described in Gonzalez-Benecke et al. (2014a), that consisted of a collection of several data sources used previously for site-specific allometric functions (further details can be found in Gonzalez-Benecke et al., 2014a). In order to estimate initial WR, we fitted a model using data from Gholz and Fisher (1982), Gibson et al. (1985) and Roth et al. (2007). The dataset for above-ground components consisted of 259 trees measured at 14 sites, including trees from 2 to 62 years old, with dbh and height ranging between 1.3 to 32.6 cm and 1.5 to 22.9 m, respectively. The dataset for WR consisted of 81 trees measured at 6 sites, including trees from 2 to 27 years old, with dbh and height ranging between 1.3 to 25.1 cm and 0.8 to 21.3 m, respectively. The data were collected across the natural range of the species distribution, under different management and stand development conditions, reflecting a variety of silvicultural inputs (planting density, soil preparation, fertilization, weed control and thinning), site characteristics (physiographic regions, soil type, and climate), genetics and age.

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) as the main predictor. For WS and WF, the data consisted of 147 trees measured at 8 sites, including trees from 1 to 4 years old, with Ht ranging between 0.45 and 5.37 m (Colbert et al., 1990; Roth et al., 2007; Manis, 1977; Gholz and Fisher, 1982). For WR, the data consisted of 64 trees measured at two sites (E.J. Jokela, unpublished data), including trees from 2 to 5 years old, with Ht ranging between 0.78 and 3.23 m. Roots 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 2 mm diameter were weighted.

The relationship between dbh and Ht was obtained from permanent plot data. A total of 172,069 paired dbh-Ht data were used, including trees from 2 to 25 years old, with dbh and H ranging between 0.3 to 37.8 cm and 1.4 to 26.3 m, respectively.

Bryars et al. (2013) used a constant bole volume ratio (Vratio) to estimate VOB from VIB (VIB is the direct output of the model, computed from WS, number of trees per hectare and basic wood specific gravity). We decided to use a variable Vratio, assuming that this ratio should be dependent on age, stand density and productivity. To create the dataset needed for model fitting, we used the growth and yield model reported by Pienaar et al. (1996), running the model for a rotation length of 30 years (well beyond the typical management scheme for slash pine pulp production), under different conditions of planting density and SI.

2.2.4. Tree mortality and self-thinning

Parameter estimates for density-independent tree mortality (stochastic mortality occurred prior to the onset of mortality due to intra-specific competition) were obtained after adapting the survival model reported by Pienaar et al. (1996). We ran the model of Pienaar et al. (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.

For density-dependent tree mortality, estimates of maximum single tree stem biomass at a stand density of 1000 trees ha^{-1} (WS $\times$ 1000, kg tree^{-1}), and the self-thinning rule parameter (thinPower) were computed from permanent plot data (Table 1), after using a species-specific general biomass equation for WS reported by Gonzalez-Benecke et al. (2014a). The dataset used for model fitting consisted of 4332 plot-level data, including trees from 2 to 25 years old, with WS ranging between 0.2 and 381 kg tree^{-1}, growing in stands with N and SI ranging between 173 to 5573 trees ha^{-1} and 17 to 31 m, respectively.

2.2.5. Canopy cover

Analysis of canopy cover was carried out using data from two studies that included the combinations of two contrasting silvicultural treatments (operational and high intensity), two contrasting planting densities (1334 and 2990 trees ha^{-1}), and six different slash pine genetic families (Table 1). Further details can be found in Roth et al. (2007). Studies included yearly data of dbh and Ht, from age 2 up to age 10 (Perry) and 12 (Waldo) years., and live crown widths at ages 3, 4 and 5 years for both studies.

2.2.6. Fertility rating

To determine FR, we correlated this value with a stand productivity index. Site index has been demonstrated to be an excellent index of stand productivity (Burkhart and Tomé, 2012) and is an important component of many growth and yield models (Weiskittel et al., 2011). As SI functions are well established and easily accessible for this species in southeastern United States (Pienaar et al., 1996; Yin et al., 1998), we used the approach of correlating FR with changes in SI. Analysis of the relationship between FR and SI was carried out using data from the long-term productivity study IMPAC (Intensive Management Practices Assessment Center; Swindel et al., 1988 and Jokela and Martin, 2000). This study was established in 1983 at a planting density of 1543 trees ha^{-1}, and included the combination of understory competition control and fertilization treatments (further details can be found in Swindel et al., 1988 and Jokela and Martin, 2000). The treatments applied in each of the 12 plots created a wide range in productivity, similar to the range of productivity found in operational and experimental plots in the southeastern United States (Jokela et al., 2010). The dataset included yearly measurements of dbh and Ht from age 3 up to age 25 years., allowing for direct determination of SI at the target index age of 25 years.

2.2.7. Needlefall and litterfall

Needlefall (NF, Mg ha^{-1} month^{-1}) dynamics were analyzed using data from the IMPAC study (Dalla-Tea and Jokela, 1991; Jokela and Martin, 2000), where NF was collected monthly, beginning at age 6 years and continuing through age 19 years, using six circular litter traps (1 m^2) installed in the 12 treatment plots. The authors corrected NF for senescence-related biomass reductions and determined monthly WF using the logistic models of foliage accretion described by Kinerson et al. (1974) and Dougherty et al. (1995). Monthly fractional rate of needlefall (γN, month^{-1}) was determined using monthly estimates of WF and NF. To estimate litterfall (LF, Mg ha^{-1} month^{-1}) we used the data from Gonzalez-Benecke et al. (2012), who assembled LF and NF data from the literature, and then determined the ratio between NF and LF (NLR) was determined. Further details can be found in Gonzalez-Benecke et al. (2012).

2.3. Parameters obtained from literature review

All other parameters estimates needed for 3-PG were obtained directly from a literature review. Those parameters estimates were: fraction of NPP allocated to roots, litter decay rate, root turnover; temperature modifier, specific needle area, light extinction coefficient, basic wood specific gravity, bark volume ratio, days of production lost per frost day, soil water modifier, fertility effects, age modifier, maximum proportion of rain interception and LAI for maximum rain interception.

2.4. Model fitting

All model fitting and data analyses were performed using SAS 9.3 (SAS Inc., Cary, NC, USA). Boundary line fitting was performed using the quantile regression procedure, with a quantile threshold of 0.98.

2.4.1. Canopy quantum efficiency and canopy conductance

Using half-hourly daytime data of gross ecosystem exchange (GEE, μmol CO_2 m^{-2} s^{-1}, assumed as identical to GPP) to intercepted photosynthetically active radiation (IPAR, μmol photon m^{-2} s^{-1}) of the AMERIFLUX dataset, α_c was determined for each year on each site by fitting a rectangular hyperbola function (Bracho et al., 2012):

$$\mathrm{GEE} = \frac{\alpha_c \cdot \mathrm{IPAR} \cdot F_{sat}}{F_{sat} + \alpha_c \cdot \mathrm{IPAR}} \quad (1)$$

where F_{sat} is the CO_2 exchange at light saturation (μmol photon m^{-2} s^{-1}). Reported values of α_c by Clark et al. (1999, 2004) were also included in order to determine an overall mean value of α_c. Appendix A show details of the methods for GEE estimations using the eddy-covariance approach.

Canopy conductance parameters were also estimated using the AMERIFLUX dataset. Using meteorological measurements recorded with an automated weather station and latent heat (λE) fluxes from eddy-covariance measurements, canopy conductance for water vapor was computed using an inverted form of the Penman-Monteith equation (Kelliher et al., 1995). Appendix A show details of the for canopy conductance estimations.

The negative exponential function that correlates canopy conductance and VPD (Landsberg and Waring, 1997) was linearized using a natural logarithm transformation. Parameter estimates were determined using linear fitting for each year on each site to the boundary line of the transformed data:

$$\ln(g_c) = \ln(\mathrm{MaxCond}) - \mathrm{CoeffCond} \cdot \mathrm{VPD} \quad (2)$$

where g_c is the canopy conductance (m s^{-1}), MaxCond is the maximum canopy conductance (m s^{-1}), CoeffCond is the stomatal sensitivity to VPD (mb^{-1}), and VPD is the vapor pressure deficit (mb). Mean values of MaxCond and CoeffCond were determined after model fitting for all measured years on both sites.

2.4.2. NPP partitioning

Using the data from Gholz and Fisher (1982), we fitted an exponential decay to a non-zero asymptote function to the relationship between stand BA and foliage to stem partitioning ratio (pFS, the ratio between NPP allocation to foliage and NPP allocation to stem):

$$\mathrm{pFS} = \mathrm{pFS1} + (\mathrm{pFS0} - \mathrm{pFS1}) \cdot e^{\left(-\ln(2)\frac{\mathrm{BA}}{\mathrm{BA_{pFS}}}\right)} \quad (3)$$

where pSF1 is the foliage to stem partitioning ratio at large BA (mature stand), pSF0 is the foliage to stem partitioning ratio at planting, and $\mathrm{BA_{pFS}}$ is the stand BA at which $\mathrm{pFS} = \frac{1}{2} \cdot (\mathrm{pFS0} + \mathrm{pFS1})$.

2.4.3. Allometric relationships

As 3-PG uses the relationships between WS and dbh to estimate dbh from a known WS, instead of WS from a known dbh, we fitted the inverse of the classical allometric function used in 3-PG, including age as a covariate. We fit dbh as a function of WS to properly minimize the errors of model fitting:

$$\mathrm{dbh} = d1 \cdot \mathrm{WS}^{d2} \cdot \mathrm{Age}^{d3} \quad (4)$$

where $d1$ to $d3$ c are curve fit parameters (denominated in 3-PG as a1Ws, n1Ws and n2Ws, respectively). Stand density (Nha) was also tested as a covariate (as suggested by Sands, 2010), but it was discarded due to inadequate results when 3-PG was run, including thinning treatments (the model including Nha performed well for simulations without thinning).

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. In the case of young stands, biomass was determined from Ht and age. For stands where dbh and Ht are known, the model selected was:

$$W_{F,S} = w1 \cdot \mathrm{dbh}^{w2} \cdot \mathrm{Ht}^{w3} \cdot \mathrm{Age}^{w4} \quad (5)$$

For young stands, when dbh is not available, the model selected was:

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

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

We determined WR as a function of total above ground biomass (AGB, the sum of WS and WF) as follows:

$$\mathrm{WR} = r0 + r1 \cdot \mathrm{AGB} \quad (7)$$

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

$$\mathrm{pBB} = \mathrm{pBB1} + (\mathrm{pBB0} - \mathrm{pBB1}) \cdot e^{\left(-\ln(2)\frac{\mathrm{Age}}{\mathrm{Age_{BB}}}\right)} \quad (8)$$

where 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 $\mathrm{pBB} = \frac{1}{2} \cdot (\mathrm{fracBB0} + \mathrm{fracBB1})$.

The relationship between dbh and Ht was fitted using several stand-level variables as covariates. The variables considered were Age, N and BA. These variables were selected as they represented different aspects of the stand, such as stocking, productivity and competition, which could affect the height-diameter relationships. Following the approach of Crescente-Campo et al. (2010) to determine which stand-level variables should be included in the final general model, a logarithm transformation was carried out and a stepwise procedure was used on the linear model with a threshold significance value of 0.15 as variable selection criteria. The variance inflation factor (VIF) was monitored to detect multicollinearity among explanatory variables. All variables included in the model with VIF larger than 5 were discarded, as suggested by Neter et al. (1996). The non-linear form of the model finally selected to estimate H was:

$$\mathrm{Ht} = 1.37 + e^{(h1 + h2 \cdot \mathrm{dbh}^{h3} + h4 \cdot \ln(\mathrm{Age}) + h5 \cdot \ln(\mathrm{Nha}) + h6 \cdot \ln(\mathrm{BA}))} \tag{9}$$

where $h1$ to $h6$ are curve fit parameters (denominated in 3-PG as aH, aHB, nHB, aHAge, aHN and aHBA, respectively).

The relationship between Vratio and VIB was fitted similar to the dbh-Ht relationship, including several stand-level variables as covariates and using a stepwise procedure and VIF criteria for variable selection. The non-linear form of the model finally selected to estimate H was:

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

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

2.4.4. Tree mortality and self-thinning

Density-independent tree mortality (γNt) was determined by fitting the model proposed by Sands (2004):

$$\gamma \mathrm{Nt} = \gamma \mathrm{N1} + (\gamma \mathrm{N0} - \gamma \mathrm{N1}) \cdot e^{\left(-\ln(2) \cdot \frac{\mathrm{Age}}{\mathrm{Age}_\gamma}\right)} \tag{11}$$

where γN1 is the mortality rate of mature stands, γN0 is the mortality rate at age = 0 (seedling mortality rate), and Age_γ is the age at which $\gamma \mathrm{Nt} = \frac{1}{2} \cdot (\gamma \mathrm{N0} + \gamma \mathrm{N1})$.

For density-dependent tree mortality, the model required two parameters: the maximum stem mass per tree at a stand density of 1000 trees per hectare (wS × 1000, kg tree^{-1}) and the exponent of the self-thinning rule (Landsberg and Waring, 1997). Values of the exponent were determined using linear fitting to the boundary line of the transformed data of mean plot WS and Nha for each year and each site:

$$\ln(\mathrm{WS}) = \mathrm{aN} + \mathrm{thinPower} \cdot \ln(\mathrm{Nha}) \tag{12}$$

where WS is mean stem biomass (kg tree^{-1}), aN is the intercept, thinPower is the slope of the self-thinning line and Nha is the total number of living trees per hectare (ha^{-1}).

2.4.5. Canopy cover

In the Eastern-PPINES dataset, in addition to dbh and Ht, live crown width was measured in two directions at ages 3, 4 and 5 years, and live crown area (CA, m^2) was determined for each measured tree assuming the crown shape as an ellipse (Gonzalez-Benecke et al., 2014b). 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:

$$\mathrm{CA} = \mathrm{a} \cdot \mathrm{dbh}^b \tag{13}$$

Using covariance analysis, no effect of site, planting density and culture was detected ($P > 0.2$, data not shown) and only the effect of genetic family was significant in the allometry of CA. The genetic families that were different ($P = 0.04$) corresponded to the extremes in productivity tested (S1, high productivity; S4, low productivity). Considering these results, we fitted a single model across all genetic families.

With the final model fitted, CA was calculated for all measured trees. The sum of CA for each plot was expressed as a proportion of the area of the plot and a CanCover was determined for each age and plot. CanCover was adjusted using a factor of $\pi/4$, the ratio between the areas of an ellipse and a rectangle of similar sides, as it was assumed that at that point the plot reached full canopy closure. After canopy closure the allometry of crown width changes (Pretzsch et al., 2012) and the relationship used in this study should not be adequate. Nevertheless, 3-PG uses a maximum value of CanCover of 1, not accounting for overlapping crowns (values of CanCover greater than 1 are assumed to be 1). In order to describe the dynamics of CanCover prior to reaching full canopy closure, a relationship between CanCover, age and other stand attributes such as BA and N was fitted.

2.4.6. Specific needle area and wood basic specific gravity

The relationships between age and specific needle area (SNA, $\mathrm{m}^2\ \mathrm{kg}^{-1}$) and basic wood specific gravity (SG) were determined by fitting the model proposed by Sands (2010):

$$\mathrm{SNA} = \sigma_1 + (\sigma_0 - \sigma_1) \cdot e^{\left(-\ln(2) \cdot \left(\frac{\mathrm{Age}}{\mathrm{Age}_\sigma}\right)^2\right)} \tag{14}$$

$$\mathrm{SG} = \rho_1 + (\rho_0 - \rho_1) \cdot e^{\left(-\ln(2) \cdot \frac{\mathrm{Age}}{\mathrm{Age}_\rho}\right)} \tag{15}$$

where σ_1 is the SNA of mature stands σ_0 is the SNA at age = 0; and Age_σ is the age at which $\mathrm{SNA} = \frac{1}{2} \cdot (\sigma_0 + \sigma_1)$, ρ_1 is the SG of mature stands, ρ_0 is the SG at age = 0, and Age_ρ is the age at which $\mathrm{SG} = \frac{1}{2} \cdot (\rho_0 + \rho_1)$.

Table 2
Summary of soil and weather data of sites used for model validation ([*]).

Project	Site	Soil Class	ASW	Tmin	Tmax	Rad-w	Rad-s	Rain	Nrain	Nfrost
AMERIFLUX	Donaldson	s	195	5.2	32.0	10.3	19.5	1183	93	15
AMERIFLUX	Mize	s	195	4.7	32.5	10.3	19.7	1188	95	16
CFGRP	Wayne	s	168	2.5	34.1	9.5	21.8	1246	98	39
CFGRP	Nassau	sl	213	5.5	32.9	10.0	21.6	1284	108	14
CFGRP	Santa Rosa	s	208	3.0	33.6	9.8	22.3	1572	96	39
CFGRP	Dooly	s	88	2.0	33.3	8.9	22.0	1258	105	37
CRIFF	Brantley	s	185	2.2	34.4	9.8	23.1	1257	98	32
E-PPINES	Perry	s	190	4.6	33.3	10.7	19.1	1307	122	27
E-PPINES	Waldo	s	175	4.4	33.2	10.3	19.6	1244	114	12
W-PPINES	Bogalusa	sl	260	4.0	33.7	8.8	21.6	1762	94	48
W-PPINES	DeRidder	sl	320	4.8	34.5	9.2	22.2	1398	77	18
W-PPINES	Kirbyville	sl	231	5.6	34.6	8.8	22.9	1397	77	39
USFS-334	Woodworth	sl	275	2.8	33.8	9.0	21.6	1538	88	27
URUGUAY	Tacuarembo	cl	260	6.1	29.6	8.8	24.5	1477	84	0
IMPAC[**]	Gainesville	s	195	6.0	32.7	10.3	19.6	1154	95	12

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: average daily minimum temperature of coolest month (°C); Tmax: average daily minimum temperature of warmer month (°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 $\mathrm{m}^{-2}\ \mathrm{day}^{-1}$); Rain: aAverage yearly total rainfall (mm year^{-1}), Nrain: average yearly total number of rainy days, Nfrost: average yearly total number of frost days.

[*] Weather data from years used for validation.

[**] Site used for FR-SI calibration.

Table 3
Description of 3-PG parameters and default values for slash pine.

Meaning/Comment	3-PG symbol	Unit	Value
Biomass partitioning and turnover			
Allometric relationships & partitioning			
Foliage:stem partitioning ratio at BA = 0	pFS0	–	0.67
Foliage:stem partitioning ratio at for mature stands	pFS1	–	0.29
BA at which foliage:stem partitioning ratio = (pFS0 + pFS1)/2	BApFS	–	11.84
Constant in the diam. v. stem mass relationship	a1Ws	–	3.630
Power in the diam. v. stem mass relationship	n1Ws	–	0.412
Power of Age in the diam. v. stem mass relationship	n2Ws	–	−0.104
Maximum fraction of NPP to roots	pRx	–	0.40
Minimum fraction of NPP to roots	pRn	–	0.144
Needlefall, litterfall, litter decay & root turnover			
Maximum needlefall rate	γFx	month^{-1}	0.13
Month at which needlefall rate has maximum value	tγFx		11
Average yearly decay rate of litter		year^{-1}	0.14
Needlefall to litterfall ratio at age 0	NF_0	–	0.733
Needlefall to litterfall ratio for mature stands	NF_1	–	1.0
Age at which Needlefall to litterfall ratio = $(\sigma_0 + \sigma_1)/2$	Age_{NLR}	year	21.5
Average monthly root turnover rate	γR	month^{-1}	0.018
NPP & conductance modifiers			
Temperature modifier (fT)			
Minimum temperature for growth	Tmin	°C	5
Optimum temperature for growth	Topt	°C	25
Maximum temperature for growth	Tmax	°C	40
Frost modifier (fFRost)			
Days production lost per frost day	kF	Day	1
Soil water modifier (fSW)			
Moisture ratio deficit for fq = 0.5	SWconst	–	0.7
Power of moisture ratio deficit	SWpower	–	9
Fertility effects			
Value of ‘m’ when FR = 0	m0	–	0
Value of ‘fNutr’ when FR = 0	fN0	–	0.3
Power of (1-FR) in ‘fNutr’	fNn	–	1
Age modifier (fAge)			
Maximum stand age used in age modifier	MaxAge	year	200
Power of relative age in function for fAge	nAge	–	1.5
Relative age to give fAge = 0.5	rAge	–	0.5
Stem mortality & self-thinning			
Mortality rate for large t	γNx	%/year	0.45
Seedling mortality rate (t = 0)	γN0	%/year	1.73
Age at which mortality rate has median value	tγN	year	7.97
Shape of mortality response	nγN	–	1
Max. stem mass per tree @ 1000 trees/hectare	wSx1000	kg tree^{-1}	220
Power in self-thinning rule	thinPower	–	1.53
Fraction mean single-tree foliage biomass lost per dead tree	mF	–	0
Fraction mean single-tree root biomass lost per dead tree	mR	–	0.2
Fraction mean single-tree stem biomass lost per dead tree	mS	–	0.4
Canopy structure and processes			
Specific needle area (σ)			
Specific needle area at age 0	σ_0	m^2 kg^{-1}	5.00
Specific leaf area for mature leaves	σ_1	m^2 kg^{-1}	3.43
Age at which specific needle area = $(\sigma_0 + \sigma_1)/2$	tσ	year	7.79
Light interception			
Extinction coefficient for absorption of PAR by canopy	k	–	0.715
Age at canopy cover	fullCanAge	year	5
BA at canopy cover	fullCanBA	m^2 ha^{-1}	10.60
Canopy cover at BA = 1 m^2 ha^{-1}	CanBA1	–	0.12
Maximum proportion of rainfall evaporated from canopy	MaxIntcptn	–	0.2
LAI for maximum rainfall interception	LAImaxIntcptn	–	5
Production and respiration			
Canopy quantum efficiency	α_c	molC molPAR^{-1}	0.056
Ratio NPP/GPP	Y	–	0.47
Canopy Conductance (gc)			
Minimum canopy conductance	MinCond	m s^{-1}	0

Table 3 (*continued*)

Meaning/Comment	3-PG symbol	Unit	Value
Maximum canopy conductance	MaxCond	$m\ s^{-1}$	0.036
LAI for maximum canopy conductance	LAIgcx	–	3
Defines stomatal response to VPD	CoeffCond	mb^{-1}	0.0598
Canopy boundary layer conductance	BLcond	$m\ s^{-1}$	0.2
Wood and stand properties			
Branch and bark fraction (pBB)			
Branch and bark fraction at age 0	pBB0	–	0.648
Branch and bark fraction for mature stands	pBB1	–	0.240
Age at which pBB = (pBB0 + pBB1)/2	tBB	year	4.751
Wood basic specific gravity			
Minimum basic density – for young trees	ρMin	–	0.371
Maximum basic density – for older trees	ρMax	–	0.550
Age at which rho = (rhoMin + rhoMax)/2	tRho	year	10.428
Stem height			
Constant in the stem height relationship	aH	–	1.0738
Constant of DBH in the stem height relationship	aHB	–	−5.4379
Power of DBH in the stem height relationship	nHB	–	−0.8544
Constant of Age in the stem height relationship	aHAge	–	0.5450
Constant of stocking in the stem height relationship	aHN	–	−0.0218
Constant of BA in the stem height relationship	aHBA	–	0.2243
Volume ratio			
Constant in the bole volume ratio relationship	aVR	–	−0.0097
Power of VIB in the bole volume ratio relationship	nVRVi	–	0.9549
Power of stocking in the bole volume ratio relationship	nVRN	–	0.0819
Power of Age in the bole volume ratio relationship	nVRAge	–	−0.0021

2.4.7. Needlefall, litterfall and forest floor accumulation

Similar to Dougherty et al. (1995), we defined the phonological month for needlefall (NMonth) starting in May (NMonth = 1) and ending in April (Nmonth = 12). After expressing γN as a proportion of annual maximum γN (γN*x*, $month^{-1}$), we fitted a non-linear model to the relationship between NMonth and the monthly average γN of all 14 years of measurements. The model finally selected was:

$$\frac{\gamma N}{\gamma Nx} = \frac{\gamma N1 + \gamma N2 * NMonth}{1 + \gamma N3 * NMonth + \gamma N4 * NMonth^2} \quad (16)$$

where γN1 to γN4 are curve fit parameters.

The relationship between age and NLR was determined by fitting the same model used for SNA and SG:

$$NLR = NF_1 + (NF_0 - NF_1) \cdot e^{\left(-\ln(2)\cdot\left(\frac{Age}{Age_{NFR}}\right)^2\right)} \quad (17)$$

where NF_1 is the NLR of mature stands NF_0 is the NLR at age = 0; and Age_{NLR} is the age at which $NLR = \frac{1}{2} \cdot (NF_0 + NF_1)$.

2.4.8. Fertility rating

At the study selected to develop a relationship between FR and SI, site specific biomass equations were developed at ages 4 (Colbert et al., 1990) and 13 years (Jokela and Martin, 2000), allowing for accurate determination of above-ground biomass (AGB, $Mg\ ha^{-1}$). After obtaining all parameters needed by 3-PG, we determined the optimum FR that minimized the error of AGB estimation for each plot. We ran the model iteratively at 0.01 FR steps until finding the value that had the minimum mean square error of the fitting between the observed and predicted AGB (including all measurements). Finally, SI was correlated with the optimum FR, obtaining a general relationship after pooling paired data from all plots.

2.5. Model evaluation

After model parameterization was completed, the performance of 3-PG for slash pine was evaluated against independent data not used in model development, from measurement plots covering a wide range of age, productivity and management. All statistical analyses were performed using SAS 9.3 (SAS Inc., Cary, NC, USA). Three measures of accuracy were used to evaluate the goodness-of-fit between the observed and predicted values for each variable: (i) root mean square error (RMSE); (ii) mean bias error (Bias); and (iii) coefficient of determination (R^2). Variables evaluated included stand basal area (BA, $m^2\ ha^{-1}$), number of surviving trees (Nha, trees ha^{-1}), bole volume over bark (VOB, $m^3\ ha^{-1}$), mean tree height (H, m) and total above-ground biomass (AGB, $Mg\ ha^{-1}$). For each plot, observed ABG was computed using the general biomass function reported by Gonzalez-Benecke et al. (2014a): $AGB = 0.0190 \cdot dbh^{2.1019} \cdot Ht^{0.8383} \cdot Age^{0.0908}$. Observed VOB was computed with the function reported by Pienaar and Rheney (1993) using observed dbh and Ht.

Model validation was carried out by running the model from age of first measurement (e.g. age 9 years for AMERIFLUX-Donaldson, or age 3 years for E-PPINES-Perry; see Table 1) to the age of last measurement (e.g. age 23 years for AMERIFLUX-Donaldson, or age 10 years for E-PPINES-Perry; see Table 1). Initial biomass pools to initialize the model were determined for each plot using the equations for WF, WS and WR reported in this study. From all datasets described previously, only the IMPAC data set was not included in model validation, as the relationship between SI and FR was fitted directly from those data. Table 1 shows a summary of stand characteristics of each study.

We included data from Eastern-PPINES and AMERIFLUX in the validation process, as each study only partially contributed to the determination of the suite of parameters. In addition to those studies, data from other sources were also included: Three studies from the Western-PPINES series of FBRC (Chmura et al., 2007); one fertilization study from the FBRC (CRIFF study located in Brantley, GA; Jokela et al., 2000); one planting density study of USFS (USFS-334 study located in Woodworth, LA; Baldwin et al., 1995) and four studies from the second cycle slash pine full-sib block-plots (FSBP) study of the Cooperative of Forest Genetics Research Program (CFGRP, 2012) at the University of Florida. At the Western-PPINES studies, due to high mortality in some plots, we selected 5 plots with more than 80% survival at each site. At the CRIFF study, that included 10 treatments repeated in 3 blocks, we selected 3 treatments that accounted for most of the variability in productivity: control (T1), herbicide competition control (T3) and fertilization plus herbicide competition control (T4). At each FSBP study, that included 50 plots of full-sib families planted as family block plots, we randomly selected 5 plots, each one containing a different full-sib family. The model was also validated against data from 10 permanent plots growing in operational stands in Uruguay (properties of Cambium Forestal Uruguay S.A.). Fig. 1 shows the location of all validation sites.

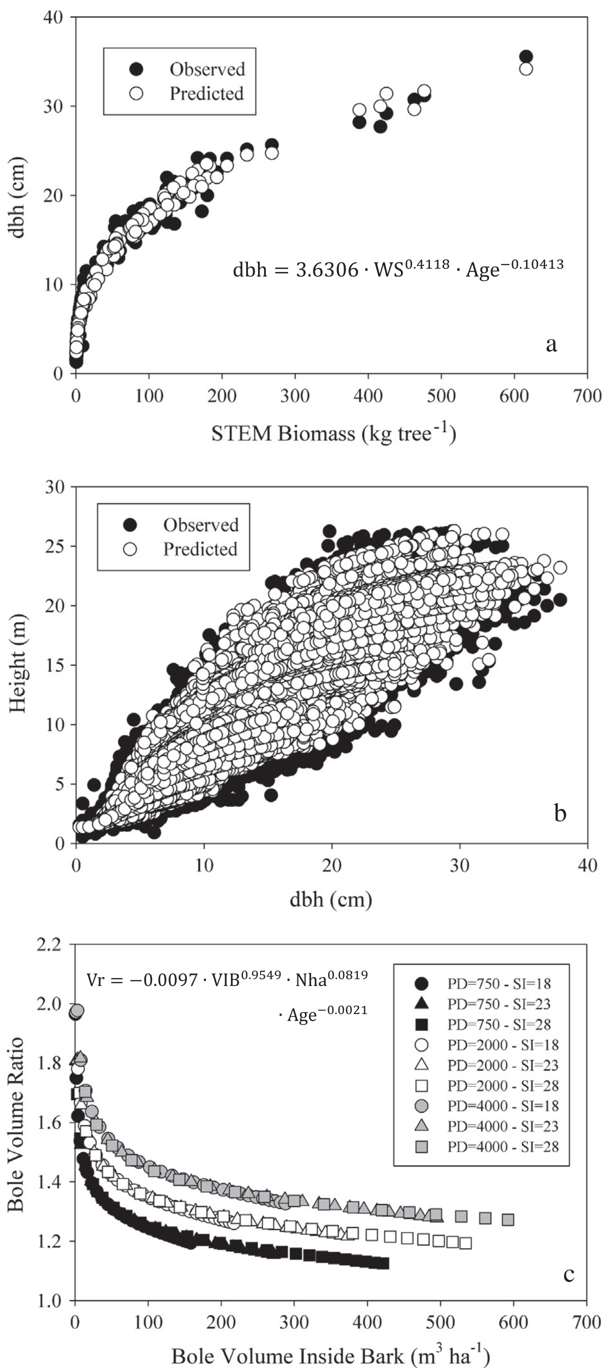

Fig. 4. Allometric relationships for (a) Stem biomass and dbh, (b) dbh and height, and (c) bole volume inside bark (VIB) and bole volume ratio (Vr) for different planting density (PD, trees ha^{-1}) and site index (SI, m).

Estimates of LAI were validated using data from both stands of the AMERIFLUX study, where projected LAI was estimated from needlefall collected monthly in 10 squared litter traps (0.81 m^2) randomly located inside the inventory plots of each site (Bracho et al., 2012), correcting for senescence-related biomass reductions and using the logistic models of foliage accretion described by Kinerson et al. (1974) and Dougherty et al. (1995). Calculations incorporated anomalous early needlefall pulses due to drought and windstorms observed in some years.

We also tested the adequacy of the estimates of stand water use by running the model for site conditions of the IMPAC study, using average SI = 22 m and varying rainfall up to 50% above and below the mean value of 1153 mm year^{-1}.

2.6. Climate and soil data

The weather data collected was monthly average daily minimum (Tmin, °C) and maximum (Tmax, °C) temperature, monthly average daily total solar radiation (MJ m^{-2} day^{-1}), monthly total rainfall (Rain, mm month^{-1}), number of rainy days (month^{-1}) and number of frost days (month^{-1}). A summary of soil and weather data of sites used for model validation is presented in Table 2. For the AMERIFLUX study, all weather data were collected from automatic weather stations installed at each site (for further details see Bracho et al., 2012). For all other sites in the U.S., daily weather data (Tmin, Tmax and Rain) were obtained online from the National Climatic Data Center (http://www.ncdc.noaa.gov/cdo-web/search), selecting the weather station nearest to each study site. Daily radiation was obtained from the National Solar Radiation Data Base (http://rredc.nrel.gov/solar/old_data/nsrdb/) of the Renewable Resource Data Center (RReDC). For sites from Uruguay, daily weather data (including radiation) were obtained online from the Instituto Nacional de Investigación Agropecuaria (http://www.inia.org.uy/online/site/gras.php), selecting the weather station from INIA-Tacuarembó. The soil data collected were texture class (s: sandy; sl: sandy-loam; cl: clay), maximum available soil water (mm) and minimum available soil (mm) water. For the AMERIFLUX studies, soils data were obtained from direct sampling. For all other 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 from Uruguay, soils data were available from soil classification maps for each site using the soil classification of Coneat (www.prenader.gub.uy/coneat/) (see Table 2).

3. Results

3.1. Model fitting

The parameter estimates for all the functions used by 3-PG are reported in Table 3. When model fitting was carried out, all parameter estimates were significant at $P < 0.05$.

Canopy quantum yield (α_c) was determined as the slope of the relationship between IPAR and gross ecosystem production (GEP) (Fig. 2a). In addition to the 12 values obtained using the AMERIFLUX data, we collected 4 more reported values from Clark et al. (1999, 2004). With all 16 data observations, we determined an average α_c of 0.0563 mol C mol^{-1} photon ($n = 16$; SE = 0.0034). The model fitted to estimate canopy conductance parameters is shown in Fig. 2b. Maximum (MaxCond), minimum (MinCond) canopy conductance and the response of canopy conductance to VPD

(CoeffCond) were 0.036 m s^{-1}, 0 m s^{-1} and 0.059 mb^{-1}, respectively (Table 3).

NPP partitioning was set as a function of BA. Foliage and stem production (Mg ha^{-1} $year^{-1}$) increased steadily up to reaching quasi-plateau values at BA larger than about 15 m^2 ha^{-1} (Fig. 3a). pFS, that was somewhat constant in early stages of stand development, declined sharply at BA larger than 10–15 m^2 ha^{-1}, reaching approximately constant values at BA larger than about 20 m^2 ha^{-1} (Fig. 3a). The parameter estimates of the new pFS function were 0.672, 0.289 and 11.93, for pFS0, pFS1 and BA_{pFS}, respectively (Table 3).

Allometric relationships for dbh (as a function of WS), Ht (as a function of dbh) and Vratio (as a function of VIB) are shown in Fig. 4. The model to estimate dbh was dependent on WS and age (Fig. 4a). In this model, the index for age was negative, indicating that for the same WS, older trees should have smaller diameters - presumably reflecting higher SG. The model to estimate Ht (Fig. 4b) was dependent on dbh, age, Nha and BA: $\mathrm{Ht} = 1.37 + e^{(1.0738075 - 5.437954 \cdot \mathrm{dbh}^{-0.854453} + 0.54002 * \ln(\mathrm{Age}) - 0.021778 * \ln(\mathrm{Nha}) + 0.224274 * \ln(\mathrm{BA}))}$ ($n = 169864$; $P < 0.001$; $R^2 = 0.99$). In this model the index for Nha was negative, indicating that trees growing in higher density stands are likely to be shorter at any given fixed value of dbh, age and BA. Bole volume ratio (Fig. 4c) was dependent on age and Nha and in this model, too, the index for age was negative, indicating that older trees are likely to have a larger bark fraction. Parameter estimates for all allometric models are given in Table 3.

Allometric relationships to estimate initial biomass pools are shown in Fig. 5. Root biomass was proportional to AGB, and that relationship was different for young trees (Fig. 5a, age 1–4 years) than for older trees (Fig. 5b, age 5–27 years). For young trees (when dbh was not available), WF and WS were dependent on Ht and age (left panel; Fig. 5c and e). When dbh data were available, WF and WS were dependent on dbh, Ht and age (right panel; Fig. 5d and f). Parameter estimates for all biomass functions are given in Table 4.

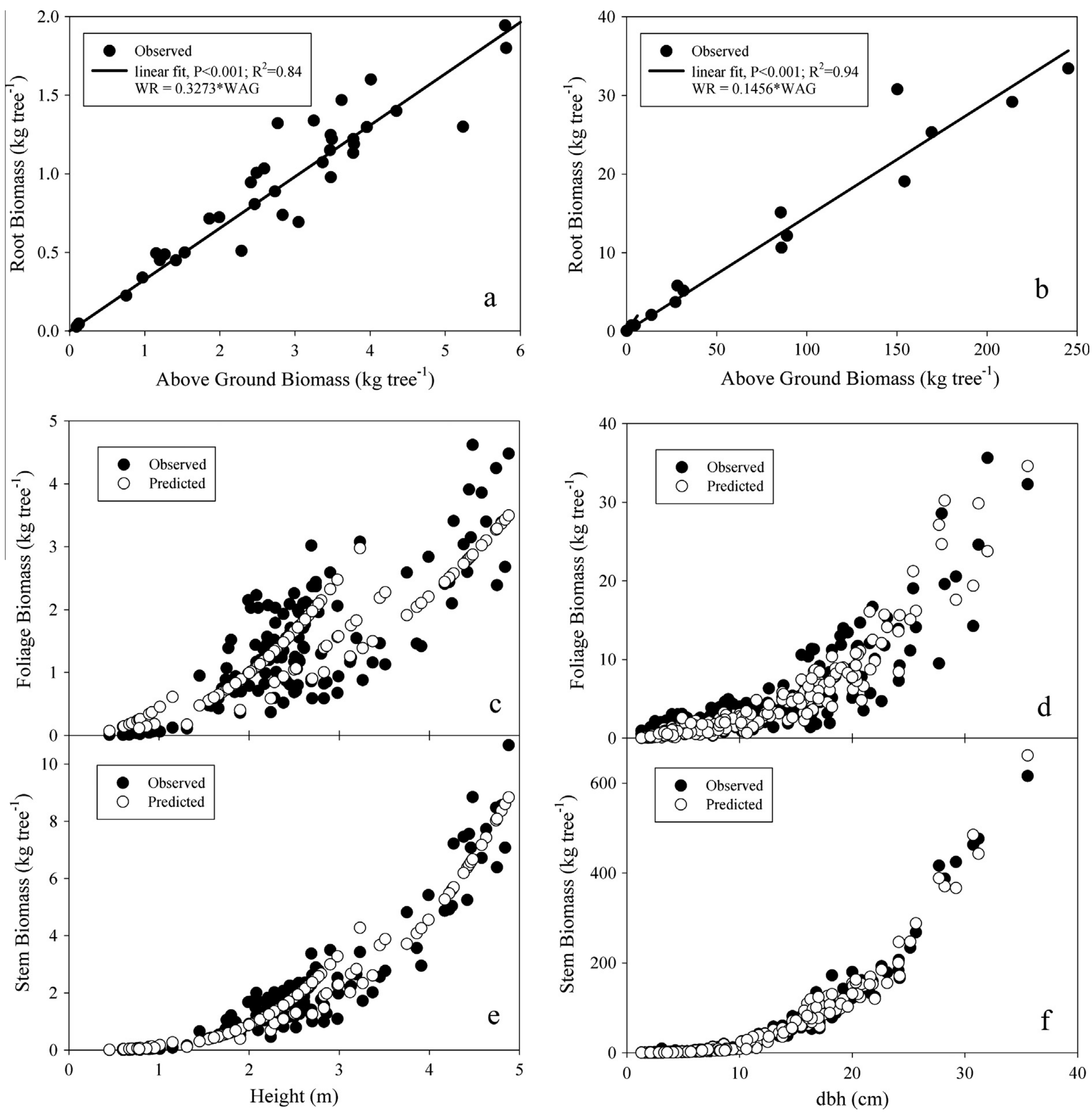

Fig. 5. Allometric relationships to estimate initial stand values for roots (a, b), foliage (c, d) and stem (e, f) biomass for young stands with no dbh (left panel; a, c, e) and for stands with dbh (right panel; b, d, f).

Tree mortality relationships are shown in Fig. 6. Examples of survival for different planting densities (PD, trees ha^{-1}) using the functions reported by Pienaar et al. (1996) are shown in Fig. 6a. When mortality rate was calculated for each PD, a single non-linear relationship was evident (Fig. 6b). 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. 6c), the slope of the self-thinning line (thinPower) was -1.5299 and the maximum stem mass per tree at 1000 trees ha^{-1} (WS $\times$ 1000) was 220 kg (Table 3).

The allometric relationship to estimate crown area was: $CA = 0.0805 \cdot dbh^{1.8539}$ ($n = 1923$; $P < 0.001$; $R^2 = 0.88$). Using this relationship, the fractional canopy cover for each plot was calculated for the three FBRC studies (E-PPINES in Waldo, E-PPINES in Perry and IMPAC). The left panels in Fig. 7 shows the effect of age, planting density and productivity on canopy cover

Table 4
Parameter estimates and fitted statistics of equations for predicting initial WF, WS and WR.

Model	Equation	Parameter	Parameter estimate	SE	R^2	RMSE	CV (%)	
Ht < 3 m	$WF = w_1 \cdot Ht^{w2} \cdot Age^{w3}$	6	$w1$	0.4446	0.0416	0.924	0.53	33.6
			$w2$	2.2907	0.1707			
			$w3$	−1.1316	0.1732			
	$WS = w_1 \cdot Ht^{w2} \cdot Age^{w3}$	6	$w1$	0.1693	0.0165	0.968	0.67	26.5
			$w2$	3.2938	0.1370			
			$w3$	−0.9131	0.1429			
	$WR = r_1 \cdot AGB$	7	$r1$	0.3273	0.0069	0.969	0.19	19.5
Ht > 3 m	$WF = w_1 \cdot dbht^{w2} \cdot Ht^{w3} \cdot Age^{w3}$	5	$w1$	0.0069	0.0033	0.888	2.47	57.3
			$w2$	2.8123	0.1726			
			$w3$	−0.2932	0.3032			
			$w4$	−0.1377	0.0816			
	$WS = w_1 \cdot dbht^{w2} \cdot Ht^{w3} \cdot Age^{w3}$	5	$w1$	0.0140	0.0021	0.990	9.37	20.5
			$w2$	2.0202	0.0466			
			$w3$	0.9804	0.0911			
			$w4$	0.1181	0.0213			
	$WR = r_1 \cdot WAG$	7	$r1$	0.1456	0.0057	0.973	2.59	24.0

WF: foliage dry mass (kg tree^{-1}); WS: stem dry mass (kg tree^{-1}); WR: root dry mass (kg tree^{-1}); AGB: total above-ground dry mass (WS + WF; kg tree^{-1}); dbh: diameter outside-bark at 1.37 m height (cm); Ht: total tree height (m); SE: standard error; R^2: coefficient of determination; RMSE; root mean square error; CV: coefficient of variation (100 RMSE/mean). For all parameter estimates: P-value < 0.001.

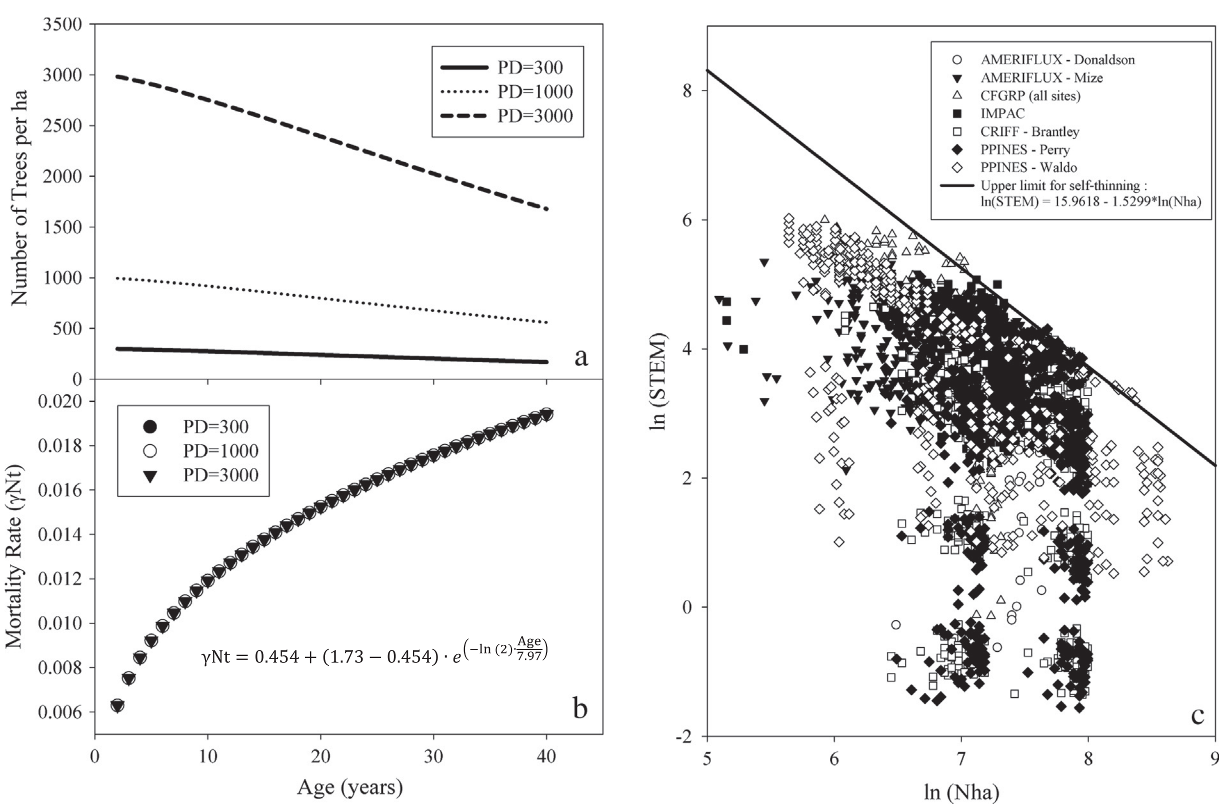

Fig. 6. Tree mortality relationships. The left panel shows the relationship between age and (a) survival for contrasting planting density (PD, trees ha^{-1}) using the model of Pienaar et al. (1996), and (b) density-independent tree mortality (γNt) for different PD. The right panel shows density-dependent tree mortality, based on the relationship between stem biomass and stand density (both in natural logarithm scale). The self-thinning line is the theoretical upper limit.

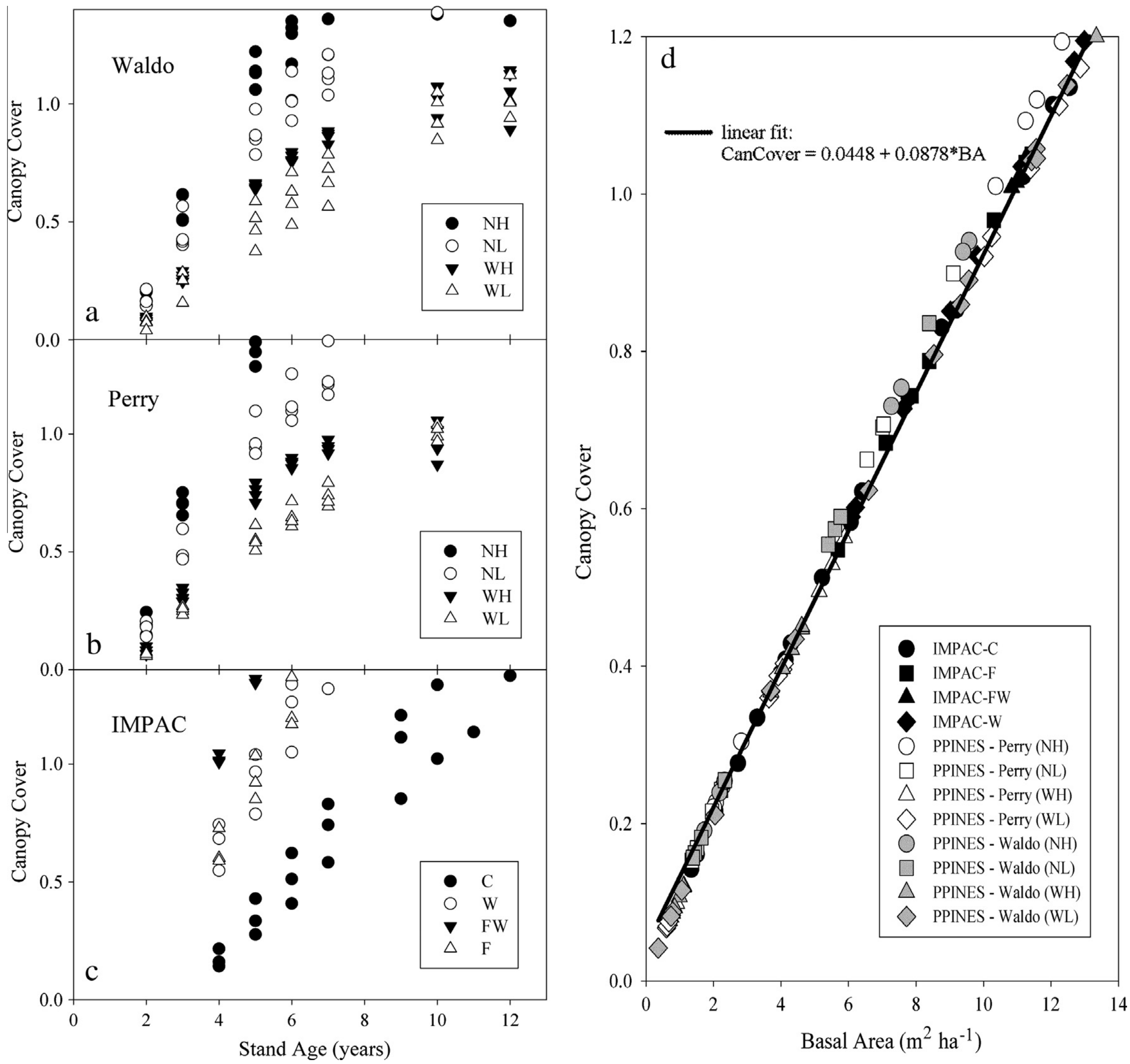

Fig. 7. Canopy Cover dynamics. The left panel shows the effect of age, stand density and culture in the development of canopy (expressed as fractional canopy cover) for three sites in North Florida (PPINES-Waldo, Fig. a; PPINES-Perry, Fig. b; IMPAC; Fig. c). The right panel shows the relationship between BA and fractional canopy cover for all three sites.

development, which affect the timing to reach full canopy closure (fractional canopy cover = 1). In the PPINES studies, plots with narrow PD and high culture (NH) reached full canopy cover at about 4 years, while plots with a wide PD and low culture (WL) reached full canopy cover at ages older than 10 years. For the IMPAC study, plots with sustained fertilization and weed control (FW) reached full canopy closure at age 4 years, while the control plots (*C*) reached full canopy closure at about age 10 years. When the fractional canopy cover was plotted against BA, a single relationship was found (Fig. 7c), even when data were included from a different study having different silvicultural treatments (IMPAC). The final model fitted was: $CanCover = 0.0448 + 0.0878 \cdot BA$ ($n = 129$; $P < 0.001$; $R^2 = 0.99$). We are aware that after canopy closure the allometry of branches changes and the relationship used in this study should not be adequate after CanCover > 1, but for 3-PG any value of CanCover greater than 1 is assumed to be 1.

Fig. 8 shows the age-dependent relationships for SNA (Fig. 8a), whole-tree SG (Fig. 8b) and NLR (Fig. 8c). For all variables, an exponential decay to a non-zero asymptote was fitted from data. Average SNA for seedlings was about 5 $m^2\,kg^{-1}$, decreasing as trees aged to values of about 3.4 $m^2\,kg^{-1}$. The model for whole-tree SG indicated that SG of seedlings was about 0.37, increasing as the trees aged to values of about 0.55 (Table 3). The model fitted for NLR predicted that for stands younger than 5 years, more than 95% of the LF corresponded to needles; for stands older than about 25 years NLR stabilized, with γN representing about 75% of γF (see also Fig. 4 in Gonzalez-Benecke et al., 2012).

Fig. 9 shows average monthly WF (Fig. 9a), NF (Fig. 9b) and γN (Fig. 9c) for the IMPAC study, where fertilization (F) and weed control (W) treatments created a wide range in foliage biomass and needlefall (Jokela and Martin, 2000). Plots that received fertilization and weed control (FW) showed higher monthly WF and NF. In general, across all 14 years of measurements, maximum and minimum WF was reached in February and July, respectively, and maximum and minimum NF was attained in November and March, respectively. When NF was expressed as a fraction of WF, all treatments showed similar γN within each month, reaching maximums and minimums in November and April, respectively. Across all treatments tested in the study, November was consistently the month when γN peaked. The final model fitted was: $\frac{\gamma N}{\gamma Nx} = \frac{0.8889 + 12.1423 * NMonth}{1 + 1.8714 \cdot NMonth + 0.1876 \cdot NMonth^2}$ ($n = 144$; $P < 0.001$; $R^2 = 0.93$). We left the model flexible to account for site-specific needlefall dynamics, allowing the user to change γNx and the month when γN reached the maximum ($t\gamma Nx$). As default values, we determined

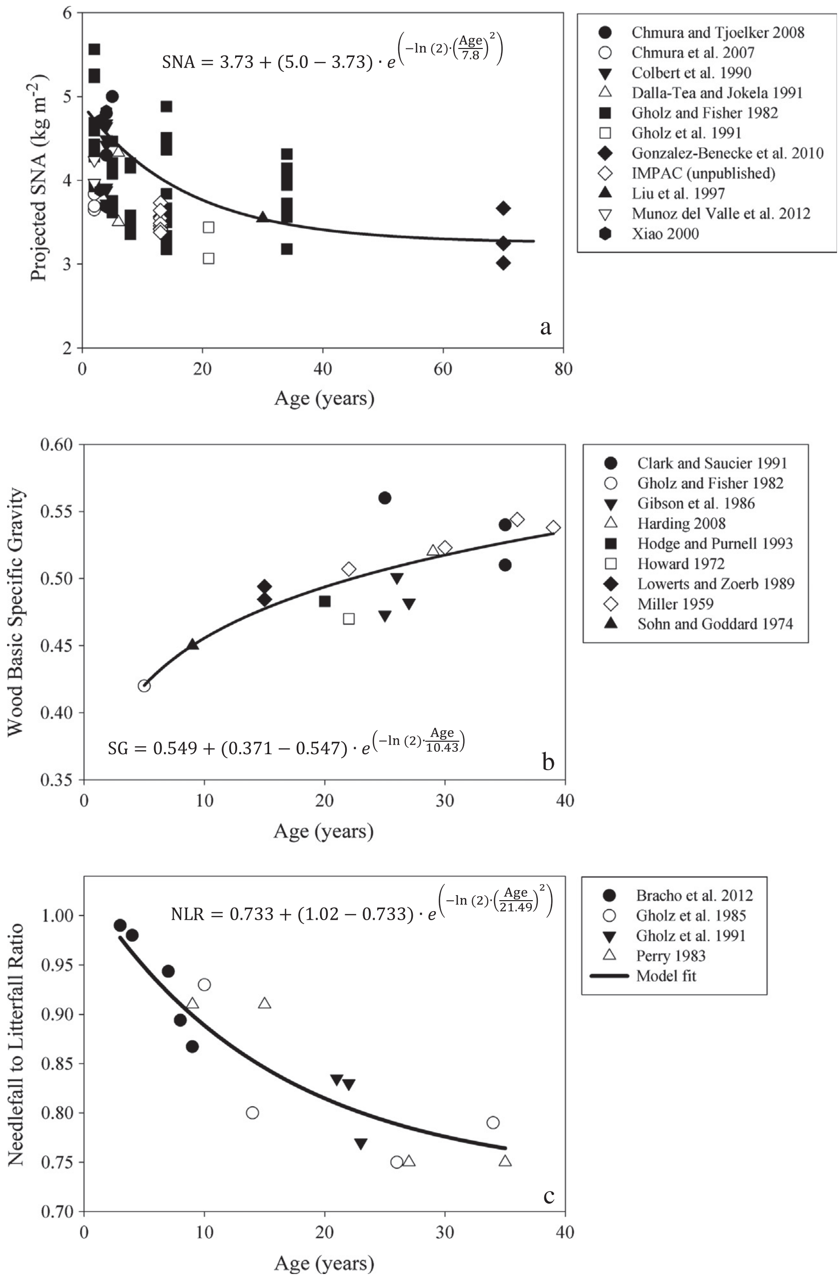

Fig. 8. Model fit for age-dependent parameters. Relationship between age and (a) specific needle area (SNA), (b) whole-tree wood basic specific gravity (SG) and (c) needlefall to litterfall ratio (NLR). (See above-mentioned references for further information.)

mean γNx of 0.13 month^{-1} ($n = 12$; SE = 0.002) and November ($t\gamma Nx = 11$) as the month when γNx peaked (Table 3). Mean monthly γN was 0.062 month^{-1}.

3.2. Iterative calibration of FR

Iterative calibration of FR was carried out using data from the IMPAC study (Jokela et al., 2010). Fertilization (F) and weed control (W) treatments applied in that study created a wide range in productivity, resulting in SI ranging between 20.4 and 28.8 m (Table 1). Fig. 10a shows examples of the iterative calibration of FR for 6 selected plots. There was a strong and linear relationship between SI and FR ($P < 0.001$; $R^2 = 0.91$; Fig. 10b). This calibration predicts a FR = 0.18 for stands with SI = 18 m and a FR = 1 for stands with SI = 29.5 m.

3.3. Parameters from literature

All other parameter estimates shown in Table 3 were obtained from a review of the literature. The minimum fraction of NPP to roots was 0.144 (Gholz et al., 1986). An average value of 0.0183 was used for monthly root turnover (Gholz et al., 1986). Values for temperature modifiers were found in Teskey et al. (1994), where Tmin, Topt and Tmax were 5, 25 and 40 °C. Using data from Dalla-Tea and Jokela (1991), Gholz et al. (1991) and Cropper and Gholz (1993) we determined an average light extinction coefficient (k) of 0.7156 ($n = 4$, SE = 0.028). The annual litter decay rate was assumed to be 0.14 (Gholz et al. 1985, 1986, 1991).

Even though species-specific parameterization was the aim of this study, a lack of information for some parameters made that impossible at this time. Consequently, we assumed those values

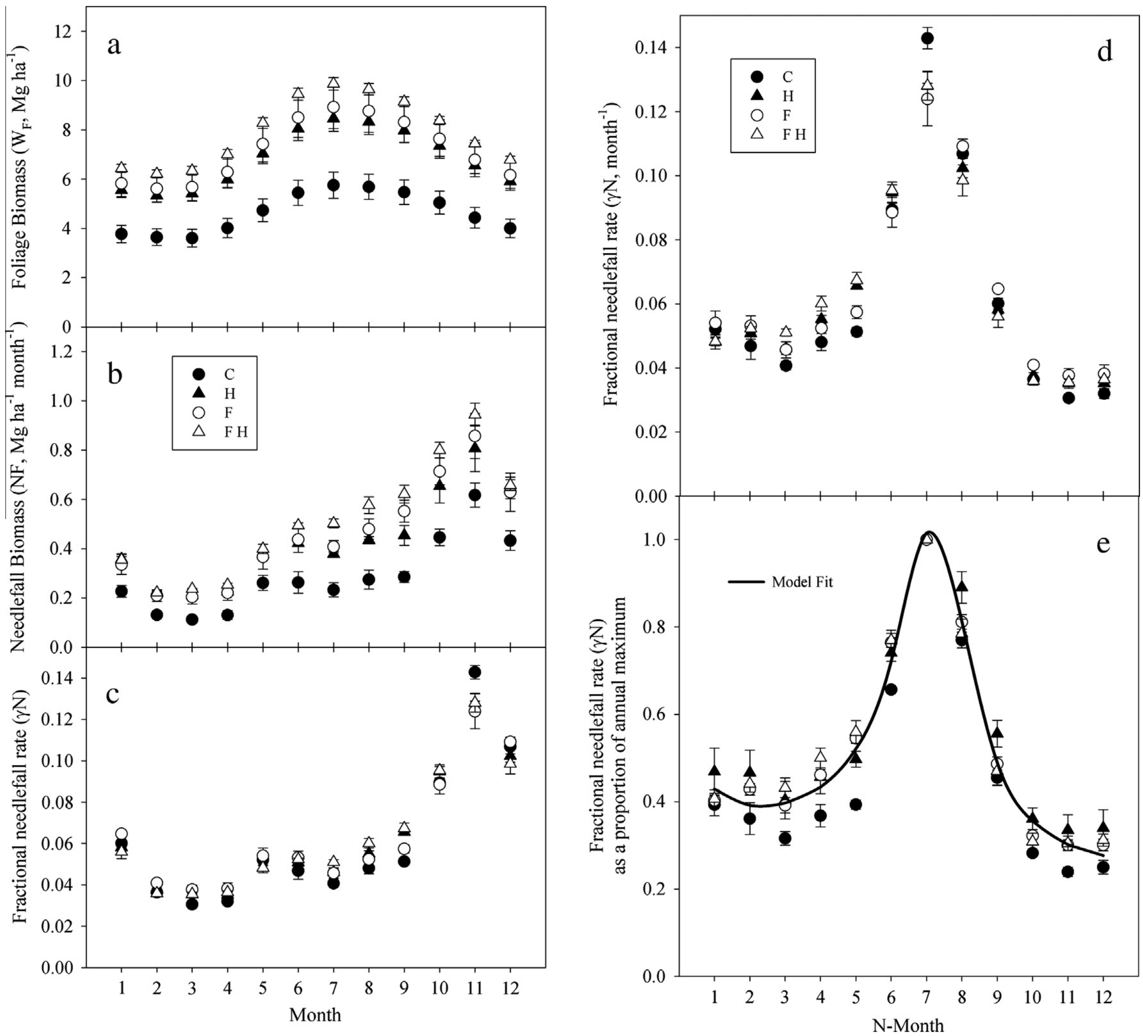

Fig. 9. Seasonal dynamics of foliage biomass and needlefall for the IMPAC study. The left panel shows average monthly (a) W_F, (b) NF and (c) γN. The right panel shows the seasonal dynamics of (d) γN and (e) γN as a proportion of annual maximum, after expressing month as phonological month for needlefall (NMonth).

to be identical to those reported for *P. taeda*, a closely related member of the subsection *Australes* of the *Pinus* genus (southern pines). These parameters included: days production lost per frost day, soil water modifier and fertility effects (from Bryars et al., 2013) and age modifier (from Sampson et al., 2006).

3.4. Model evaluation

There was a good agreement between observed and predicted values, with no clear tendencies to over or under-estimate for any of the variables tested. Across all sites, the slope and the intercept of the relationship between predicted and observed values were not statistically different from one ($P > 0.11$) and zero ($P > 0.07$), respectively (Fig. 11).

All model performance tests showed that AGB, BA, H, Nha and VOB estimations agreed well with measured values (Table 5). Across all sites (ALL) and for all estimations, the RMSE ranged between 7.2% and 19.1%. The Bias ranged between 6.9% underestimations for BA and 4.1% over-estimations for VOB, with no clear tendency to over- or under-estimate. Estimated and observed values were highly correlated, with R^2 values greater than 0.89.

LAI estimations the model performed well, predicting monthly values within the range of observed LAI. For the young sand (Site Mize; Fig. 12a), projected LAI increased until reaching maximum of about 3.1 m^2 m^{-2} at age 7 years. For the mid-rotation sand (Site Donaldson; Fig. 12b), LAI changed seasonally, ranging around mean LAI of about 1.5 m^2 m^{-2}.

When testing stand water use estimations the model performed well, predicting that, across a 25-year rotation, stand transpiration (*T*, mm) and evapotranspiration (ET, mm) were about 80–95% and 84–101% of annual rainfall, respectively (Fig. 13), similar to previous estimates reported for slash pine plantations (Cropper, 2000). Fractional *T* and ET were closer to 1 as rainfall was reduced, implying a depletion of soil water under reducing water availability. Mean daily ET ranged between 1.6 and 4.0 mm day^{-1}, for rainfall conditions ranging between 576 and 1730 mm year^{-1}. For average rainfall conditions (1153 mm year^{-1}), mean daily ET was about 3.1 mm day^{-1}.

4. Discussion

The set of parameters estimates values described in this study allowed for accurate growth predictions and dynamics of slash pine using the 3-PG model. The new approaches presented in this study provide new algorithms for NPP allocation dynamics, canopy cover dynamics and the fertility rating. These processes in the standard 3-PG model are problematic when applying the model to new species, and may be difficult for users to correctly estimate.

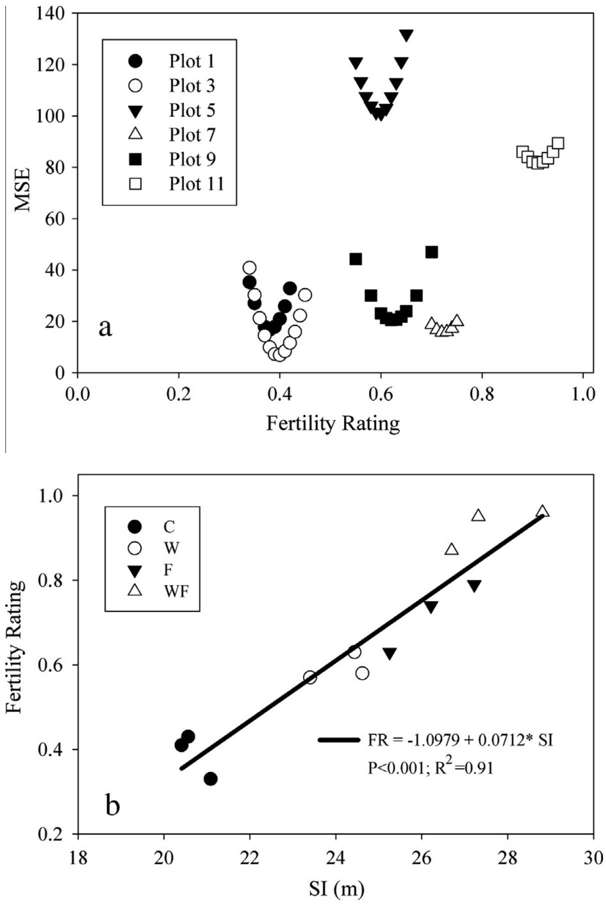

Fig. 10. Fertility rating iterative calibration showing (a) examples of the iterative calibration of FR for 6 selected plots in IMPAC study, and (b) relationship between SI and FR.

Even though there is often good performance of the 3-PG model, Landsberg and Sands (2011) remarked that the generality of the relationships used for biomass allocation remains to be established. Our rationale that stand productivity and competition were correlated with changes in NPP allocation was supported with the robust relationship between BA and pFS. For mature stands the modified model predicted pFS values of about 0.28, and were similar to the value of 0.25 reported for *P. taeda* trees of 20 cm dbh by Bryars et al. (2013). In our case, the estimation of NPP allocation to foliage and stem based on BA rather than using dbh, resulted in realistic stand biomass predictions.

Our estimate of α_c, based on stand level assessments using the eddy-covariance approach, is about 10% larger than the value currently used in the model for *P. taeda*, where the parameter was determined from leaf-level measurements (Dr. Robert Teskey, personal communication). However, our value of α_c is within the range of values reported for other species. Sands and Landsberg (2002), Whitehead et al. (2002), Almeida et al. (2004) and Coops et al. (2005), reported values of 0.070, 0.055, 0.068 and 0.045 mol C mol^{-1} photon, for *E. globulus*, *D. cupressium*, *E. grandis* and *P. ponderosa*, respectively.

When the adequacy of stand water use was tested, the model performed well, giving realistic estimations of stand transpiration. For average rainfall conditions, mean daily evapotranspiration was about 3.1 mm day^{-1}, similar to the values reported by Cropper (2000), Gholz and Clark (2002) and Powell et al. (2005). These authors also reported that fractional ET (ET as a proportion of rainfall) ranged between 1.01 and 0.84, similar to the values shown in Fig. 13. These results support the suitability of the parameters used for canopy conductance for this species.

In recent versions of the model, the fractional canopy cover was set as a function of stand age. Different values of fullCanAge have been given for different species, such as Xenakis et al. (2008), Pérez-Cruzado et al. (2011) or Bryars et al. (2013), who reported fullCanAge values of 18, 3 and 2 years, for *Pinus sylvestris* L., *E. nitens* and *P. taeda*, respectively. Other authors have even used a fullCanAge value of 0 years, such as Whitehead et al. (2002), Dye et al. (2004) and Sands (2004). Based on field observations over a wide range of sites, we concluded that the use of a single age to determine the moment when the stand reaches full canopy closure was not adequate. Moreover, Radtke and Burkhart (1999) concluded that the age to reach full canopy on *P. taeda*, depended on planting density, site productivity and genetics. The allometric relationship between dbh and CA used to determine the fractional canopy cover was similar for 5 of the 6 families tested, but was different for two contrasting genotypes. The model reported here should be a good descriptor of the relationship between dbh and CA for most of the genetic variability in crown architecture within this species; although the genetic differences detected in this study raises the possibility for future family or clonal specific calibrations. When canopy cover was determined under different conditions of stand age, density and productivity, a single relationship between fractional canopy cover and BA was adequate, supporting our rationale that the year to reach full canopy cover was correlated with stand density and productivity. This relationship makes the estimations of absorbed PAR independent of arbitrary model tuning.

Most previous applications of the 3-PG model relied on using arbitrary FR values that better fit with the data used for calibration, giving adequate results, but lacking of mechanism, or at least, independence. For example, Whitehead et al. (2002), Coops et al. (2005), Almeida et al. (2004) and Coops et al. (2010) used fixed FR values of 0.02, 0.4, 0.8 and 0.7, respectively. Other authors have used iterative simulations for parameter calibration of FR in relation to a reference site with an assumed FR. For example, Stape et al. (2008) and Bryars et al. (2013) calibrated the model for a high fertility site, assigning a FR = 1, and then scaling FR for other sites based on comparisons to the initial site. Sampson et al. (2006) used an opposite approach, calibrating the model for a low fertility site, assigning a FR = 0.01, and then scaling up FR for the other sites. Other authors such as Xenakis et al. (2008), Almeida et al. (2010) and Pérez-Cruzado et al. (2011), used soil attributes to estimate FR. The former correlated a Nitrogen availability index with FR, while the last two authors used an empirical index that included fertility, water, oxygen, management and topography limitation levels. In order to maintain a model that is easy to apply across a range of sites, especially for a regional analysis, we decided to correlate FR with SI, a widely available stand productivity index that is assumed as a proxy of the growth potential of the site. The original idea came from Dye et al. (2004), but those authors did not provide any regression parameter estimates. The model predicts a maximum FR = 1 for stands with SI = 30 m, a value that is above the range of observed plots (in our dataset consisting of 118 plots, only two plots had SI larger than 30 m, and those plots corresponded to studies with sustained weed control and fertilization evaluated at age = 10 years.), ensuring the applicability of the model for a wide range of stand productivity and making model estimations less dependent on arbitrary tunings.

When the adequacy of LAI estimations was tested, the model performed well, giving realistic estimations of seasonal dynamics of monthly LAI. We are aware of the limitations of the model, that cannot account for the effects of severe drought or wind storms, as the case of the last year of measurements in Fig. 12 (see age = 8 and 18 years for stands Mize and Donaldson, respectively), where a

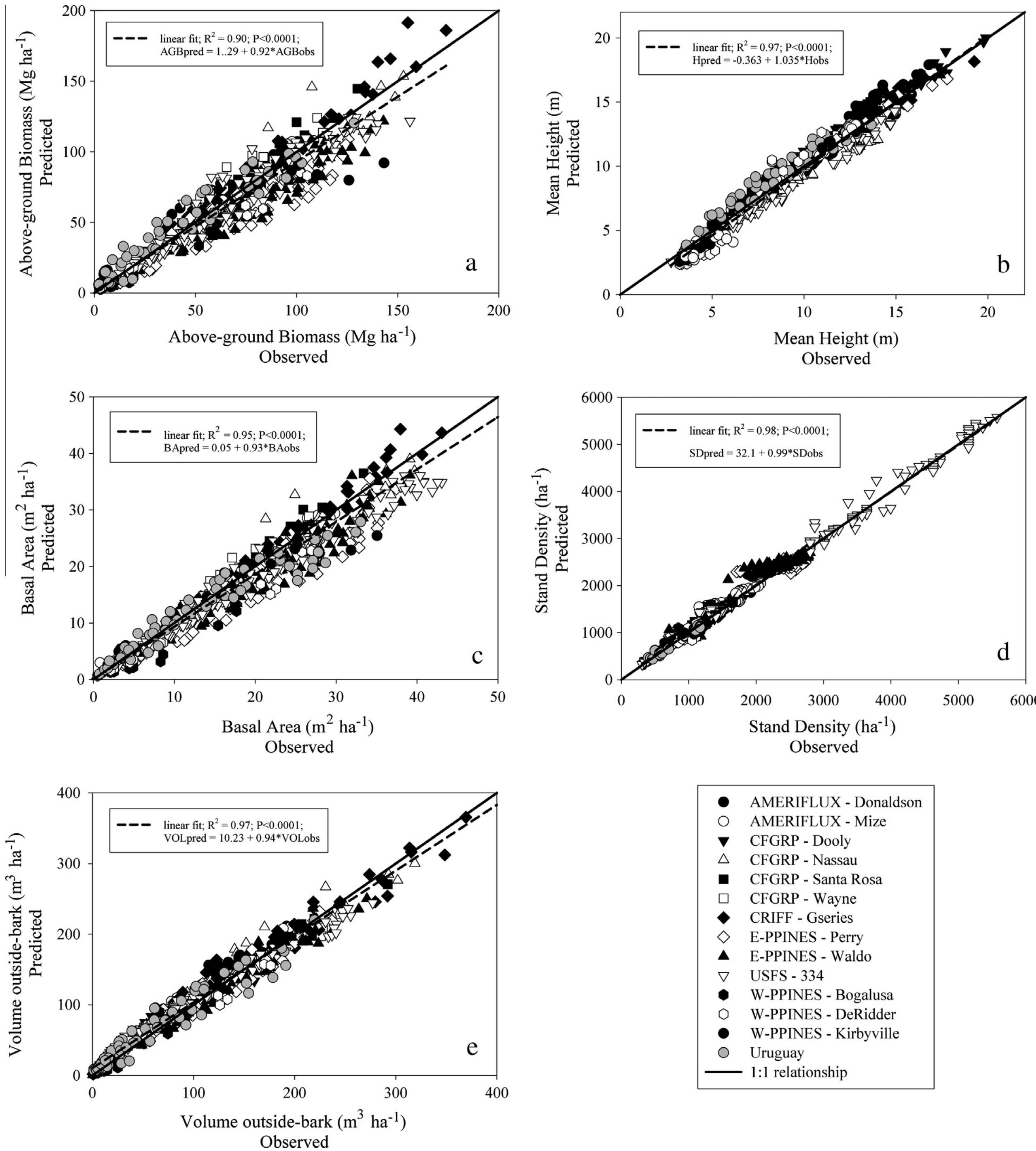

Fig. 11. Model validation for 14 tested sites. Observed *versus* predicted (simulated with 3-PG) values of (a) total above ground biomass (AGB, Mg ha^{-1}), (b) mean tree height (H, m), (c) stand basal area (BA, m^2 ha^{-1}), (d) Stand density (SD, trees ha^{-1}) and (e) Bole volume over-bark (VOL, m^3 ha^{-1}). Dotted line represents linear fit between observed and predicted values and solid lines correspond to the 1-to-1 relationship.

decline in LAI was associated to high needlefall due to Hurricane Katrina (Bracho et al., 2012). Further research is needed to better simulate the effects of climate on LAI dynamics. Additionally, it is possible that extra flushes of needles or unusual retention of some needles beyond two years could alter LAI time series.

Needlefall is an important factor in the model, as it directly affects LAI estimations. Sands and Landsberg (2002) included an age-dependent function that described the increase in foliage litterfall as trees developed from seedlings to canopy closure, assuming that after that point the stand reached a constant maximum mean monthly needlefall rate (Sands and Landsberg, 2002; Almeida et al., 2004; Dye et al., 2004; Coops et al., 2005; Bryars et al., 2013). Plant materials comprising the litter in pine forests include more than only pine needles: it contains cones and twigs, and understory leaves and twigs, as well as bark and woody stems (Smith and Heath, 2002). The NLR used in this study accounted for those components of the forest floor, which, in conjunction with the inclusion of decay estimates, allowed for estimations of forest floor accumulation. Running the model for site conditions of the IMPAC study and using SI ranging between 20 and 28 m, the forest floor biomass accumulation at age 25 years ranged between 22 and 38 Mg ha^{-1} (data not shown). These estimates were within the

Table 5
Summary of model evaluation statistics for AGB, BA, H, Nha and VOB estimations.

Variable	Project/site	$\bar{O}$	$\bar{P}$	n	RMSE (%)	Bias (%)	R^2
AGB	AMERIFLUX	65.1	66.0	96	8.97	1.36	0.931
	CFGRP	90.8	96.0	40	14.58	5.71	0.786
	CRIFF	91.0	98.1	45	11.09	7.81	0.922
	E-PPINES	66.2	54.2	176	24.10	−18.01	0.808
	W-PPINES	33.9	28.3	45	41.68	−16.65	0.885
	USFS-334	57.2	54.0	150	16.88	−5.68	0.930
	URUGUAY	43.0	47.8	44	23.30	11.03	0.907
	ALL	63.1	59.7	596	19.14	−5.36	0.894
BA	AMERIFLUX	19.0	18.5	104	6.31	−2.38	0.969
	CFGRP	21.8	22.4	59	10.81	3.1	0.902
	CRIFF	23.6	24.4	54	7.08	3.55	0.963
	E-PPINES	17.1	14.8	207	20.16	−13.44	0.903
	W-PPINES	8.2	6.7	61	36.74	−18.41	0.900
	USFS-334	16.2	14.6	174	16.21	−9.49	0.944
	URUGUAY	13.4	12.6	56	22.27	−6.04	0.896
	ALL	17.0	15.8	715	16.09	−6.94	0.932
H	AMERIFLUX	11.4	11.7	96	5.90	2.52	0.957
	CFGRP	14.0	14.2	40	4.28	1.44	0.923
	CRIFF	13.5	14.1	45	5.56	4.66	0.940
	E-PPINES	8.7	8.1	172	8.66	−6.35	0.954
	W-PPINES	6.7	6.3	45	14.97	−6.7	0.917
	USFS-334	8.2	8.5	125	6.75	3.72	0.962
	URUGUAY	8.6	9.4	44	11.21	8.66	0.867
	ALL	9.6	9.7	567	7.61	0.37	0.962
Nha	AMERIFLUX	1637	1702	104	7.25	3.94	0.937
	CFGRP	1185	1220	59	7.36	3.01	0.923
	CRIFF	1418	1431	54	3.97	0.86	0.778
	E-PPINES	1777	1773	208	8.61	−0.27	0.957
	W-PPINES	1035	1016	61	7.96	−1.84	0.679
	USFS-334	2095	2113	175	5.19	0.86	0.996
	URUGUAY	681	665	57	5.59	−2.43	0.971
	ALL	1609	1622	718	7.16	0.82	0.987
VOB	AMERIFLUX	114.1	122.2	104	10.23	7.07	0.953
	CFGRP	145.0	152.6	60	12.85	5.19	0.933
	CRIFF	166.2	174.1	54	11.58	4.73	0.958
	E-PPINES	84.0	83.3	204	13.58	−0.82	0.975
	W-PPINES	37.0	37.4	60	31.29	1.15	0.951
	USFS-334	68.5	73.7	150	18.18	7.57	0.963
	URUGUAY	67.2	70.8	54	24.03	5.37	0.927
	ALL	91.6	95.3	686	14.86	4.1	0.968

AGB: above-ground biomass (Mg ha^{-1}); BA: stand basal area (m^2 ha^{-1}); H: mean tree height (m); Nha: trees per hectare (ha^{-1}); VOB: stand bole volume outside bark (m^3 ha^{-1}); ALL: average value for all projects/sites; $\bar{O}$: mean observed value; $\bar{P}$: mean predicted value; n: number of observations; RMSE: root of mean square error (m); Bias: absolute bias (m); R^2: coefficient of determination. Values of RSME and Bias are percentage relative to observed mean.

range reported by Gholz et al. (1985), Harding and Jokela (1994) and Vogel et al. (2011). Our model estimates the variable monthly needlefall rate, which should produce more realistic estimates of needlefall and forest floor accumulation, nevertheless, further research is needed to better simulate the effects of climate and substrate quality on forest floor decomposition.

The inclusion of the mortality function reported by Pienaar et al. (1996) in the form of the model proposed by Sands (2004) greatly improved the estimations of stand density, another part of the model identified for improvement (Sands and Landsberg, 2002; Pinjuv et al., 2006). Unsatisfactory results were found by Pinjuv et al. (2006), who reported 18% under-estimations, or Sands and Landsberg (2002) and Bryars et al. (2013), who concluded that the largest discrepancy in model performance was in stand density estimations, remarking that the model failed to predict the gradual onset of mortality early in the stand. In our study, when tested on contrasting planting densities, the overall bias was less than 1%.

The estimates of VOB also showed high accuracy, reflecting adequate performance of the functions to estimate PBB, SG and Vratio, as these variables partially contribute to the estimation of VOB. Instead of using a single value for SG (Sands and Landsberg, 2002; Sampson et al., 2006), we used an age-dependent estimation. A similar approach was used by Bryars et al. (2013), but they used a segmented extrapolation instead of a continuous non-linear model. Vratio was set dependent on Age and stand density, adding more plasticity to the estimations that used a single value Bryars et al. (2013).

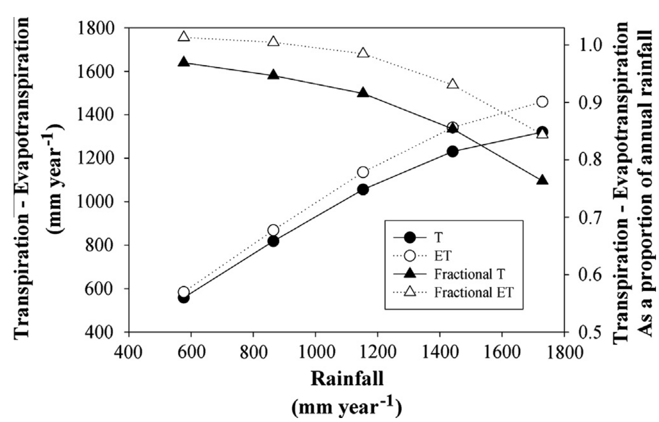

Fig. 13. Examples model performance of stand water use determinations for IMPAC study under varying rainfall.

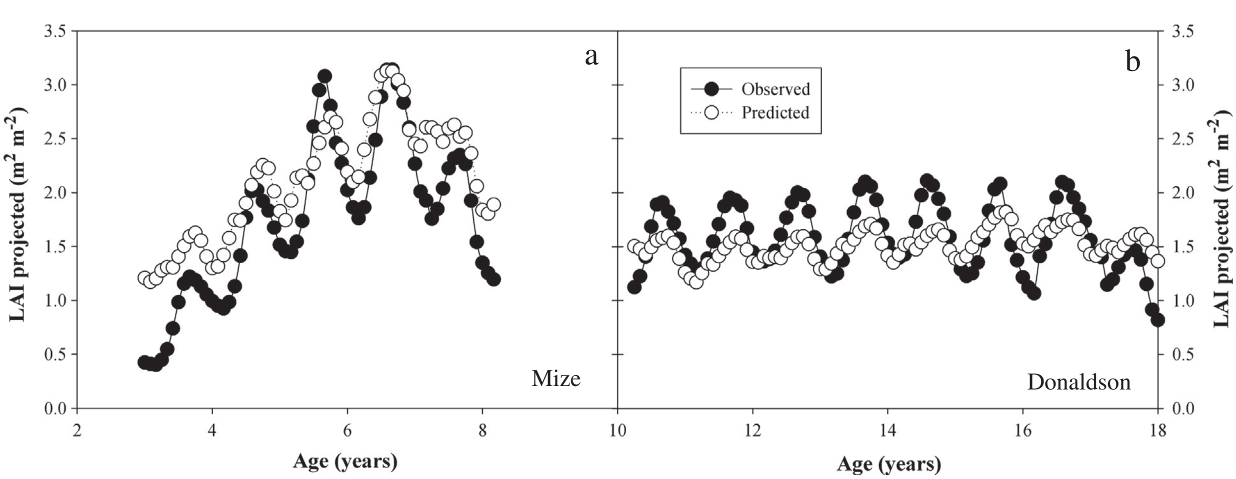

Fig. 12. Examples model performance of monthly LAI determinations for AMERIFLUX study, showing observed and predicted LAI for (a) young and (b) mid-rotation stands.

Another improvement in the model was the inclusion of allometric functions to estimate initial biomass pools. Sands and Landsberg (2002) highlighted the importance of the initial biomass conditions, showing high sensitivity for initial canopy development. Most of the parameter estimates and relationships presented in this study have a wide range of applicability, and not only for 3-PG. For example, the general SG, dbh-height and biomass functions, that can be incorporated into the C balance model reported by Gonzalez-Benecke et al. (2011), or the parameters for canopy conductance dynamics, that can be used in eco-hydrological models to determine stand water dynamics (Dye and Olbrich, 1993; Sun et al., 2011; Wang et al., 2009).

The model was validated under variable stand and site conditions, covering zones beyond the natural distribution, including stands growing in Uruguay. Overall, the model showed satisfactory predictions over a range of climate and soil conditions. Although other factors such as disease and pests could be important, the model performed well with site-specific model inputs, showing high agreement between observed and predicted values for all variables tested.

5. Conclusion

This paper reports the first set of 3-PG parameter estimates for slash pine. Using data from the literature and long-term productivity studies we developed new functions for estimating NPP allocation dynamics, biomass pools at any starting age, canopy cover dynamics, density-independent tree mortality and FR. We developed a new method to estimate FR based on a strong and positive correlation with SI. The model was tested against data from plots covering a wide span of stand characteristics, distributed beyond the species distribution range in the southeastern United States, including stands in Uruguay, South America. The model can be applied to assess the impact of future climate scenarios on stands growing over a large geographical area and across a wide range of ages and stand characteristics.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.04.030.

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